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ΔΙΔΑΚΤΟΡΙΚΗ ΔΙΑΤΡΙΒΗ

Διερεύνηση οικολογίας-δυναμικής πληθυσμών της θαλασσιάς χελώνας *Caretta caretta* στο βιότοπο αναπαραγωγής του κόλπου Λαγάνα με τη χρήση συγχρόνων μεθόδων

Loggerhead sea turtle (*Caretta caretta*) behaviour, ecology and population dynamics in the breeding area of Laganas Bay, Zakynthos Greece using direct observation and remote technology

Gail Schofield (B.Sc.)

Αγρίνιο 2009

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ΔΙΔΑΚΤΟΡΙΚΗ ΔΙΑΤΡΙΒΗ

Που υποβλήθηκε στο Διαπανεπιστημιακό Μεταπτυχιακό Πρόγραμμα
Σπουδών Αειφορική Διαχείριση Προστατευόμενων Περιοχών
για την απόκτηση του τίτλου του Διδάκτορα
στην Αειφορική Διαχείριση Προστατευόμενων Περιοχών

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ΕΠΤΑΜΕΛΗΣ ΕΞΕΤΑΣΤΙΚΗ ΕΠΙΤΡΟΠΗ

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ΠΡΟΛΟΓΟΣ / PREFACE

Η παρούσα διατριβή έχει μια δομή που αποτελείται από έξι κεφαλαία, καθένα από τα οποία έχει δημοσιευτεί σε επιστημονικό περιοδικό. Η έρευνα πραγματοποιήθηκε από την υποψήφια διδάκτορα η Gail Schofield και έγινε δυνατή με τη βοήθεια των επιβλεπόντων καθηγητών. Η σύνταξη των επιστημονικών άρθρων έγινε από την Gail Schofield, ελέχθηκαν και διορθώθηκαν από τους επιβλέποντες καθηγητές μου. Οι συν-συγγραφείς που αναφέρονται σε κάθε επιστημονικό άρθρο, βοήθησαν με διάφορους τρόπους: με το να μου παρέχουν τη δυνατότητα να μελετήσω τα ζώα και να έχω στη διάθεση μου τον κατάλληλο εξοπλισμό, με την παροχή συμβουλών στο σχεδιασμό της έρευνας, με εποικοδομητική κριτική σε πρόχειρες εκδόσεις άρθρων και με τη βοήθεια τους στη στατιστική ανάλυση.

This thesis takes the form of six chapters, all of which have been published in refereed journals. The research was conceived by myself and realised with the support of my supervisors. The manuscripts were written by myself, Gail Schofield, and overseen by my supervisors. My co-authors, who are listed at the start of each manuscript, helped in various ways: by providing me with access to study animals and equipment, by offering advice on experimental design, by constructive criticism of earlier drafts of the manuscripts and by giving statistical advice.

ΕΛΛΗΝΙΚΗ ΠΕΡΙΛΗΨΗ

Η ορθολογική διαχείριση και προστασία των βιοτόπων κ'των ειδών που απειλούνται, απαιτεί την κατανόηση της δομής του πληθυσμού, της ηθολογίας και των προτύπων μετακίνησης και διασποράς τους. Έτσι παρέχονται τα απαραίτητα εργαλεία στους ερευνητές, ώστε να κατανοήσουν πως ένα απειλούμενο ειδος επηρεάζει την περιβάλλουσα κοινότητα, καθώς επίσης και τις λειτουργίες, την οργάνωση και την απόκριση σε πιθανές διαταραχές του οικοσυστήματος. Οι θαλάσσιες χελώνες, οι οποίες είναι απειλούμενα είδη παγκοσμίως, περνούν όλη τους τη ζωή στη θάλασσα, εκτός από το μικρό χρονικό διάστημα κατά το οποίο οι θηλυκές βγαίνουν στην παραλία για να ωοτοκήσουν. Η μελέτη τέτοιων μεγάλων σπονδυλωτών στο φυσικό τους περιβάλλον είναι δύσκολη. Γι' αυτό το λόγο, το μεγαλύτερο μέρος της έρευνας στηρίζεται στη χρήση της απομακρυσμένης τεχνολογίας για την παρακολούθηση της συμπεριφοράς και των κινήσεων των χελωνών. Αποτέλεσμα αυτού είναι η έρευνα να πραγματοποιείται κυρίως στις θηλυκές χελώνες, καθώς μόνο αυτές βγαίνουν στην παραλία για να γεννήσουν, παρέχοντας έτσι την ευκαιρία για την τοποθέτηση σ' αυτές εξοπλισμού ο οποίος θα καταγράψει τις δραστηριότητές τους κατά την υπόλοιπη περίοδο ωοτοκίας. Ο κόλπος Λαγανά, στο νησί της Ζακύνθου, είναι ο μεγαλύτερος βιότοπος αναπαραγωγής της θαλάσσιας χελώνας *Caretta caretta* στη Μεσόγειο. Εδώ συχνάζουν αρκετές εκατοντάδες θαλάσσιες χελώνες και αρκετές χιλιάδες τουρίστες κάθε καλοκαίρι. Η τοποθεσία των παραλιών ωοτοκίας και οι σχετικές πυκνότητες φωλεοποίησης χρησιμοποιήθηκαν για να προσδιοριστεί ο βαθμός προστασίας που προσφέρουν οι θαλάσσιες ζώνες προστασίας στον κόλπο του Λαγανά. Μετά την ίδρυση του Εθνικού Θαλάσσιου Πάρκου Ζακύνθου (ΕΘΠΖ) ήταν προφανής η ανάγκη λήψης βασικών δεδομένων σχετικά με τις μετακινήσεις των χελωνών στη θάλασσα, ώστε να αξιολογηθούν και να βελτιωθούν τα υφιστάμενα μέτρα προστασίας στη θαλάσσια περιοχή.

Στόχος της παρούσας διατριβής ήταν η απόκτηση στοιχείων τόσο για τις αρσενικές, όσο και για τις θηλυκές θαλάσσιες χελώνες, σχετικά με τη δομή του πληθυσμού, τη συμπεριφορά και τη χρήση του βιοτόπου αναπαραγωγής του είδους στη Ζάκυνθο, με

συνδυασμό της άμεσης παρατήρησης και της χρήσης απομακρυσμένης τεχνολογίας. **Στο Κεφάλαιο 1**, παρουσιάζονται τα αποτελέσματα αξιολόγησης του δυναμικού των φυσικών σημαδιών του προσώπου για την αναγνώριση των ατόμων θηλυκών και αρσενικών χελωνών, ώστε να αποκτηθούν βασικές πληροφορίες για το μέγεθος του πληθυσμού και την αναλογία των φύλων. Δεδομένα συμπεριφοράς των θαλάσσιων χελωνών, συνδυάστηκαν στη παρούσα μελέτη και παρουσιάζονται στο **Κεφάλαιο 2**. Εδώ καταγράψαμε και κατηγοριοποιήσαμε όλες τις μονήρεις και τις κοινωνικές συμπεριφορές των αρσενικών και θηλυκών χελωνών, από τις οποίες την τεκμηρίωση των συμπεριφορών της αναζήτησης τροφής, του καθαρισμού και της διαμάχης μεταξύ θηλυκών, για πρώτη φορά δημοσιεύσαμε εμείς σε περιοχές. Καθώς η επιθετική συμπεριφορά (διαμάχη) μεταξύ θηλυκών του ίδιου είδους δεν είναι ευρέως τεκμηριωμένη, ειδικά για τα θαλάσσια σπονδυλωτά, στο **Κεφάλαιο 3** εξετάσαμε τη δομή και τη λειτουργία των ενδοειδικών ανταγωνιστικών αλληλεπιδράσεων μεταξύ των θηλυκών χελωνών. Τα αποτελέσματα έδειξαν ότι συγκεκριμένες περιοχές στο βιότοπο αναπαραγωγής, μπορεί να προτιμούνται από τις θηλυκές θαλάσσιες χελώνες τις οποίες και οι θαλάσσιες χελώνες επιπρόσθετα υπερασπίζονται. Αυτό μας οδήγησε στο ερώτημα, εάν η προτίμηση αυτή οφειλόταν: (i) στο ότι οι θηλυκές έβρισκαν καταφύγιο στις περιοχές αυτές από την ενεργοβόρα αλληληπίδραση με αρσενικά τα οποία περιπολούσαν, ή (ii) στο ότι στις περιοχές αυτές, οι θηλυκές έβρισκαν θερμότερα νερά ώστε να επιταχυνθεί η ωρίμανση των αυγών.

Για να απαντήσουμε σε αυτά τα ερωτήματα, τοποθετήσαμε μεγάλης ακρίβειας καταγραφείς GPS και TDRs (Time-Depth recorders) σε θηλυκά άτομα πριν από την έναρξη της ωοτοκίας, ώστε να ερευνήσουμε τα πρότυπα μετακινήσεων όταν η θερμοκρασία της θάλασσας δεν ήταν η βέλτιστη για την ανάπτυξη των αυγών. Στο **Κεφάλαιο 4** παρουσιάζονται τα αποτελέσματα αυτής της έρευνας, τα οποία δείχνουν ότι οι θηλυκές χελώνες χρησιμοποιούν πρωτίστως την περιοχή κοντά στη ακτή και το στατιστικό μοντέλο έδειξε ότι υπεύθυνες για τις μετακινήσεις τους μπορεί να είναι κοινές βιο-φυσικές διεργασίες. Λόγω του ότι είναι σημαντικό να κατανοήσουμε το πως όλα τα στοιχεία του πληθυσμού χρησιμοποιούν τη θαλάσσια περιοχή, στο **Κεφάλαιο 5** εξετάσαμε τα πρότυπα μετακινήσεων των αρσενικών και θηλυκών θαλάσσιων χελωνών. Τα αρσενικά βρέθηκε ότι χρησιμοποιούν μια παρόμοια με τις θηλυκές περιοχή κοντά στην ακτή. Ως εκ τούτου η έρευνά μας έδειξε ότι η προστατευόμενη θαλάσσια περιοχή στο Εθνικό Θαλάσσιο Πάρκο Ζακύνθου μπορεί να μην περιλαμβάνει τους πιο κρίσιμους (ζωτικούς) οικότοπους για τις θαλάσσιες χελώνες *Caretta caretta* στη διάρκεια της αναπαραγωγικής περιόδου. Με την ίδια έρευνα αποκτήσαμε πρωτότυπα δεδομένα σχετικά με τα αρσενικά και τις μετακινήσεις τους στη Μεσόγειο, από τις περιοχές αναπαραγωγής έως τις περιοχές διατροφής και διαχείμανσης. Στο **Κεφάλαιο 6** συγκεντρώνονται τα ερωτήματα τα οποία προέκυψαν κατά τη μελέτη της συμπεριφοράς και των μετακινήσεων, μέσω της διερεύνησης των προτύπων μετακίνησης των θηλυκών σε σχέση με τη θερμοκρασία του θαλάσσιου περιβάλλοντος. Εδώ καταδεικνύεται ότι στην αρχή της αναπαραγωγικής περιόδου, οι χελώνες μετακινούνται καθημερινά ώστε να βρίσκονται σε παροδικά θερμές κηλίδες (τμήματα) της θάλασσας η παρουσία των οποίων σχετίζεται με τη διεύθυνση του ανέμου. Καθώς η θάλασσα θερμαινόταν περισσότερο κατά το καλοκαίρι, η παραπάνω επιλογή δεν ήταν πια εμφανής. Παρόμοια συμπεριφορά δεν έχει μέχρι τώρα αναφερθεί ξανά για μια περιοχή αναπαραγωγής θαλάσσιων χελωνών. Η επιλογή των θερμότερων νερών στην αρχή της περιόδου προφανώς επιταχύνει την ωρίμανση των αυγών πριν την ωοαπόθεση και ως εκ τούτου, η ενεργή επιλογή των παράκτιων θερμών νερών μπορεί να επιτρέπει στις χελώνες την έναρξη της ωοτοκίας νωρίτερα. Αυτό θα μπορούσε να εξηγήσει και να τεκμηριώσει την επιθετικότητα των θηλυκών μεταξύ τους, η οποία αναφέρθηκε στο Κεφάλαιο 3.

Συμπερασματικά, τα ευρήματα της παρούσας διατριβής αποτελούν πρωτότυπες παρατηρήσεις και ιδέες σχετικά με τη βιολογία των θαλάσσιων χελωνών, με πολλές εφαρμογές στη διαχείριση και προστασία και λόγω των θερμικών προσαρμογών αυτού του πληθυσμού στην κλιματική αλλαγή και την παγκόσμια αύξηση της θερμοκρασίας.

ENGLISH SUMMARY

Rational conservation and protected area management of endangered species requires the understanding of population structure, behaviour ecology, movement patterns and distribution. This provides researchers with a means to understand how an animal may impact the surrounding community as well as ecosystem function, organisation and response to disturbance. Sea turtles, which are endangered globally, spend their entire lives at sea, except for the brief period adult females emerge on the beach to nest. The study of such large migratory vertebrates in their natural marine habitats is difficult. Therefore most research depends on remote technology to track turtle behaviour and movement. As a result there remains a research bias towards female turtles because they come ashore to nest, providing an easy opportunity to attach tracking equipment to record activity during and following the nesting period. Laganas Bay, on the island of Zakynthos in Greece, is the largest loggerhead sea turtle (*Caretta caretta*) rookery in the Mediterranean, frequented by several hundred sea turtles and several hundred thousand tourists each summer. Nesting beach locations and relative nesting densities were used to delineate the degree of protection offered by marine protection zones in Laganas Bay. Following the establishment of the National Marine Park of Zakynthos (NMPZ) in 1999, it was apparent that empirical data about in-water sea turtle movement was necessary to validate and improve existing management maritime protection actions.

The objective of this thesis was to obtain information about both male and female loggerhead breeding population structure, behaviour and area-use at the Zakynthos rookery through a combination of direct observation and remote technology. **Chapter 1** presents the results of an assessment validating the potential of natural facial markings to identify individual male and female loggerheads, to obtain baseline population size and sex-ratio information about the breeding population. Behavioural information was assimilated within this study, the results of which are presented in **Chapter 2**. Here we record all solitary and social behaviour categories of males and females, including the presentation of the first published documentation of foraging, cleaning and female-female contests for loggerheads at breeding areas. Because aggressive behaviour between females of the same species is not widely documented, particularly in marine vertebrates, in **Chapter 3** we examine the structure and function of antagonistic

interactions between female loggerheads. The results indicated that certain sites may be preferentially sought after and defended by sea turtles, leading us to question whether this arose to (i) take refuge from energetically costly interactions with reproductively active patrolling males or (ii) to seek out warmer water to accelerate gestation.

To answer these questions we attached fine-scale GPS loggers and TDRs (Time-Depth recorders) to females prior to the onset of nesting, to investigate movement patterns when the sea temperature was sub-optimal for egg development. **Chapter 4** presents the movement results of this study indicating that females primarily use the nearshore area, and statistical modelling indicated common biophysical processes might be driving their movements. Because it is important to understand how all components of the population utilise the marine area, in **Chapter 5** we investigated both male and female movement patterns. Males were found to occupy a similar nearshore area to females, hence our research demonstrated that the protected marine area of the National Marine Park of Zakynthos may not include the most critical habitats for loggerhead sea turtles during the breeding period. Through the same study we obtained novel tracking information of males in the Mediterranean from local breeding to regional wintering/foraging areas. **Chapter 6** consolidates the questions raised in the behaviour and movement chapters through investigating female movement patterns in relation to the thermal marine environment. Here it is demonstrated that at the start of the breeding season turtles repositioned themselves daily to reside in transient patches of warm water, correlated to wind direction. As the sea warmed in the summer, this selection was no longer evident. Such behaviour has not been reported at a sea turtle breeding site previously. This early season warm-water selection presumably speeds up egg maturation rates before oviposition, hence, active selection of nearshore warm waters may allow turtles to initiate nesting at an earlier date; which may justify the observed female aggression recorded in Chapter 3.

In conclusion, this thesis presents many novel observations and concepts with respect to sea turtle biology, with far-reaching implications with respect to conservation management and, due to the thermal adaptations of this population, climate change.

ΠΕΡΙΕΧΟΜΕΝΑ / CONTENTS

ΓΕΝΙΚΗ ΕΙΣΑΓΩΓΗ

Η προστασία των απειλούμενων ειδών είναι απαραίτητη, ειδικά λόγω του ότι παρατηρείται μείωση των πληθυσμών τους σε παγκόσμιο επίπεδο. Η θαλάσσια χελώνα *Caretta caretta* είναι ένα από αυτά τα είδη για τα οποία απαιτείται η ανάληψη δράσης, τόσο σε τοπικό όσο και σε περιφερειακό επίπεδο, ώστε να περιοριστούν οι κίνδυνοι που τιν απειλούν. Για την αποτελεσματική προστασία, θα πρέπει να ληφθούν υπόψη οι ιδιαίτερες βιολογικές και οικολογικές συνθήκες του είδους.

Φυλογένεση και Μορφολογία

Οι χελώνες εμφανίστηκαν στα τέλη της Τριασικής περιόδου, πριν από περίπου 200 εκατομμύρια χρόνια (Pritchard, 1997). Οι θαλάσσιες χελώνες αποτελούν ένα ξεχωριστό κλάδο ο οποίος αποσπάσθηκε από τις υπόλοιπες χελώνες τουλάχιστον πριν από 110 εκατομμύρια χρόνια κατά τη διάρκεια της Κρητιδικής περιόδου. Την ίδια περίοδο, οι θαλάσσιες χελώνες διασπάστηκαν σε δύο οικογένειες, οι οποίες υπάρχουν έως σήμερα: στην οικογένεια Dermochelyidae, η οποία αποτελείται από ένα μόνο είδος, τη δερματοχελώνα (*Dermochelys coriacea*) και στην οικογένεια Cheloniidae στην οποία εντάσσονται έξι είδη (*Caretta caretta, Eretmochelys imbricata, Lepidochelys olivacea, Lepidochelys kempi, Chelonia mydas* και *Natator depressus*). Η φυσιολογία και οι βιολογικές προσαρμογές των θαλάσσιων χελωνών παρέμειναν χωρίς καμία αλλαγή για εκατομμύρια χρόνια, με αρκετά χαρακτηριστικά να είναι κοινά σε όλα τα είδη των θαλάσσιων χελωνών, τα οποία τις διαχωρίζουν από τα υπόλοιπα είδη των Testudines. Τέτοια χαρακτηριστικά είναι, τα μη συσπώμενα άκρα, τα ενισχυμένα κρανιακά οστά, η μετατροπή των άκρων σε πτερύγια και οι δακρυϊκοι αδένες από τους οποίους αποβάλεται το περίσσιο αλάτι. Παρόλα αυτά, τα είδη των θαλάσσιων χελωνών διαφέρουν μεταξύ τους όσον αφορά στο χρόνο δημουργιάς τους, στη δυναμική του πληθυσμού τους και στην παγκόσμια κατανομή τους.

Οικολογία και Κατανομή

Οι οικότοποι των θαλάσσιων χελωνών απαντώνται κυρίως σε τροπικές περιοχές. Αυτό συμβαίνει διότι είναι εξώθερμα ζώα και η θερμοκρασία του περιβάλλοντος επηρεάζει άμεσα τη θερμοκρασία του σώματός τους. Επηρεάζει επομένω τις κινήσεις τους

(Etnoyer *et al.*, 2006), την απόκτηση τροφής (Broderick *et al.*, 2001a), την εποχικότητα της αναπαραγωγής (Godley *et al.*, 2002; Weishampel *et al.*, 2004), την περιοδικότητα της ωοτοκίας (Sato *et al.*, 1998; Hays *et al.*, 2002a) και τα διαστήματα μετανάστευσης (Solow *et al.*, 2002). Επομένως η ικανότητα τους εντοπίσουν θερμοκρασιακά κατάλληλες περιοχές, όπου η θερμοκρασία θα κυμαίνεται εντός ενός συγκεκριμένου εύρους τιμών, είναι ζωτικής σημασίας. Η *Caretta caretta* διαφέρει από τα άλλα είδη θαλάσσιων χελωνών στο ότι είναι κοσμοπολίτικο είδος και οι περιοχές αναπαραγωγής της απαντώνται σε πιο εύκρατα γεωγραφικά πλάτη των 19-36º βόρεια και νότια του ισημερινού (Dodd, 1988), ενώ μεμονωμένα περιστατικά ωοτοκίας έχουν παρατηρηθεί σε γεωγραφικό πλάτος έως και 41ºN (Bentivegna *et al.*, 2005; SWOT website http://www.seaturtlestatus.org) (Σχήμα 1). Στη Μεσόγειο υπάρχουν αναπαραγωγικοί πληθυσμοί δύο εκ των επτά ειδών θαλάσσιων χελωνών, της *Caretta caretta* (Linnaeus, 1758) και της πράσινης χελώνας (*Chelonia mydas*, Linnaeus, 1758), ενώ παρατηρούνται και σποραδικές επισκέψεις για αναζήτηση τροφής από δερματοχελώνες (*Dermochelys coriacea*, Camiñas, 1998). Η γενετική έρευνα έδειξε ότι ο πληθυσμός της *Caretta caretta* στη Μεσόγειο προήλθε από αυτόν του Δυτικού Ατλαντικού πριν από περίπου 12.000 χρόνια μετά την τελευταία περίοδο των παγετώνων (Laurent *et al.*, 1998).

Προστασία και Διατήρηση

Οι θαλάσσιες χελώνες χρειάζονται και αξιοποιούν μια ποικιλία ενδιαιτημάτων. Αμμώδεις παραλίες για να αφήσουν τα αυγά τους, ρηχές θαλάσσιες περιοχές διατροφής και βαθιούς ωκεάνιους διαδρόμους μετανάστευσης, οι οποίοι εκετείνονται από τους τροπικούς έως τα απομακρυσμένα βόρεια και νότια γεωγραφικά πλάτη. Οι θαλάσσιες χελώνες σε παγκόσμιο επίπεδο αντιμετωπίζουν μια ποικιλία απειλών. Στις παραλίες ωοτοκίας, οι θαλάσσιες χελώνες απειλούνται από την τουριστική και τοπική ανάπτυξη η οποία δημιουργεί τεχνητό φωτισμό, κατασκευές και αλλαγή στα χαρακτηριστικά και τη χρήση της παραλίας (Lohmann *et al.*, 1997; Kikukawa *et al.*, 1999; Weishampel *et al.*, 2004), καθώς επίσης και επιδείνωση των παραλιών ωοτοκίας από τις καλλιέργειες, τον ευτροφισμό των εδαφών, την περίφραξή τους, την εξόρυξη άμμου και τη θήρευση των αυγών (Ackerman, 1997). Στη θάλασσα, οι θαλάσσιες χελώνες αντιμετωπίζουν την απευθείας θήρευση, τη θνησιμότητα εξαιτίας της αλιείας (Epperly *et al.*, 1995), καθώς επίσης και άλλες απειλές όπως η μόλυνση από πετρελαιοειδή (Sims *et al.*, 2006a), τα απορρίμματα (Balazs, 1985), τις καταστροφικές πρακτικές αλιείας όπως το ψάρεμα με δυναμίτη και κυάνιο (Bjorndal, 1996; Pilcher & Oakley, 1997), τις άγκυρες και τις προπέλες των σκαφών, την εναπόθεση φερτών υλών και τη χρήση συρόμενων αλιευτικών εργαλείων σε θαλάσσια λιβάδια ποσειδωνίας (Bjorndal, 1996). Η παγκόσμια αύξηση της θερμοκρασίες προσθέτει νέες απειλές τόσο στις παραλίες ωοτοκίας, όσο και στη θάλασσα.

Κατά συνέπεια, όλα τα είδη των θαλάσσιων χελωνών συμπεριλαμβάνονται στο Παράρτημα 1 της CITES και απαγορεύεται η εμπορία τους για όλα τα κράτη – μέλη. Σε πολλές χώρες, η ελλειπής εφαρμογή της νομοθεσίας, η ανεπαρκής ενημέρωση και ευαισθητοποίηση και συμμετοχή στα μέτρα προστασίας συμβάλλουν στη μείωση των πληθυσμών των θαλάσσιων χελωνών. Η *Caretta caretta* χαρακτηρίζεται ως απειλούμενο παγκοσμίως είδος σύμφωνα με το Κόκκινο Βιβλίο της IUCN (2000), το οποίο βασίζεται στο ότι τα επίπεδα ενόχλησης και εκμετάλλευσης υποδεικνύουν μια μείωση τουλάχιστον κατά 50% τα επόμενα 10 χρόνια ή τις 3 επόμενες γενίες, βάσει άμεσων παρατηρήσεων (Weimerskirch *et al.*, 2002). Επιπλέον, οι οικότοποι της *Caretta caretta* προστατεύονται και με βάση το Ευρωπαϊκό Οικολογικό Δίκτυο “Natura 2000” (Οδηγία 92/43/ΕΕ) καθώς και από μια πληθώρα συμβάσεων που έχουν υπογραφεί από την Ελλάδα (π.χ. Barcelona Convention, Bern Convention, CITES). Παρόλα αυτά, πάνω από το ένα τέταρτο των χωρών της Μεσογείου πρέπει να προσθέσουν ή και να βελτιώσουν τη νομοθεσία τους, ώστε να ενισχυθεί η προστασία των θαλάσσιων χελωνών.

Παράμετροι του αναπαραγωγικού πληθυσμού της Μεσογείου

Οι κύριοι αναπαραγωγικοί πληθυσμοί της *Caretta caretta* απαντώνται στην Ανατολική Μεσόγειο, σε χώρες όπως η Ελλάδα, η Τουρκία και η Κύπρος. Θεωρείται ότι οι θαλάσσιες χελώνες δεν γεννάνε στη Δυτική Μεσόγειο διότι τα νερά είναι πιό ψυχρά από ότι απαιτείται από αυτές. Η τεκμηριωμένη ωοτοκία της *Caretta caretta* στη Μεσόγειο φτάνει τις 5.031 φωλιές ανά περίοδο, από τις οποίες το 60.6% στην Ελλάδα, το 27.2% στην Τουρκία και το 11.4% στην Κύπρο. Μικρότερα ποσοστά ωοτοκίας παρατηρούνται στη Λιβύη, στην Τυνησία, στην Αίγυπτο, στο Ισραήλ, στην Ιταλία και στην Ισπανία. Οι θαλάσσιες χελώνες που ωοτοκούν στη Μεσόγειο είναι αρκετά πιο μικρές από τις θαλάσσιες χελώνες σε άλλα μέρη του κόσμου, γεγονός το οποίο πιθανά οφείλεται στο ότι ζούν σε μια από τις πιο ολιγότροφες περιοχές του κόσμου (Miller, 1997). Οι μελέτες δείχνουν ότι το ποσοστό των θηλυκών στους νεοσσούς είναι πολύ υψηλό σε όλη τη Μεσόγειο (Godley *et al.*, 2001b).

Η πλειονότητα της ωοτοκίας της *Caretta caretta* στη Μεσόγειο, πραγματοποιείται ανάμεσα στις αρχές Ιουνίου και στις αρχές Αυγούστου, με σποραδική ωοτοκία από τα μέσα Μαΐου έως τις αρχές Σεπτεμβρίου. Κατά την αναπαραγωγική περίοδο, οι χελώνες χρησιμοποιούν τη θαλάσσια περιοχή για το ζευγάρωμα, την ανάπτυξη και την ωρίμανση των αυγών τους πριν την ωοαπόθεση, πριν και ενδιάμεσα της περιόδου ωοτοκίας. Οι παραλίες παίζουν σημαντικό ρόλο στον κύκλο ζωής των θαλάσσιων χελωνών, καθώς σε αυτές βγαίνουν οι θηλυκές για να αφήσουν τα αυγά τους. Το επιτυχές ζευγάρωμα υπολογίζεται ότι συμβαίνει περίπου 15 με 30 ημέρες πριν από την πρώτη ωοαπόθεση (Booth & Peters, 1972; Wood & Wood, 1980), με μια περίοδο 12 έως 20 ημερών ανάμεσα στις ωοαποθέσεις, ανάλογα με τη θερμοκρασία της θάλασσας (Sato *et al.*, 1998; Hays *et al.*, 2002a). Τα αρσενικά θεωρείται ότι αναχωρούν από την αναπαραγωγική περιοχή αμέσως μετά την περίοδο του ζευγαρώματος (Limpus, 1993; Godley *et al.*, 2002; Rostal, 2005), ενώ οι θηλυκές αμέσως μετά την περίοδο ωοτοκίας (Broderick *et al.*, 2002; Zbinden *et al.*, 2007a). Στη Μεσόγειο, έχει καταγραφεί ότι τα θηλυκά άτομα ωοτοκούν 2 έως πέντε φορές σε μία περίοδο, ενώ μεταναστεύουν εκ νέου στην περιοχή αναπαραγωγής κάθε 2 έως 3 χρόνια κατά μέσο όρο (Broderick *et al.*, 2002; Zbinden *et al.*, 2007a). Σε άλλες περιοχές του κόσμου, έχει παρατηρηθεί ότι τα αρσενικά μεταναστεύουν στις περιοχές αναπαραγωγής κάθε χρόνο (Limpus, 1993). I θαλάσσιες χελώνες, *Caretta caretta*, έχει παρατηρηθεί ότι μεταναστεύουν έως και 1.500 χιλιόμετρα μακρυά από τις περιοχές αναπαραγωγής, στις περιοχές διαχείμανσης και διατροφής σε άλλα τμήματα της Ανατολικής και της Δυτικής Μεσογείου (Broderick *et al.*, 2007; Zbinden *et al.*, 2008).

Η περιοχή αναπαραγωγής στη Ζάκυνθο

Οι *Caretta caretta* είναι οι μόνες θαλάσσιες χελώνες οι οποίες ωοτοκούν στην Ελλάδα (Margaritoulis *et al.*, 2003) και προστατεύονται από την εθνική νομοθεσία ήδη από το

1980. Ο κόλπος του Λαγανά στη Ζάκυνθο είναι ο μεγαλύτερος βιότοπος αναπαραγωγής για τις *Caretta caretta* στην Ελλάδα, στην Ευρώπη και προς το παρόν στη Μεσόγειο. Στον κόλπος Λαγανά πραγματοποιείται το 42,4% της συνολικής ωοτοκίας στην Ελλάδα και το 25,7% της ωοτοκίας στη Μεσόγειο (Margaritoulis, 2005). Στην περιοχή αυτή υπάρχουν έξι ξεχωριστές παραλίες ωοτοκίας, με μέσο ετήσιο αριθμό φωλιών 1.245 για τα έτη 1984 έως 2007 (SD± 302; range: 833-2018). Ο κόλπος του Λαγανά συμπεριλαμβάνεται στο Ευρωπαϊκό Οικολογικό Δίκτυο “Φύση 2000” (Directive 92/43/EEC: GR2210002). Το 1999, για την καλύτερη προστασία ης περιοχής, η περιοχή του κόλπου Λαγανά χαρακτηρίστηκε ως Εθνικό Θαλάσσιο Πάρκο Ζακύνθου (Ε.Θ.Π.Ζ.) με Προεδρικό Διάταγμα (ΦΕΚ 906/Δ/1999). Ο Φορέας Διαχείρισης του Ε.Θ.Π.Ζ. ανέπτυξε και έθεσε σε εφαρμογή μέτρα πρόστασίας ώστε να μειώσει την οικολογική πίεση στο βιότοπο αναπαραγωγής του κόλπου Λαγανά τόσο στις παραλίες ωοτοκίας, όσο και στη θαλάσσια περιοχή.

Στη Ζάκυνθο, όλα τα τμήματα γης που συνορεύουν με τις παραλίες ωοτοκίας είναι ιδιωτικά, επομένως η πιο σημαντική απειλή γι’αυτό το βιότοπο αναπαραγωγής της *Caretta caretta* είναι η ανάπτυξη των παράκτιων περιοχών και ο τουρισμός (Arianoutsou, 1988). Μέτρα προστασίας τέθηκαν σε εφαρμογή κατά τη δεκαετία του '90, πριν από τη θεσμοθέτηση του Ε.Θ.Π.Ζ. Καθώς η χρήση συσκευών αναμετάδοσης (π.χ. τηλεμετρία) την περίοδο εκείνη βρισκόταν σε πρώιμα στάδια, ο βαθμός προστασίας που καθορίστηκε για τις θαλάσσιες ζώνες του κόλπου Λαγανά, βασίστηκε στη θέση των παραλιών ωοτοκίας και στις σχετικές πυκνότητες φωλεοποίησης (Σχήμα 2, Arapis & Margaritoulis, 1996). Η ζώνη Α περιλαμβάνει 3 παραλίες ωοτοκίας οι οποίες αντιπροσωπεύουν το 70% της φωλεοποίησης στο βιότοπο, και σ’αυτή δεν επιτρέπεται η παρουσία κανενός πλωτού μέσου. Η ζώνη Β περιλαμβάνει 3 παραλίες ωοτοκίας, με 30% φωλεοποίηση, και σ’αυτή τα πλωτά μέσα έχουν όριο ταχύτητας τα 6 μίλια την ώρα και δεν μπορουν να αγκυροβολήσουν. Η ζώνη Γ δεν περιλαμβάνει καμία παραλία ωοτοκίας. Σ’αυτή τα πλωτά μέσα έχουν όριο ταχύτητας τα 6 μίλια την ώρα και μπορούν να αγκυροβολήσουν.

Δημοσιευμένες έρευνες για τις θαλάσσιες χελώνες στη Ζάκυνθο

Η έρευνα των θαλάσσιων χελωνών, ιστορικά έχει ως επίκεντρο τη βιολογία τους η οποία είναι συνδεδεμένη με την ξηρά π.χ. ωοαπόθεση και την επιτυχία εκκόλαψης, με τις απομακρυσμένες τεχνολογίες να επικεντρώνονται στη συμπεριφορά των θηλυκών κατά το διάστημα ανάμεσα στις ωοαποθέσεις και στη μετανάστευση.

Πληροφορίες σχετικά με την ωοτοκία έχουν διεξοδικά καταγραφεί από το 1984, από τη Μ.Κ.Ο. ΑΡΧΕΛΩΝ (Margaritoulis, 1982; Margaritoulis, 1983; Margaritoulis, 1985; Margaritoulis *et al.*, 2003; Margaritoulis, 2005). Οι πληροφορίες αυτές χρησιμοποιήθηκαν για την προστασία των παραλιών ωοτοκίας (Arianoutsou, 1988; Arapis & Margaritoulis, 1996; Kornaraki *et al.*, 2006), καθώς και για το σχεδιασμό θεωρητικών μοντέλων ωοτοκίας. Τέτοια μοντέλα περιλαμβάνουν την επιλογή της θέσης της φωλιάς (Mazaris *et al.*, 2006), την ανά χρόνο ποικιλότητα και πιστότητα των τάσεων του πληθυσμού σε προσομοιώσεις που βασίστηκαν σε πραγματικούς αριθμούς θηλυκών ατόμων (Mazaris *et al.*, 2005; Mazaris *et al.*, 2008b) και την επίδραση της θερμοκρασίας στη δραστηριότητα της ωοτοκίας (Mazaris *et al.*, 2004). Από τη θεσμοθέτηση του Ε.Θ.Π.Ζ. και μετά έχουν πραγματοποιηθεί έρευνες σχετικά με τη διαχείριση, οι οποίες αποτίμησαν τη διαχείριση της παράκτιας περιοχής σε σχέση με την νομοθεσία, με τους επισκέπτες και την ωοτοκία των θαλάσσιων χελωνών (Togridou *et al.*, 2006b; Togridou *et al.*, 2006a; Mazaris *et al.*, 2008a). Η επιστημονική έρευνα έδειξε ότι η αναλογία των θηλυκών στους νεοσσούς είναι μεγαλύτερη (Zbinden *et al.*, 2006; Zbinden *et al.*, 2007b) και οι γενετικές μελέτες υποδεικνύουν υψηλά επίπεδα πολλαπλής πατρότητας (Zbinden *et al.*, 2007c), καθώς και νέες ιδέες σχετικά με τη μετανάστευση των θηλυκών και τη χρήση της περιοχής, εφαρμόζοντας μεθόδους δορυφορικής τηλεμετρίας (Zbinden *et al.*, 2007a; Zbinden *et al.*, 2008). Παρόλα αυτά, για την ικανοποιητική προστασία του αναπαραγωγικού πληθυσμού της *Caretta caretta*, θα πρέπει να γίνει κατανοητός ο τρόπος με τον οποίο τόσο τα αρσενικά, όσο και τα θηλυκά χρησιμοποιούν το θαλάσσιο περιβάλλον στις περιοχές αναπαραγωγής και διατροφής, συμπεριλαμβανομένου του πληθυσμού, της συμπεριφοράς, των μετακινήσεων και της κατανομής σε σχέση με το βιότοπο, το περιβάλλον και την υφιστάμενη νομοθεσία.

Οι περιοχές αναπαραγωγής των θαλάσσιων χελωνών παρέχουν μια μικρή αλλά πολύ σημαντική ευκαιρία για τον προσδιορισμό της βιολογίας της αναπαραγωγής και της ωοτοκίας του είδους. Οι βασικοί κανόνες και τα κριτήρια, με βάση την έγκυρη επιστημονική έρευνα, είναι πολύ σημαντικά ώστε οι διαχειριστές και οι ερευνητές να αποφασίσουν πότε και γιατί να αναπτύξουν μια συγκεκριμένη διαχειριστική μέθοδο, πως να εφαρμόσουν αποτελεσματικά την επιλογή τους και να αποτιμήσουν τα αποτελέσματά της (Sutherland *et al.*, 2004).

Περιγραφή της υπό μελέτη περιοχής

Ο κόλπος Λαγανά βρίσκεται στο νοτιο-ανατολικό τμήμα της νήσου Ζακύνθου (37° 43’ N, 20° 52’ E). Ο κόλπος είναι γενικά αβαθής με μέγιστο βάθος τα 50 μ, μέση θερμοκρασία στην επιφάνεια της θάλασσας που κυμαίνεται από 15°C το Μάρτιο έως 28°C τον Αύγουστο (Comprehensive Ocean Atmosphere Data Sets (COADS) database, www.cdc.noaa.gov/ coads/). Ο κόλπος Λαγανά έχει μήκος 12 χιλιόμετρα και πλάτος 8 χιλιόμετρα, ενώ η ακτογραμμή του έχει μήκος 27.8 χιλιόμετρα από τα οποία 6.16 χιλίομετρα είναι παραλίες ωοτοκίας της θαλάσσιας χελώνας *Caretta caretta*.

Η πιλοτική έρευνα ανά τομείς, η οποία πραγματοποιήθηκε στο πλαίσιο της παρουσίας διδακτορικής διατριβής από την συγγραφέα (G.S.), ως προς την κατανομή των θαλάσσιων χελωνών κατά την περίοδο 2003 – 2005 στον κόλπο του Λαγανά έδειξε ότι οι θηλυκές χελώνες συγκεντρώνονται κυρίως κατά μήκος της ακτογραμμής σε ένα τμήμα μήκους 5 χιλιομέτρων, ανάμεσα στον Άγιο Σώστη και στο Καλαμάκι (Schofield *et al.*, 2008c). Γι’αυτό το λόγο η παρούσα διατριβή επικεντρώνεται σε αυτή την περιοχή (Σχήμα 3) (αυτό επιβεβαιώθηκε αργότερα με τη χρήση της απομακρυσμένης τεχνολογίας, Schofield *et al.*, 2007a).

Στόχοι της έρευνας

Κύριος στόχος της έρευνα ήταν η συλλογή πληροφοριών σχετικά με τη βιολογία των θαλάσσιων χελωνών, ώστε να διαπιστωθεί η αποτελεσματικότητα των μέτρων προστασίας στην αναπαραγωγική περιοχή του Ε.Θ.Π.Ζ. και να προταθούν σχετικές τροποποιήσεις. Οι έρευνες στη Ζάκυνθο τα προηγούμενα χρόνια είχαν τα προηγούμενα επικεντρωθεί στις παραλίες ωοτοκίας. Ωστόσο, και οι έρευνες στο νερό με απευθείας παρατήρηση της συμπεριφοράς των θαλάσσιων χελωνών είναι σπάνιες παγκοσμίως, εξαιτίας της δυσκολίας παρατήρησης στη θάλασσα. Επομένως, η παρούσα έρευνα δεν είχε προηγούμενες πληροφορίες στις οποίες μπορούσε να βασιστεί. Τα Κεφάλαια 1 έως 3 παρουσιάζουν τα αποτελέσματα της απευθείας παρατήρησης που αφορούν την ταυτοποίηση των ατόμων και τις παρατηρήσεις συμπεριφοράς. Στα Κεφάλαια 4 έως 6, με τη χρήση της απομακρυσμένης τεχνολογίας επιβεβαιώνονται οι προηγούμενες παρατηρήσεις μας και τα ερωτήματα που προέκυψαν από τις εν λόγω παρατηρήσεις. Συνεπώς, η διατριβή αυτή παρουσιάζει την ανάπτυξη και υλοποίηση των ερευνητικών ιδεών που η σύλληψή τους έγινε σε διαδοχικές αναπαραγωγικές περιόδους. Ως αποτέλεσμα αυτής της μεθόδου κατέστη δυνατή η ανάπτυξη νέων προσεγγίσεων μελέτης της βιολογίας κ'συμπεριφοράς των θαλάσσιων χελωνών, συμπεριλαμβανόμενων παραμέτρων της δυναμικής του πληθυσμού, της ηθολογίας και των προτύπων μετακίνησης, στον σημαντικότερο και λιγότερο μελετημένο βιότοπο αναπαραγωγής της θαλάσσιας χελώνας στη Μεσόγειο.

Η δομή της παρούσας διατριβής έχει ως εξής:

1) Στο Κεφάλαιο 1, περιγράφεται μια απλή και γρήγορη τεχνική φωτο-αναγνώρισης των ατόμων της θαλάσσιας χελώνας *Caretta caretta*.
2) Στο Κεφάλαιο 2, αναλύονται με λεπτομέρειες οι διαφορετικές συμπεριφορές που παρατηρήθηκαν σε αρσενικά και θηλυκά άτομα της θαλάσσιας χελώνας *Caretta caretta* στην περιοχή αναπαραγωγής.
3) Στο Κεφάλαιο 3, εξετάζονται η δομή και οι λειτουργίες της ανταγωνιστικής συμπεριφοράς ανάμεσα στις θηλυκές θαλάσσιες χελώνες.
4) Στο Κεφάλαιο, 4 διερευνώνται οι μετακινήσεις των θηλυκών θαλάσσιων χελωνών, με τη χρήση της τεχνολογίας GPS, εντός της περιοχής αναπαραγωγής και οι πιθανές εφαρμογές τους στη διαχείριση της περιοχής.
5) Στο Κεφάλαιο 5 εξετάζονται τα σχετικά πρότυπα μετακινήσεων των αρσενικών και θηλυκών ατόμων, στα οποία είχε τοποθετηθεί πομπός GPS, μέσα στη περιοχή αναπαραγωγής γαι την εφαμογή τους στη διαχείριση της περιοχής. Παράλληλα, δίνονται νέες πληροφορίες σχετικά με τη μετανάστευση των αρσενικών μετά το ζευγάρωμα στις μακρινές περιοχές διατροφής και διαχείμανσης.

6) Στο Κεφάλαιο 6, συνδυάζονται τα δεδομένα που συλλέχθηκαν ώστε να καθοριστεί η ύπαρξη της επιλογής μικρο-οικοτόπων από τις θαλάσσιες χελώνες σε ένα δυναμικό θερμοκρασιακά περιβάλλον, εξετάζοντας τις πιθανές αιτίες και διερευνώντας τις πιθανές στρατηγικές.
7) Στη Συζήτηση αναλύοναι τα επιστημονικά συμπεράσματα της παρούσας ερευνάς και συσχετίζονται με τη διαχείριση και την προστασία σε τοπικό και περιφερειακό επίπεδο, καθώς και με τις ανάγκες για μελλοντική έρευνα.

Σκοπός του Κεφάλαιου 1 ήταν η δημιουργία ενός αντικειμενικού εργαλείου ώστε να κατασκευαστεί μια βάση δεδομένων του πληθυσμού χρησιμοποιώντας τη φωτο-αναγνώριση. Η ρεαλιστική εκτίμηση του μεγέθους του πληθυσμού και το ιστορικό της ζωής των ατόμων είναι πολύ σημαντικά για την αποτελεσματική διαχείριση της άγριας ζωής, αλλά συχνά είναι δύσκολο να μετρηθούν σε θαλάσσια ζώα τα οποία ζουν πολλά χρόνια και πραγματοποιούν μακρινές μεταναστεύσεις (Caughley, 1994). Πολλά ερευνητικά προγράμματα θαλάσσιων χελωνών χρησιμοποιούν μαρκάρισμα με συμβατικές μεθόδους (π.χ. plastic, monel, titanium) ώστε να αποκτήσουν πληροφορίες σχετικά με το ιστορικό ζωής των θηλυκών θαλάσσιων χελωνών στις περιοχές αναπαραγωγής, ή πληροφορίες σχετικά με τις ηλικιακές κλάσεις στις περιοχές διατροφής (Chaloupka & Limpus, 2001; Balazs & Chaloupka, 2004). Η αναπόφευκτη απώλεια των σημάνσεων (π.χ. εξαιτίας λανθασμένης τοποθέτησης ή εξαιτίας χτυπήματος/δαγκώματος) μπορεί να αποδειχτεί σημαντικό πρόβλημα για ορισμένα είδη (Limpus, 1992), διακόποντας έτσι τη συνέχεια μακροχρόνιων προγραμμάτων παρακολούθησης για είδη που ζουν πολλά χρόνια (Sibly *et al.*, 2005). Η εφαρμογή της τεχνικής της φωτο-αναγνώρισης παρότι έχει διερευνηθεί σε διάφορα είδη θαλάσσιων χελωνών (Bennett *et al.*, 1999; Richardson *et al.*, 2000; Rodriguez & Sarti, 2000; Schofield *et al.*, 2004; White, 2006; Wood, 2006), δεν έχει ακόμα καθοριστεί η χρησιμότητα της ως εργαλείο βιο-παρακολούθησης σε μεγάλους πληθυσμούς. Έτσι, θέσαμε δύο στόχους: (i) να καθορίσουμε τη χρησιμότητα της τεχνικής της φωτο-αναγνώρισης σε ένα μεγάλο πληθυσμό (ο οποίος ξεπερνά τα 400 άτομα), δοκιμάζοντας την στον μεγαλύτερο βιότοπο αναπαραγωγής της *Caretta caretta* στη Μεσόγειο (που αρκετές εκατοντάδες χελωνών συγκεντρώνονται κάθε καλοκαίρι) και (ii) να καθορίσουμε εάν ανεκπαίδευτοι χρήστες μπορούν γρήγορα και αξιόπιστα να μάθουν την τεχνική της φωτο-αναγνώρισης, ώστε να ταυτοποιήσουν άτομα της θαλάσσιας χελώνας. Η μέθοδος έπρεπε να είναι εύκολη στη χρήση για έμπειρους και άπειρους χρήστες, καθώς και αξιόπιστη και αποτελεσματική για την ταυτοποίηση αρσενικών και θηλυκών ατόμων, ώστε να χρησιμοποιηθεί για τη βιο-παρακολούθηση του πληθυσμού, τις μελέτες συμπεριφοράς τη διαχείριση και την προστασία.

Σκοπός του Κεφάλαιου 2 ήταν η συλλογή πληροφοριών σχετικά με τη συμπεριφορά των αρσενικών και θηλυκών θαλάσσιων χελωνών *Caretta caretta* στο θαλάσσιο περιβάλλον κατά την αναπαραγωγική περίοδο. Και αυτό διότι οι απευθείας παρατηρήσεις ενός ζώου στο φυσικό του περιβάλλον, παρέχουν πολύτιμες πληροφορίες για το πως αυτό το είδος προσαρμόζεται στο ιδιαίτερο περιβάλλον του. Εξαιτίας των δυσκολιών στη μελέτη μεγάλων θαλάσσιων σπονδυλωτών στο φυσικό τους περιβάλλον (π.χ. η κατάσταση της θάλασσας, το βάθος, η ορατότητα, και οι φυσικοί κίνδυνοι), οι περισσότερες μελέτες συμπεριφοράς των θαλάσσιων χελωνών βασίζονται στα συμπεράσματα που εξάγονται από συσκευές που τοποθετούνται στα ζώα, όπως καταγραφείς δεδομένων ράδιο- και δορυφορικής-τηλεμετρίας (Hopkins-Murphy *et al.*, 2003; Hochscheid *et al.*, 2005a; Myers & Hays, 2006). Παρόλα αυτά, χωρίς τη σύγκριση με αξιόπιστες απευθείας παρατηρήσεις της συμπεριφοράς, υπάρχει κίνδυνος λανθασμένης ερμηνείας των δεδομένων, ή ακόμα η παράβλεψη πλευρών της βιολογίας των θαλάσσιων χελωνών, όπως απέδειταν οι Houghton *et al.*(2002). Η εκτενέστερη μελέτη της συμπεριφοράς των θαλάσσιων χελωνών με απευθείας παρατηρήσεις προέρχεται από τους Booth and Peters (1972), την οποία έχουν συμπληρώσει και άλλες μελέτες (Whittow & Balazs, 1982; Dodd, 1988; Losey *et al.*, 1994; Frick *et al.*, 2000; Heithaus *et al.*, 2002b). Καθώς οι θαλάσσιες χελώνες συγκεντρώνονται κοντά στη ακτή, στον κόλπο του Λαγανά και διαμένουν στα ρηχά και γενικά καθαρά νερά, μας δόθηκε η ευκαιρία να καταγράψουμε και να τεκμηριώσουμε τη συμπεριφορά των θαλάσσιων χελωνών με απευθείας παρατηρήσεις, σε μία εύκρατη αναπαραγωγική περιοχή. Επομένως οι στόχοι της μελέτης ήταν: (i) να καταγράψουμε και να τεκμηριώσουμε τη μονήρη και την κοινωνική συμπεριφορά των θαλάσσιων χελωνών και (ii) να ερευνήσουμε τον τρόπο με τον οποία οι διαφορές στη συμπεριφορά των αρσενικών και των θηλυκών χελωνών μπορεί να αντικατοπτρίζουν στρατηγικές που οφείλονται στο φύλο. Τέτοιες πληροφορίες είναι βασικές για την αποτελεσματική προστασία και διαχείριση των ζώων στο φυσικό τους περιβάλλον (Mills *et al.*, 2005), παρέχοντας τον τρόπο κατανόησης του πως ένα ζώο μπορεί να επηρεάζει την κοινότητα γύρω του, καθώς και τη λειτουργία, την οργάνωση και την απόκριση σε πιθανή διαταραχή του οικοσυστήματος (Piraino *et al.*, 2002).

Στο Κεφάλαιο 3 γίνεται αναλυτική διερεύνηση μιας πλευράς της συμπεριφοράς των χελωνών, (η οποία αναγνωρίστηκε στο Κεφάλαιο 2) που αφορά την ανταγωνιστική αλληλεπίδραση των θηλυκών χελωνών. Παρότι υπάρχουν κάποια στοιχεία σχετικά με την επιθετική αλληλεπίδραση μεταξύ χελωνών όταν βρίσκονται η μία κοντά στην άλλη (Herbst & Jacobson, 2000; Limpus & Limpus, 2003), η επιθετικότητα ανάμεσα σε αναπαραγωγικά ενήλικες θηλυκές χελώνες δεν έχει καταγραφεί στο παρελθόν. Επιπλέον, υπάρχουν ελάχιστες καταγραφές επιθετική συμπεριφορά ανάμεσα σε θηλυκά του ίδιου είδους από το ζωϊκό βασίλειο (Liker & Székely, 1997). Στην περίπτωση τέτοιων θηλυκών, η επιθετικότητα σχετίζεται συχνά με παράγοντες που επηρεάζουν την επιβιωσή τους ή αυτή των απογόνων τους: για παράδειγμα η τροφή, οι ερωτικοί σύντροφοι, οι περιοχές ωρίμανσης των αυγών, οι περιοχές ωοτοκίας και οι περιοχές στις οποίες αποφεύγουν τους θηρευτές (Gowaty & Wagner, 1988; Liker & Székely, 1997; Woodley & Moore, 1999). Οι στόχοι της μελέτης αυτής ήταν: (i) να περιγράψει τα στάδια κλιμάκωσης από τις παθητικές επιδείξεις μέχρι την επιθετική διαμάχη, (ii) να καταγράψει τους τρόπους με τους οποίους οι αντίπαλοι ανταλλάσσουν πληροφορίες σχετικά με την ικανότητα και το κίνητρό τους, βασιζόμενοι σε υπάρχοντα μοντέλα ανταγωνισμού, και (iii) να εξετάσει πιθανές αιτίες της επιθετικής συμπεριφοράς ανάμεσα στις θηλυκές *Caretta caretta*. Λόγω του ότι μια πληθώρα παραγόντων που σχετίζονται με την ικανότητα ή/και την αξία των φυσικών πηγών για κάθε ανταγωνιστή, επηρεάζει το κίνητρό του και επομένως το αποτέλεσμα της διαμάχης (Parker, 1974; Maynard Smith, 1982; Enquist & Leimar, 1983; Kotiaho *et al.*, 1999; Cressman *et al.*, 2004), παρόμοια συμπεριφορά μπορεί να υποδεικνύει προσαρμοστικότητα σε έναν οικότοπο. Συνεπώς, με την απευθείας συλλογή βασικών πληροφοριών συμπεριφοράς, οι ηλεκτρονικές συσκευές καταγραφής μπορεί επιπλέον να χρησιμοποιηθούν ως ένα ισχυρό εργαλείο για τη συλλογή ειδικών πληροφοριών σε σχέση με τις τάσεις της κοινωνικής συμπεριφοράς των ζώων και τη χρήση του οικοτόπου.

Στα Κεφάλαια 4 και 5, η χρήση της απομακρυσμένης τεχνολογίας υλοποιείται με τη μορφή των μονάδων GPS και TDRs (Time-Depth Recorders), ώστε να επιβεβαιώσουμε τη χρήση από τις χελώνες της περιοχής κοντά στην ακτή, η οποία διαπιστώθηκε κατά την έρευνα του πληθυσμού με απευθείας παρατήρηση. Η απόκτηση αξιόπιστων και υψηλής ακρίβειας και λεπτομέρειας δεδομένων ιχνηλάτησης, μπορεί να είναι πολύ σημαντική για τη λήψη ορθολογικών, προσαρμοζόμενων και δυναμικών διαχειριστικών αποφάσεων για ένα φυσικό οικότοπο, για ένα απειλούμενο είδος και για άλλες σχετικές πολιτικές προστασίας του φυσκού περιβάλλοντος τόσο σε τοπικό, όσο και σε περιφερειακό επίπεδο (Argardy, 1994; Thompson *et al.*, 2000; Parra *et al.*, 2006). Τα συμβατικά συστήματα τηλεμετρίας έχουν περιορισμένη εφαρμογή όταν απαιτούνται υψηλής ακρίβειας και λεπτομέρειας δεδομένα, και όταν συνεκτιμώνται τα πρότυπα μετακινήσεων με τις βιοφυσικές παραμέτρους σε μικρή κλίμακα (Wilson *et al.*, 2002; Bradshaw *et al.*, 2007b). Παρότι οι μονάδες GPS έχουν ακρίβεια μερικών δεκάδων του μέτρου, το γεγονός ότι τα θαλάσσια ζώα βγαίνουν στην επιφάνεια του νερού σε σποραδικά διαστήματα, περιορίζει τη χρονική περίοδο κατά την οποία οι μονάδες GPS μπορούν να λάβουν σήμα από τους δορυφόρους (Sisak, 1998; Jay & Garner, 2002; Ryan *et al.*, 2004; Yasuda & Arai, 2005; Petersen *et al.*, 2006; Sheppard *et al.*, 2006). Οι υπάρχουσες μελέτες για τις θηλυκές θαλάσσιες χελώνες στις περιοχές αναπαραγωγής, χρησιμοποίησαν όλες συμβατική τεχνολογία και η πλειοψηφία τους πραγματοποιήθηκε με το τέλος της περιόδου ωοτοκίας (Hays *et al.*, 1991; Hays *et al.*, 2002a; Houghton *et al.*, 2002; Hays *et al.*, 2003a; Hopkins-Murphy *et al.*, 2003). Εξαιτίας της ανάγκης για σύλληψη μέσα στο νερό, που βέβαια απαιτεί μεγάλη φυσική προσπάθεια και έρευνα (Ehrhart & Ogren, 1999), η γνώση σχετικά με τη χρήση της περιοχής από τα αρσενικά στις περιοχές αναπαραγωγής είναι σπάνια (αλλά βλέπε Limpus, 1993; Plotkin *et al.* 1996; Sakamoto *et al.*, 1997; Hays *et al.*, 2001; James *et al.*, 2005; Shaver *et al.*, 2005a; Godley *et al.*, 2008). Παρόλα αυτά, για τον αντικειμενικό καθορισμό του εάν τα υπάρχοντα ή τα προτεινόμενα διαχειριστικά μέτρα σε τοπικό (για παράδειγμα εντός μιας προστατευόμενης περιοχής), εθνικό και περιφερειακό επίπεδο είναι τα κατάλληλα, απαιτούνται υψηλής ακρίβειας και λεπτομέρειας δεδομένα ιχνηλάτησης για τα άτομα του πληθυσμού. Επιπρόσθετα, στη Μεσόγειο, στις περιοχές διατροφής των θαλάσσιων χελωνών δεν υφίστανται μέτρα προστασίας (Margaritoulis *et al.*, 2003; Zbinden *et al.*, 2008). Επομένως, η επιβεβαίωση της χρήσης συγκεκριμένων περιοχών από τις αρσενικές και τις θηλυκές θαλάσσιες χελώνες μπορεί να συνεισφέρει με το να δώσει τα αποδεικτικά στοιχεία τα οποία θα οδηγήσουν στη θεσμοθέτηση προστατευόμενων περιοχών. Συνοψίζοντας, οι στόχοι στα δύο αυτά Κεφάλαια ήταν: (i) να διερευνηθούν με λεπτομέρεια και ακρίβεια οι μετακινήσεις των αρσενικών και θηλυκών θαλάσσιων χελωνών *Caretta caretta* στην προστατευόμενη περιοχή του κόλπου Λαγανά, (ii) να προσδιοριστεί κατά πόσο τα πρότυπα μετακινήσεων των θηλυκών σε τοπικό επίπεδο είναι τυχαία, (iii) να συνδυαστούν τα δεδομένα της φώτο-αναγνώρισης με αυτά από τα GPS ώστε να υπολογιστεί μια λειτουργική αναλογία φύλου για τον πληθυσμό, (iv) να εξακριβωθεί η αναχώρηση των αρσενικών από την αναπαραγωγική περιοχή και να προσδιοριστεί η τοποθεσία των περιοχών διατροφής, σε σχέση με αυτές των θηλυκών, (v) να εξεταστεί πως μπορούν να δεδομένα μας να συνεισφέρουν στη βελτίωση των μέτρων προστασίας και της νομοθεσίας σε τοπικό και περιφεριακό επίπεδο.

Στο Κεφάλαιο 6 αναζητούμε τις αιτίες της επιθετικής συμπεριφοράς για τις περιοχές ανάπαυσης κοντά στη ακτή και τα πρότυπα μετακινήσεων των θηλυκών χελωνών που καταγράφτηκαν. Ο βιότοπος της Ζακύνθου στον κόλπο του Λαγανά, είναι ασυνήθιστος γιατί σε αυτόν συγκεντρώνεται ένας σχετικά μεγάλος αριθμός ατόμων (Margaritoulis, 2005), παρότι βρίσκεται στα όρια ενώς γεωγραφικού πλάτους που το είδος μπορεί να ανεχτεί (Dodd, 1988). Η σημασία της επιλογής θερμοκρασίας σε ένα δυναμικό περιβάλλον μπορεί να είναι ιδιαίτερα σημαντική στα όρια κατανομής του είδους, όπου οι περιβαλλοντικές συνθήκες μπορεί να αγγίζουν όρια καταλληλότητας, και επομένως, οι συνέπειες της επιλογής θερμών οικοθέσεων είναι μεγαλύτερη. Τέτοιες καταστάσεις μπορεί να είναι ιδανικές για τη διερεύνηση της πρακτικής της επιλογής θερμοκρασίας σε ένα δυναμικό περιβάλλον. Σε γενικές γραμμές, η θερμοκρασία του νερού επηρεάζει άμεσα τη θερμοκρασία σώματος των θαλάσσιων χελωνών και επομένως τις μετακινήσεις τους (Etnoyer *et al.*, 2006), την αναζήτηση τροφής (Broderick *et al.*, 2001a), την εποχικότητα αναπαραγωγής (Godley *et al.*, 2002; Weishampel *et al.*, 2004), την περιοδικότητα ωοαπόθεσης (Sato *et al.*, 1998; Hays *et al.*, 2002a) και τις περιόδους μετανάστευσης (Solow *et al.*, 2002). Συνεπώς, η ικανότητα εντοπισμού θερμοκρασιακά κατάλληλων περιοχών, όπου η θερμοκρασία του νερού βρίσκεται σε συγκεκριμένα όρια διακύμανσης είναι ζωτικής σημασίας. Στο κεφάλαιο αυτό: (i) εξετάζεται εάν οι θαλάσσιες χελώνες στη Ζάκυνθο παρουσιάζουν θερμοκρασιακή επιλογή και (ii) διερευνάται η πιθανότητα οφέλους από αυτή την επιλογή, με την έννοια της επιτάχυνσης της ωρίμανσης των αυγών που επιτρέπει στην πρώτη ωοαπόθεση να πραγματοποιηθεί νωρίτερα γεγονός που μπορεί να βελτιώσει την αναπαραγωγική ικανότητα. Η παρούσα έρευνα, δεν δείχνει μόνο τη σημασία της επαρκούς προστασίας των θαλάσσιων περιοχών κοντά στην ακτή, οι οποίες χρησιμοποιούνται από τις θηλυκές χελώνες στις αρχές της αναπαραγωγικής περιόδου, αλλά μπορεί επίσης να υποδείξει πως τα πρότυπα επιλογής οικοθέσεων και τα όρια κατανομής ενός είδους μπορούν να επηρεαστούν σε σχέση με την παγκόσμια αλλαγή του κλίματος.

Η παρούσα διατριβή έχει μια δομή που αποτελείται από έξι κεφαλαία, καθένα από τα οποία έχει δημοσιευτεί σε επιστημονικό περιοδικό. Η έρευνα πραγματοποιήθηκε από την υποψήφια διδάκτορα η Gail Schofield και έγινε δυνατή με τη βοήθεια των επιβλεπόντων καθηγητών. Η σύνταξη των επιστημονικών άρθρων έγινε από την Gail Schofield, ελέχθηκαν και διορθώθηκαν από τους επιβλέποντες καθηγητές μου. Οι συν-συγγραφείς που αναφέρονται σε κάθε επιστημονικό άρθρο, βοήθησαν με διάφορους τρόπους: με το να μου παρέχουν τη δυνατότητα να μελετήσω τα ζώα και να έχω στη διάθεση μου τον κατάλληλο εξοπλισμό, με την παροχή συμβουλών στο σχεδιασμό της έρευνας, με εποικοδομητική κριτική σε πρόχειρες εκδόσεις άρθρων και με τη βοήθεια τους στη στατιστική ανάλυση.

GENERAL INTRODUCTION

Protecting threatened species is necessary, given the accelerated decline noted in the populations of most of these species around the world. Sea turtles represent one such species for which action is needed at both a country and regional level to provide the most favourable conditions for reducing the threats to the sea turtle populations. For effective protection, the biological and ecological conditions that are specific to the sea turtle species must be considered.

Phylogeny & Morphology

Turtles appeared in the late Triassic about 200 million years ago (Pritchard, 1997). Sea turtles constitute a single radiation that was distinct from all other turtles at least 110 million years ago during the Cretaceous period. During that radiation, sea turtles split into two main subgroups, which still exist today: the unique family Dermochelyidae, comprising a single species, the leatherback (*Dermochelys coriacea*); and the six species of hard-shelled sea turtle in the family Cheloniidae (the loggerhead *Caretta caretta*, the Hawksbill *Eretmochelys imbricata*, the Olive ridley *Lepidochelys olivacea*, the Kemp’s ridley *Lepidochelys kempi*, the Green *Chelonia mydas* and the Flatback *Natator depressus*). The physiological design and biological adaptations of sea turtles have remained unchanged for millions of years, with several key features that are common to all sea turtle species and which set them apart from other Testudines; these include non-retractile limbs, extensively roofed skulls, limbs converted to paddle-like flippers, and salt glands to excrete excess salt. However, the sea turtle species’ differ between one another in generation time, population dynamics and global distribution.

Ecology & Distribution

Sea turtles habitats primarily occur in the tropics. This is because they are ectotherms, whereby water temperature strongly influences turtle body temperature and hence influences movement (Etnoyer *et al.*, 2006), food acquistion (Broderick *et al.*, 2001b), reproductive seasonality (Godley *et al.*, 2002; Weishampel *et al.*, 2004; Rostal, 2005), internesting periodicity (Sato *et al.*, 1998; Hays *et al.*, 2002a) and remigration interval (Solow *et al.*, 2002). Therefore, the ability to locate thermally suitable sites, where water temperature lies within a certain range, is of fundamental importance. Loggerheads are different to other sea turtle species in that they are a circumglobal species; nesting areas are concentrated at more temperate latitudes of 19-36º north & south of the equator (Dodd, 1988), with isolated nesting events being recorded up to 41ºN (Bentivegna *et al.*, 2005; SWOT website http://www.seaturtlestatus.org). (Figure 1). The Mediterranean sea holds breeding populations of just two of the seven sea turtle species, the loggerhead (*Caretta caretta*, Linnaeus, 1758) and the green (*Chelonia mydas*, Linnaeus, 1758), with infrequent foraging visits by the leatherback sea turtle (*Dermochelys coriacea*, Camiñas, 1998) into the region. Genetic research has shown that the localised populations of loggerheads that have evolved in the Mediterranean diverged genetically from western Atlantic stocks about 12,000 years ago after the last glacial period (Laurent *et al*, 1998).

Conservation issues

Sea turtles require a range of habitats to complete their life cycles; sandy beaches for egg deposition, shallow foraging sites and deep ocean migratory routes extending from the tropics to far northern and southern latitudes. Sea turtle species worldwide are subject to a diverse range of potential threats. On the nesting beaches turtles are threatened by tourist and residential development creating artificial lighting, building structure and changes in beach characteristics and beach use (Lohmann *et al.*, 1997; Kikukawa *et al.*, 1999; Kolbe & F.J., 2001; Weishampel *et al.*, 2004), as well as the loss or deterioration of nesting beach habitat from agriculture, nourishment, armouring and sand mining and/or nest predation (Ackerman, 1997). At sea, turtles face the risk of direct exploitation, fishery mortality (Epperly *et al.*, 1995) and a number of other threats, such as oil pollution, marine debris (Balazs, 1985), destructive fishing practices such as blast and cyanide fishing (Bjorndal, 1996; Pilcher & Oakley, 1997), anchors and propellers, siltation and the use of bottom trawls in seagrass ecosystems (Bjorndal, 1996). Global warming poses additional threats on both the nesting beach and marine environment.

Consequently sea turtle species are listed on Appendix 1 of CITES prohibiting any international trade among contracting parties. In many countries insufficient enforcement of existing legislation and inadequate public awareness and participation in conservation measures also contribute to the depleted status of these sea turtle populations. The loggerhead sea turtle is globally categorized as endangered on the 2000 IUCN red list, based on an index of abundance and levels of exploitation suggesting a reduction of at least 50% over the last 10 years or three generations based on known records (Weimerskirch *et al.*, 2002). Mediterranean loggerhead habitats are also protected under the European Natura 2000 Habitats Directive (EEC 92/43) as well as several international conventions ratified by Greece (e.g. Barcelona Convention, Bern Convention, CITES). Despite this, more than one quarter of the Mediterranean countries have yet to pass laws and finalise the legislative process to strengthen protection for marine turtles.

Breeding population parameters in the Mediterranean

The main loggerhead nesting concentrations are found in the Eastern Mediterranean basin countries of Greece, Turkey and Cyprus. It is assumed that turtles do not nest in the west Mediterranean because the sea is cooler than that required by turtles. The documented loggerhead nesting effort in the Mediterranean reaches an average of 5031 nests per season; of these 60.6% are in Greece, 27.2% are in Turkey and 11.4% are in Cyprus. Lower levels of nesting activity occur in Libya, Tunisia, Egypt, Lebanon, Israel, Syria, Italy and Spain. Nesting loggerheads in the Mediterranean are significantly smaller than those in other parts of the world, which is believed to be a result of their living in one of the most nutrient poor seas in the world (Miller, 1997). Studies indicate highly female-biased sex ratios in hatchling production across the Mediterranean (Godley *et al.*, 2001b).

The vast majority of loggerhead sea turtle nesting in the Mediterranean occurs between the beginning of June and early August, with sparse nesting from mid-May to early September. During the breeding period, sea turtles utilise the marine area for mating and egg development prior to egg laying during the pre- and inter-nesting periods. The beaches are instrumental in the life cycle of sea turtles, as this is where female loggerheads emerge to lay their eggs. Successful mating has been predicted to occur approximately 15-30 days prior to the first clutch being laid (Booth & Peters, 1972;

Wood & Wood, 1980), with an inter-nesting duration of 12-20 days, depending on sea temperature (Sato *et al.*, 1998; Hays *et al.*, 2002a) between each subsequent clutch. Males are believed to depart the breeding areas immediately after the mating period (Limpus, 1993; Godley *et al.*, 2002; Rostal, 2005), and females immediately after the nesting period (Broderick *et al.*, 2002; Zbinden *et al.*, 2007a). In the Mediterranean, females have been recorded nesting 2-5 times within a season, re-migrating every 2-3 years on average (Broderick *et al.*, 2002; Zbinden *et al.*, 2007a). In other parts of the world, males have been indicated to remigrate annually (Limpus, 1993). Loggerhead females have been observed to migrate at distances as far as 1500km from nesting grounds to wintering and foraging areas in other parts of the eastern and western Mediterranean (Broderick *et al.*, 2007; Zbinden *et al.*, 2008).

The breeding area of Zakynthos

Loggerheads are the only sea turtle species that nest in Greece (Margaritoulis *et al.*, 2003) and have been protected by national legislations since 1980. Laganas Bay, on Zakynthos Island, is the largest nesting rookery for loggerhead sea turtles (*Caretta caretta*) in Greece, Europe and, at present, the Mediterranean. Laganas Bay represents 42.4% of the total loggerhead nesting effort in Greece and 25.7% of that in the Mediterranean (Margaritoulis, 2005). There are six discernable nesting beaches on Zakynthos, with an average estimated nesting effort of 1245 nests annually between 1984 and 2008 (SD± 302; range: 833-2018). Laganas Bay was designated as one of the regions ratified for protection by the European Union Habitats Directive in 1992 (Directive 92/43/EEC: GR2210002). In 1999, for more effective protection of the region, the Democratic President of the Greek Republic decreed the formation of the National Marine Park of Zakynthos (NMPZ) (Gov. Gazette 906/D 22 December 1999). The NMPZ implement and enforce protection measures to reduce disturbance to the loggerhead sea turtle breeding habitats of Laganas Bay, including both the nesting beaches and marine area.

On Zakynthos, all land adjacent to the nesting beaches is privately owned, hence the most important threat for this particular loggerhead nesting area is considered to be coastal development and tourism (Arianoutsou, 1988). Protective legislation in Laganas

Bay was implemented during the 1990s prior to the formation of the National Marine Park of Zakynthos. Because transmitters were in their infancy during this period, the degree of protection offered by the maritime zones was delineated based on nesting beach locations and relative nesting densities (Figure 2, Arapis & Margaritoulis, 1996). Maritime Zone A holds three nesting beaches representing 70% of the rookery nesting effort. Here where no sea vessels are permitted. Maritime Zone B holds three nesting beaches and 30% of the nesting effort. Here sea vessels are permitted to travel at 6 knots but cannot anchor. Maritime Zone C holds no nesting activity, and here sea vessels are permitted to travel at 6 knots and may anchor.

Published sea turtle research on Zakynthos

For logistical reasons, the study of marine turtles has historically focused on aspects of their biology, which are tied to the land, e.g. nesting activities and hatchling success, with remote technology studies focusing on female internesting behaviour and post-nesting migration.

Information on nesting activity has been comprehensively gathered by Archelon since 1984 (Margaritoulis, 1982; Margaritoulis, 1983; Margaritoulis, 1985; Margaritoulis *et al.*, 2003; Margaritoulis, 2005). This data has been used towards conservation issues related to the nesting beaches (Arianoutsou, 1988; Arapis & Margaritoulis, 1996; Kornaraki *et al.*, 2006) and applied to theoretical models of sea turtle nesting activity. Such models include analysis of nest site selection (Mazaris *et al.*, 2006), the interannual variability and reliability of population trend simulations based on observed numbers of females (Mazaris *et al.*, 2005; Mazaris *et al.*, 2008b) and the influence of sea temperature on the onset and activity levels of sea turtle nesting (Mazaris *et al.*, 2004). Since the formation of the National Marine Park of Zakynthos, management related studies have been conducted assessing coastal area management actions in relation to legislation, visitors and sea turtle nesting activity (Togridou *et al.*, 2006a; Togridou *et al.*, 2006b; Mazaris *et al.*, 2008a). Science based research indicated female biased hatchling sex ratios (Zbinden *et al.*, 2006; Zbinden *et al.*, 2007b) and genetic studies inferring high levels of multiple paternity (Zbinden *et al.*, 2007c), as well as new insights into female loggerhead migration and area-use from satellite telemetry

(Zbinden *et al.*, 2007a; Zbinden *et al.*, 2008). However, to adequately protect all aspects of the breeding population, the way in which both male and female sea turtles utilise the marine environment at breeding and foraging grounds must be understood; including population, behaviour, movement and distribution parameters in relation to the habitat, environment and existing / proposed legislation.

Sea turtle breeding areas provide a narrow but important window of opportunity for assessing reproduction and nesting biology. Standard guidelines and criteria based on sound scientific research are essential in order for policy-makers and field workers to decide when and why to invoke one management option over another, how to effectively implement the chosen option, and evaluate success (Sutherland *et al.*, 2004).

Description of study area

Laganas Bay is situated at the southeastern part of the Greek island of Zakynthos (37° 43’ N, 20° 52’ E). The bay is generally shallow, reaching a depth of about 50 m, with sea surface temperatures of 15°C in March rising to 28°C in August (Comprehensive Ocean Atmosphere Data Sets (COADS) database, www.cdc.noaa.gov/ coads/). Laganas Bay is about 12 km long by 8 km wide, with a coastline of 27.8km in length, along 13km of which there is 6.16 km of loggerhead sea turtle nesting beaches.

Pilot transect surveys conducted by the author (GS) of turtle distribution during 2003-2005 indicated that female turtles tended aggregate along a 5 km section of coast (between Agios Sosits and Kalamaki) within Laganas Bay (Schofield *et al.*, 2008c). For this reason the thesis research effort was focused in this area (Figure 3) (and later validated by remote technology, Schofield *et al.*, 2007a).

Study aims

The overall aim of this study was to obtain information on sea turtle marine biology in order to ascertain the effectiveness of existing protecting measures within the breeding area of the National Marine Park of Zakynthos, and suggest amendments. Studies on Zakynthos had previously concentrated on the nesting beaches, while in-water studies directly observing sea turtle behaviour are sparse worldwide due to the difficulties of working in the marine environment. Therefore the research conducted in this study had no direct precedent or local information on which to build. Chapters 1-3 present the results of direct observation work in the form of identification and behavioural observations. Chapters 4-6 utlise remote technology to confirm these observations and address questions raised through these initial observations. The thesis therefore presents the development of research ideas built up across consecutive nesting seasons. As a result of this approach I was able to develop new insights into sea turtle marine biology, including population parameters, behavioural ecology and movement patterns, at the Mediterranean's largest loggerhead sea turtle rookeries, with limited existing research.

The structure of the thesis is as follows:

1) Chapter 1 describes a simple, rapid method for photographic-identification of loggerhead sea turtles.
2) Chapter 2 details the different behaviours observed by male and female loggerheads at the breeding area.
3) Chapter 3 examines the structure and function of antagonistic behaviour between female turtles
4) Chapter 4 investigates fine-scale movement of female turtles using GPS technology within the breeding area and its potential application to conservation management
5) Chapter 5 compares relative movement patterns of males and females attached with GPS units within the local breeding area for application to protection measures, while providing a new insight into male post-breeding migration to distant foraging/wintering areas.
6) Chapter 6 applies the assimilated data to determine the presence of microhabitat selection by sea turtles in a dynamic thermal marine environment, considering possible reasons and search strategy mechanisms
7) The discussion considers the new scientific findings of the research, conservation implications at a local and regional scale and the focus for future research.

The aim of **Chapter 1** was to construct an objective tool on which to build a population database using photo-identification. Realistic estimates of population size and life history parameters are central to effective wildlife management, but are often difficult to measure in long-lived and elusive migratory marine vertebrates (Caughley, 1994). Many sea turtle research programmes use some form of conventional tagging method (i.e. plastic, monel, titanium) to obtain life history information about nesting females at breeding areas or of different age classes at foraging areas (Chaloupka & Limpus, 2001; Balazs & Chaloupka, 2004). The inevitable loss of identification markers (i.e. from incorrect attachment or being knocked/bitten off) (Limpus, 1992) can become problematic in some species, interrupting the continuity of long-term studies of long-lived species of conservation concern (Sibly *et al.*, 2005). Hence, photo-identification has been explored in several sea turtle species (Bennett *et al.*, 1999; Richardson *et al.*, 2000; Rodriguez & Sarti, 2000; White, 2006; Wood, 2006; Schofield *et al.*, 2008c), the utility of this approach as a bio-monitoring tool when population sizes are large has not been established. We therefore set out with two objectives (i) to establish the utility of photo-identification in a large population (exceeding 400 unique individuals) by testing the technique at the Mediterranean's largest loggerhead turtle rookery, where several hundred turtles aggregate each summer and (ii) to establish whether naïve users could easily and reliably learn to use photo-identification to recognise individual sea turtles. The method had to be easy to use for experienced and non-experienced personnel and is credible and effective for individual recognition of male and female turtles for application in population bio-monitoring, behaviour studies and conservation.

The objective of **Chapter 2** was to gather information about the behaviour of male and female loggerhead sea turtles in the marine environment during the breeding period. This is because direct observation of animals in their natural environment contributes important information about how species adapt to a particular environment. Due to the difficulties of studying large marine vertebrates in their natural habitats (e.g. sea state, depth and visibility, physical danger), most behavioural studies of sea turtles rely on inferences from animalborne devices, such as data-loggers, radio and satellite telemetry (Hopkins-Murphy *et al.*, 2003; Hochscheid *et al.*, 2005a; Myers & Hays, 2006). However, without reliable comparative direct behavioural observations there is a risk of misinterpreting or even overlooking aspects of sea turtle biology (as shown by Houghton *et al.*, 2002). The most comprehensive study of sea turtle behaviour from direct-observations is by Booth and Peters (1972), to which several studies have subsequently contributed (Whittow & Balazs, 1982; Dodd, 1988; Losey *et al.*, 1994; Frick *et al.*, 2000; Heithaus *et al.*, 2002b). Because turtles aggregate close to shore in Laganas Bay, inhabiting shallow and generally clear waters, this provided an opportunity to document sea turtle behaviour through direct observation at a temperate breeding area. Therefore the aims of this study were to (i) document the solitary and social behaviour of loggerhead sea turtles, and (ii) evaluate how differences in the proportions of observed male and female behaviour may reflect gender-specific strategies. Such information is fundamental for the effective conservation of animals in their natural habitats (Mills *et al.*, 2005), providing a means to understand how an animal may impact the surrounding community as well as ecosystem function, organisation and response to disturbance (Piraino *et al.*, 2002).

Chapter 3 focused on a detailed assessment of one aspect of animal behaviour identified in Chapter 2, antagonistic interactions between females. While anecdotal evidence of aggressive interactions between individual turtles when in close proximity to one another exists (Herbst & Jacobson, 2000; Limpus & Limpus, 2003), aggression between reproductively adult female turtles has not been previously recorded. Furthermore, aggressive behaviour between females of the same species across the animal kingdom is not frequently documented (Liker & Székely, 1997). In the case of females, aggression is usually related to factors that affect their own and/or their offspring’s survival: for instance food, mates, gestation sites, nest sites and sites to evade predators (Gowaty & Wagner, 1988; Liker & Székely, 1997; Woodley & Moore, 1999). The aims of this study were to (i) describe the stages of contest escalation from passive displays to aggressive combat (ii) suggest how opponents communicate information on capability and motivation, based on existing games models of competition, and (iii) consider possible reasons for aggressive behaviour among female loggerhead sea turtles. As a range of factors associated with individual fitness and/or resource value may affect competitor motivation and hence contest outcome (Parker, 1974; Maynard Smith, 1982; Enquist & Leimar, 1983; Kotiaho *et al.*, 1999; Cressman *et al.*, 2004), such behaviour may indicate an adaptation to a habitat. Hence, by collecting direct baseline behavioural information, electronic devices could be subsequently used as a powerful tool to acquire specific information with respect to trends in marine animal social behaviour and habitat use.

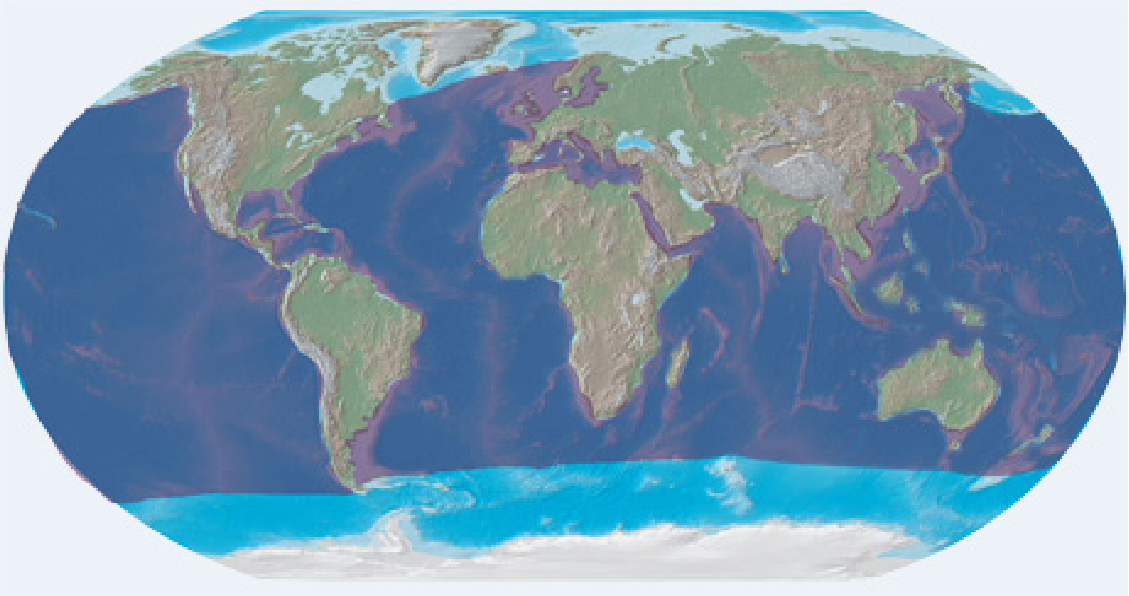
In **Chapters 4 and 5** remote technology is used in the form of GPS units and TDRs (Time-Depth Recorders) to confirm the nearshore use by turtles observed during direct-observation studies of population and behaviour. The acquisition of high resolution tracking information may be important in formulating rational, adaptive and dynamic management decisions for nature reserves, endangered species and related conservation policies at both a local and regional level (Argardy, 1994; Thompson *et al.*, 2000; Parra *et al.*, 2006). Conventional biotelemetry systems have limited application at finer spatial resolutions, and when quantifying movement patterns in relation to biophysical parameters at small scales (Wilson *et al.*, 2002; Bradshaw *et al.*, 2007b). While GPS units provide an accuracy to within 10s of metres, due to the infrequent surfacing behaviour of marine animals, there is a limited time period when the units are available for acquiring satellite signals interval (Sisak, 1998; Jay & Garner, 2002; Ryan *et al.*, 2004; Yasuda & Arai, 2005; Petersen *et al.*, 2006; Sheppard *et al.*, 2006). Existing studies of female sea turtles at breeding areas used conventional technology and were primarily conducted following the onset of nesting (Hays *et al.*, 1991; Hays *et al.*, 2002a; Houghton *et al.*, 2002; Hays *et al.*, 2003a; Hopkins-Murphy *et al.*, 2003). Due to the necessity for inwater capture, which requires high levels of physical and search effort (Ehrhart & Ogren, 1999), knowledge about male area use and occupancy at breeding grounds is sparse (but see Limpus, 1993; Plotkin *et al.*, 1996; Sakamoto *et al.*, 1997; Hays *et al.*, 2001b; James *et al.*, 2005a; Shaver *et al.*, 2005b; Godley *et al.*, 2008). However, to objectively determine whether existing or suggested protection measures at local (i.e. within a national park or reserve), national and regional level is appropriate, high resolution tracking of all segments of the population actively using the area is required. Furthermore, in the Mediterranean sea turtle foraging areas remain largely absent of protective legislation (Margaritoulis *et al.*, 2003; Zbinden *et al.*, 2008), hence confirmation of the use of certain areas by both adult males and females following migration from breeding areas may contribute towards providing evidence supporting the establishment of much needed protection sites. Therefore, the aims of these two chapters were to (i) investigate the fine scale movement of male and female loggerhead turtles (*Caretta caretta*) within the protected area of Laganas Bay, (ii) assess the randomness in fine-scale movement patterns of females (iii) combine the results of the in-water photo-identification surveys with turtle GPS location information to calculate an operational sex-ratio for the breeding population, (iv) assess the departure of males from the breeding grounds and identify the location of foraging sites in relation to known female foraging sites, and (v) consider how our data might be applied towards contributing to sea turtle conservation measures, policies and legislation at a local and regional scale.

Chapter 6 seeks reasons for aggression over resting space and broadly similar nearshore use and movement patterns recorded in females in the previous chapters. The rookery on Zakynthos island (Greece) in the semi-enclosed Laganas Bay is unusual in that the population is relatively large (Margaritoulis, 2005) despite being situated at the latitudinal margins of the species' breeding range (Dodd, 1988). The importance of thermal selection in a dynamic environment may be particularly acute at the limits of species distributions where environmental conditions may be at the margins of suitability, and hence, the implications of thermal habitat selection are greater. Such situations might, therefore, be ideal for testing the existence of fine-scale thermal selection in a dynamic thermal environment. In general, water temperature strongly influences turtle body temperature and hence movement (Etnoyer *et al.*, 2006), food acquistion (Broderick *et al.*, 2001b), reproductive seasonality (Godley *et al.*, 2002; Weishampel *et al.*, 2004), internesting periodicity (Sato *et al.*, 1998; Hays *et al.*, 2002a) and remigration interval (Solow *et al.*, 2002). Therefore, the ability to locate thermally suitable sites, where water temperature lies within a certain range, is of fundamental importance. This chapter examines if (i) sea turtles at Zakynthos show thermal selection, and (ii) considers the possible benefits in terms of increasing egg maturation rates before oviposition, thereby allowing the seasons' first clutch to be laid earlier which may enhance reproductive fitness. The implications of this research not only shows the importance of adequately protecting the nearshore areas used by female turtles in the early part of the breeding season, but may also serve to indicate how patterns of habitat selection and species range distribution might alter with respect to global climate change.

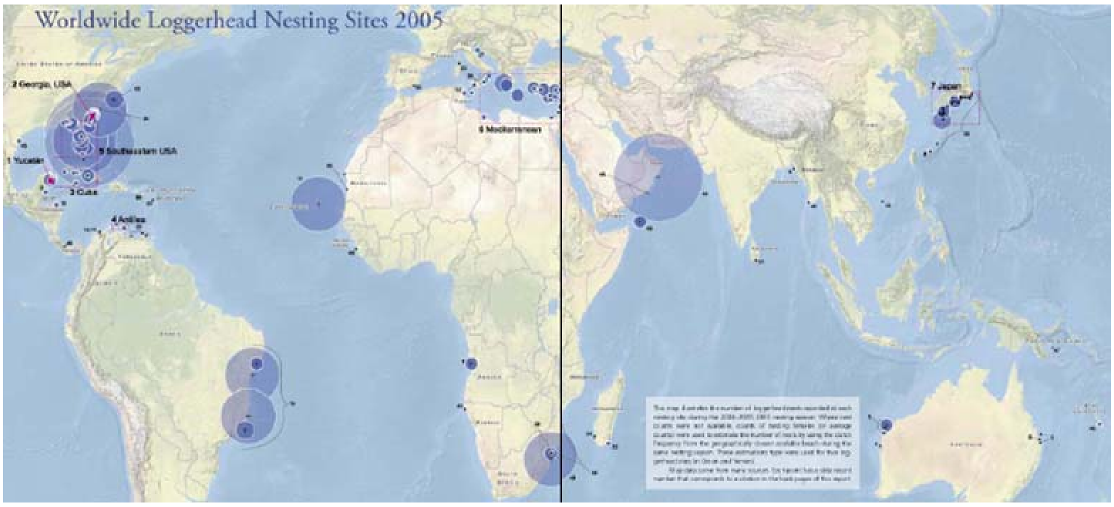
This thesis takes the form of six chapters, all of which have been published in refereed journals. The research was conceived by myself and realised with the support of my supervisors. The manuscripts were written by myself, Gail Schofield, and overseen by my supervisors. My co-authors, who are listed at the start of each manuscript, helped in various ways: by providing me with access to study animals and equipment, by offering advice on experimental design, by constructive criticism of earlier drafts of the manuscripts and by giving statistical advice.

FIGURES

Figure 1. Loggerhead sea turtle (*Caretta caretta*) distribution (a) worldwide in temperate and tropical habitats (http://www.seaworld.org;), although (b) nesting is limited to latitudes of 19-36° north and south of the equator (SWOT website http://www.seaturtlestatus.org)



(a)



(b)

Figure 2. Map of Laganas Bay containing National Marine Park of Zakynthos (NMPZ) marine protection and ecotourism zones. Zone A = no boating zone (nesting beaches of Gerakas, Daphni and Sekania), zone B = boating permitted at 6km hr-1 but no mooring (nesting beaches of Crystal, Kalamaki and Marathonisi), zone C = boating permitted at 6km hr-1 and mooring, Ecotourism zone = including a swim zone 0-200 m from shore and an NMPZ endorsed turtle-watching business zone 200-1400 m from shore (adapted from map of NMPZ www.nmp-zak.org)

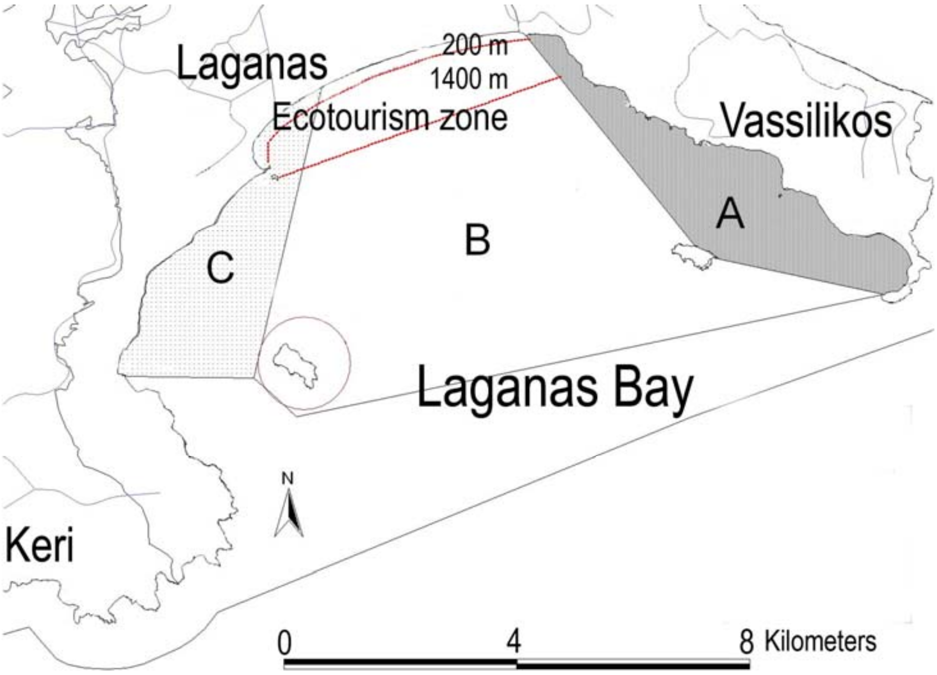
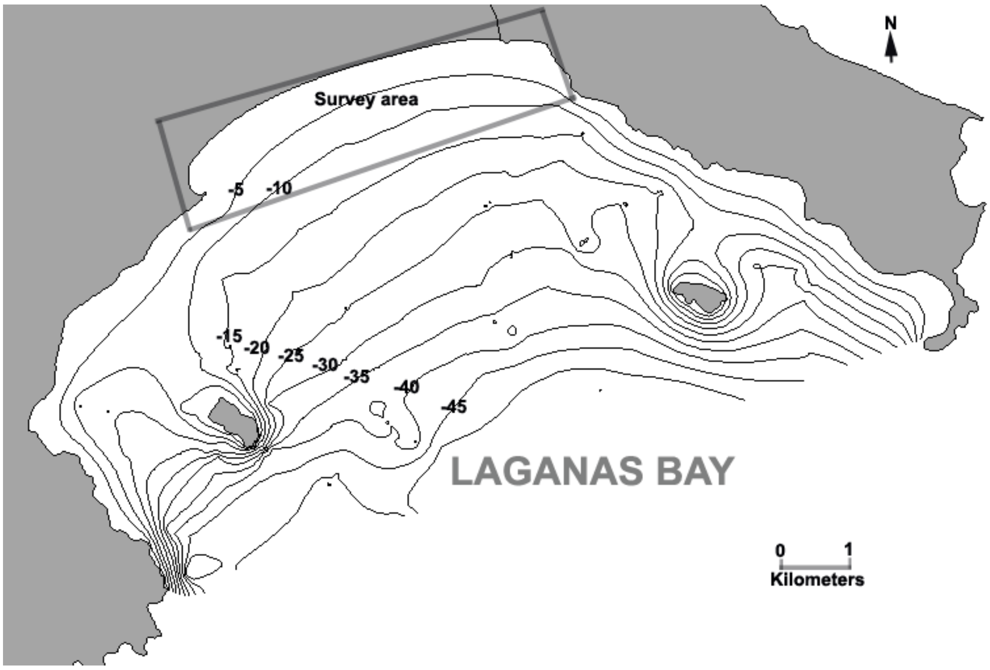
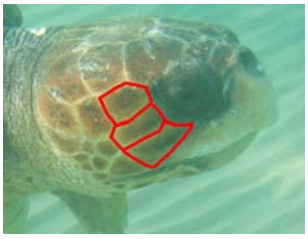


Figure 3. Map of Laganas Bay situated on the southern part of Zakynthos island, showing bathymetry (isobars at 5 m seadepth intervals) and the PhD survey area



ΚΕΦΑΛΑΙΟ / CHAPTER 1. Investigating the viability of photo-identification as an objective tool to study endangered sea turtle populations



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Peer-reviewed journal citation (manuscript in Appendix 3)*:*
***Schofield, G.**, K.A. Katselidis, P. Dimopoulos, J.D. Pantis. 2008. Investigating the viability of photo-identification as an objective tool to study endangered sea turtle populations. Journal of Experimental Marine Biology & Ecology 360:103-108*

Affiliated conference presentation (poster in Appendix 4**):**
***Schofield, G.**, K. Katselidis, & J. Pantis. 2008. Assessment of photo-identification and GIS as a technique to collect in-water information about loggerhead sea turtles in Laganas Bay, Zakynthos Greece (poster presentation). Proceedings of the Twenty-fourth Annual Symposium on Sea Turtle Biology & Conservation U.S. Dept. Commerce. NOAA Tech. Memo. NMFS-SEFSC. Pp152-153*

INTRODUCTION

The ability to identify individuals within a population is often a starting point for ecological and conservation studies (Thompson *et al.*, 2000; Sibly *et al.*, 2005; Lusseau *et al.*, 2006; Bradshaw *et al.*, 2007a; McMahon *et al.*, 2007). Realistic estimates of population size and life history parameters are central to effective wildlife management, but are often difficult to measure in long-lived and elusive migratory marine vertebrates (Caughley, 1994). Most studies with free-ranging animal populations rely on the physical capture of animals and the placement of artificial tags, brands or other objects to allow their subsequent identification (Wilson & Wilson, 1989; McMahon *et al.*, 2007). Such approaches have often been used successfully although there are sometimes problems such as stress to the animals through capture, handling and tag attachment and impacts of the marker itself. For example flipper bands have been shown to increase mortality in penguins as have some flipper tags used in sea turtle research (Nichols & Seminoff, 1998; Dugger *et al.*, 2006). Furthermore, the inevitable loss of identification markers (i.e. from incorrect attachment or being knocked/bitten off) (Limpus, 1992) can become problematic in some species, interrupting the continuity of long-term studies of long-lived species of conservation concern (Sibly *et al.*, 2005).

An alternative to attaching markers to wildlife, is to use visual identification of individuals. The ability to recognize individuals from naturally occurring features has many advantages over conventional marking techniques, including: animals are not physically captured, identifiable characteristics are stable over time, and the behaviour of the animal is less likely to be affected by the identification system (Hammond, 1990; Blackmer *et al.*, 2000). Photographic identification, in which researchers photographically capture these natural markings to identify and re-identify individuals, has proven to be a useful tool in long-term monitoring of wild animal populations (Thompson *et al.*, 2000; Forcada & Aguilar, 2003; Bradshaw *et al.*, 2007a). For example, whisker patterns are used in lions, facial scale patterns in sea turtles, pelage spot patterns in whale-sharks, fin shape and scarring in dolphins (Richardson *et al.*, 2000; Thompson *et al.*, 2000; Arzoumanian *et al.*, 2005; Ogutu *et al.*, 2006).

Many sea turtle research programmes use some form of conventional tagging method (i.e. plastic, monel, titanium) to obtain life history information about nesting females at breeding areas or of different age classes at foraging areas (Chaloupka & Limpus, 2001; Balazs & Chaloupka, 2004). Flipper tagging studies tend to preferentially target adult female turtles due to their accessibility on the nesting beaches, resulting in a skewed picture of the adult population structure. Furthermore, significant levels of tag loss often reduce the reliability and scientific value of data collected (Mrosovsky, 1976; Limpus, 1992; Witzell, 1998; Broderick & Godley, 1999). Alternative more endurable methods have recently been used, including passive integral transponders (PIT) (McDonald & Dutton, 1996), natural genetic markers (Bowen, 1995) and photo-identification using head scalation patterns (Richardson *et al.*, 2000).

While photo-identification has been explored in several sea turtle species (Bennett *et al.*, 1999; Richardson *et al.*, 2000; Rodriguez & Sarti, 2000; Schofield *et al.*, 2004; White, 2006; Wood, 2006), the utility of this approach as a bio-monitoring tool when population sizes are large has not been established. Furthermore while experienced workers may have a good ability to visually discriminate individuals (Douglas-Hamilton & Douglas-Hamilton, 1975), a photographic database can potentially be used more widely, and have longevity beyond the career of the originator, if other users can be trained to reliably use the data-base.

The aim of this work is to construct an objective tool based on photo-identification which is easy to use for experienced and non-experienced personnel and is credible and effective for individual recognition of male and female turtles for application in population bio-monitoring, behaviour studies and conservation. We therefore set out with two objectives:

1. to establish the utility of photo-identification in a large population by testing the technique at the Mediterranean's largest loggerhead turtle rookery, where several hundred turtles aggregate each summer
2. to establish whether naïve users could easily and reliably learn to use photo-identification to recognise individual sea turtles.

MATERIALS & METHODS

Data source

Still photographs were taken of male and female loggerheads in the sea. An Olympus Digital 500 (5.0 megapixel) camera with underwater housing was used, while snorkeling at a distance of 2-7m from the target animal. Images were collected between late April and early August during five years of surveying, 2003-2007. Animal gender was determined based on tail length dimorphism (Casale *et al.*, 2005).

For the purpose of the trials, between one and five digital photographs were selected for each of 170 ‘confirmed' individuals, validated by the presence of external plastic flipper tags (attached within the framework of the NGO Archelon beach monitoring programme). The tags were attached prior to the onset of the study and the selected turtles retained the same tag(s) in all subsequent sightings as confirmation of their identity. All photographs were of the right lateral head region of the turtle, and were selected based on two criteria:

1. all images of the same turtle were from different sighting events separated by at least 1 day,
2. only high digital photographs (300-pixel resolution) were used in which all facial scales were visible. Before use, each image was assigned a unique identification number.

Group-assignation and photographic matching

Using an identification tree split into four sequential fields, we divided individuals into ten groups based on the relative shapes of the post-ocular scales (Fig. 1). Each group contained < 100 individuals. We used the lateral facial scale patterns to differentiate between different individuals within each group (Fig. 2a & b). Comparison and matching of photographs within each group was made by subjective observation of three different sets of facial scale groups:

1. the numbering and pattern of tympanic and central scales
2. the relative shapes of the sub-temporal scales, and

3. the relative shapes of the temporal scales.

Within each group turtles are separated into ‘male’, ‘female’ and ‘unknown’ categories. This means that if the sex is not determined when the animal is photographed, the individual can be matched following separation into one of the groups.

Expert observer validation against flipper tagged turtles

The lead author (GS) who has observed turtles in the water for many years conducted a trial to validate her ability to consistently sort and match 200 photographs from known turtles identified with flipper tags. This trial was conducted twice with two different sets of 200 images (i) without and (ii) with the aid of the identification tree. In both versions, the observer was given a catalogue containing 50 unique turtle images. A separate set of 150 unsorted images was provided, each of which could be assigned as a ‘new capture’ or a ‘re-capture’ when compared to the images in the primary catalogue (Table 1a). The average number of images per individual was 2.7 (range 1-5) for both data sets respectively. In both versions, the trial was repeated on three different occasions separated by an interval of at least one day. The time taken to complete each trial run was recorded.

Naïve observer trials

Trial 1: separating turtles into groups

A trial was conducted to assess observer ability to allocate turtles into the correct groups when a reasonably large number of captures is involved (Appendix 2 Trial 1). Each observer was given instructions on how to use the ‘identification tree’ and was asked to allocate 40 images into one or more groups (Table 1b), or state if unable to place the image. The average number of images per individual turtle was 1.3 (range 1- 2). The trial was conducted twice, separated by an interval of at least one day. In the first run of the trial, all observers (n=44) were inexperienced. Before the second run of the trial, part of the group (n=24) received training. The time taken to complete each trial was recorded.

Trial 2: matching turtles within groups

A trial was conducted to assess observer ability to correctly match turtles within one group when a reasonably large number of captures is involved (Appendix 2. Trial 2). Each observer was given a catalogue containing 15 unique images. A separate set of 20 unsorted images was provided, each of which could be assigned as a ‘new capture’ or ‘re-capture’ when matching against the provided catalogue (Table 1c). The average number of images per individual turtle was 1.8 (range 1-4). The trial was conducted twice, separated by an interval of at least one day. In the first run of the trial, all observers (n = 49) were inexperienced. Before the second run of the trial, part of the group (n = 23) received training. The time taken to complete each trial was recorded.

In all trials, the observers were permitted to re-order the displayed ‘capture’ images to assist with the sorting/matching process, and were allowed to set aside images given during sequential identification to return to at the end.

Trial analyses

To quantify observer ability, five photo-matching categories were defined:

1. a Match-Match (MM) indicates that the observer correctly matched the photograph to the correct group or individual
2. the New-New (NN) category indicates that the observer correctly placed the photograph as a new group/individual not found in the existing database,
3. a New-Match (NM) category indicates that the observer correctly matched a new photograph to another newly added image to the database,
4. a False-Match (FM) was determined when an observer incorrectly matched a photograph to a different group/individual in the photographic database (false positive error),
5. a False-New(FN) category was defined as when an observer incorrectly classified a photograph as a new image but it was already in the photographic database (false negative error). We demonstrated the consistency and reproducibility of observer judgement within trials by providing multiple photographs of single individuals.

We used paired Students t-tests to examine the relative improvement in skill and time requirement within and between observer groups.

RESULTS

Expert observer validation against flipper tagged turtles

The accuracy and consistency of photographic matching of turtles validated from flipper tags was extremely high; without use of identification tree (98%), with use of identification tree (100%). Incorrect matching occurred for the same three images in all three runs of the first version of the trial (without identification tree), with turtles being incorrectly specified as new captures (i.e. inflation of the population). The use of the identification tree to group turtles before matching resulted in turtles being matched at a significantly faster rate (paired Student’s t-test, t=33.1, df=4, Pb0.001) with a 50% reduction in matching time required; from 2.26 to 1.14 minutes per image (Table 2).

Naïve observer trials

Trial 1: separating turtles into groups

In the first run of the trials when all observers were naïve, a mean accuracy of 69% was obtained with observers taking 42 minutes on average to complete the trial. Student t-tests indicated no significant difference in ability in the first run of the trial between those that did and did not receive subsequent training (Student's *t*-test, t=0.18, *df*=42, *P*=0.8). Repetition of the trials indicated a slightly significant improvement in the untrained group (mean 76%, paired Student's *t*-test, t=2.11, *df* =38, *P*=0.04) and a highly significant improvement in the trained group (mean 83%, paired Student's *t*-test, t=4.27, *df*=46, *P*<0.0001) (Fig. 3). Trial repetitions took an average 30 minutes in both trained and untrained groups and were not found to be significant in either group. Detailed statistics of the results of these trials are shown in Table 3.

Trial 2: matching turtles within groups

In the first run of the trials when all observers were naïve, a mean accuracy of 71% was obtained with observers taking 47 minutes on average to complete the trial. Student t-tests indicated no significant difference in ability in the first run of the trial between those that did and did not receive training (Student's *t*-test, t=0.07, *df*=47, *P*=0.07). Repetition of the trials, indicated no significant improvement in the untrained group (mean 78%, Student's *t*-test, t=1.57, *df*=50, *P*=0.1) and a highly significant improvement in the trained group (mean 87%, Student's *t*-test, t=3.74, *df*=44, *P*<0.0001) (Fig. 4). Detailed statistics of the results of these trials are shown in Table 4.

Trial repetitions took an average 37 minutes in both trained and untrained groups and were not found to be significant in either group. In the first run of the trials when all observers were naïve, 32% of the images were matched incorrectly, of which 16% were false negative (no match found), 28% were false positive (new images matched with existing) and 56% of the images were mis-matched existing images. In the second run of the trials, there was no significant difference in the untrained group, whereas in the trained group a significant decline in false positive (Student's *t*-test, t=3.04, *df*=44, *P*=0.004) and mismatching (Student's *t*-test, t=2.62, *df*=44, *P*<0.001) was found.

DISCUSSION

Photo-identification of natural markings is increasingly being used to collect data on individual animals for application to demographic studies (Thompson *et al.*, 2000; Lusseau *et al.*, 2006; Bradshaw *et al.*, 2007a). Although information obtained from photo-identification is highly valuable (Hammond, 1990; Blackmer *et al.*, 2000), processing data in large catalogues can be labour-intensive and subject to human error (Kelly, 2001). Through the use of trials, our study demonstrated the validity (i.e. accuracy) and reliability (i.e. precision) of natural markings for assignation of individual loggerhead sea turtles to groups according to a simple identification tree, and that once an image has been assigned to a group, its markings can be used to correctly match it to existing catalogue images of the same individual present in that group.

The size of sea turtle populations is typically assessed by counting tracks of females on nesting beaches (Demetropoulols & Hadjichristophorou, 1995; Godley *et al.*, 2001a;

Broderick *et al.*, 2002; Margaritoulis, 2005). However this ignores the size of the male component of the adult population. Yet, identifying male turtles is also important to assess population size and sex-ratio. It relatively easy to estimate hatchling sex ratios by, for example, recording incubation temperatures or incubation durations (Broderick *et al.*, 2001a; Zbinden *et al.*, 2007b). Furthermore it is possible to reconstruct long-term trends in hatchling sex ratios from environmental proxies such as air temperature (Hays *et al.*, 2003b). However, how hatchling sex ratio projects through to adult sex ratio is not known. Hence nothing is known about long-term trends in adult sex-ratios for sea turtles and implications of climate change for this important demographic parameter. Photo-id, when combined with in-water surveys, clearly has the potential to start providing estimates of the number of males at breeding sites and hence also adult sex-ratios.

As well as a lack of information on adult sex-ratios, there is also very little known in general about the ecology of male turtles. Direct observations have been used to infer mating seasonality and the departure time of male turtles from breeding areas (e.g. Godley *et al.*, 2002), while paternity in clutches can be assessed without sampling adult males themselves from which inferences about male-female encounters and male movements (Lee *et al.*, 2007; Lee, 2008) can be made. However, very few male turtles are identified by tagging because this requires logistically challenging capture at sea (e.g. Hays *et al.*, 2001b; James *et al.*, 2005b) as males very rarely emerge onto land (but see Rice & Balazs, 2008). Photo identification will allow a new era of experimental and ecological studies of male turtles, allowing, for example, the behaviours of known individuals to be assessed (Schofield *et al.*, 2006; Schofield *et al.*, 2007b). In addition, photoidentification will allow the interval between successive breeding seasons (the remigration interval) to be established. For female turtles, remigration intervals may be several years, presumably because it takes a long time for individuals to attain a threshold body condition before they embark on breeding migrations (e.g. Hays, 2000; Broderick *et al.*, 2001b; Chaloupka *et al.*, 2008). However, the remigration interval of male turtles are poorly understood, although it is possible that they may be appreciably shorter that for females (Chaloupka & Limpus, 2001), since males do not invest resources in egg production and hence they may lose less condition during breeding seasons.

The accuracy and reliability of photographic matching may be impeded by image quality (i.e. light intensity and sea clarity in underwater photographs) and/or database size (Whitehead *et al.*, 1997; Forcada & Aguilar, 2003; Beekmans *et al.*, 2005). As a consequence, mistakes may result in the wrong inferences being made about the biology of animals. For example, false negative errors (failing to find a match) inflate population estimates, while false positive errors (matching new individuals to an existing database image) deflate population estimates. We recorded a very low error rate during the course of the trials, with that of false positive errors (matching two photographs from different animals) being slightly more frequent than false negative errors. Hence, the accumulation of errors over time in our database, leading to over or under estimations of population size (Stevick *et al.*, 2001), is likely to be negligible.

Our results showed that while in all trials the success rate in photographic matching was very high, experience and training improved the reliability to match individuals (Douglas-Hamilton & Douglas-Hamilton, 1975). Furthermore, at present we have overcome the difficulty of manually comparing and matching a large volume of photographic images (>400) by dividing turtles into several groups of <100 images based on variations in one set of facial features. As our photographic catalogue expands, it may become necessary to develop a computer-assisted matching programme, as has been designed for several other vertebrate species with large photographic population databases (Kelly, 2001; Hillman *et al.*, 2003; Beekmans *et al.*, 2005). However, confirmation is required of the stability of the natural features (i.e. colouration and relative scale sizes) being used (Forcada & Aguilar, 2003; Arzoumanian *et al.*, 2005).

Accurate information about the population structure and ecology is not only vital to address the conservation needs of the Zakynthos sea turtle rookery, but could serve as an indicator of adult survival after departure from the breeding area (Chaloupka & Limpus, 2002). Such insights could provide a quantitative foundation for the re-evaluation of the regional, national and global conservation status of this species, thus strengthening international maritime protection policies amongst Mediterranean countries (Thompson *et al.*, 2000; Sibly *et al.*, 2005; Fagan & Holmes, 2006). For example, the creation of photo-libraries at local, national and regional scales, within which individual life-histories could be developed as well as knowledge about small and large scale migrations of male and female turtles, e.g. between islands or across the Mediterranean basin and how this impacts micro- and macro-population dynamics. The permanency of photographic data not only permits retrospective analyses as research objectives evolve, but also provides an opportunity to investigate other parameters that may also influence species conservation management and ecological risk assessments such as site fidelity, patterns of interaction, physical condition, health indicators and the impact of anthropogenic activity (Burger & Garber, 1995; Bennett *et al.*, 1999; Pettis *et al.*, 2004; Lusseau *et al.*, 2006).

In conclusion, our study has validated the accuracy, reliability and ease of training of using natural facial markings to identify individuals in a breeding population of loggerhead sea turtles. Within the framework of a long-term monitoring programme, our photographic matching technique could potentially be used to obtain new insights about sea turtle population trends, behaviour, ecology and conservation status. Ultimately, appropriate wildlife management depends on the acquisition of realistic life history information, and photo-identification is a proven technique, facilitating the continuity of long-term studies for long-lived species of conservation concern.

FIGURE & TABLE CAPTIONS

Figure 1. Identification tree separating the turtle images into ten groups based on the relative shapes of the post-ocular scales.

Fig. 2. (a) Lateral head scales of loggerhead turtle used for matching images in this study. (b) Sample lateral facial scale data sets from the photo-identification database. Raw images (top row) from newly submitted (right) and catalogued (left) encounters are processed by comparison of different sets of scale groups (bottom row).

Figure 3. Success in placing turtles into the correct groups; (1a) first run of group that received no training (mean 69%) (1b) second run of group that received no training (mean 76%; improvement p = 0.04) (2a) first run of group before training provided (mean 69%) (2b) second run of group following training (mean = 83%, improvement p = <0.0001).

Figure 4. Success in matching turtles within a group; (1a) first run of group that received no training (mean 71%) (1b) second run of group that received no training (mean 79%; improvement p = 0.1) (2a) first run of group before training provided (mean 71%) (2b) second run of group following training (mean = 87%, improvement p = <0.0005).

Table 1. The photographic image categories for each trial (a) expert observer validation (b) naïve observers separating images into groups (c) naïve observers matching turtles within groups

Table 2. Expert observer validation of photo-identificationt technique using confirmed turtle images

Table 3. Naïve observer trials separating images into groups

Table 4. Naïve observer trials matching individuals within groups

Appendix 2. Trial 1 worksheet.

Appendix 2. Trial 2 worksheet.

Figure 1. Identification tree separating the turtle images into ten groups based on the relative shapes of the post-ocular scales.

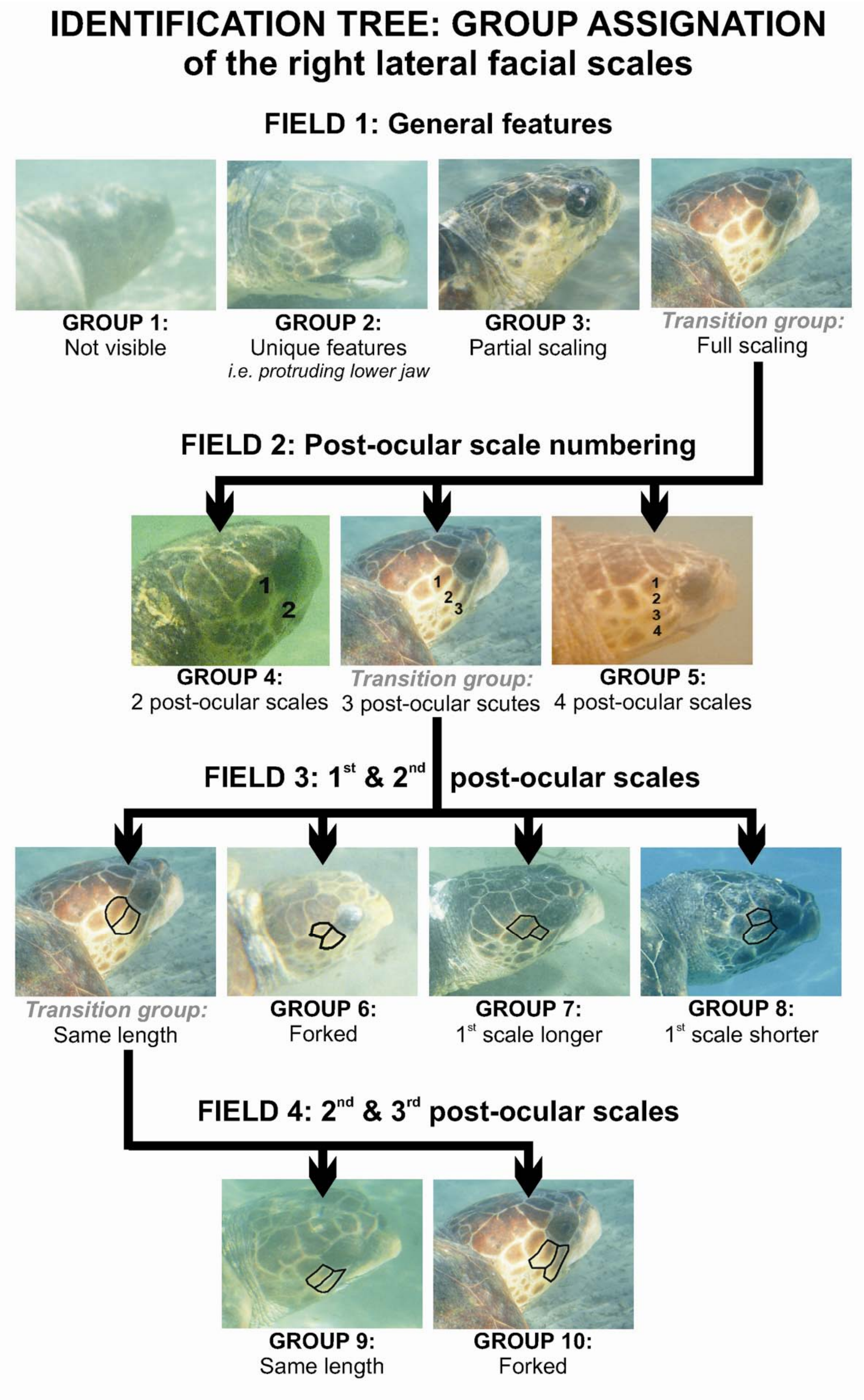

Fig. 2. (a) Lateral head scales of loggerhead turtle used for matching images in this study. (b) Sample lateral facial scale data sets from the photo-identification database. Raw images (top row) from newly submitted (right) and catalogued (left) encounters are processed by comparison of different sets of scale groups (bottom row).

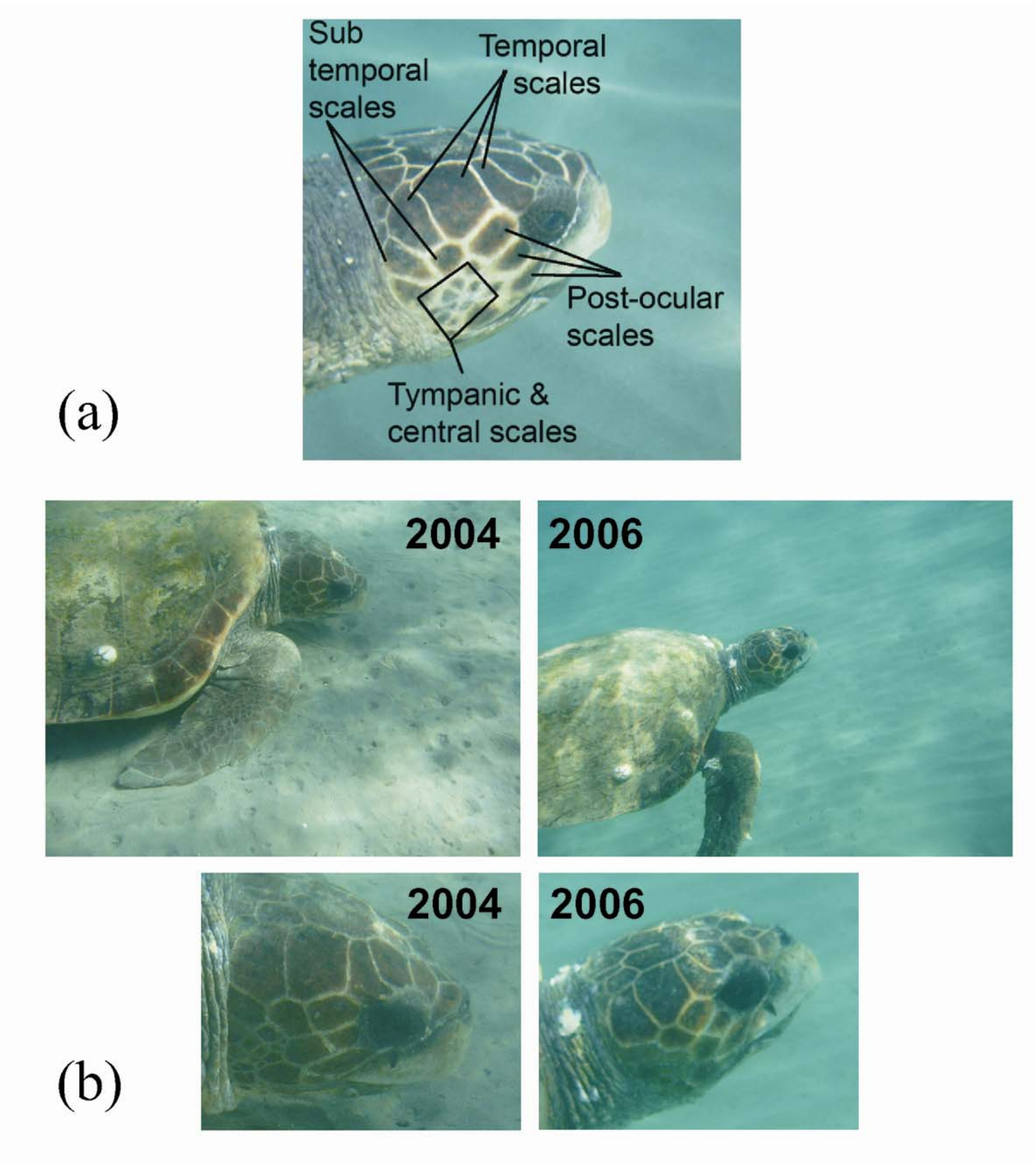

Figure 3. Success in placing turtles into the correct groups; (1a) first run of group that received no training (mean 69%) (1b) second run of group that received no training (mean 76%; improvement p = 0.04) (2a) first run of group before training provided (mean 69%) (2b) second run of group following training (mean = 83%, improvement p = <0.0001).

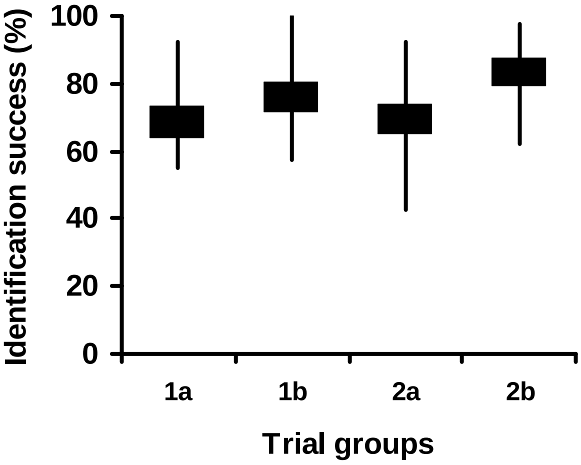

Figure 4. Success in matching turtles within a group; (1a) first run of group that received no training (mean 71%) (1b) second run of group that received no training (mean 79%; improvement p = 0.1) (2a) first run of group before training provided (mean 71%) (2b) second run of group following training (mean = 87%, improvement p = <0.0005).

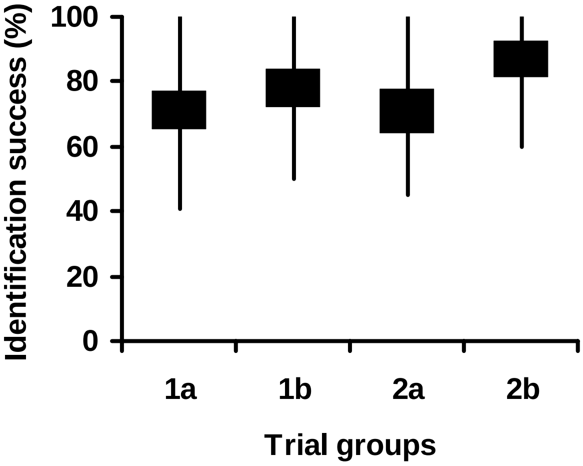

Table 1. The photographic image categories for each trial (a) expert observer validation (b) naïve observers separating images into groups (c) naïve observers matching turtles within groups

(a)

Trial type	Total images	Database images	Images to match	Catalogue image matches					New catalogue images	New catalogue image matches				
				0	1	2	3	4		0	1	2	3	4
Matching not using groups	200	50	150	15	8	11	9	7	31	9	2	9	8	3
Matching by using groups	200	50	150	12	12	17	6	3	35	5	7	11	8	4

(b)

Total images	Database images	Images to match	Group matches										Singles	Duplicates
			1	2	3	4	5	6	7	8	9	10		
50	10	40	1	2	5	1	1	4	6	7	8	5	22	9

(c)

Total images	Database images	Images to match	Catalogue image matches					New catalogue images	New image matches				
			0	1	2	3	4		0	1	2	3	4
35	15	20	6	6	2	1	0	4	2	1	1	0	0

Table 2. Expert observer validation of photo-identification technique using confirmed turtle images

Task	Run	Time to complete / min	Matching time per image /min	Images to match/ trial	Average correct photo-matches	Average false matches (false positive errors)	Average failed matches (false negative errors)	Per trial group/ % success
Matching without grouping	1	346	2.3	150	146	0	4	97
	2	333	2.2	150	147	0	3	98
	3	345	2.3	150	147	0	3	98
Matching with grouping	1	178	1.18	150	150	0	0	100
	2	168	1.12	150	150	0	0	100
	3	172	1.14	150	150	0	0	100

Table 3. Naïve observer trials separating images into groups

		Group 1		Group 2	
		run 1	run 2	run 1	run 2
	participants	20	20	24	24
identification success / %	mean	68,6	75,9	69,3	83,1
	median	67,5	75	70	85
	standard deviation	12,7	9,6	10,8	10,9
	minimum	55	57,5	42,5	62
	maximum	92,5	100	92,5	97,5
	upper 95% confiden	63,1	71,27	64,65	78,5
	lower 95% confiden	73,54	80,48	73,89	87,75
time taken / minutes	mean time taken / n	42	31	41	29
	median	40	30	37,5	30
	standard deviation	17	9	19	14
	minimum	11	15	20	15
	maximum	90	60	100	75

Table 4. Naïve observer trials matching individuals within groups

		Group 1		Group 2	
		run 1	run 2	run 1	run 2
	participants	26	26	23	23
identification success / %	mean	71	77,9	70,7	86,7
	median	70	77,5	75	90
	standard deviation	16,5	15,2	16,8	11,9
	minimum	40	50	45	60
	maximum	100	100	100	100
	upper 95% confiden	64,72	71,64	63,67	80,61
	lower 95% confiden	77,2	84,13	77,63	92,86
time taken / minutes	mean time taken / n	48,3	36,5	45,1	37,5
	median	47,5	32,5	40,0	35,0
	standard deviation	20,7	15,1	19,0	12,6
	minimum	20	20	25	20
	maximum	120	90	105	65

ΚΕΦΑΛΑΙΟ / CHAPTER 2. Behaviour analysis of the loggerhead sea turtle *Caretta caretta* from direct in-water observation

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Peer-reviewed journal citation (manuscript in Appendix 3)*:*
Schofield, G.*, K.A. Katselidis, J.D. Pantis, P. Dimopoulos, G.C. Hays. 2006. Behaviour analysis of the loggerhead sea turtle (Caretta caretta) from direct in-water observation. Endangered Species Research 2:71-79*

Affiliated conference presentation (poster in Appendix 4; DVD in Appendix 5**):**
Schofield, G., K.A. Katselidis, J.D. Pantis, P. Dimopoulos & G.C. Hays. 2006. Preliminary documentation of loggerhead solitary and social behaviour in the maritime breeding area of Laganas Bay, Zakynthos, Greece. Twenty-Sixth International Symposium on Sea Turtle Biology and Conservation. Pp110-112

INTRODUCTION

Direct observation of animals in their natural environment contributes important information about how species adapt to a particular environment. Information about behaviour and interactions at the level of individuals is key to understanding how an animal may impact the surrounding community as well as ecosystem function, organisation and response to disturbance (Piraino *et al.*, 2002). Hence, studies of behaviour in the field are fundamental for the effective conservation of animals in their natural habitats (Mills *et al.*, 2005).

Direct observations in the marine realm are often restricted due to sea depth and state, underwater visibility, natural light availability, physical danger and adequate access to the study animal (Hooker & Baird, 2001). Due to the difficulties of studying large marine vertebrates in their natural habitats, most studies of their behaviour have relied on inferences from animalborne devices. For example, in sea turtle research devices such as data-loggers, radio and satellite telemetry are used (Hopkins-Murphy *et al.*, 2003; Hochscheid *et al.*, 2005a; Myers & Hays, 2006). While useful, these techniques cannot describe the full range of behavioural patterns of wild animals that direct first person observations can (Houghton *et al.*, 2002; Houghton, 2003). To date, there have been few quantitative observational studies of sea turtles (Booth & Peters, 1972; Whittow & Balazs, 1982; Dodd, 1988; Losey *et al.*, 1994; Frick *et al.*, 2000); however, the development of animal-borne cameras has provided the opportunity to observe and confirm the underwater behaviour of these and other marine vertebrates (Davis *et al.*, 1999; Heithaus *et al.*, 2002b; Reina *et al.*, 2005; Hays *et al.*, 2006).

Sea turtles are endangered worldwide, therefore a detailed understanding of their behaviour is a key factor to be considered when drawing up effective conservation management policies. This is particularly important in coastal areas where marine oriented tourism is focused on sea turtles (Meadows, 2004). On Zakynthos island in Greece, high densities of reproductively active loggerhead sea turtles and turtle-watching enterprises co-exist in a very restricted area each summer. Currently turtle watching protocols and permitted observation zones are evolving under the guidance of the National Marine Park of Zakynthos. However, due to the lack of knowledge about sea turtle behaviour and habitat use in this and similar coastal reproductive areas, decisions are not currently scientifically based.

Laganas Bay, in the National Marine Park of Zakynthos, is an ideal location for investigating the behaviour of loggerhead sea turtles *Caretta caretta* at a temperate breeding area. Several hundred adult turtles are found at nearshore aggregations for about 4 months following migration into the bay each spring (Margaritoulis, 2005). In sea turtles, mating and first nesting occur up to 6 weeks apart (Wood & Wood, 1980; Miller *et al.*, 2003), with females storing sperm to fertilize several clutches laid during the season at intervals of around 14 d (Hays *et al.*, 2002a).

The aim of this study was to gather information about the behaviour of male and female loggerhead sea turtles in the marine environment during the breeding period. In this paper we:

1. document the solitary and social behaviour of loggerhead sea turtles, and
2. discuss how differences in the proportions of observed male and female behaviour may reflect gender-specific strategies.

MATERIALS AND METHODS

In-water surveys have been conducted annually since 2003 to collect information about loggerhead sea turtle marine ecology from April to July during the breeding season. The nesting season runs from approximately late-May to early September (Margaritoulis *et al.*, 2003). Hence, our surveys spanned the time during which there was still some mating activity, but many females had started nesting.

Surveys were conducted in Laganas Bay along a 5.5 km stretch of nearshore water, extending 1 km into the sea to depths of up to 10 m. Surveys were conducted over a total of 287 h on 104 d across 3 yr (2003 to 2005). Surveys were primarily concentrated in the afternoons between 12:00 and 18:00 h, lasting an average of 3 h (minimum 1, maximum 7 h). Observers entered the water from a boat, a kayak or directly from the shore.

Boat surveys (405 km, 137 h) were conducted by 2 to 3 observers in April and May of 2003 on a 4 m boat with an outboard engine. Sessions lasted an average of 5 h (minimum 4, maximum 7 h) at a maximum boat speed of 4 knots km^{-1}. Line transects across the entire survey area were performed during each survey session that ran parallel to shore at sea depths of 10, 7, 5 and 3 m. Kayak surveys (77 km, 33 h) were conducted by 2 observers in May and June of 2004 on 2 sea-kayaks at randomly selected sites within the survey area. Sessions lasted an average of 2 h (minimum 1, maximum 3 h). A 2 km line transect was conducted at a sea depth of 5 m and returning at a sea depth of 3 m during each session. Snorkel-swim surveys (163 km, 117 h) were conducted by 1 to 2 observers in May and June of 2004 and 2005 at randomly selected sites within the survey area. Sessions lasted an average of 1.7 h (minimum 1, maximum 3 h). A 1 km line transect was conducted with the observer swimming parallel to shore at a sea depth of 3 m and returning by wading at a sea depth of 1 m.

On sighting a sea turtle, the GPS location was recorded (using a GARMIN Etrex-legend) while the observer entered the water from the boat/kayak at a distance of at least 5 to 10 m from the target animal(s) and approached until within underwater visual range (subject to daily variations in underwater visibility, approx. average 4, minimum 0.5, maximum 8 m), to minimise disturbance of ongoing behaviour. On encountering the animal(s), photographic records were collected in addition to biological, environmental and behavioural observations (including response to underwater observer presence). Photographs were taken using an Olympus Digital 500 (5.0 megapixel) with underwater housing. Video footage, using a Sony DCR-HC32E Handycam with housing, was collected to classify observed behaviours and inter-specific interactions. Sex was estimated using tail length (Casale *et al.*, 2005).

Analyses included only the initial behaviour observed at each sighting event. Non-parametric Chi-square statistics were used for comparative analysis of the behaviour sighting data. We regarded the results to be significant when $p < 0.05$.

RESULTS

General survey information

The behaviour of loggerhead sea turtles at initial sighting was recorded at 1534 sighting events of solitary (n = 80 male, n = 1335 female) and social (n = 65 same sex, n = 54 mixed sex) activity. This bias towards female turtles partly reflects their location closer to shore where surveys were concentrated. However this ratio may also reflect the highly skewed bias towards females found in hatchling loggerhead turtles in Mediterranean populations (Godley *et al.*, 2001b; Mrosovsky *et al.*, 2002).

On average, 1.5 sightings km^{-1} were made by boat (n = 615), 3 sightings km^{-1} were made by kayak (n = 237) and 4 sightings km^{-1} were made by snorkel-swim surveys. Sightings lasted 2.7 min on average (SD ± 4 min, minimum 1, maximum 65 min). We grouped observed behaviour into 4 solitary and 2 social behaviours (Fig. 1) comprising 14 sub-categories (Table 1).

Solitary behaviour descriptions

Resting. This incorporates both resting on the sea bed and surface-basking (Table 1, Fig. 2A-B, Video clips 1 to 3, see Appendix 5). When resting on the seabed the head, body and flippers were lowered on the substrate. Females never rested within visual range of one another. At 4 sightings large fish (>0.5 m body length) were recorded in close proximity to resting females. At 34 sightings, juvenile saddled bream *Oblanda melanura* (2 to 4 cm body length) were observed feeding opportunistically on resting turtles that neither solicited nor appeared to respond to this activity. Surface-basking turtles rested at the sea surface or up to 1 m beneath the sea surface with the head and flippers lowered.

Swimming. This includes along the seabed, in the water column and near the sea surface as well as patrolling by males (Table 1, Fig. 2C-D, Video clips 4 to 6, see Appendix 5). At 29 sighting events, 6 different fish species (adult and juvenile) were recorded swimming in close proximity to turtles (in the folds of the hind flipper body join, or above or beneath the carapace or head). Four males patrolling for females were each followed at close proximity by the in-water observer for an average of 43 min (SD ± 17 min). The males all appeared to swim parallel to shore at sea depths of 0.5 to 3 m. On detecting a female the male swam faster, generally approaching the female side on and nudging/biting at her carapace initiating courtship behaviour. By combining all data sets, we estimated that patrolling males encountered a female every 9 min on average (SD ± 3).

Foraging. Both males and females were observed mining for bivalves (Table 1, Fig. 2E, Video clips 7 & 8, see Appendix 5). Females made sporadic attempts, but none were observed to be successful. Males foraged close to shore in areas where females also aggregate to rest. Bouts lasted a minimum of 30 min, which was defined as periods when turtles dug in the sand and ended when no digging was reported for 5 min. The males swam along the seabed, and on detecting bivalves in the sand they dug in the sand with their beak using the flippers for momentum. Successful attempts were recognised by the expulsion of segments of crushed mollusc shell from both the nares and oral cavity. By combining all data sets, we estimated that males made digging attempts about twice a minute (mean 38 s, SD = 7) with a 45% foraging success rate (n = 148 attempts).

Cleaning. This includes both self-cleaning and fish cleaning symbiosis (Table 1, Fig. 2F-G, Video clips 9 & 10, see Appendix 5). When self cleaning, turtles repetitively rubbed their heads, flippers and carapace against submerged rocks or anchors. Algae, barnacles and limpets were visibly removed, and distinctive parallel markings were created running the length of the carapace. Based on this uniformity of scratch patterns (different to that created by claw/carapace scratches during mating/ fighting), we were able to detect if this behaviour had been performed recently in all sighted turtles. We found that 55% of females and 19% of males sighted had performed this activity at least once during the survey period. Female turtles were observed visiting a specific cleaning station and actively soliciting cleaning by juvenile sheepshead bream *Diplodus puntazzo* (12 to 14 cm body length). The solicitation posture was held until fish approached; the turtle extended her head, with her hind limbs sprawled and the forelimbs stretched forward, and the body slightly raised above the seabed. Turtles were cleaned by an average of 13 fish (SD ± 4.8) at any one time. Bream are omnivorous, and were assumed to be primarily feeding on micro-organisms on the turtles soft and hard body surfaces; however, epidermal skin lesions were also targeted. This caused turtles to react by flicking the head, twisting the body, swimming fast, biting at their own flippers or fish or on rocks, or to depart the cleaning zone altogether. Within an hour of departure 2 turtles returned for repeat cleaning.

Social behaviour descriptions

Contest. This included female–female and male–male interactions (Table 1, Fig. 2H-I, Video clips 11 to 13, see Appendix 5). Female contests lasted on average 3.4 min (SD ± 1.02 min) and involved ritualized escalation in behaviour from passive threat displays (e.g. head–tail circling) to aggressive combat (e.g. sparring, biting and chasing). The presence of intruder females triggered a response in 76% of observed cases. Contests were usually initiated when the intruder entered the visual range of the resident; however, for 12% of instances, contests were initiated by tactile advances (nuzzling/biting of carapace) from the intruder. Male contests followed the same pattern of escalation as that of female competition. During fights males would bite, spar, lock flippers while plastron to plastron, attempt to mount, and repeatedly swim to and from each other at speed, until one opponent retreated. In all instances, the retreating male curled its tail under the carapace while the winner held its tail straight.

Reproduction. This includes courtship and copulation with and without male attendants (Table 1, Fig. 2J-L, Video clips 14 to 19, see Appendix 5). Courtship was initiated by a male entering the visual range of a female, advancing quickly and biting at the carapace (Video clip 14). The male would attempt to get behind the female and mount; however, if the female was not receptive, she would counter his actions by attempting to (1) take a vertical position in the water with the plastron facing the male, which sometimes led to the male locking plastrons with the female (Video clips 15 & 16), (2) maintain head–head position preventing the male from circling around, often trying to obtain a higher horizontal position in the water than the male (Video clip 17), (3) spin out from under a male attempting to mount (Video clip 18), (4) attempt to get behind the male and bite at his tail (Video clip 19). Males attempting to court females during the inter-nesting period were never observed to successfully mount and mate.

Mating was observed on 20 occasions during the pre-nesting period, both on the sea surface and on the seabed. Copulation had already begun when the turtles were initially observed, and males were mounted for periods of at least 40 min (the total duration was not recorded). Mounted males hooked their fore-flipper claws over the anterior rim of the female carapace and were observed repeatedly biting at the necks of females. Mating appeared to occur more frequently:

1. during rough sea conditions when underwater visibility was low (90%, 18 pairs) and
2. during April (70%, 14 pairs). Copulation with interference by attendant males was recorded on 5 occasions.

Only one attendant was recorded at any one time with mating pairs. One mounted male was successfully dislodged by attendant interference. Attendant behaviour included fast swimming to and from the mating pair and aggressive biting of the mounted male’s (and on occasion female’s) fore and hind flippers, neck, tail and carapace. During attacks mounted females would attempt to evade the attendant by diving to the seabed and swimming along it, ceasing all movement between attacks.

Female behaviour

At 1449 female sightings (Fig. 2), significantly more were observed in solitary (92%) than social (8%) behaviour (x_1^2 = 1020, P < 0.001). Solitary females were more likely to be found inactive (68%) than active (32%) (x_1^2 = 164, P < 0.001). While cleaning behaviour only accounted for 1.5% of observations, very similar uniform scratch patterns on the carapace (different to that of mating scratches) were documented at over 50% of female sighting events.

Male behaviour

At sighting events with male loggerheads present (Fig. 2, n = 139), analysis of initial behaviour observations indicated that they were just as likely to be found in solitary (57%) as social states (43%; x_1^2 = 2.33, *P* = 0.1). There was no significant difference in the occurrence of active (61%) and inactive (39%) solitary states (x_1^2 = 3.24, *P* = 0.07). Uniform scratch patterns, identical to that of females observed performing self cleaning, were found on the carapace of males at 19% sighting events. The proportion of social behaviour observed in males (43%) was 5 times greater than that of females (8%). Furthermore, the proportion of active solitary behaviour observed in males (62%) was double that of females.

DISCUSSION

Through intensive in-water observations of loggerhead sea turtles during the breeding season, we found that a broad range of behavioural activities were exhibited. Our research differed from existing studies at breeding areas (courtship and internesting) in that, rather than specifically addressing courtship and mating behaviour (Booth & Peters, 1972; Dodd, 1988; Frick *et al.*, 2000), or inter-nesting movement patterns (Hopkins-Murphy *et al.*, 2003), we sought to investigate the behavioural ecology of sea turtles during this period.

Our results indicated that in general males were more active and social than females, which probably reflected the need to acquire multiple mates to maximise fitness, whereas female fitness would be maximised by energy conservation to divert resources towards egg development (Hays *et al.*, 2002a; Hopkins-Murphy *et al.*, 2003). However, we observed female loggerheads investing in active behaviours previously unobserved in loggerheads during the breeding period, i.e. that of foraging, cleaning (self-cleaning and fish-cleaning symbiosis) and female–female contests. Contests between individuals over space has received anecdotal mention in sea turtle literature (Limpus & Limpus, 2003), yet our research indicated that antagonistic interactions are a noteworthy component of female loggerhead activity during the breeding period. It is possible that females may be benefiting from:

1. thermally optimal sites to enhance egg development, or
2. space to obtain refuge from energy consuming encounters with males patrolling for receptive mates (Booth & Peters, 1972; Whittow & Balazs, 1982; Lee & Hays, 2004).

Both self-cleaning (e.g. green turtles Chelonia mydas, Heithaus *et al.*, 2002b) and cleaning symbioses have been recorded in other sea turtle species at foraging and breeding grounds (e.g. green turtles: Losey *et al.*, 1994; hawksbill turtles Eretmochelys imbricata: Sazima *et al.*, 2004). However, high carapace epibiont loads (Frick *et al.*, 1988) and a recent animal-borne sea turtle study (Heithaus *et al.*, 2002b) have led researchers to suggest that loggerheads do not invest as heavily in cleaning behaviour as other sea turtle species (Bjorndal, 2003). Yet, while we only observed self-cleaning and fish cleaning symbiosis on a few occasions, evidence of self-cleaning behaviour was apparent from the uniform scratch patterns on the carapaces of a large proportion of surveyed male and female turtles, indicating that loggerheads at Laganas Bay do invest in cleaning activity.

Herbivorous foraging behaviour has been documented in one Mediterranean population of female green turtles at a breeding area (Hays *et al.*, 2002b). Similarly, we observed sporadic feeding attempts for molluscs by both female and male loggerheads at Laganas Bay. However, time spent foraging was relatively short, presumably because of the need to spend time and energy on other activities (e.g. males searching for females), and possibly because prey densities were sufficiently low that sometimes it was more profitable (e.g. for females) to simply rest than attempt to feed.

Direct observations of loggerhead sea turtle mating systems in the wild remain rudimentary (Dodd, 1988; Frick *et al.*, 2000). Courtship and mating behaviour of loggerheads have been found to follow similar patterns to that documented in other sea turtle species (Booth & Peters, 1972; Godley *et al.*, 2002; Rostal, 2005). In courtship bouts with unreceptive females we corroborated and expanded on the use of avoidance manoeuvre sequences. Furthermore, we recorded that females would attempt to circle behind persistent males to make offensive advances biting at their tails. As with other species, we observed that males competitively search for receptive females (Jessop *et al.*, 1999) in the form of patrolling but we also documented the presence of male–male combat, possibly for primary mate acquisition. Furthermore, while the presence of antagonistic attendant males in the company of copulating pairs has been recorded in other species of sea turtle (Booth & Peters, 1972), this was not documented in loggerheads (Frick *et al.*, 2000) until the current research.

Direct observations of turtle behaviour are of great value and provide many interesting insights that are difficult, or impossible, to gain from more indirect methods or animal-borne imaging. Studies, comparing direct and indirect methodologies of animal behaviour, have shown that remote-sensing data can distinguish between active and inactive states, however it cannot reliably distinguish the different behaviour patterns within those states (Hansen *et al.*, 1992; Heithaus *et al.*, 2001). Our findings have shown that loggerhead sea turtles exhibit a wider range of behaviour than has previously been documented at breeding areas. It is therefore likely that indirect inferences about movement patterns made from remote-sensing data analysis may be subject to error (as shown by Houghton *et al.*, 2002). It is also possible that jaw activity patterns may be subject to misclassification (Hochscheid *et al.*, 2005b) due to the failure to document activities such as sparring and biting in contests and courtship, biting at cleaner fish during cleaning, or biting themselves during self cleaning. The recent development of animal-borne cameras has given researchers of marine vertebrates, such as sea turtles, the opportunity to observe and confirm underwater behaviour (Davis *et al.*, 1999; Heithaus *et al.*, 2002b; Reina *et al.*, 2005; Hays *et al.*, 2006). Hence, knowledge about free-living behaviour, obtained from direct observations, is essential towards improving the accuracy of remote-data interpretation of marine wildlife.

To implement effective wildlife management and conservation plans, accurate information about animal behaviour, habitat use and population dynamics are essential. On Zakynthos, our data may be used to improve the existing national park conservation policies. The protection zones should be amended to take into consideration the function of different habitats with respect to sea turtle activities. Furthermore, sea turtle watching protocols should be refined, limiting in-water watching activities to regions where behaviour is minimally impacted. In conclusion, direct observational studies in the marine environment are of great value in developing our knowledge of marine vertebrate behaviour, validating remote technologies and contributing towards ecosystem research and environmental monitoring.

FIGURE & TABLE CAPTIONS

Table 1: Summary table of the breakdown of loggerhead sea turtle behaviour at each sighting event during surveying (M = male, F = Female)

Figure 1: The relative proportions of behaviour exhibited by male (black, n = 139) and female (hatched, n = 1449) loggerhead sea turtles (Caretta caretta) at initial sighting

Figure 2: Photographic slides showing sea turtle behaviour

Appendix 5: Observed behaviour video clips

Table 1. Summary table of the breakdown of loggerhead sea turtle behaviour at each sighting event during surveying (M = male, F = Female)

Status	**# Sighting Events**	**Behaviour category**	**# Sighting Events**	**Behaviour sub-category**	**Sex**	**# Sighting Events**
SOLITARY	1415	Resting	933	*Resting on seabed*	*M*	27
					F	676
				Surface-basking	*M*	4
					F	226
		Swimming	452	*Along seabed*	*M*	8
					F	89
				In water column	*M*	12
					F	197
				Near surface	*M*	21
					F	121
				Patrolling	*M*	4
					F	0
		Foraging	9	*Infaunal mining*	*M*	4
					F	5
		Cleaning	21	*Self-cleaning*	*M*	0
					F	6
				Fish cleaning symbiosis	*M*	0
					F	15
SOCIAL	119	Competition	65	*Male-male*	*M+M*	5
				Female-female	*F+F*	60
		Reproduction	54	*Courtship*	*M+F*	34
				Copulation	*M+F*	15
				Copulation with interference by attendant(s)	*(M+F)+M*	5
TOTAL	**1534**		**1534**			**1534**

Figure 1. The relative proportions of behaviour exhibited by male (black, n = 139) and female (hatched, n = 1449) loggerhead sea turtles (*Caretta caretta*) at initial sighting

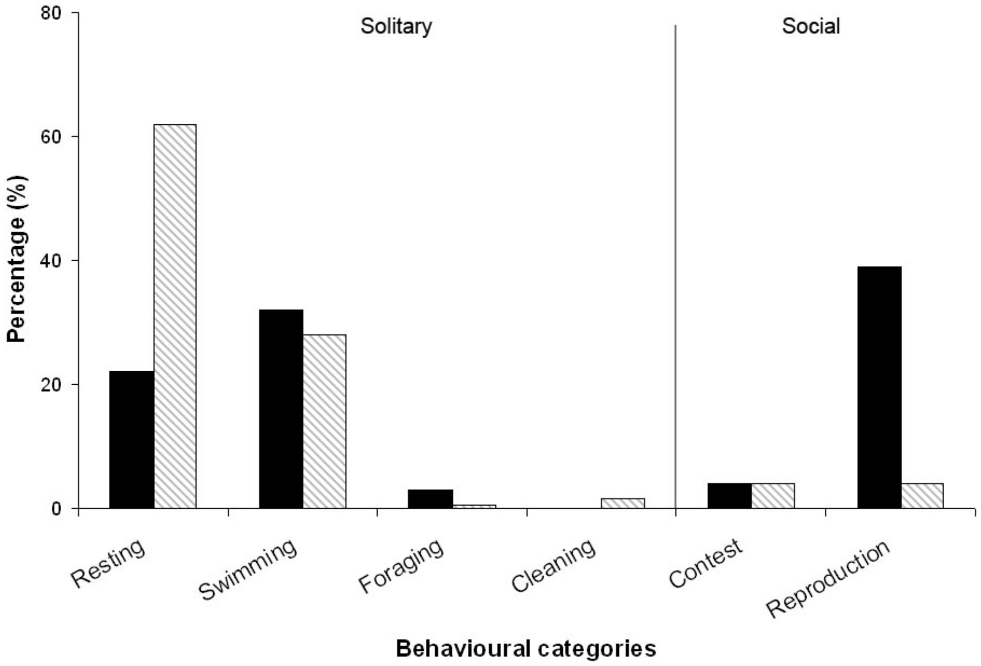

Figure 2. Photographic slides showing sea turtle behaviour

A. Female loggerhead resting on the seabed

B. Female loggerhead surface-basking

C. Female loggerhead swimming

D. Male loggerhead patrolling for females

E. Male loggerhead foraging for molluscs

F. Female loggerhead rubbing against an anchor

G. Female loggerhead posing at a fish cleaning station manned by sheepshead bream (*Diplodus puntazzo*)

H. Antagonistic female loggerhead interaction

I. Antagonistic male loggerhead interaction

J. Loggerhead courtship activity

K. Loggerheads copulating

L. Loggerhead copulation with antagonistic attendant male

ΚΕΦΑΛΑΙΟ / CHAPTER 3. Female-female aggression: structure of interaction and outcome in loggerhead sea turtles

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Peer-reviewed journal citation (manuscript in Appendix 3)*:*
Schofield, G*., K.A. Katselidis, J.D. Pantis, P. Dimopoulos, G.C. Hays. 2007. Female-female aggression: structure of interaction and outcome in loggerhead sea turtles. Marine Ecology Progress Series 336: 267-274*

Affiliated conference presentation (poster in Appendix 4**):**
Schofield, G*., K.A. Katselidis, J.D. Pantis, P. Dimopoulos & G.C. Hays. 2007. Female-female aggression in loggerhead sea turtles: structure of interaction and outcome. Twenty-Seventh International Symposium on Sea Turtle Biology and Conservation. Myrtle Beach, South Carolina. Pp59*

INTRODUCTION

Although aggression between males is a widespread phenomenon, the same behaviour between females is less frequently documented (Liker & Székely, 1997). Aggressive behaviour primarily arises to exclude intruders from defended areas in order to avoid competition for resources (Petrie, 1984). Intra-specific aggression usually serves to establish hierarchy among individuals for access to resources. In the case of females, aggression is usually related to factors that affect their own and/or their offspring's survival: for instance food, mates, gestation sites, nest sites and sites to evade predators (Gowaty & Wagner, 1988; Liker & Székely, 1997; Woodley & Moore, 1999). Such behaviour requires an individual to invest in defence (e.g. to expend energy and/or time) so that some kind of benefit can be obtained (e.g. improved ranking or exclusive access to a limited resource). Because the relative importance of each defended resource can vary in space and time, it is often difficult to explain the origin of aggression. However, the degree of aggression is usually correlated with opponent capability and/or resource availability (Brown, 1964). Confrontations between 2 individuals are usually characterised by specific stereotypical behaviour that is divided into stages of escalating aggression (Ruby, 1978) in which individuals evaluate and test the ability of the opponent (Parker, 1974; Maynard Smith, 1994).

Contests are usually resolved through low cost displays of physical attributes (Ruby, 1978), and only escalate into costly aggressive (agonistic) interaction if neither competitor retreats (Enquist & Leimar, 1983). The outcome of escalated contests depends on a range of parameters such as competitive ability (resource holding power) and occupancy of a territory or hierarchical rank (prior residency effect). The residing individual is usually expected to win because, over time, the optimal sites/ranks are occupied by superior competitors (evolutionary stable strategies; Maynard Smith & Price, 1973; Parker, 1974). However, a range of factors associated with individual fitness and/or resource value may also affect competitor motivation and hence contest outcome (pay-off asymmetries such as contest duration and previous encounters; Kotiaho *et al.*, 1999; Cressman *et al.*, 2004).

Although aggressive behaviour and contest escalation is widely documented for many vertebrates and invertebrates, direct observations of the aggressive behaviour of free-living animals in the marine environment is primarily limited to captive studies, usually of fish (Bisazzo & Pilastro, 1997). Most research on large free-living marine animals relies on the attachment of electronic devices, such as data-loggers and satellite transmitters, to elucidate animal behaviour (e.g. of fish, seabirds, seals, whales, dolphins and sea turtles) related to diving and migratory activity. Although electronic devices have the capacity to record a range of animal movements, physiological processes and environmentally related parameters, at present they cannot—with the exception of camera systems—be used to infer intra- and inter-species interactions. Yet such interactions may be key to establishing how individuals utilise habitats and function within larger marine ecosystems.

Sea turtles are deep–diving migratory marine vertebrates; hence, remote technology has played an important role in understanding their aquatic activity (Hays *et al.*, 2002a; Myers *et al.*, 2006). However, without reliable comparative direct behavioural observations (Booth & Peters, 1972; Whittow & Balazs, 1982; Houghton, 2003) there is a risk of misinterpreting or even overlooking aspects of sea turtle biology (as shown by Houghton *et al.*, 2002). For instance, telemetry studies have shown that sea turtles are solitary, even when individuals of a particular species share overlapping home ranges at foraging or breeding site aggregations (Hays *et al.*, 2002b; Hopkins-Murphy *et al.*, 2003). Nevertheless, there is anecdotal evidence of aggressive interactions between individuals when in close proximity to one another (Herbst & Jacobson, 2000; Limpus & Limpus, 2003).

Laganas Bay on the island of Zakynthos (Greece) is a major breeding area for loggerhead sea turtles *Caretta caretta* (Margaritoulis, 2005). Several hundred turtles seasonally aggregate nearshore, making it relatively easy to acquire quantitative information on their aquatic behaviour through direct observation. As part of an ongoing in-water survey, we recorded repeated instances of female–female interactions. In the present study, we describe the stages of contest escalation from passive displays to aggressive combat. Based on existing theoretical game models of competition, we suggest how opponents communicate information on capability and motivation, and we discuss possible reasons for aggressive behaviour among female loggerhead sea turtles.

MATERIALS AND METHODS

Since 2003, in-water surveys have been conducted at Zakynthos annually between April and July, thus encompassing the loggerhead sea turtle breeding season (courtship and inter-nesting periods). Surveys were organised to cover a range of daylight hours between 08:00 and 20:00 h. They lasted 2 to 6 h depending on the method used (e.g. boat, kayak or snorkelling) and weather conditions. Boat, kayak and snorkel surveys were concentrated along a 5.5 km stretch of nearshore area at sea depths of up to 10 m, depths at which large numbers of female loggerhead sea turtles tend to aggregate during the breeding season.

On sighting a sea turtle from the boat or kayak, the distance to the individual and the GPS location were recorded. The observer then entered the water at a distance of at least 5 m from the target animal(s) and approached until within underwater visual range. Surveys were only conducted when the underwater visual range (which varied according to sea state) exceeded 2m, in order to minimize disturbance of ongoing behaviour. On encountering the animal(s), photographs were taken, and biological, environmental and behaviour observations (ongoing behaviour and behavioural response to the presence of the underwater observer) were recorded. Written records were made of all behavioural observations. In events involving social interactions, the start and end times were recorded and the position in which the tail was held at the beginning and end of interactions was documented in writing. During 2005, video footage was collected to classify all observed solitary and social behaviour as well as inter-species interactions. Sex was estimated using previously documented tail-length dichotomies for mature adult male and female turtles (Casale *et al.*, 2005).

We calculated mean and standard deviation for normally distributed metric data. We used non-parametric chi-square statistical analysis to assess the correlation between behavioural states and confrontation data (passive versus aggressive). We regarded results to be significantly different from H_0 when $p < 0.05$.

RESULTS

Female–female interactions comprised 4% of all female loggerhead sea turtle sighting events (n = 60 out of 1449 events) during the 3 yr survey. Male–female interactions comprised an additional 4% of sighting events while 92% of sighting events were of solitary females. We recorded the structure of 60 contests each lasting an average of 3.4 min (SD ± 1; Range 1–6 min), comprising a total of 3.1 h of observations.

Prior to contests, the behaviour of the resident turtle was always solitary and consisted of resting on the seabed, 65% (n = 39); surface-basking, 13.5% (n = 8); swimming, 18.5% (n = 11); or fish cleaning symbiosis, 3% (n = 2). Female interactions during fish cleaning symbiosis were excluded from the data set owing to the small sample size and because fish cleaning was only observed in the survey area during 1 season.

Confrontation structure

Turtles displayed a stereotyped sequence of escalating behaviour during contests. We divided contest escalation into 4 stages that could be concluded at any stage by the retreat of 1 opponent. The stages were:

1. initial contact, stimulated by visual or tactile cues
2. passive confrontation, comprising wide head–tail circling, with individuals maintaining a distance of 1.5 m from one another
3. aggressive confrontation, involving violent physical contact
4. separation, with both turtles leaving or one fleeing and the other chasing.

The confrontation structure and the outcomes of confrontations are presented in Figure 1.

Initial contact

Initial contact occurred when intruders entered the visual range of residents. In all encounters of intruders with basking or swimming residents (100%, n = 19) both turtles responded. However, while contact was made in the majority of encounters of intruders with residents resting on the seabed (82%, n = 32), it was not always by both individuals. Three scenarios were presented by resident turtles resting on the seabed (n = 39) when an intruder entered their occupied space:

1. in 18% (n = 7) of encounters the intruder passed by, either unnoticed or ignored
2. in 54% (n = 21) of encounters the intruder advanced on the resident turtle, obtaining visual contact and a defensive response by 91% (n = 19) of resting site residents (Fig. 2) in which the anterior body and head were raised with mouth gaping (as observed by Limpus & Limpus, 2003)
3. in 28% (n = 11) of encounters the intruder advanced on the resident, obtaining no visual contact or defensive response, and proceeded to attack the resting turtle by nuzzling or biting the carapace (Fig. 3), thus stimulating a response in 73% (n = 8) of interactions.

Passive phase

Once visual contact was made with the left or right eye (depending on which side the intruder entered visual range), it was not broken until separation. At this point, passive confrontation was initiated in the form of wide head–tail circling, with individuals maintaining a distance of 1.5 m. All intruder interactions with basking and swimming turtles (n = 19) led to a passive response, whereas residents resting on the seabed responded on only 69% of occasions (n = 27). The majority of confrontations that progressed to the passive phase were actually resolved in that phase, i.e. 88% (n = 7) of surface-basking, 91% (n = 10) of swimming confrontations (89.5% combined) and 63% (n = 17) of seabed resting site confrontations. A significantly higher proportion of confrontations with resting site residents developed into aggressive confrontation than did those with surface-basking/swimming residents ($x_1^2 = 4.92, P < 0.02$; 37% (n = 10) and 10.5% (n = 2) respectively)

Aggressive phase

Aggressive confrontation was triggered when one turtle stopped circling to face the other head-on. A sequence of physically violent interactions was initiated, starting with sparring, in which the turtles snapped at each others' jaws (Fig. 4), with one or both turtles holding offensive 'horizontal' or defensive 'vertical' positions in the water column. This progressed to close circling in which the turtles snapped at the opponent's posterior carapace and/or flippers, followed by chasing and snapping at the neck and/or central carapace. All aggressive confrontations involved sparring and 36% (n = 4) progressed to close circling; of these 75% (n = 3) progressed to chasing and biting before separation.

Separation

Separation was either mutual, with both turtles initially swimming away in generally opposite directions, or involved one opponent briefly chasing the other out of the immediate vicinity. Although the prehensile tail of adult male sea turtles has been documented to serve the primary function of curling under the female carapace for penile penetration (Miller et al. 2003), the present study noted that the prehensile tails of females being used significantly often during confrontations ($x_1^2 = 3.89, P < 0.04$), possibly as a signal of the opponent's intention. In 70% (n = 21) of passive and 80% (n = 12) of aggressive interactions, the first turtle to depart visibly curled its tail immediately prior to separation.

Separation of intruders and resident surface-basking or swimming turtles was generally mutual (62.5% [n = 5] and 63.5% [n = 7] respectively; 63% combined), with no significant difference observed between the frequency of capitulation (i.e. departure) of intruders and residents ($x_1^2 = 0.6, P < 0.4$). In confrontations with resting site residents, there was a 96% (n = 26) probability that one of the opponents would flee rather than both depart mutually. Intruders were significantly more likely to depart first during passive and aggressive confrontations with resting site residents ($x_1^2 = 19.18, P < 0.001$), with an intruder win rate of 15% (n = 5) that was reduced by a further 5% during aggressive confrontations.

DISCUSSION

Our research illustrates that interactions between female loggerhead sea turtles are subject to escalation, the degree of which appears to differ with respect to behavioural state. Aggressive behaviour between females may arise:

1. as a side-effect of elevated reproductive hormones (Woodley & Moore, 1999) or
2. as a side-effect of fending off male advances once receptivity has passed.

However, resident females initially respond to males entering their visual range by holding a vertical ‘refusal’ pose (Booth & Peters, 1972), which is not observed until the aggressive phase of female–female interactions. Although heightened olfactory senses (Bartol & Musick, 2000) may enable residents to identify and respond to intruders accordingly, prior to their entrance into residents’ visual range, this does not account for the incidence of aggressive behaviour also observed in foraging individuals and captive juveniles (Herbst & Jacobson, 2000; Limpus & Limpus, 2003). Our observations indicate that interactions were more aggressive when they involved resting site locations than when basking and swimming turtles were concerned, and that these locations were noticeably sought after by intruders. Marine environments are not homogeneous, and this behaviour indicates that turtles could be competing over a scarce high quality resource. These observations support the population ‘interference’ model derived from the ‘Ideal Free Distribution’ (Fretwell, 1972; Sutherland & Parker, 1986) in that seabed resting sites may represent an optimal resource over which individuals compete, whereas surface-basking and swimming states occur at suboptimal sites subject to less competition.

In some breeding areas, female turtles have been observed to take refuge from energetically costly interactions with reproductively active patrolling males by occupying nearshore waters (Booth & Peters, 1972; Lee & Hays, 2004). In this instance, space may be the limiting factor, whereby females resting in close proximity to one another would attract unwanted male attention. This may also account for the incidence of beach-basking behaviour of green turtles *Chelonia mydas* at Hawaii (Whittow & Balazs, 1982). Therefore, the size of the defended aquatic sites may correlate with the visual range of the resident, which is controlled by dynamic physical parameters such as light or sea clarity (Val dimarsson & Metcalfe, 2001).

Alternatively, detailed research has shown that, in gestating reptiles, environmental temperature affects the developmental rate and viability of offspring as well as adult growth and survival (e.g. lizards: Wapstra, 2000; snakes: Ladyman *et al.*, 2003). It is therefore possible that female turtles, particularly in temperate breeding areas, are responding to thermal cues in the environment by seeking out warmer water to accelerate gestation. Temperature regulation may also serve as an alternative explanation for Hawaiian green turtle beach-basking behaviour (Whittow & Balazs, 1982). This theory is further supported by comparative studies of sea turtle distribution in temperate and tropical breeding areas: in the former, where ambient sea temperatures are cooler, turtles form dense nearshore aggregations, whereas in the latter they remain more dispersed (e.g. Hays *et al.*, 2002b).

In contests between female loggerhead sea turtles, we observed that established residents at seabed resting sites were more likely to win both passive (73%) and escalated aggressive (68%) contests, supporting established evolutionary ecology competition models (e.g. Parker, 1974; Maynard Smith, 1982; Enquist & Leimar, 1983). Competition escalation models predict that differences in opponent fighting ability should determine the outcome, usually favouring the stronger opponent. It is likely that initial resident status depends on time of arrival, whereas the length of residency depends on how rested the individuals are prior to each encounter combined with individual competitive ability.

Motivation to fight is influenced by many parameters related to individual fitness and resource value, and is subject to regular re-evaluation by each opponent, with respect to confrontation frequency, intensity and duration (e.g. Kotiaho *et al.*, 1999; Cressman *et al.*, 2004). We found that confrontations at surface-basking or swimming locations were more likely to mutually terminate at the passive stage; hence, resource value may also play an important role in determining fight duration and escalation (e.g. Kotiaho *et al.*, 1999). We suggest that a combination of size assessment and resource value could account for the 3 initial contact categories observed between occupants and intruders at resting sites. In cases with ‘no contact’, the intruder passes over an occupant with superior competitive ability or at a site of low resource value. In instances with a ‘visual response’, the intruder establishes visual contact, initiating a confrontation sequence with an equally matched resting site occupant.

Finally, in interactions provoked by a ‘tactile response’, high resource value may motivate some intruders to provoke confrontations with opponents of superior competitive ability, although they have little chance of winning. Intruders that select the right opponent may have more to gain or less to lose than the established resident, resulting in the resident giving way to the intruder (Kotiaho *et al.*, 1999), independent of the resident’s holding power and strength. When confronted with an opponent, competitors must acquire appropriate information about each other prior to initiating a fight. Such information is usually obtained through a set of passive threat displays (Ruby, 1978). In sea turtles, passive head–tail circling behaviour may represent a ‘cheap’ way to determine opponent strength through size evaluation, while the position in which the prehensile tail is held may be an energetically inexpensive signal for motivational intent (with no correlation with animal strength). We suggest that tail position may be used to obtain information about the opponent’s willingness to escalate or abort conflict at any stage of the combat sequence. An extended tail signals willingness to proceed, whereas tail curling at any part of conflict escalation indicates a competitor’s decision to abort. Hence, when a contestant’s decision to continue beyond passive head–tail circling is ‘borderline’, just a quick visual assessment of the opponent’s tail position could determine intent.

Although cheap signals invite cheating (e.g. Parker, 1974; Maynard Smith, 1994), use of the tail to signal intent may be evolutionarily stable as long as both opponents benefit. While the costs of circling are low (in terms of energy and lost time), the expense of escalation to physical contact are high (risk of injury) and may keep cheating under control. Therefore, while sparring is not potentially dangerous, it may present an honest indicator of opponent strength and motivation (e.g. Kotiaho *et al.*, 1999). The way in which individuals of a species compete over resources allows researchers to objectively measure the importance of a particular environment, habitat or ecosystem to animals.

Direct observation of free living marine animals is subject to a number of limitations; for instance, our study was limited by time of day, sea conditions and sea depth. Because of such limitations, use of remote technology is becoming increasingly common. However, without corroborated observational research, such technology only produces informed guesswork of animal behavioural activities. Advances in electronics are making underwater video cameras economically viable, giving the researcher the opportunity to obtain direct observational information within a wide range of marine settings (e.g. cameras may be hand-held or attached to the seabed, boat, remote-vehicle or study animal). By collecting direct baseline behavioural information, electronic devices could be subsequently used as a powerful tool to acquire specific information with respect to trends in marine animal social behaviour and habitat use. A useful goal for future studies would be to attempt to quantify the competitive abilities of fighting sea turtles and assess how their ability impacts the outcome of encounters. For example, it might be that competitive ability is related to body size or length of residency, as is the case in some other vertebrates (Downes & Shine, 1998; Gray *et al.*, 2002). Our study can be considered a first step towards application of remote technology in order to specifically investigate possible causes of social interactions between sea turtles.

FIGURE & TABLE CAPTIONS

Figure 1. Flow-chart showing the stages of female-female loggerhead competition. The percentage values on the arrows indicate the outcomes from different interactions.

Figure 2. Visually provoked response of resident to intruder

Figure 3. Tactile provoked response by intruder to resident

Figure 4. Aggressive sparring between females

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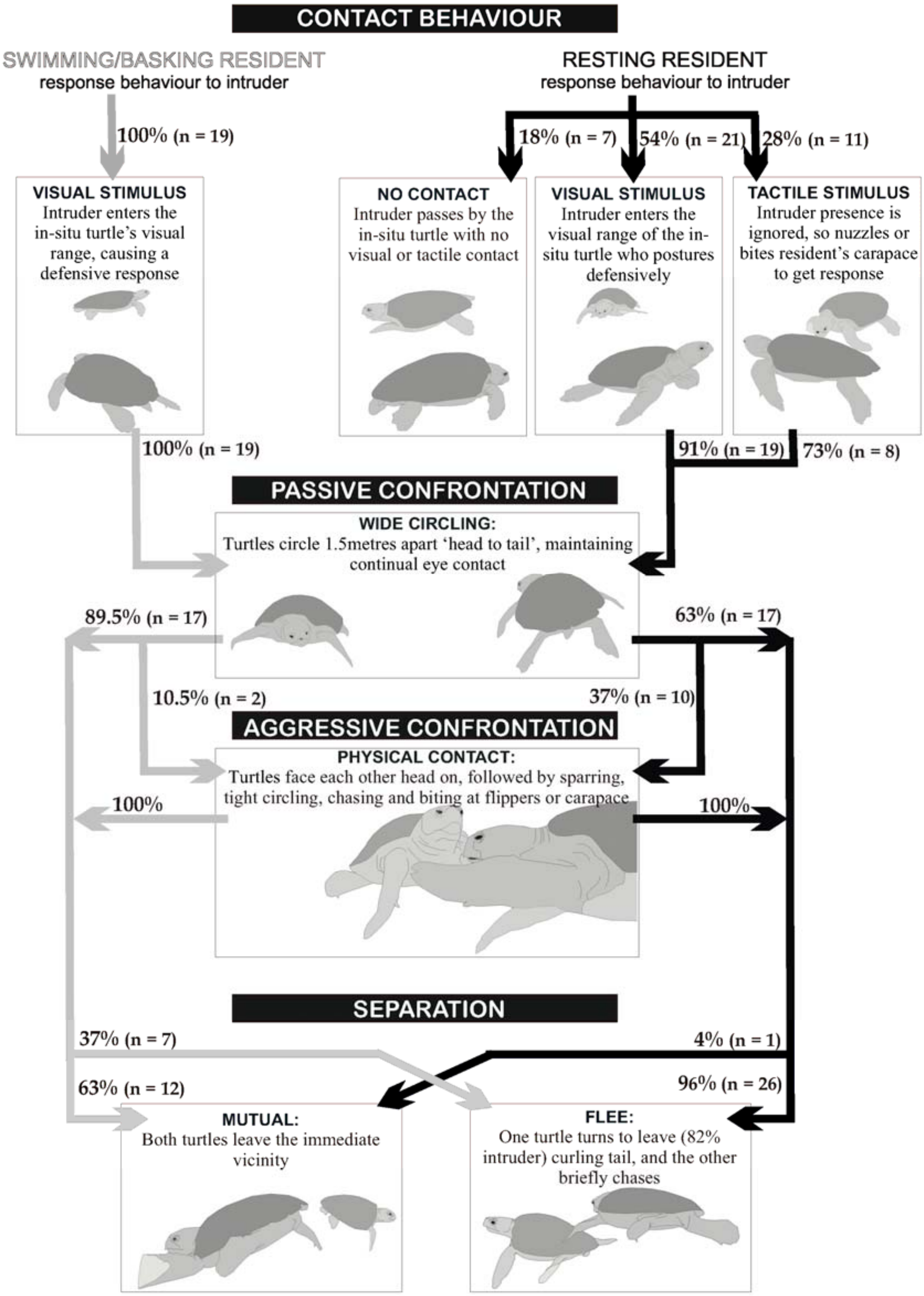

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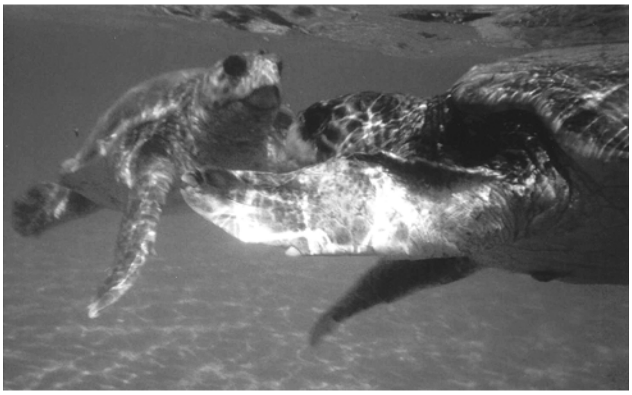

ΚΕΦΑΛΑΙΟ / CHAPTER 4. Novel GPS tracking of sea turtles as a tool for conservation management

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Peer-reviewed journal citation (manuscript in Appendix 3)*:*
Schofield, G.*, C.M. Bishop, G. MacLean, P. Brown, M. Baker, K.A. Katselidis, P. Dimopoulos, J.D. Pantis, G.C. Hays. 2007. GPS tracking of sea turtles as a tool for conservation management. Journal of Experimental Marine Biology and Ecology. 347: 58-68*

Affiliated conference presentation (poster in Appendix 4**):**
Schofield, G.*, C.M. Bishop, G. MacLean, P. Brown, M. Baker, K.A. Katselidis, P. Dimopoulos, J.D. Pantis, G.C. Hays. 2007. GPS tracking for fine-scale conservation management: following sea turtles within a marine protected area. Presented at the Twenty-Eighth International Symposium on Sea Turtle Biology and Conservation. Loreto, Baja California Sur, Mexico. Pp69*

INTRODUCTION

Understanding movement patterns and the factors that affect animal distribution are integral components of behavioural ecology, conservation and protected area management. Conventional animal biotelemetry systems, such as radio and satellite transmitters, have revolutionised the ability to track wildlife movement over vast spatial and temporal scales (Maehr *et al.*, 2002; Luschi *et al.*, 2003; Sale *et al.*, 2006; Sims, 2006). Despite this, variable accuracies and infrequent intervals between fixes (Hays *et al.*, 2001a; Hulbert & French, 2001) limit their application at finer spatial resolutions, and when quantifying movement patterns in relation to biophysical parameters at small scales (Wilson *et al.*, 2002; Bradshaw *et al.*, 2007b). However, the acquisition of high resolution tracking information may be important in formulating rational, adaptive and dynamic management decisions for nature reserves, endangered species and related conservation policies (Argardy, 1994; Thompson *et al.*, 2000; Parra *et al.*, 2006).

Loggers based on the Global Positioning System (GPS) are an important new technology allowing wildlife to be studied with unparalleled accuracy, often to within ranges of 10 m (Moen *et al.*, 1997; Hulbert & French, 2001). However the level of accuracy has been found to vary among animals depending on terrain, habitat and behaviour (Moen *et al.*, 1997; Friar *et al.*, 2004). While GPS loggers, some linked to transmitters to relay the positional data, are routinely used for terrestrial and aerial animals (Douglas-Hamilton *et al.*, 2005; Biro *et al.*, 2006), tracking marine vertebrates with GPS loggers has proved more problematic. This is because infrequent surfacing behaviour limits the time when loggers are available for acquiring satellite signals. For marine species therefore, the current challenge is, in as short a time possible, to acquire sufficient information in order to calculate GPS positions when an animal surfaces. There are several initiatives underway to achieve this goal and some limited success has been achieved, depending on species and surfacing interval (Sisak, 1998; Jay & Garner, 2002; Ryan *et al.*, 2004; Yasuda & Arai, 2005; Petersen *et al.*, 2006; Sheppard *et al.*, 2006).

While satellite and VHF telemetry studies have been effectively used to investigate sea turtle oceanic migratory routes (Luschi *et al.*, 2003; Hays *et al.*, 2004b; Sale *et al.*, 2006) to coastal foraging or breeding grounds, details about behaviour and habitat use at these regions of seasonal residency remain limited (Heithaus *et al.*, 2002b; Houghton *et al.*, 2002; Seminoff *et al.*, 2002; Hopkins-Murphy *et al.*, 2003; Yasuda & Arai, 2005). Existing studies of female sea turtles at breeding areas using remote technology have been primarily conducted following the onset of nesting (Hays *et al.*, 1991; Hays *et al.*, 2002a; Houghton *et al.*, 2002; Hays *et al.*, 2003a; Hopkins-Murphy *et al.*, 2003). These studies indicate that internesting females tend to inhabit sea depths of 15 m or less, and may be found as much as 10 km from the nesting beaches, often exhibiting movements parallel to the coast.

Laganas Bay, on the island of Zakynthos in Greece, is the largest loggerhead sea turtle (*Caretta caretta*) rookery in the Mediterranean (Margaritoulis, 2005). It is visited by several hundred sea turtles and several hundred thousand tourists each summer (Arianoutsou, 1988). Sea turtles often begin residency in Laganas Bay as early as April, before nesting starts in late May, and are frequently observed in close proximity to shore (Schofield *et al.*, 2006). Nesting beach locations and relative nesting densities were used to delineate the degree of protection offered by marine protection zones in Laganas Bay (Arapis & Margaritoulis, 1996). The no-boating zone encompasses three nesting beaches (out of a total of six), which account for about 70% of nesting activity (Margaritoulis, 2005). Since establishment of the National Marine Park of Zakynthos (NMPZ) in 1999, stricter regulation of nearshore tourism and turtle-watching activities in the two boating zones has been introduced, however empirical data about in-water sea turtle movement is necessary to validate and improve existing management actions.

Many coastal regions are subject to anthropogenic pressure, in the form of fisheries, coastal development and tourism (Arianoutsou, 1988; Hays *et al.*, 2003c; Parra *et al.*, 2006). It is therefore important to obtain information about where, when and why endangered species, such as sea turtles, use these areas, in order to implement rational and effective protective legislation and management of human activities (Argardy, 1994; Thompson *et al.*, 2000). The aim of this study was to investigate sea turtle movement and habitat use at the internationally important rookery of Zakynthos. We used recently developed, low-powered, TrackTag™ GPS loggers to follow individual sea turtle movements and evaluate the effectiveness of existing marine protection zones.

METHODS

Study animal

TrackTag™ GPS loggers were deployed onto four adult female loggerhead sea turtles (curved carapace lengths 81–89 cm) in Laganas Bay, Zakynthos, Greece (37°43′N 20°53′E), during the pre-nesting period in May 2006 and removed during the inter-nesting period in June 2006. In one case, deployment problems caused the logger to malfunction so that no data were collected. Hence data were collected from three turtles. In addition, six time–depth recorders (TDR) were deployed and retrieved from all four turtles plus another two female turtles. The attachment of all devices was conducted under licenses from the Greek Ministry of Agriculture. A 4 m research boat was used to find turtles resting on the seabed at depths less than 1.5 m. The turtles were captured using the turtle-rodeo technique (Ehrhart & Ogren, 1999) and lifted onto the boat. Following capture, the curved carapace length was measured and then a GPS logger and/or TDR attached using a standard method we have widely employed before with various transmitters and loggers (Hays *et al.*, 2003a). In brief, the carapace was cleaned and then the logger embedded in quick setting two-part epoxy resin (Powerfastners Inc., New Rochelle, NY, USA) with wooden baffles positioned at the anterior to help prevent impacts to the equipment (see Fig. 1). Loggers and TDRs were removed from the animals by one of two methods:

1. using the rodeo capture technique, or
2. by recovery on the beach immediately following nesting.

GPS loggers

We used recently developed, low-powered, archival Navsys Ltd. TrackTag™ GPS devices (http://www.navsys.com). Battery-life is saved due to TrackTag requiring < 60 ms to be powered up and acquire enough data for a navigational fix. This speed of acquisition is made possible because the positions are calculated during post-processing. Our devices had a memory capacity of 32,750 positions. The logger was housed in a stream-lined, pressure tight, ABS plastic casing measuring 101–34–26 mm (L × W × H). The mass of the device, including battery and housing, was 55 g (c. 0.001% of estimated sea turtle mass). Loggers had a saltwater switch so that they only attempted to acquire information from the GPS satellites when the turtle was at the surface. This system helps to extend memory capacity along with battery life. Navsys estimates accuracy of locations to be around 30 m (2dRMS) 95% of the time using a horizontal and stationary receiver in the UK. Prior to deployment, the GPS loggers were charged and programmed using Navsys TrackTag™ software to record in continuous mode at 30 s intervals when the saltwater switch indicated the units were not submerged. The housing was sealed using ABS water-resistant glue requiring a 6 h drying period. GPS co-ordinates were recorded with a spatial resolution of 0.0001° (11 m for latitude and 8.8 m for longitude at 37°N).

On retrieval, all GPS locations were plotted to examine the turtles' movements. Data when the turtles were ashore (nesting or on aborted nesting attempts) were removed from all analysis and were confirmed by direct field observation, GPS onshore location and/or by TDR analysis of depth and temperature values. Due to the surfeit of data we also explored various filters to remove potentially erroneous locations. These methods included:

1. removal of visually erroneous locations, such as those that fell well on land or were completely spatially different to previous and successive fixes within the same time frame,
2. using a maximum rate of travel of 5 km h^{-1} between successive locations (Hays *et al.*, 2004a; Tremblay *et al.*, 2006) which was selected based on calculations from 3 or more consecutive fixes occurring at 10–20 min intervals
3. using the 'dilution of precision' (DOP), measuring the quality of satellite geometry, in which values below 10 are retained (Adrados *et al.*, 2002) and
4. using the 'satellite visibility' (SV) with a threshold of > 4 satellites following previous work (Sea Mammal Research Unit SMRU, http://smub.st-and.ac.uk).

TDR devices

To record the diving behaviour of turtles we used time–depth recorders (TDRs); LOTEK LTD_1100 model TDRs (LOTEK Marine Technologies, St. John's, Newfoundland). The TDRs weighed 5 g in air, sampled depth with a precision of 2 cm, temperature with a precision of 0.2 °C and stored up to 16,384 readings for each parameter (http://www.lotek.com/ltd1100.htm). The TDRs employed "time-extension" sampling whereby the sampling interval was adjusted so that data continued to be collected regardless of the length of deployments. Hence, the sampling frequency was approximately the length of the deployment divided by 16,384, which, in our study, equated to a sampling interval of < 1 min to around 4 min. For each data set we conducted a zero point offset, whereby we determined the shallowest depth recorded every 4 h. We would expect this depth to be the surface (0 m) and so all the raw depth values from the loggers were adjusted accordingly, typically by a maximum of a few 10 s of cm. This process of zero point calibration is standard within TDR studies (see for example, Hays *et al.*, 2007). Data when the turtles were ashore (nesting or on aborted nesting attempts) were removed from further analysis. These events were confirmed by direct field observation and/or by analysis of depth and temperature values indicating that the turtle was ashore.

Turtle spatial area use

Using the Geographic Information Systems (GIS) package ArcView 3.1 we identified key area use by overlaying the turtle GPS fixes on existing features, including:

(i) sea depth parameters,
(ii) Natura 2000 marine habitats and
(iii) National Marine Park of Zakynthos maritime zones.

To obtain an objective measure of sea turtle key area use in relation to the selected features, we initially filtered the GPS fixes by selecting one fix per hour for each turtle (Tremblay *et al.*, 2006). The GIS programme provided the attributes of the polygons for each feature within the maps. The location of turtle GPS fixes was analysed (using the "query" and "summarise" tools) with respect to the chosen features, to indicate areas that are in need of increased protection.

Turtle movement model simulations

Two turtles that were tracked moving around Laganas Bay at the same time (GPS2 and GPS3) seemed to show broadly the same pattern of movement rather than moving randomly with respect to each other. We therefore compared their movements against two random walk models. First we calculated the distance separating these two turtles every 3 h between 24/5/2006 and 6/6/2006, excluding days on which turtles nested (31/5/2006). In model 1 we assumed that each turtle moved randomly within Laganas Bay (defined by latitudes 37°70′–37°74′ N and longitudes 20°84′-20°96′E). Given that the bay at its widest point is about 12 km, we assumed that within 3 h a turtle could travel anywhere in the bay. We therefore divided the bay into grid squares (178 m in latitude by 211 m longitude) and randomly selected grid squares for each modelled turtle at 3 h intervals. At each time we calculated the distance apart between the two modelled turtles. In model 2, we constrained the movements of the modelled turtles so that they moved randomly but only within 900 m of the shore in Laganas Bay. For both models, 1000 movement steps were generated. The differences in observed distribution of actual and random walks were calculated using Kolmogorov–Smirnov tests.

RESULTS

TrackTag™ GPS loggers

Excluding deployment and retrieval days, the three turtles equipped with GPS loggers were tracked for a total of 73 complete days (17, 31 and 25 days respectively) between 20 May and 23 June 2006. All three turtles nested at the same beach (Sekania, in maritime zone A) during the period of GPS logger attachment.

A total of 5488 GPS fixes were obtained, of which 1278 were from when the turtles were making nesting attempts, leaving 4210 in-water locations. On filtering the data for visually erroneous locations, 457 fixes were removed, leaving 3753 GPS fixes (89%), with an average daily fix rate of 51 locations (Table 1, Fig. 2a–c). Alternative filtrationmethods of the in-water locations, using the speed filter left 64% of locations, while 40% and 62% of locations were retained respectively using the DOP and SV based filtration methods (Table 1). In all cases the tracks, either with raw or filtered locations, were very similar and the high number of daily locations allowed accurate assessment of each turtle's movement (Fig. 3a–f) (Hays *et al.*, 2004a). Hence, we selected to base subsequent data analysis on GPS locations that remained following the removal of ‘visually erroneous’ locations.

The GPS loggers indicated that all three turtles primarily used an 18.5 km section of the 27.8 km coastline of Laganas Bay; with 100%, 100% and 84% of in-water GPS locations for each turtle respectively (Fig. 4a–c and Appendix 5). Only GPS4 left the breeding area during the survey period. Analysis of hourly turtle locations against bathymetry, corroborated this coastal preference, suggesting that 79% of time was spent at sea bed depths < 5 m. Analysis of turtle distance from shore at hourly intervals indicated that 89% of hourly locations occurred within 0.5 km of shore, 76% within 0.2 km of shore and 56% within 0.1 km of shore (Figs. 5 and 6a). Analysis of our dataset using GIS overlays of Natura 2000 habitats suggested that the turtles do not uniformly inhabit shallow waters, but prefer habitats comprising submerged sandbanks (63% fixes) over other near-shore habitats, such as shallow rocky reefs (37% fixes) (Fig. 6b).

Analysis of hourly GPS locations with respect to the National Park maritime zones indicated that turtles spent on average 25%, 29% and 42% GPS of time in maritime protection zones A, B and C respectively. The turtles spent on average 56% (range 34%–94%) of time within the ecotourism zone straddling maritime zones B–C. GPS4 spent 4% of the survey period outside of the three protection zones (Fig 6c).

TDR devices

The near-shore movements of the three turtles equipped with GPS loggers was reflected in their patterns of depth utilisation with the vast majority of their time spent at very shallow depths. For example, all three turtles spent > 95% of their time at sea depths shallower than 4m (Fig. 7). Similarly for a further three turtles equipped with TDR loggers only, for a total of 67 days (31, 12 and 21 days respectively) between 16 May and 27 June, their patterns of depth utilisation were also very shallow (Fig. 7) with all these turtles similarly spending > 95% of their time shallower than 4 m.

Turtle movement and simulations

Analysis of comparative locations of actual GPS2 and GPS3 turtles at three-hourly intervals indicated that they occurred at distances of ≤ 1.5 km apart on 55% of occasions (average 1.6 km, range 0.01–5.44). Analysis of comparative locations of GPS4 with GPS2 and GPS3 indicated that they occurred at ≤ 1.5 km of both GPS2 and GPS3 on 38% of occasions (average 2.6 km, range 0.01–8.3). In both models the frequency distribution for the distances apart between the two modelled turtles was different to that in the observed data (Fig. 8), with GPS2 and GPS3 generally being more closely associated than that predicted by both random walk models (Kolmogorov–Smirnov tests, D=0.4245, P<0.001 and D=0.5031, P<0.001 respectively). In other words, this evidence suggests that turtles 2 and 3 were moving in the same manner within the bay.

DISCUSSION

Increasing development and settlement of human populations in coastal locations has become an important issue worldwide, threatening the sustainability of many marine and coastal resources (Arianoutsou, 1988; Argardy, 1994; Parra *et al.*, 2006). To facilitate wildlife conservation and sustainable use of marine areas, it is essential to understand the relationship between populations and their habitats (Castilla, 2000; Canadas *et al.*, 2005), with knowledge about the impacts of environmental and anthropogenic parameters providing additional benefit (Thompson *et al.*, 2000; Tisdell & Wilson, 2002; Douglas-Hamilton *et al.*, 2005; Preisler *et al.*, 2006). However, quantification of such parameters is often difficult hence the ‘precautionary approach’ to protect wildlife is applied in many areas, whereby measures are introduced, such as the regulation of boating activity, to minimise disturbance across general regions (Thompson *et al.*, 2000; Wilson *et al.*, 2004; Lusseau, 2006; Sorice *et al.*, 2006). In the case of sea turtles, nesting beach locations and relative nesting densities have been used to delineate the degree of protection offered by adjacent marine protection zones

(Arapis & Margaritoulis, 1996). While this approach has shown relatively good success in general, core protection areas may not reflect actual areas of wildlife habitat use, as we have demonstrated in our study at the largest sea turtle rookery in the Mediterranean.

The fine-scale detail of movement patterns obtained using the GPS loggers during this study, could not have been replicated using conventional telemetry (Hays *et al.*, 2001a; Hulbert & French, 2001; Tremblay *et al.*, 2006; Bradshaw *et al.*, 2007b). This has been made possible because the TrackTag™ GPS system calculates the position during post-processing rather than in real time (http://www.navsys.com). We have shown here how TrackTag™ GPS loggers can now obtain large numbers of locations for marine species. The volume of data and degree of accuracy obtained using the TrackTag™system are greatly improved in comparison to that obtained in previous GPS studies of marine wildlife (Sisak, 1998; Arai & Ono, 2002; Jay & Garner, 2002; Yasuda & Arai, 2005; Petersen *et al.*, 2006), facilitating fine-scale analysis and application to protected area management.

While the movement models we have used in this study are very basic, a number of more refined models could potentially be explored. For example, correlated random walk models, which randomly draw step lengths from the measured step-length frequency distribution, may provide a more refined test of whether animals are moving randomly (e.g. Heithaus *et al.*, 2002a). Similarly techniques such as fractal analysis and first passage time analysis provide mathematical approaches for exploring the details of habitat use by tracked animals, so that habitat preferences can be identified (e.g. Pinaud & Weimerskirch, 2005; Bailey & Thompson, 2006). One of the great advantages of the high resolution tracks provided by GPS loggers (high accuracy of locations combined with very frequent locations) is that a range of quantitative movement analysis can be performed on the data, with the biological signal not being compromised by artefacts introduced by measurement errors (Bradshaw *et al.*, 2007b). Hence the technology we have introduced here has great utility for tracking a wide range of marine vertebrates that surface to breathe including mammals and birds (C.M. Bishop unpublished). Furthermore, tethered GPS data-loggers may work for those non airbreathing animals (e.g. some fish) that do not surface to breathe but nevertheless come close to the surface.

During our study, while female sea turtles spent the majority of time outside of the no-boating maritime protection zone, a significant proportion of the population nest on one or more of the beaches in this region (Katselidis *et al.*, 2004), and our data indicated that turtles are likely to preferentially frequent the region adjacent to the nesting beach in the days preceding nesting. As a result, this zone remains one of extreme conservation importance. The movement and depth data indicated that female turtles preferentially inhabit very shallow water in areas of submerged sand-banks. These criteria are only found in the two lesser protected boating zones. Our findings clarify that for maritime zones to provide the necessary protection, they should be based on sea turtle key area use (i.e. sea depth, proximity to shore and habitat preference), and not only the location of nesting beaches as has been done until now. While the national park has acted on an existing transect based survey (Schofield *et al.*, 2008c) to form an ‘ecotourism zone’ to improve regulation of turtle-watching activities, our data suggest that this zone needs to be extended by about another 4 km, with the implementation of stronger regulations on marine area use within this region. Since female turtles occupied this zone for over 50% of time, it is important to quantify the impact of all near-shore human activities (including wading, swimming, private boat hire and turtle-watching), as has been done with other marine vertebrate species impacted by humans (Lusseau, 2006).

Turtles spend their time at sea during the breeding season engaged in a variety of activities such as mating, cleaning and resting (Booth & Peters, 1972; Schofield *et al.*, 2006). Resting on the sea bed has been widely reported for hard-shelled turtles including green, loggerhead and hawksbills turtles (Houghton *et al.*, 2002; Seminoff *et al.*, 2002; Hopkins-Murphy *et al.*, 2003; Houghton, 2003). Often female turtles are reported resting at depths of 15 m or less, and this relatively deep resting is reflected in the data provided from TDR deployments. However, in this study it was striking that female loggerhead turtles at the Zakynthos rookery almost never dived to sea bed depths of more than 4 m during May and June. This pattern of shallow diving was seen both in the turtles equipped with GPS loggers and TDRs (n=3) and those carrying only TDRs (n=3). The fact that both groups showed similar patterns of depth utilisation implies that the near-shore movements in shallow water we saw for the three GPS-equipped individuals might occur generally for female loggerhead turtles at this time of year at the Zakynthos rookery. The turtles may be inhabiting regions close to shore to avoid males (Booth & Peters, 1972). However, since turtles appear to selectively change sites on a daily basis and individuals had similar movement patterns, this suggests other processes may drive these near-shore movements.

Our study has demonstrated how GPS tracking can be used to obtain accurate spatio-temporal information about the fine-scale movement patterns of a marine vertebrate, illustrating the value of this technique for wildlife conservation management and improvement of protection measures.

FIGURE & TABLE CAPTIONS

Figure 1. Loggerhead sea turtle following TrackTagTM GPS logger attachment

Figure 2. Histograms of the number of daily GPS locations for each turtle. (a). GPS2, (b). GPS3, (c). GPS4.

Figure 3. Graph showing the difference between GPS logger locations retained with the different filtration methods. (a). all GPS in-water locations, (b). visually erroneous locations filter, (c). speed filter 5 km hour-1 (d). satellite visibility filter >4 (e). Dilution of precision filter <10 (f). hourly positional locations

Figure 4. GPS logger tracks including nesting beach emergence fixes. (a). GPS2, (b). GPS3, (c). GPS4

Figure 5. The cumulative frequency distribution for the distances from shore using hourly GPS logger locations of all three GPS turtles combined (thick solid black line) and each turtle separately. GPS2 fine black line, GPS3 thick grey line, GPS4 fine grey line.

Figure 6. GIS maps showing the hourly GPS logger locations of all three turtles with respect to (a). bathymetry (b). Natura 2000 habitats; submerged sandbanks (orange), reefs (brown) and Neptune's seagrass (pale green) (c). NMPZ maritime protection zones and ecotourism zone (swim 0-200 m from shore, turtle-watching 200-1400 m from shore).

Figure7. Histogram and complementary table (beneath) of TDR data from six sea turtles showing the percentage of shallow pattern of depth utilization. (a). GPS2 solid black bar, (b). GPS3 solid grey bar, (c). GPS 4 solid white bar, (d). TDR1 diagonal grey lined bar, (e). TDR2 horizontal grey lined bar, (f). TDR3 diagonal black lined bar.

Figure 8. The cumulative frequency distribution for the distances apart of GPS2 and GPS3 turtles measured every 3 h between 24/5/2006 and 6/6/2006 (dashed line) and modelled turtles moving within the bay following random walk models. Thick solid grey line = random walk model 1, thick black solid line = random walk model 2. The observed distribution differed significantly from both random walk models (Kolmogorov-Smirnov tests, $D = 0.4245$, $P < 0.001$ and $D = 0.5031$, $P < 0.001$ respectively)

Table 1. Presentation of TrackTagTM GPS logger locations acquired and those remaining following filtration. (CCL = curved carapace length of turtle, CCW* = curved carapace width of turtle)*

Appendix 5: A video animation showing the day by day movements of the three turtles with GPS loggers from attachment to retrieval (applying the Maptool program, www.seaturtle.org *) (Animated gif).*

Figure 1. Loggerhead sea turtle following TrackTagTM GPS logger attachment

Figure 2. Histograms of the number of daily GPS locations for each turtle. (a). GPS2, (b). GPS3, (c). GPS4.

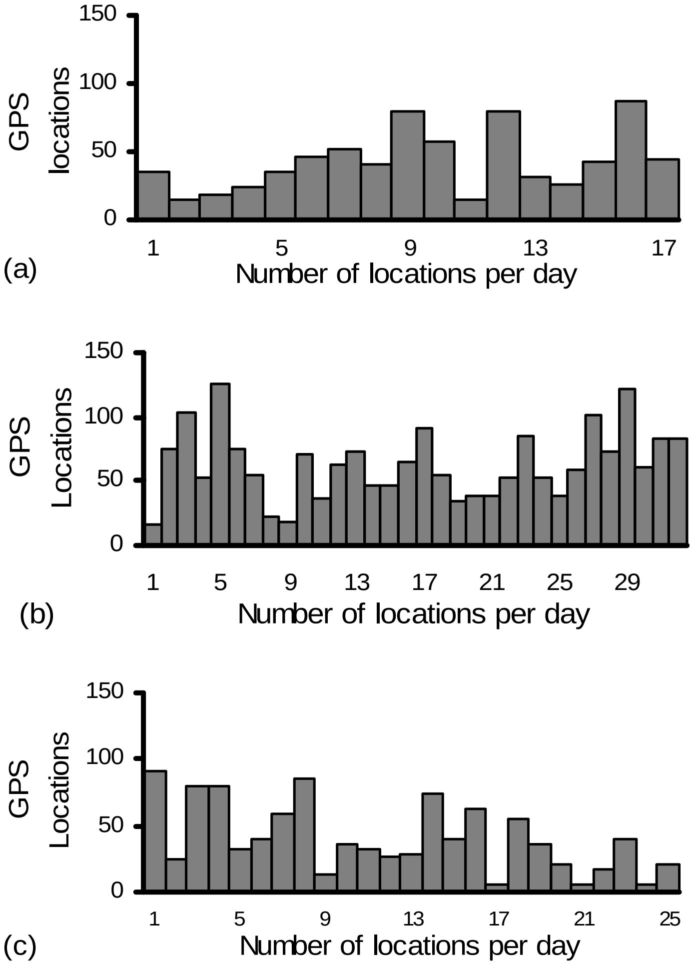


Figure 3. Graph showing the difference between GPS logger locations retained with the different filtration methods. (a). all GPS in-water locations, (b). visually erroneous locations filter, (c). speed filter 5 km $hour^{-1}$ (d). satellite visibility filter >4 (e). Dilution of precision filter <10 (f). hourly positional locations

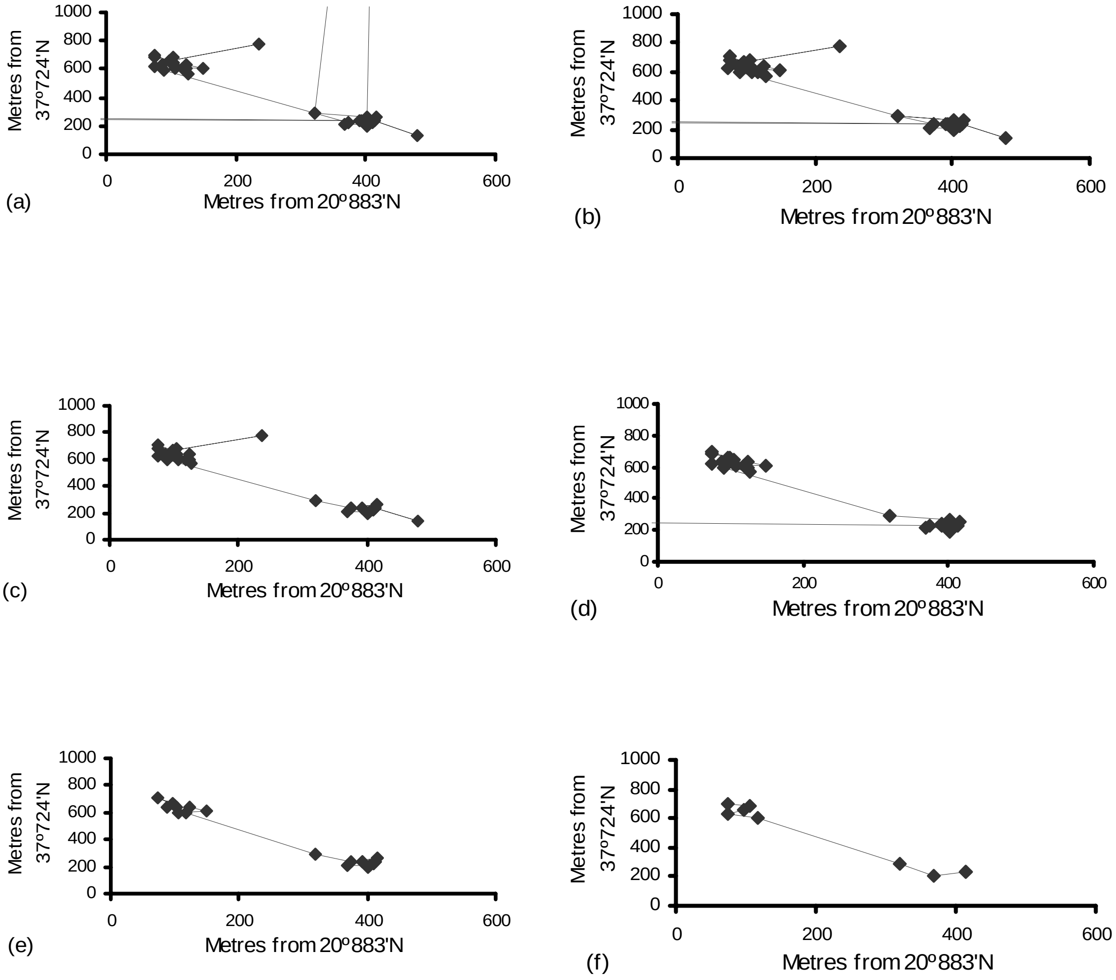


Figure 4. GPS logger tracks including nesting beach emergence fixes. (a). GPS2, (b). GPS3, (c). GPS4

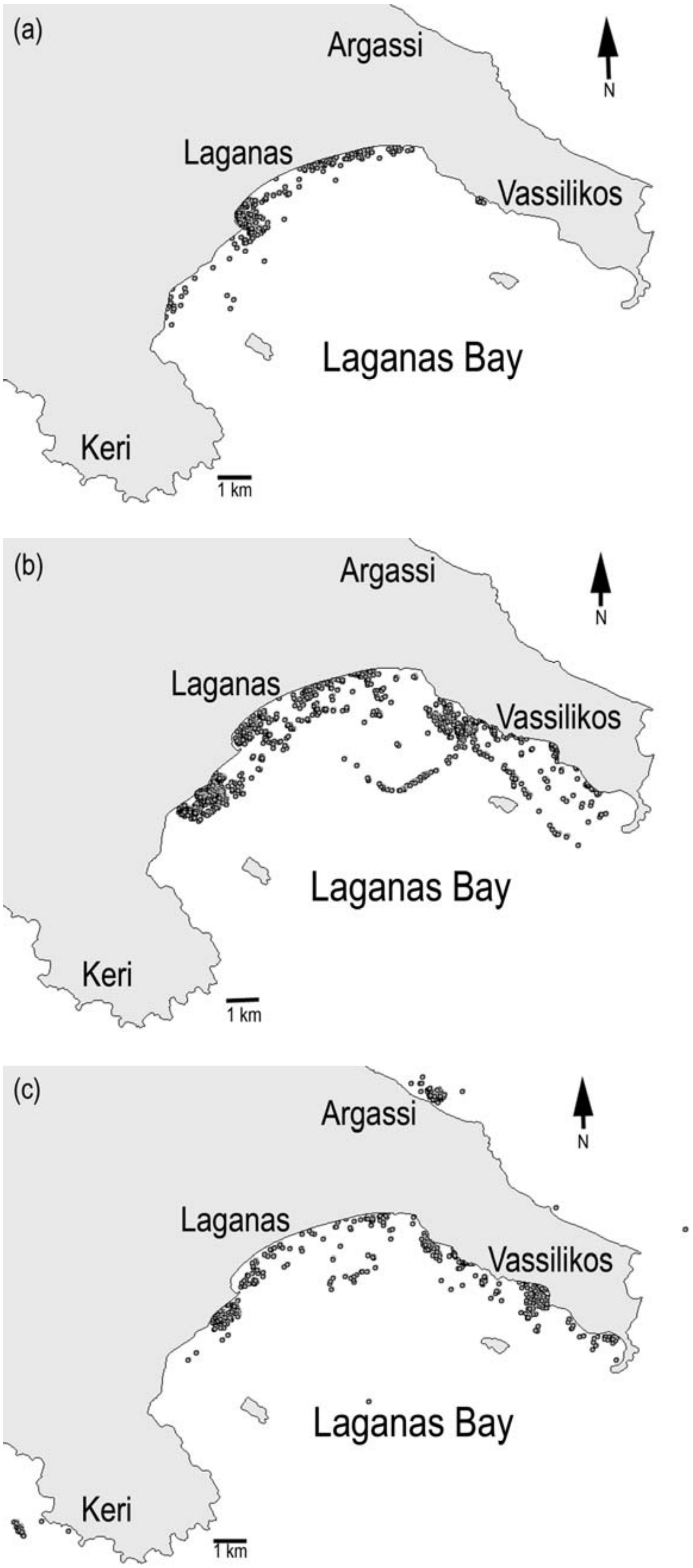


Figure 5. The cumulative frequency distribution for the distances from shore using hourly GPS logger locations of all three GPS turtles combined (thick solid black line) and each turtle separately. GPS2 fine black line, GPS3 thick grey line, GPS4 fine grey line.

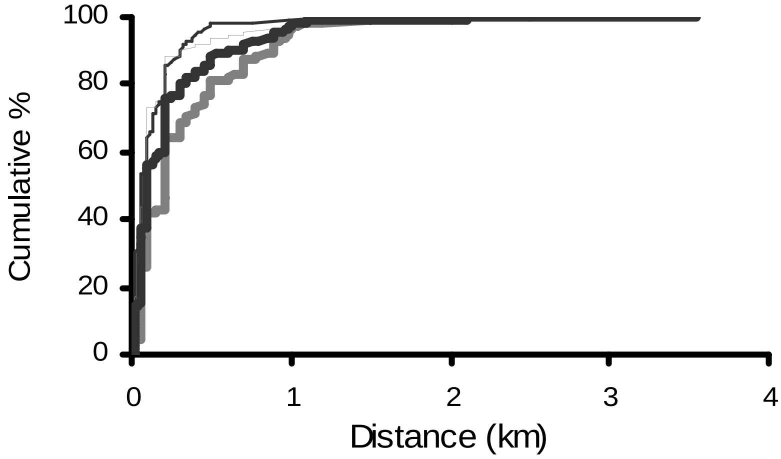
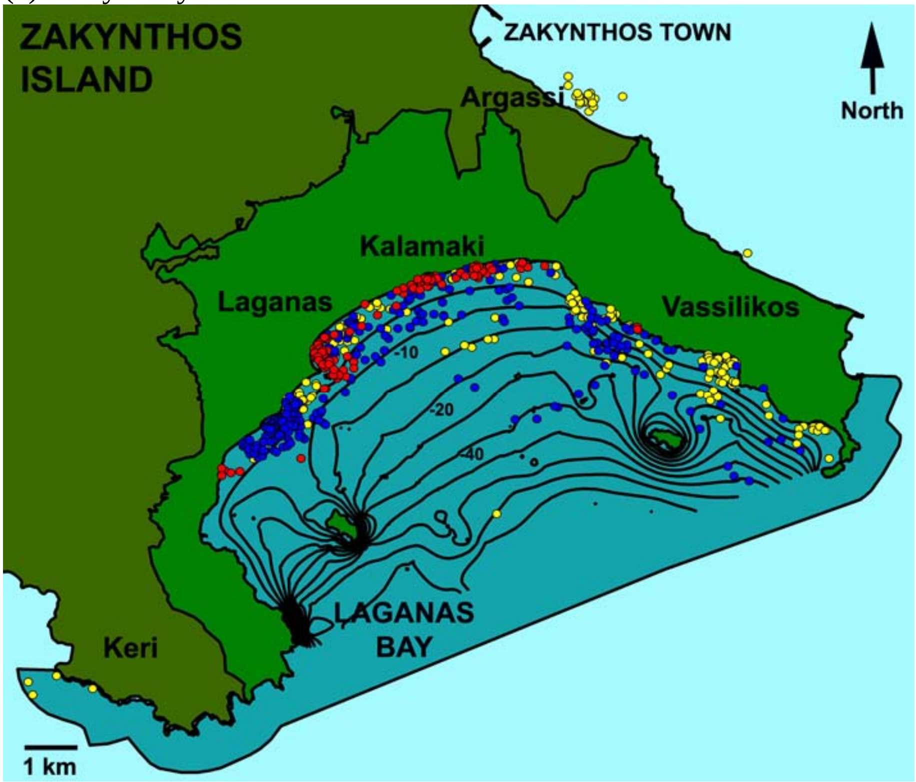
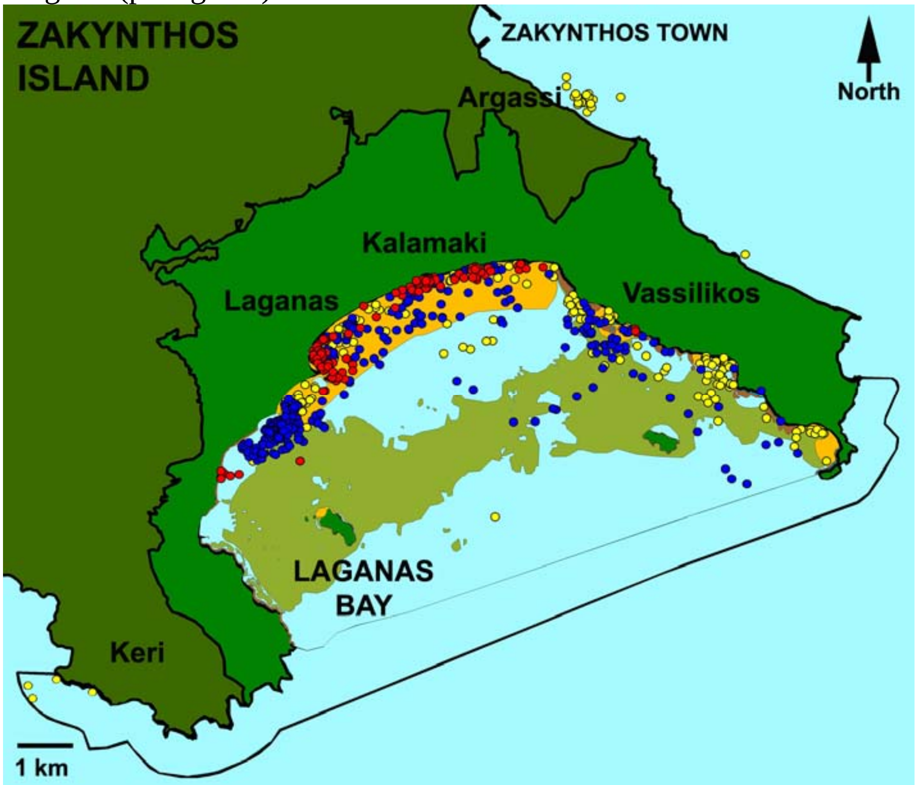


Figure 6. GIS maps showing the hourly GPS logger locations of all three turtles with respect to:

(a) bathymetry



(b) Natura 2000 habitats; submerged sandbanks (orange), reefs (brown) and Neptune's seagrass (pale green)



(c). NMPZ maritime protection and ecotourism zone (swim 0-200 m from shore, turtle-watching 200-1400 m from shore).

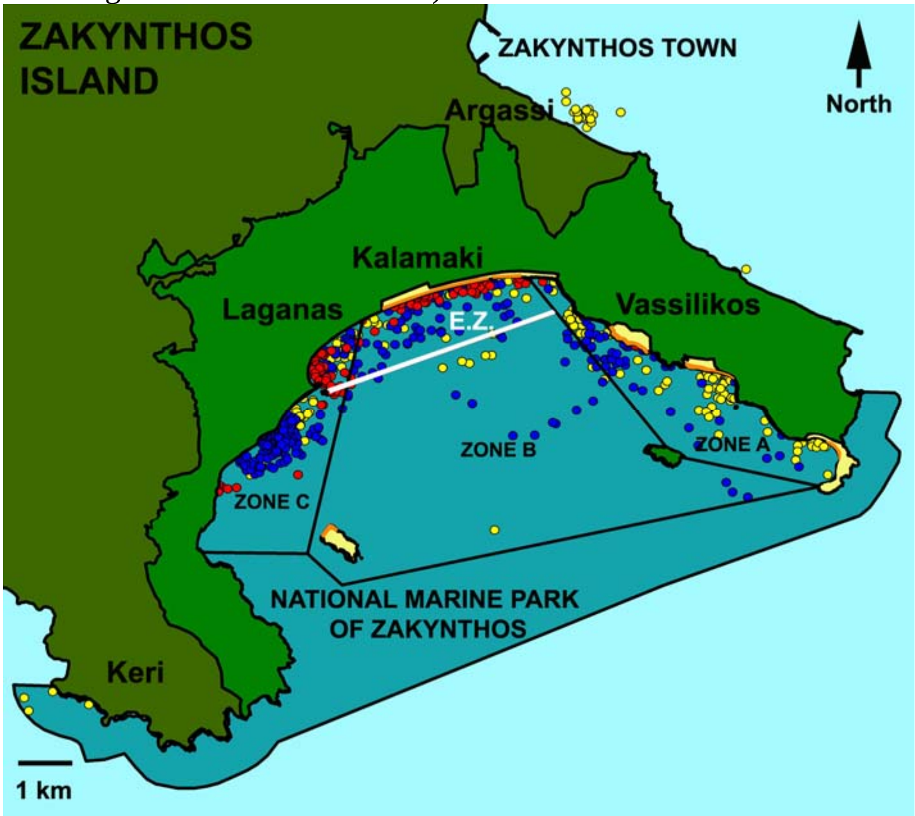
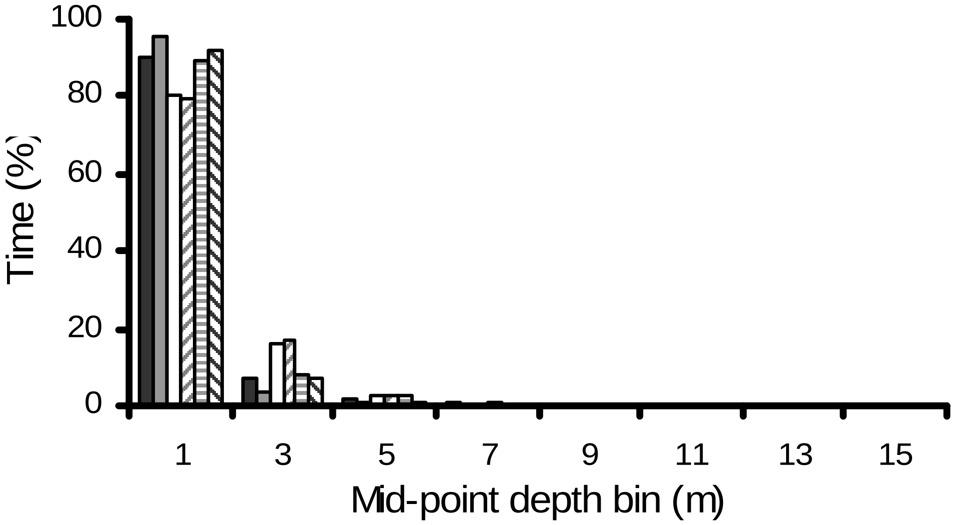


Figure 7. Histogram and complementary table (beneath) of TDR data from six sea turtles showing the percentage of shallow pattern of depth utilization. (a). GPS2 solid black bar, (b). GPS3 solid grey bar, (c). GPS 4 solid white bar, (d). TDR1 diagonal grey lined bar, (e). TDR2 horizontal grey lined bar, (f). TDR3 diagonal black lined bar.



	Percent of time at mid-point depth bin / metres				
Animal id	1	3	5	7	11
GPS2	89.92	7.12	2.05	0.74	0.01
GPS3	95.34	3.42	1.21	0.02	0
GPS4	80.75	16.03	3.05	0.15	0.01
TDR1	79.69	16.68	2.80	0.46	0.12
TDR2	89.23	7.99	2.61	0.12	0.02
TDR3	91.89	7.39	0.57	0.14	0

Figure 8. The cumulative frequency distribution for the distances apart of GPS2 and GPS3 turtles measured every 3 h between 24/5/2006 and 6/6/2006 (dashed line) and modelled turtles moving within the bay following random walk models. Thick solid grey line = random walk model 1, thick black solid line = random walk model 2. The observed distribution differed significantly from both random walk models (Kolmogorov-Smirnov tests, D = 0.4245, P < 0.001 and D = 0.5031, P < 0.001 respectively)

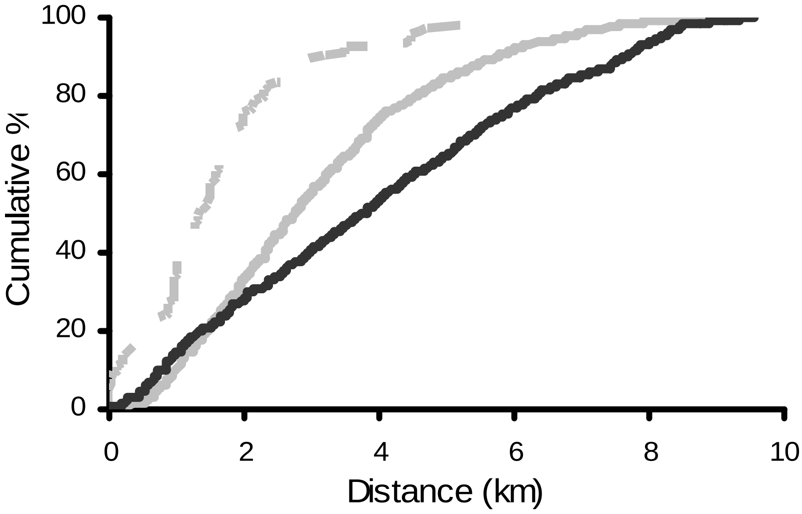


Table 1. Presentation of TrackTagTM GPS logger locations acquired and those remaining following filtration. (CCL* = curved carapace length of turtle, CCW* = curved carapace width of turtle)

GPS logger	**Turtle parameters**		**GPS logger information**			**Full no. days attached**	**All GPS locations**		*Locations removed*	**In-water GPS locations**		***Filtering processes of in-water locations***									
												Visually erroneous		**Speed**		**SV**		**DOP**		**Hourly**	
	CCL* /cm	CCW* /cm	Date attached	Date retrieved	Date of nesting		Total	*av. fix/ day*	*Nesting beach*	Total	*av. fix/ day*	Total	*av. fix/ day*	Total	*av. fix/ day*	Total	*av. fix/ day*	Total	*av. fix/ day*	Total	*av. fix/ day*
GPS 2	81	73,5	19/5/2006	6/6/2006	31/5/2006	17	1076	*63*	*214*	862	*51*	*734*	*43*	519	*31*	721	*34*	437	*21*	181	10
GPS 3	89	76	23/5/2006	26/6/2006	25/6/2006	31	3077	*99*	*817*	2260	*73*	*2007*	*65*	2189	*69*	1761	*57*	1160	*37*	479	15
GPS 4	87	72	24/5/2006	18/6/2006	7/6/2006	25	1335	*53*	*247*	1088	*44*	*1012*	*40*	818	*33*	907	*36*	588	*24*	266	11
						73	**5488**	***75***	*1278*	**4210**	***58***	***3753***	***51***	**3526**	***48***	**3389**	***46***	**2185**	***30***	**926**	**13**

ΚΕΦΑΛΑΙΟ / CHAPTER 5. Conservation implications of intense spatial area use by breeding male and female loggerheads at the Mediterranean's largest rookery

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Peer-reviewed journal citation (manuscript in Appendix 3):
Schofield, G., *M.K.S. Lilley, C.M. Bishop, P. Brown, K.A. Katselidis, P. Dimopoulos, J.D. Pantis, G.C. Hays. 2009. Conservation hotspots: intense space use by breeding male and female loggerheads at the Mediterranean's largest rookery.Endangered species research. doi: 10.3354/esr00137*

INTRODUCTION

Effective conservation management of wide ranging marine vertebrates requires quantitative information at both a local and regional level (Hyrenbach *et al.*, 2000). In recent decades satellite telemetry has facilitated the tracking of wildlife movement over thousands of kilometres. Invaluable information has been provided on migratory corridors and the essential resources that they link, such as reproductive and foraging grounds (Morreale *et al.*, 1996; Sheppard *et al.*, 2006; Rasmussen *et al.*, 2007; Zbinden *et al.*, 2008). While such corridors are rarely protected, partly due to their often traversing political borders, the prime resource sites which they connect may meet 'siting' criteria for inclusion within national protected area management schemes (Gardenfors, 2001; Campbell, 2007; Lawton, 2007; Wood & Dragicevic, 2007). To formulate effective protective zoning and associated conservation legislation and policies, objective and quantitative evidence is required with respect to key species habitat preferences and core area use within such sites (Sutherland *et al.*, 2004; Togridou *et al.*, 2006a). This is of particular consequence in coastal zones where increasing levels of human settlement, leisure and fishing activities may already be placing pressure on endangered species populations and the natural resources on which they depend (Martien *et al.*, 1999; Zbinden *et al.*, 2007a). However, conventional satellite transmitters provide only fairly coarse spatial resolution and are primarily useful in documenting broad-scale movements (Hays *et al.*, 2001a). Recently, tracking units based on GPS technology have become available to wildlife researchers, with an accuracy of metres (Hulbert & French, 2001). For this reason, GPS technology is an increasingly important tool to quantitatively address the conservation management requirements of wide ranging terrestrial and marine species both within and between the reserves designated to protect them (Ryan *et al.*, 2004; Douglas-Hamilton *et al.*, 2005; Schofield *et al.*, 2007a)

For the globally endangered sea turtle species', much information is now available on the periodic broad-scale movements of adult females as they migrate between nesting and foraging areas, which is usually derived from Argos satellite transmitters (e.g. Luschi *et al.*, 2003; James *et al.*, 2005b; Broderick *et al.*, 2007; Zbinden *et al.*, 2008).

Habitat use within breeding and foraging areas has been inferred using mark-recapture, radio, sonic and/or satellite telemetry (van Dam & Diez, 1998; Hopkins-Murphy *et al.*, 2003; Zbinden *et al.*, 2007a), and more recently GPS units (Yasuda & Arai, 2005; Schofield *et al.*, 2007a). However there remains a bias towards female oriented research because they come ashore to nest, providing an easy opportunity to attach tracking equipment. At temperate breeding areas, satellite and sonic telemetry studies of female loggerheads indicate use of sea bed depths of within 15 m (Hopkins-Murphy *et al.*, 2003; Zbinden *et al.*, 2007a), and recent GPS tracking indicates possible use of depths as shallow as <4 m (Schofield *et al.*, 2007a).

In comparison to females, far less is known about male turtle movement patterns (but see Limpus, 1993; Plotkin *et al.*, 1996; Hays *et al.*, 2001b; James *et al.*, 2005a; Shaver *et al.*, 2005b), due to the necessity for inwater capture which requires high levels of physical and search effort (Ehrhart & Ogren, 1999). Existing research indicates that males may occupy sea depth of up to 40 m at breeding grounds (Shaver *et al.*, 2005a), and following a protracted mating period appear to exhibit similar migration patterns to adult female conspecifics (for overview see Sakamoto *et al.*, 1997; Godley *et al.*, 2008). To objectively determine whether existing or suggested protection measures at local (i.e. within a national park or reserve), national and regional level is appropriate, high resolution tracking of all segments of the population actively using the area are required (Seminoff *et al.*, 2002). Furthermore, in the Mediterranean sea turtle foraging areas remain largely absent of protective legislation (Zbinden *et al.*, 2008), hence confirmation of the use of certain areas by both adult males and females following migration from breeding areas may contribute towards providing evidence supporting the establishment of much needed protection sites.

The island of Zakynthos, Greece hosts the largest known breeding population of loggerheads in the Mediterranean (Margaritoulis, 2005). Several hundred loggerhead turtles enter Laganas Bay at the southern part of Zakynthos to breed from mid-April onwards (Schofield *et al.*, 2006), and female turtles generally nest from late-May until early-August, with an average of 1300 clutches per season (Margaritoulis, 2005). Existing marine protection zones were delineated based on nesting beach locations and relative nesting densities (Arapis & Margaritoulis, 1996). Since the formation of the National Marine Park of Zakynthos in 2000, regulation of recreational nearshore activities (particularly organised and incidental turtle watching activities) has been strengthened, however for new legislation to be passed accurate information on marine area use by adult male and female turtles are essential. During in-water surveys to assess turtle distribution and behaviour between 2003-2005 (Schofield *et al.*, 2006; Schofield *et al.*, 2008b), we noted a strong bias towards female sightings (n = 80 male, n = 1335 female), and accredited this at the time to differential spatial use by males and females in Laganas Bay. Preliminary research using highly accurate GPS TrackTag loggers indicates that female turtles primarily utilise 18.5 km of nearshore coastline at seabed depths of <5 m (or up to 1 km distance from shore) (Schofield *et al.*, 2007a), however it was not known whether males exhibited similar behavioural movement patterns.

The aim of our study is to investigate the fine scale movement of male and female loggerhead turtles (*Caretta caretta*) within a major breeding rookery using GPS tracking units. We also assess the departure of males from the breeding grounds and identify the location of foraging sites. We consider how our data might be applied towards contributing to sea turtle conservation measures, policies and legislation at a local and regional scale. At the local scale we evaluate the status of protection measures in the National Marine Park of Zakynthos, while at the regional scale we contribute information for protection across international borders of male sea turtles through linking breeding and foraging areas.

MATERIALS AND METHODS

Tracking units & turtle capture technique

During 2006 and 2007 GPS tracking units were placed on adult male and female loggerheads; GPS transmitters were placed on males due to the low likelihood of resighting for data retrieval while GPS loggers were placed on females with a high likelihood of resighting due to their nesting at least 3 times per breeding season (see

Zbinden *et al.*, 2007a). In 2006 and 2007, TrackTag^{TM} GPS loggers (Navsys Ltd, Edinburgh UK, http://www.navsys.com) were deployed onto four and five adult female loggerhead turtles (curved carapace lengths 77-89 cm) respectively, during the pre-nesting period in May and removed during the inter-nesting period in June (see Schofield et al., 2007 for detailed logger information). In two cases (one in each year) loggers malfunctioned due to deployment problems so that no data were collected. In 2007 four Fastloc GPS-Argos tags (Sirtrack Ltd, Havelock North New Zealand, http://www.sirtrack.com) and one conventional Kiwisat 101 PTT Argos unit (Sirtrack Ltd) were deployed onto males (curved carapace lengths 79-91 cm). The Fastloc GPS-Argos transmitters relayed GPS information remotely via the Argos system. In addition the Fastloc data was stored on-board so that in the event of instrument recovery all the acquired Fastloc-GPS data could be downloaded directly to a computer. One coat of antifoulant was painted on all Sirtrack units.

Navsys estimate the accuracy of TrackTag locations to be around 30 m (2dRMS) for 95% of locations recorded using a horizontal and stationary receiver in the UK. Fastloc units have an accuracy of 55 m in 95% of locations recorded and 20 m in 50% of locations recorded (Sirtrack Fastloc webpage http://www.sirtrack.com). The conventional Argos unit accuracy is categorised by location classes (LC); LC 3, LC 2, LC 1 or LC 0 locations which are classified as within 150 m, >150-350 m, >350-1000 m or >1000 m respectively. Locations classified as classes A and B have ill defined, but probably poor accuracy (particularly LC B) (Hays *et al.*, 2001a).

A 4 m research boat was used to find turtles at water depths of 1 to 7 m. Turtles were captured at random along the central 12 km stretch of coastal waters over submerged sandbanks only (for safety reasons) using the turtle-rodeo technique (Ehrhart & Ogren, 1999), and were swum into a semi-submerged wooden box attached to the side of the boat (Figure 1a). Following capture, the curved carapace length was measured and then a GPS logger/transmitter was attached using a standard method which we have employed before with various transmitters/loggers (Hays *et al.*, 2003a). In brief, the carapace was cleaned and then the logger embedded in quick setting two-part epoxy resin (Powerfastners Inc., New Rochelle, NY, USA) with wooden baffles positioned at the anterior to help prevent impacts to the equipment (Figure 1b & 1c). The reproductively active status of the captured individuals was determined through in-water observation of courtship and mating activity. The attachment of all devices was conducted under licenses from the Greek Ministry of Agriculture. All GPS loggers and one GPS transmitter were retrieved from the animals by one of two methods, (i) using the rodeo capture technique or (ii) by recovery on the beach immediately following nesting.

Data analysis

All GPS transmitter and logger locations were first plotted to allow a quick initial visual inspection. The data were filtered by (i) subjectively removing visually erroneous locations (i.e. on land or spatially different fixes to previous and successive fixes within the same timeframe), (ii) using a maximum rate of travel of five km hour^{-1} between successive locations (Hays *et al.*, 2004a) which was selected based on calculations from 3 or more consecutive fixes occurring at 10-20 minute intervals and (iii) removing data when the turtles were onshore (nesting and/or aborted nesting attempts). We then calculated the mean GPS location per hour for each turtle (Tremblay *et al.*, 2006). We calculated the daily mean location of each turtle from the hourly datasets, from which the daily distance from shore of different turtles was calculated. We divided the 27.8 km coastline of Laganas Bay into three equal nine km coastline sections (the eastern, middle and western section), and used hourly datasets to determine general area use. Note the eastern section of coastline falls in the highly protected no-boating park zone while the eastern and middle sections fall in the low protected zones where boating is permitted. An estimate of migratory distance for the males was calculated by summing up distance travelled between daily locations. A measure of directness of the route was obtained by dividing the distance travelled by the displacement (i.e. the straight-line distance between the breeding and foraging area). For the data from the conventional Argos PTT unit, locations were filtered using a maximum rate of travel of 5km hour^{-1} between successive locations (Hays *et al.*, 2004a).

In order to correlate male departure times with respect to the onset of nesting, information on the daily nest number in 2007 was obtained from the National Marine

Park of Zakynthos for all beaches in Laganas Bay. The number of new nests from the previous night was assessed from tracks. The mean date of nesting for 2007 (3 July, day of year: 184) was determined by:

$$\text{Mean date of season} = \frac{\Sigma\, x f}{\Sigma\, f}$$

where x = day of year and f = number of nests. The nesting 'peak' described the date at which the greatest number of nests were recorded (27 June, day of year: 178).

The mean date at which the transition between the pre-nesting (phase prior to the first nesting event) and internesting (phase between first and last nesting events) period occurred was calculated from the first nesting event for each female from the GPS datasets (Table 1). This was identified when locations were being consistently recorded at 30 second intervals for a minimum of 30 minutes, indicating that the turtle was on land. If more than one event was recorded in a five day period, the last event was selected as the successful nesting event, with the preceding events being recorded as non-nesting emergences. Subsequent nesting events were also identified in five of the tracked turtles, and this information was used to calculate internesting intervals. For correlation with the dataset of the male that remained in the breeding area, we also separated the two periods by identifying the date from which nests were recorded daily thereafter. In 2006 and 2007 the first nest was laid on 29 May (day of year: 149) and 17 May (day of year: 137) respectively, with regular daily nesting being recorded from 29 May (day of year: 149) and 1 June (day of year: 152) onwards respectively.

Near-shore surveys

In the current study we revisit the in-water sea turtle distribution and behaviour datasets from 2003 when the most robust surveys were conducted by boat (Schofield *et al.*, 2006; Schofield *et al.*, 2008b). On 27 fair weather days from 14 April to 31 May 2003, daily line transects were made at seabed depths of 3 m, 5 m, 7 m and 10 m (i.e. up to one km from shore) along a 5.5 km stretch of nearshore coastline within Laganas Bay (for map see Schofield et al., 2006). Boat surveys (405 km, 137 h) were conducted by two to three observers on a 4 m boat with an outboard engine. Sessions lasted an average of 5 h (minimum 4, maximum 7 h) at a maximum boat speed of four knots h^{-1}. The survey period covered a range of daylight hours between 09:30 and 19:30. GPS locations of turtle sightings were recorded using Garmin E-Trex hand-held units and stills-photographs were taken underwater when snorkelling at a distance of 2-7 m from the target animal using an Olympus Digital 500 (5.0 megapixel) camera with underwater housing. Animal gender was determined based on tail-length dimorphism (Casale *et al.*, 2005) and presence/absence of external identification-tags (only females are tagged).

We used the natural scalation patterns on the lateral facial region to identify individual turtles. The accuracy of the technique was validated by assessing the ability to match ‘known’ turtles, i.e. individuals with existing external identification-tags, which accounted for 58% of profiled female turtles. An accuracy of 98% was obtained, with difficulty arising in low quality images or when the turtle was positioned at an awkward angle to the camera.

RESULTS

Tracking data

Excluding deployment and retrieval days, we tracked three female turtles equipped with TrackTag GPS loggers in 2006 and 2007 for a mean 34 days each (range 17-52 days). The four males equipped with Fastloc GPS-Argos transmitters were tracked for a mean 29 days each (range 3-51 days). The one male equipped with a conventional Argos transmitter was tracked for 128 days (Table 1). The volume of useable locations obtained from the different devices (TrackTag GPS loggers, unretrieved Fastloc GPS-Argos transmitters, retrieved Fastloc GPS-Argos transmitter and conventional Argos satellite transmitter are presented in Table 1. The retrieved TrackTag loggers and Fastloc transmitter provided a much greater volume of data compared to that relayed via Argos. As expected given their greater accuracy, all GPS units provided very detailed information on sea turtle area use, in contrast to the conventional Argos unit from which only the general location of the turtle could be inferred (Figure 2a & b).

Male and female area use in the breeding area

The data from the GPS units (loggers and transmitters) indicated that both male and female turtles primarily used the marine area close to shore (from hourly positional datasets) (Figure 2a & Appendix 5). Before and after the onset of nesting, 82% of all seven female GPS locations in Laganas Bay occurred within 500 m of the shore (Figure 3a) (approx. seabed depth <5 m). In the pre-nesting period, 92% of all four male GPS locations also occurred within 500 m of the shore in Laganas Bay (Figure 3b).

The GPS units not only indicated this nearshore preference, but also that the tracked males and females appear to preferentially use certain stretches of coastline within Laganas Bay. We found that before the onset of nesting, 100% of male GPS locations and 77% of female GPS locations occurred along the middle section of coastline. Only one GPS-tracked male remained in Laganas Bay following the onset of the nesting season and appeared to restrict all its activity to the middle section of coastline before and after the onset of nesting. Of the seven tracked females, activity was confined within Laganas Bay before the onset of nesting (99% of GPS locations), with some movement out of Laganas Bay occurring after the nesting season had started in June (79% of GPS locations in Laganas Bay).

After the onset of nesting, females continued to preferentially frequent the middle section of coastline (54% of GPS locations). Before and after the onset of nesting, 21% of female GPS locations occurred along the eastern section of coastline (containing three nesting-beaches representing 70% of rookery nesting effort), which appeared to be associated with nesting-activity with turtles in general moving to this section of coastline three to five days before nesting. Just 0.2% of female GPS locations occurred in the western section of coastline.

Female movement in the vicinity of the breeding area

Of the seven females tracked using GPS loggers, four remained in Laganas Bay before and after the onset of nesting. Three turtles exited Laganas Bay on six occasions. One turtle in 2006 exited Laganas Bay on two occasions, frequenting the island’s west-coast for one day during the pre-nesting period and the island’s east-coast for four days following the first nesting event. In 2007, one turtle exited Laganas Bay on one occasion during the internesting period and occupied the east-coast for four days. One turtle exited Laganas Bay on three occasions prior to the first nesting to the east-coast for one day on each occasion. The day following the first nesting (indicated by the GPS data), the same turtle travelled 96 km to Kyparissia Bay in the Peleponesse for a 15 day period (Figure 4); travelling for four days directly to the Peleponesse, remaining for eight days and returning over three days. Five days later the turtle nested again on Zakynthos, with an internesting interval of 20 days. It is unlikely that the turtle nested when in Kyparissia, as no locations were continuously recorded at 30 second intervals to indicate the turtle was out of water, and we also documented a mean internesting interval of 17 days (SD ± 3.3) in five of the tracked turtles.

Male movement following the onset of the nesting season

Males departed from the breeding grounds of Laganas Bay between 14 and 23 May (Table 1), which averaged three days after the first recorded nest (17 May, day of year 137), 12 days before the start of regular nesting activity (1 June, day of year 152), 38 days before the nesting peak (27 June, day of year 178) and 44 days before the mean date of peak nesting (3 July, day of year 183) (Figure 5).

Four of the males departed in disparate directions; two departed in a south-easterly direction, one in a south-westerly direction and one in a north-westerly direction (Figure 6a). One male remained in Laganas Bay and was last sighted on the 27 August (when the Fastloc GPS-Argos transmitter was retrieved), still inhabiting the same nearshore section.

Two males were tracked to their foraging areas (Figure 6b). The male with the Fastloc GPS-Argos transmitter swam to a foraging area between the islands of Olib and Silba in

Croatia, 721 km north of the nesting area. It travelled a total distance of 762 km over 21 days, and was recorded to arrive at the foraging grounds on 12 June, remaining until 30 June when transmissions terminated. The male equipped with the conventional Argos transmitter swam to a foraging area in the Bay of Izmir in Turkey, 597 km north east of the nesting area. The turtle travelled a total distance of 927 km (calculated from daily mean locations) to reach the foraging area over an 18 day period, and was recorded to arrive on 10 June and was still transmitting from the same vicinity on 12 September.

Of interest, the male that remained in Laganas Bay changed its spatial area use in the periods before and after the onset of nesting activity from mainly within 500 m to more than 500 m from shore (Figure 3b).

Population parameters

In the current study we combine the results of the in-water surveys with turtle GPS locations information to calculate an operational sex-ratio for the breeding area. We crudely estimated the mean female seasonal breeding population size to be 463 individuals by dividing the mean number of nests recorded between 1984 and 2002 (1293.7 nests; Margaritoulis, 2005) with an estimated mean clutch frequency of three (based on information from Jensen *et al.*, 2006; Zbinden *et al.*, 2007a).

During 2003, photographic records were collected at a total 460 loggerhead sightings, across 27 surveys in April and May. From these records, we identified 38 unique males and 127 unique females, with an average resighting rate of three times per individual across surveys. From this information we calculated a 76.7% female bias (1 male to 3.3 females) in the operational sex ratio. We also recorded the average sex-ratio in each field survey and found a significant temporal change in sex-ratio across the survey period, from 66.7% male bias (2 males to 1 female) in April to a 90% female bias (1 male to 9 females) in late May ($F_{1,22} = 71.3$, $r^2 = 0.75$, $p < 0.001$) (Figure 7).

The GPS tracks from our 11 male and female turtles indicated that 100% of male and 77% of female hourly locations occurred along the middle nine km of coastline during May. Therefore the Zakynthos seasonal operational sex ratio recorded in 2003 may be representative of the population. We combined the sex-ratio data with the mean female seasonal population size, to predict a total mean seasonal population size of about 593 individuals; 130 males and 463 females. If sea turtle densities were uniform across Laganas Bay, there would be 5.3 turtles/km^2. However, based on our GPS data, if 100% males and 77% females utilise nine km^2 nearshore area during May, we would expect densities of 54 turtles/km^2.

DISCUSSION

The combined fine-scale movement patterns recorded for male and female loggerhead turtles in this study provide information on critical habitat use to guide management decisions fundamental to their conservation.

Our data strongly indicated that before the onset of nesting both males and females use the same nearshore area, along a specific nine km stretch of coastline and primarily within 500 m of shore (or within 5 m sea depths) in Laganas Bay. These observations support existing work in which females use sea depths up to 15 m when in the breeding area (Hopkins-Murphy *et al.*, 2003), however our results indicate a much narrower area use by males than previously recorded sea depths of up to 40 m (Shaver *et al.*, 2005b). One of the tracked males remained in the breeding area, with a noticeable shift in sea depth use to deeper water following the onset of nesting. This shift may have reflected a change in the status of a resident, i.e. from breeding to foraging, and may explain the greater depth range recorded for males in other breeding areas (Shaver *et al.*, 2005b).

Our observations suggest it is unlikely that females are successfully using the nearshore habitat as a refuge from males following mating (Booth & Peters, 1972; Whittow & Balazs, 1982). For example, females maintained the same pattern of nearshore habitat use in the first month following the onset of nesting, despite the fact that most males had migrated out of the breeding area by this time. The reason why females prefer nearshore water during this period remains obscure, however males may be found close to shore because they follow the females to maximise their mating opportunities. By restricting area use, females may conserve energy expenditure during the reproductive season when they may lay several clutches across several months (Hays *et al.*, 1999; Wallace *et al.*, 2005). Furthermore, as turtles utilising the nearshore area of Laganas Bay have been found to experience water temperatures around 5ºC above the that in waters >10 m depth (Schofield *et al.*, 2008a), which would decrease the duration between nestings (Sato *et al.*, 1998; Hays *et al.*, 2002a) and would therefore be energetically beneficial. In 2006 one of the three tracked turtles utilised waters outside of Laganas Bay (Schofield *et al.*, 2007a), and was not discussed due to the small sample size and probability of this being anomalous for this population (see Zbinden *et al.*, 2007a). However, the results of the 2006 and 2007 tracking data indicated that several of the tracked females moved at spatial scales beyond the main breeding, which is consistent with previous suggestions that loggerheads may show poorer beach fidelity (Stoneburner, 1982; Hays & Sutherland, 1991; Katselidis *et al.*, 2004) than other sea turtle species (Mortimer & Portier, 1989). The discrepancy in observations between Zbinden et al (2007a) and our study in the same breeding area, may be attributed to the former study recording movement in late June to August and the latter study recording movement in May to late June, possibly indicating change in behavioural patterns across the nesting period. The level of internesting movement may depend on the habitat needs of each species, such as foraging in leatherbacks (Georges *et al.*, 2007), or possibly prospecting alternative nesting sites in loggerheads. This suggestion is supported by the fact that nesting activity does occur on the east coast of Zakynthos and Peleponesse where the turtles in our study were recorded. If these broad-scale movements occur regularly within the population, then current protective measures of the Zakynthos breeding area may require re-evaluation.

The use of GPS tracking in this study, defined the fine-scale habitat use by both males and females of the sea turtle breeding population and, therefore the critical site in which heightened protection measures are required (Sutherland *et al.*, 2004; Wood & Dragicevic, 2007). Our research was conducted in collaboration with the National Park Authority on Zakynthos to evaluate the effectiveness of existing protective zoning. Of management interest, GPS tracking of females in 2006 and 2007 indicated preferential nearshore area use outside of the core marine protected area, with similar patterns being recorded in tracked males. Our findings support the experimental introduction of the national park 'ecotourism zone' in 2006 to reduce disturbance to turtles through strengthened boating regulations (Lusseau, 2004), and expansion to include the prime section of coastline used by both sexes. However, governmental legislative action is required to reform existing zones, which is difficult to secure (Togridou *et al.*, 2006a; Campbell, 2007; Lawton, 2007). Our study also indicated the possible presence of resident turtles, hence research to determine winter area use around Zakynthos is important to improve protection measures particularly with respect to the fishery industry bycatch (Martien *et al.*, 1999). With the advent of GPS tracking facilitating fine-scale analysis of wildlife movement patterns, we strongly recommend its use in the delineation of protection zones to ensure the habitat requirements of the species are met (Martien *et al.*, 1999; Sutherland *et al.*, 2004; James *et al.*, 2005b).

Climate change may impact turtle population dynamics, hence an understanding of sex ratios at different life stages is vital towards effective protection At the Zakynthos rookery, we inferred a highly female-biased adult sex-ratio using our photo-identification and GPS tracking information. Highly skewed female sex-ratios of 60-99% have already been documented for loggerhead hatchlings in the Mediterranean (see Zbinden *et al.*, 2007b for overview) and other populations around the world (Mrosovsky & Provancha, 1989; Marcovaldi *et al.*, 1997). Studies of juveniles indicate that skewed ratios may be balanced by males originating elsewhere (Henwood, 1987), though this may be as a result of sex-related dispersal (Casale *et al.*, 2006). The nearshore use by both sexes shown in our GPS tracking study, indicated that the 77% female bias recorded during in-water surveys in 2003 (Schofield *et al.*, 2006) may not be the result of nearshore sampling bias. While we combined in-water surveys and GPS data from different years, the tracking data of females across two years strongly indicated that the pattern of movement was similar. Estimates of total population numbers and sex-ratios depend on recruitment-rates and the return-rates of both males and females; females are believed to return bi-annually (Hays & Sutherland, 1991) and data from Australia suggest annual return-rates in males (Chaloupka & Limpus, 2001). If this is the case an 85% female bias may exist in the total adult population, which is similar to the 75% female bias in hatchling sex ratios predicted by Zbinden et al. (2007b) on Zakynthos.

We found that sea turtle density in the breeding area may be ten-times greater than expected, based on an estimate of seasonal population size combined with our observed sex-ratio data. This high density arises because our GPS data show that sea turtles primarily aggregate along 9km^2 of coastline, rather than uniformly using the 89km^2 area of Laganas Bay. Hence, this area should be the first priority for the management plan and legislation of the National Marine Park of Zakynthos. It should be noted that for the purposes of these calculations we used a clutch-frequency of three, however this number is highly variable within loggerhead populations and requires confirmation (Dodd, 1988). The high density of turtles may explain the unusually high multiple paternity recorded at the Zakynthos rookery (Zbinden *et al.*, 2007c) despite it being a small loggerhead population relative to other rookeries exhibiting high levels of multiple paternity (Jensen *et al.*, 2006; Lee, 2008).

In support of the literature, we observed a male-bias in the adult population at the start of the nesting season, yet most tracked males departed prior to the onset of nesting (Plotkin *et al.*, 1996; Godley *et al.*, 2002; James *et al.*, 2005a). Both males and females undertake long migrations to breeding areas, where limited foraging is available, resulting in a massive energy cost depending on the level of activity and period of residency (Jessop *et al.*, 1999; Luschi *et al.*, 2003). Once at the breeding area, to maximise reproductive output, males must competitively search for receptive females, invest in male-male combat and mate (Booth & Peters, 1972; Schofield *et al.*, 2006). Literature on sperm competition of other species in which multiple paternity occurs have shown that the first male to mate with a female is more likely to sire the most offspring in a clutch (Zamudio & Sinervo, 2000). Also, female turtles only need to mate once as they have the capacity to store sperm and can fertilise subsequent clutches, and are likely to resist mating again (Booth & Peters, 1972; Lee & Hays, 2004). Therefore there is a trade-off for male turtles when away from the foraging area; to maximise paternity rates they must arrive at the breeding area early enough to mate with unmated females, but not so early that they waste energy waiting for females to arrive. Males that remain at the breeding ground all year would save on the energetic cost of migration, and have the potential to mate with more females, especially in populations where female arrival is variable. While some individuals may forage year-round on Zakynthos, prey availability is not adequate to sustain the population resulting in different dispersal strategies as indicated by Shaver et al. (2005). Hence, the majority of tracked males migrated out of the breeding area prior to the onset of nesting. Logically, males should depart the breeding area when the reproductive benefit to the male is reduced, i.e. when most females have been mated and are no longer receptive (Plotkin *et al.*, 1996; Hays *et al.*, 2001b; Godley *et al.*, 2002; James *et al.*, 2005b), hence the female bias in our dataset recorded at the onset of nesting was likely to be comprised primarily of unreceptive females.

Adult male turtles monitored by satellite have been recorded to travel large distances from breeding grounds (Sakamoto *et al.*, 1997; Hays *et al.*, 2001b; James *et al.*, 2005a). One of the few studies to follow both sexes was for adult leatherbacks tracked in the North Atlantic where similar long distance movements for the sexes were seen (James *et al.*, 2005b). Our results suggest that males showed broadly similar dispersal and migratory patterns to that recorded in post-nesting females (Zbinden *et al.*, 2008), with disparate distant foraging grounds. Two of the males in our study were tracked to distant foraging or wintering areas in Turkey and Croatia, identified due to the tracking locations being concentrated in one area. By combining tracking data of sex and age classes with local empirical studies it may be possible to identify other foraging sites in need of national and trans-boundary conservation management action (Gardenfors, 2001; Campbell, 2007; Wood & Dragicevic, 2007).

Our study supports the value of GPS tracking towards understanding spatial area use of marine vertebrates such as sea turtles, at both local and regional scales. At the local scale GPS tracking contributes to the evaluation of conservation measures, policies and legislation, while at the large scale it can be applied to create integrated networks of protected areas encompassing breeding, migratory and foraging areas at national, trans-boundary and global levels. Our study indicated that while retrievable GPS units produce a much larger volume of data, GPS transmitters provide the opportunity to track the fine-scale movement of more elusive components of the population (i.e. males) within the protected area and at post migratory foraging grounds. This is of particular importance due to the low male sex ratios recorded in the Zakynthos population, which appears to continue throughout development. In conclusion, fine-scale GPS tracking of wildlife movement patterns may contribute towards enhancing national and international efforts to identify, delineate and develop of new and effective protected areas.

FIGURE & TABLE CAPTIONS

Figure 1. Adult male loggerhead sea turtle (Caretta caretta) (a) at capture (b) during Sirtrack Fastloc GPS-Argos transmitter attachment and (c) immediately following release (photos by Mike and Jeanette Sheldon).

Figure 2. Daily mean (a) GPS logger locations for males (n = 4, 72 locations, square markers) and females (2006: n = 3, 109 locations, triangle markers; 2007: n = 4, 124 locations, circle markers) in Laganas Bay and (b) male satellite transmitter locations (n = 1, 16 locations). We considered fixes falling on land as belonging to the closest point off the coast. Bay divisions: (w) western (c) central, (e) eastern.

Figure 3. Distance from shore before (black bars) and after (white bars) the onset of the nesting season for (a) females (n = 7) and (b) males (n = 4 before and n = 1 after) obtained from hourly positional datasets.

Figure 4. Internesting migration from Zakynthos to the Peleponesse by one female during 2007.

Figure 5. 2007 daily nesting numbers (circles) and days of departure of the four tracked male turtles (arrows) (nesting data obtained from NMPZ archives).

Figure 6. (a) Disparate departure directions of the four males that migrated away from Zakynthos. (b) Long distance migration of two male turtles from the breeding area of

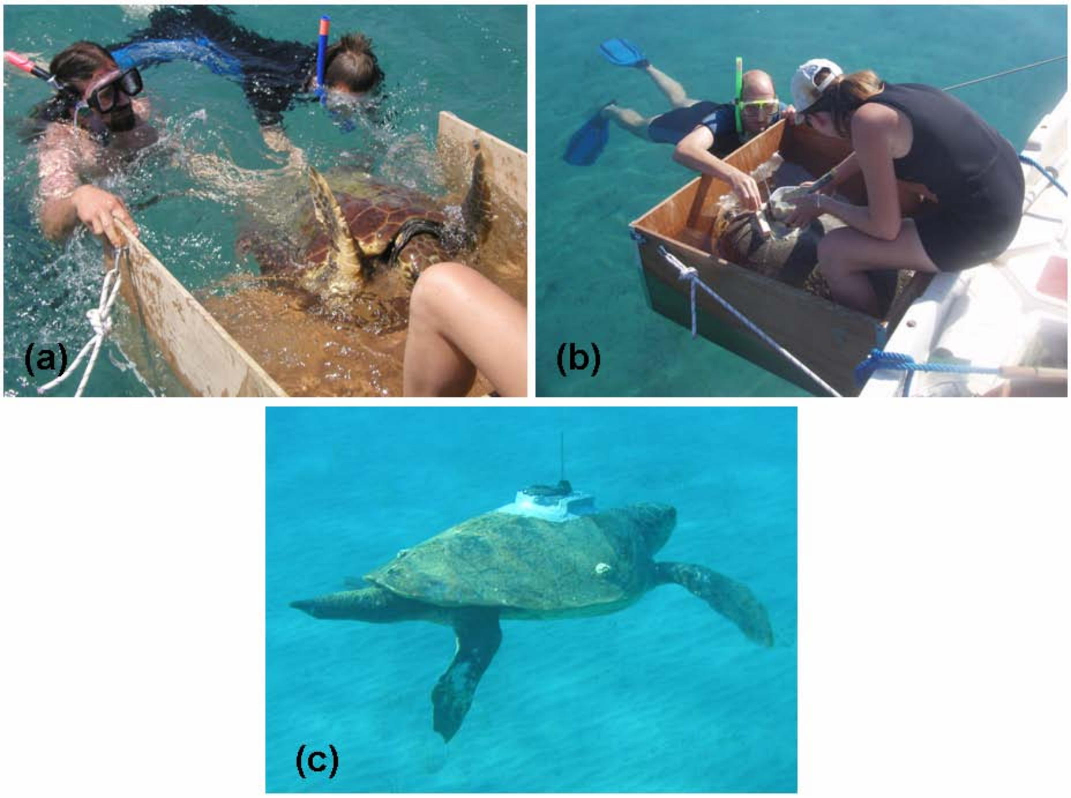
Zakynthos; one GPS transmitter track to the islands of Olib and Silba in Croatia and one satellite transmitter track to the Bay of Izmir in Turkey.

Figure 7: The proportion of male loggerheads present in the nearshore waters of Laganas Bay showing a significant decline between 14 April and 31 May in 2003 ($F_{1,22} = 71.3$, $r^2 = 0.75$, $p < 0.001$*).*

Table 1. GPS logger and transmitter locations acquired and those remaining following filtration. (CCL = curved carapace length of turtle, CCW* = curved carapace width of turtle)*

Appendix 5: An animation showing the day by day movements of the
eleven turtles across a 55 day period with GPS loggers from attachment to retrieval; blue range squares = 2007 males (n = 4), green range triangles = 2006 females (n = 3), red range circles = 2007 females (n = 4) (Animated gif).

Figure 1. Adult male loggerhead sea turtle (*Caretta caretta*) (a) at capture (b) during Sirtrack Fastloc GPS-Argos transmitter attachment and (c) immediately following release (photos by Mike and Jeanette Sheldon).



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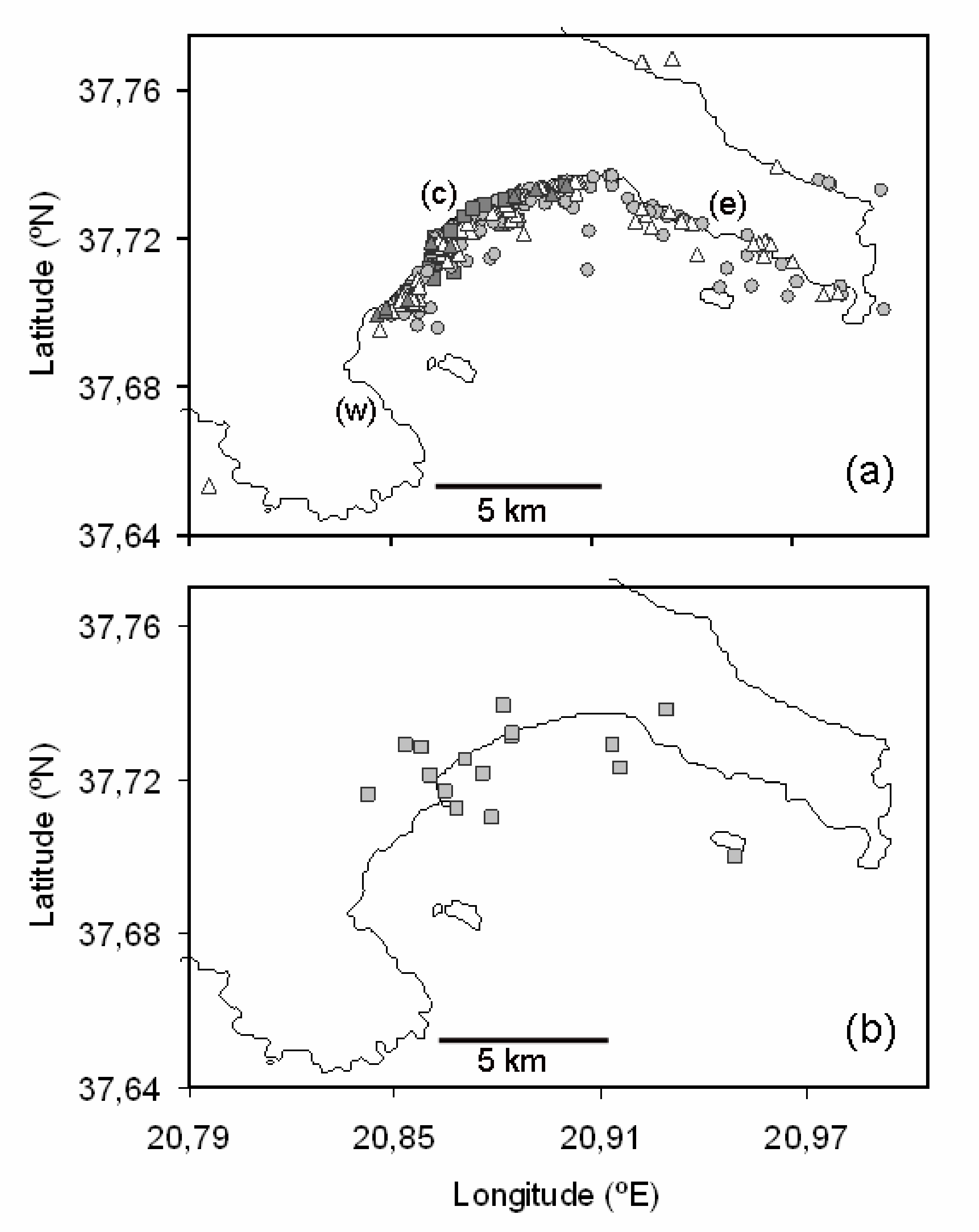

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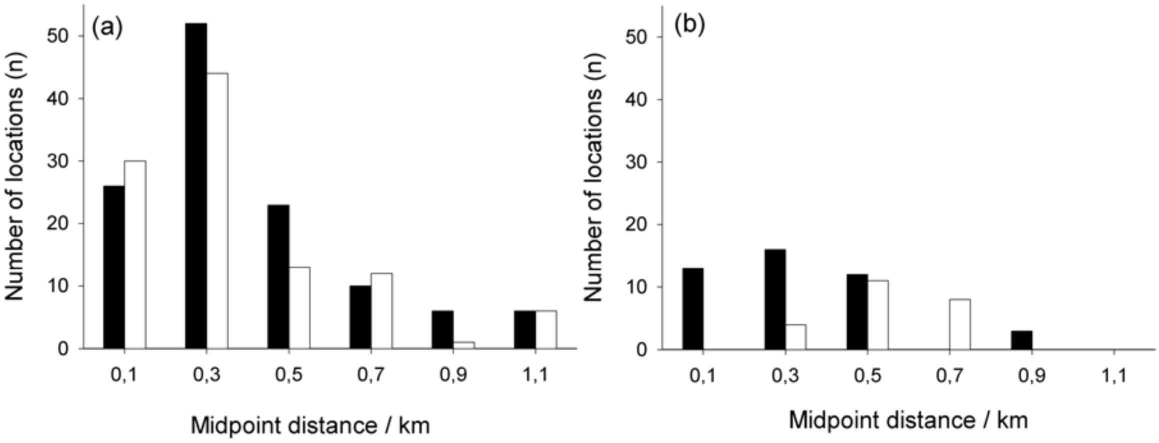


Figure 4. Internesting migration from Zakynthos to the Peleponesse by one female during 2007.

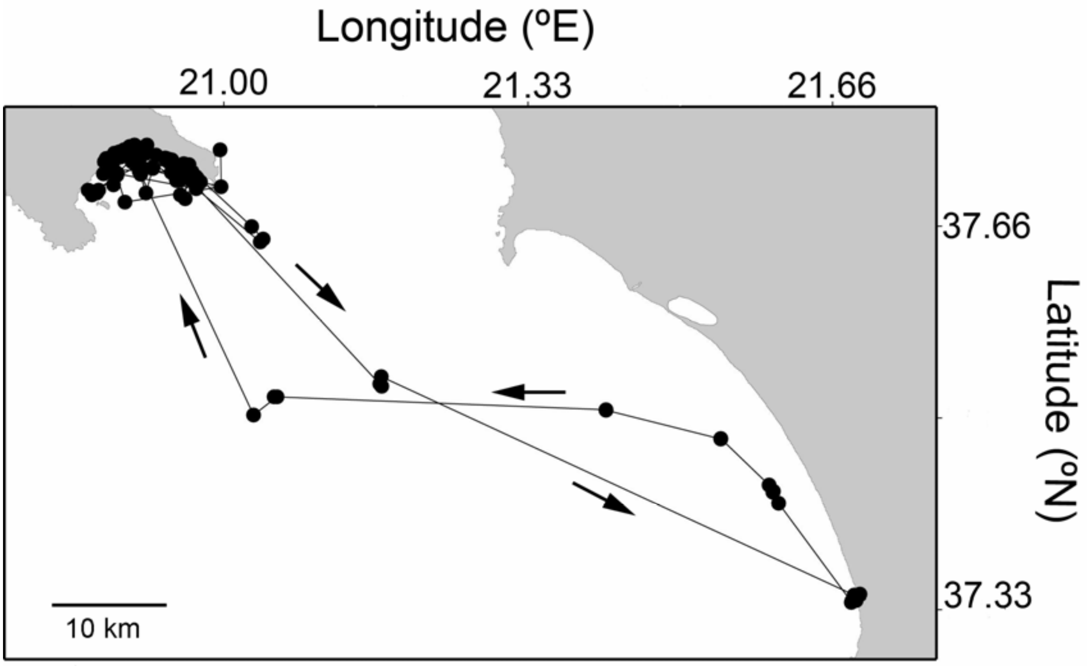
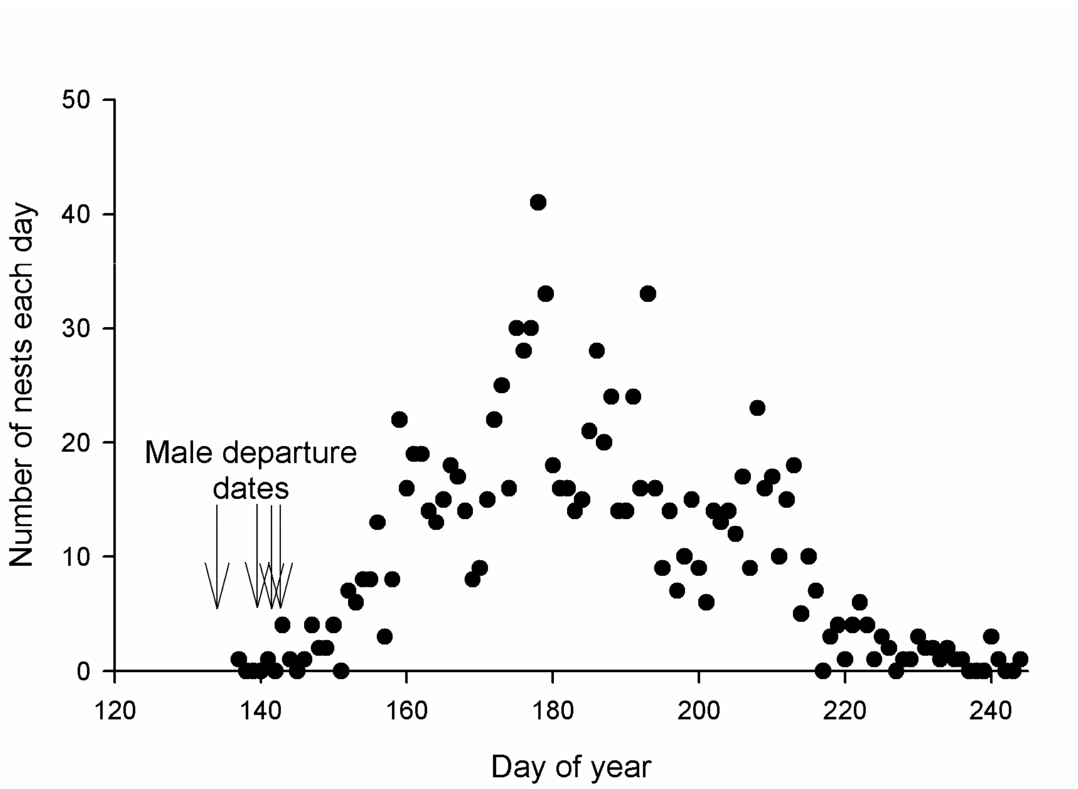


Figure 5. 2007 daily nesting numbers (circles) and days of departure of the four tracked male turtles (arrows) (nesting data obtained from NMPZ archives).



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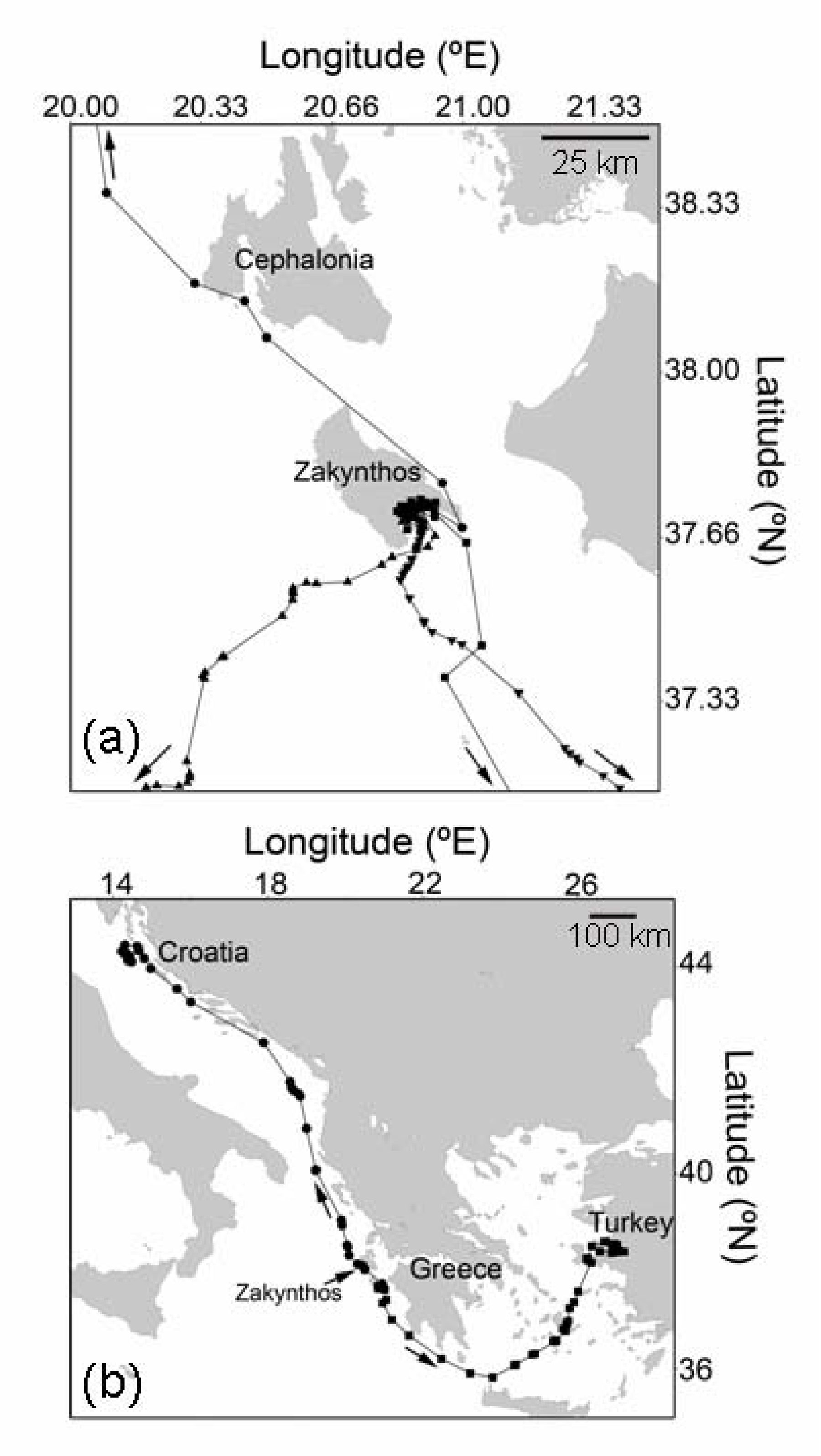

Figure 7: The proportion of male loggerheads present in the nearshore waters of Laganas Bay showing a significant decline between 14 April and 31 May in 2003 ($F_{1,22} = 71.3$, $r^2 = 0.75$, $p < 0.001$).

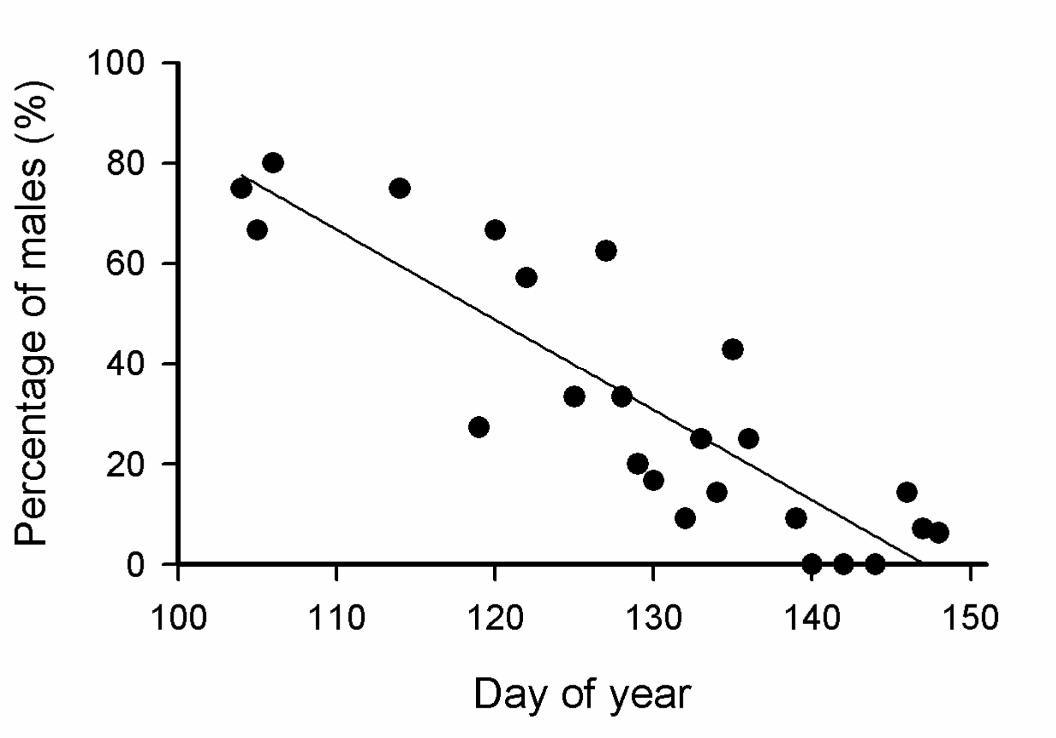

Table 1. GPS logger and transmitter locations acquired and those remaining following filtration. (CCL* = curved carapace length of turtle, CCW* = curved carapace width of turtle)

Year	Turtle id	Device	Turtle parameters/cm		Date GPS attached	Date GPS stopped/removed	Day of first nesting	Day of departure	No operational days	Post filtering locations	
			CCL*	CCW*						Total	Mean per day
2006	Female_1	TrackTag GPS	81	73.5	19/5/2006	6/6/2006	21/5/2006	n/a	**17**	519	**31**
2006	Female_2	TrackTag GPS	89	76	23/5/2006	26/6/2006	25/6/2006	n/a	**31**	2198	**69**
2006	Female_3	TrackTag GPS	87	72	24/5/2006	18/6/2006	7/6/2006	n/a	**25**	818	**33**
								n/a			
2007	Female_4	TrackTag GPS	83	75	4/5/2007	25/6/2007	5/6/2007	n/a	**52**	2081	**25**
2007	Female_5	TrackTag GPS	84	77	8/5/2007	11/6/2007	3/6/2007	n/a	**34**	909	**27**
2007	Female_6	TrackTag GPS	81	74	9/5/2007	26/6/2007	23/5/2007	n/a	**48**	1779	**37**
2007	Female_7	TrackTag GPS	77	66	11/5/2007	12/6/2007	21/5/2007	n/a	**35**	1377	**39**
2007	Male_1	Sirtrack GPS	81	72	8/5/2007	26/6/2007	n/a	n/a	**49**	1110	**23**
2007	Male_2	Sirtrack GPS	91	81	10/5/2007	30/6/2007	n/a	20/5/2007	**51**	53	**1**
2007	Male_3	Sirtrack GPS	81	74	14/5/2007	17/5/2007	n/a	14/5/2007	**3**	38	**13**
2007	Male_4	Sirtrack GPS	79	70	10/5/2007	25/5/2007	n/a	22/5/2007	**15**	44	**1**
2007	Male_5	Sirtrack satellite	90	83	7/5/2007	12/9/2007	n/a	23/5/2007	**128**	100	**0.8**
								Total	**488**	**11026**	**22.5**

ΚΕΦΑΛΑΙΟ / CHAPTER 6. Microhabitat selection by sea turtles in a dynamic thermal marine environment

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Peer-reviewed journal citation (manuscript in Appendix 3)*:*
***Schofield, G.**, C.M. Bishop, K.A. Katselidis, P. Dimopoulos, J.D. Pantis, G.C. Hays. 2009. Microhabitat selection by sea turtles in a dynamic thermal environment. Journal of Animal Ecology 78(1):14-21*

Affiliated conference presentation (oral presentation abstract in Appendix 4**):**
***Schofield, G.**, C.M. Bishop, K.A. Katselidis, P. Dimopoulos, J.D. Pantis, G.C. Hays. No time to chill out: GPS tracking reveals micro-habitat selection by breeding loggerhead turtles. Oral presentation at the Twenty-Ninth International Symposium on Sea Turtle Biology and Conservation. Brisbane, Australia, February 2009*

INTRODUCTION

Habitat selection, and its impact on reproductive fitness, has long been one of the cornerstones of ecological research (e.g. Loe *et al.*, 2006; Parra *et al.*, 2006). Moreover, recent concern over the implications of climate change has heightened interest in how patterns of habitat selection might change in the future (e.g. Braschler & Hill, 2007). From the suite of possible environmental parameters, temperature often plays a key role in influencing habitat preferences over a range of spatial scales. For example, over the broad scale (e.g. across ocean basins), temperature may influence the distribution of species and their seasonal movements (McMahon & Hays, 2006), while on smaller scales of metres or kilometres, temperature may drive the specific microhabitat selected by individuals. For example, features such as rocks or scrub are used to make adjustments in body temperature for terrestrial species (e.g. frogs, Hamer *et al.*, 2003; baboons, Hill, 2004; snakes, Shine *et al.*, 2005). Similarly, some aquatic species have been shown to preferentially select sites near water outflows from power stations where the water is warmer (e.g. alligators, Murphy & Brisbin, 1974; manatees, Laist, 2005; sea turtles, Lyon *et al.*, 2006). Thermal selection has also been demonstrated for freshwater turtles (e.g. Parmenter, 1980).

We can liken this ecological problem of thermal selection to animals searching for patchily distributed prey, where individuals are constantly having to make decisions on where to reposition themselves to maximize resource acquisition. For animals searching for prey, the pattern of movement may be fundamentally impacted by whether animals have a good knowledge of what drives the prey distribution within their environment (Sims *et al.*, 2005; Sims *et al.*, 2006a). Likewise, when the resource of interest is temperature, rather than prey, we might predict different search patterns depending on the animal’s knowledge of its environment as well as its physiological state and ecological needs.

The importance of thermal selection in a dynamic environment may be particularly acute at the limits of species distributions where environmental conditions may be at the margins of suitability, and hence, the implications of thermal habitat selection are greater. Such situations might, therefore, be ideal for testing the existence of fine-scale thermal selection in a dynamic thermal environment.

Loggerhead sea turtles (*Caretta caretta*) are fairly widely distributed across subtropical and temperate latitudes (Dodd, 1988). The rookery on Zakynthos island (Greece) in the semi-enclosed Laganas Bay is unusual in that it is relatively large (Margaritoulis, 2005) despite being situated at the latitudinal margins of the species' breeding range. When turtles migrate to Zakynthos to mate in March–May, sea surface temperatures are generally cool (*c.* 13–22ºC) before increasing towards mid-summer. Therefore, the size of the breeding population at Zakynthos, despite these cold conditions, is a conundrum. It might be predicted that turtles display thermal selection to overcome cold conditions, although such thermal selection has not been demonstrated before in sea turtles. Certainly it is widely known that in lakes and semi-enclosed water bodies, the wind direction may cause warm near-surface water to accumulate at the down-wind end of the water mass (e.g. Barnes & Mann, 1991). Hence, it is possible that there may be heterogeneous water temperatures at Zakynthos, offering the possibility of thermal selection by sea turtles at this site. Here we examine if sea turtles at this site show thermal selection and consider the possible benefits in terms of increasing egg maturation rates before oviposition, thereby allowing the seasons' first clutch to be laid earlier which may enhance reproductive fitness.

MATERIALS & METHODS

Relative rookery nesting density

As part of the current study, we compiled a database containing information about (1) nesting numbers (2) nesting beach length, and (3) latitude at known loggerhead rookeries found in the Northern Hemisphere. The first two parameters were combined to acquire nesting density (n.km^{-1}). Data was acquired from the State of the World's Sea Turtles website (SWOT http://www.seaturtlestatus.org) and the 'Loggerhead Sea Turtles Book' (Bolten & Witherington, 2003).

Transect surveys

Transect surveys were conducted to obtain information on (i) sea surface and seabed temperature, and (ii) sea turtle distribution across Laganas Bay. Five transect lines (T1–T5), each with three temperature stations at 1-, 3- and 5-m sea depths were delineated along a pre-selected 5-km section of near-shore water (Fig. 1). We used a 4-m boat with an outboard engine, with travel speeds of four knots between stations. Each transect line was 0·75 km in length, at a minimum distance of 1 km from adjacent station start points, set on a north–south line, except for the first transect which was set on a northeast–southeast line (due to land form characteristics). The global positioning system (GPS) location of each transect station was recorded using GARMIN eTrex-legend (Olathe, KS, USA). Between 9 May and 13 July 2006, 34 morning and afternoon line transects were conducted, each spanning a 2-h period. Forty-five per cent of transects were conducted between 09·00 and 11·00 h and 55% of transects were conducted between 15·00 and 17·00 h. Seventy-five per cent of transects were conducted in a west–east order, while 25% were conducted in an east–west order to allow for time-dependent variations in temperature/turtle records. At each temperature station, the sea surface and seabed temperatures were recorded for a 3-min interval using Tinytag TGP- 4204 (Gemini Data Loggers, Chichester, West Sussex, UK) external probe (rapid response) and TGP-4017 (Gemini Data Loggers, Chichester, West Sussex, UK) internal probe (slower response) loggers respectively. Between stations, the loggers were placed in a bucket of seawater to reduce the time required to adjust to ambient water temperature. Validation experiments showed both types of instrument consistently recorded the temperature to within 0·01ºC of one another. The 3-min measurement period was selected on the basis of the thermal response time of the TGP-4017 logger, that is, after this time there was no change in the measured temperature.

All turtle sightings, whether at the surface or submerged and within 20 m of the boat, were recorded by two observers (i) at each temperature station, (ii) between temperature stations, (iii) on the outgoing (east–west transect order) or return (west–east transect order) journey from port. On sighting a turtle, the time, sea depth, turtle depth and turtle behaviour were recorded. All surveys were conducted in a good sea state, to reduce the impact of conditions on sighting probability.

Environmental data

Weather data were recorded in three independent ways to try and remove any impact of very local weather conditions on land impacting our interpretation of the weather in Laganas Bay. (i) Wind direction, cloud cover and sea state were recorded approximately at the start and end of each survey by direct observation, (ii) a WS-2300 weather station (La Crosse Technology Ltd, La Crosse , WI, USA) positioned 100 m in land (Fig. 1) was set to record a range of parameters (including air temperature, wind direction and speed) at 30-min intervals (and downloaded bi-weekly onto computer) between 8 May and 31 July 2006, and (iii) hourly data sets were provided by the Zakynthos Airport weather station located 1 km inland from Laganas Bay (Fig. 1) for the period of 1 May to 31 July 2006. Where readings from the WS-2300 and airport weather stations were in agreement, we took the mean of these observations. When they differed appreciably (e.g. due to local topography influencing wind direction), then the weather station record was selected which showed a wind direction that most closely matched that observed visually during the surveys at sea.

Animalborne Loggers

Navsys Ltd. TrackTag TM GPS loggers (Colorado Springs, CO, USA; http://www.navsys.com) were attached to three female loggerhead sea turtles for a total of 73 complete days (17, 31 and 25 days respectively) between 20 May and 23 June 2006. In addition, we used time-depth recorders (TDRs) that recorded ambient temperature and depth; LOTEK LTD_1100 model TDRs (LOTEK Marine Technologies, St. John’s, NF, Canada). These were attached to the three females fitted with GPS loggers plus three others for a total of 140 days (17, 31, 25 and 31, 12, 21 days respectively) between 16 May and 27 June. For GPS and TDR system parameters and attachmentretrieval methodology, see Schofield *et al.* (2007a).

Validation trials were conducted to confirm the equivalence of temperature readings made by the different temperature devices. In a controlled experiment, we compared the sea temperature readings of the Tinytag TGP-4204 external probe (n = 1), Tinytag TGP-4017 internal probe (n = 1) and Lotek TDRs (n = 6) used during the research.

All equipment readings were simultaneously taken for 10 min at 30-s intervals at the surface, 1-, 3-, 5- and 7-m sea depths. We found that the two Tinytag loggers consistently recorded temperature to within 0·01ºC of one another at the sea surface (the external probe was not used at lower depths). The TDRs recorded temperature on average 0·09ºC lower than the Tinytag TGP-4017 internal probes (range –0·01 to –0·16, SD ± 0·04). These small differences were corrected in the data analysis.

Water temperature further from the sea

We were unable to conduct our own surveys of water temperature far from the shore for logistic reasons. Therefore, we used the *in-situ* temperature readings made by equipped turtles to assess water temperature further from the shore, since water depth increased in the middle of the bay (Fig. 1).

Turtle distribution analyses

We investigated whether turtle distribution, recorded both on transect surveys and with GPS tracked turtles, was linked to wind direction. For the surveys in Laganas Bay, we calculated the mean turtle position on transects by assessing their angular distribution around the bay from a central reference point and then applying circular statistics (Fig. 1, Oriana version 2·00). To obtain an objective measure of area use for GPS tracked turtles, we initially filtered the GPS fixes (average of 51 fixes turtle^{-1} day^{-1}) by selecting the central location for each hour for each turtle (Tremblay *et al.*, 2006). Subsequently, we calculated the daily mean GPS derived position for each tracked turtle. All GPS locations occurring outside of the Laganas Bay area were removed. All GPS locations in the 3 days before egg laying were removed, as existing literature indicates a pattern of increasing activity as a nesing event approaches (Hays *et al.*, 1991; Hays *et al.*, 1999) that may be driven by active nesting beach selection rather than immediate environmental parameters.

Turtle temperature analyses

We investigated if individual turtles fitted with TDRs (n = 6) experienced warmer water than expected by chance. To do this, we examined the water temperatures measured on transects in Laganas Bay. For each survey (either morning or afternoon), we determined the mean and maximum water temperature measured by the Tinytag temperature devices. During the same sampling period at which each survey was conducted, we determined the mean temperature measured by the TDRs attached to individual turtles.

RESULTS

Relative rookery nesting density

From a sample of 121 loggerhead rookeries in which nesting number and beach length information were available, we found there was a significant correlation between nesting density and latitude ($F_{1,111}$ = 17.9, r^2 = 0.37, p < 0.001; Fig. 2a-c). Whereby, there is a decline in the density of loggerhead populations with increasing latitude. However the Zakynthos rookery was unusual in having a high nesting density (235 nests km^{-1}; Margaritoulis *et al*., 2003) as well as having a high latitudinal location.

Wind direction versus sea temperature

Within the 5-km transect area, there was variability in the sea temperature between different transects, and we found that this variability was strongly correlated with wind direction. For example, when the wind blew from the south-east, the warmest water was found in the north-west part of the bay. Overall, the mean wind direction explained 55% of the variation in the location of the warmest sea temperature recorded on each transect survey ($F_{1,30}$ = 36·3, r^2 = 0·55, P < 0·001) (Fig. 3a). This wind–temperature relationship was even stronger during afternoon surveys ($F_{1,16}$ = 47·7, r^2 = 0·75, P< 0·001) (Fig. 3b).

Turtle Distribution

A total of 351 turtle sightings were made during 34 surveys in the 5-km study area. On average, 10 individuals were sighted per survey (range 0–38 sightings survey^{-1}). There was strong link between turtle distribution and wind direction. For example, Fig. 4 shows the distribution of turtles on 2 days of contrasting wind direction and shows how when the wind blew from the east, turtles were concentrated in the western part of the bay, while when the wind blew from the south the turtles were seen in the northern part of the bay.

This relationship between wind direction and turtle distribution was always significant but improved when we selected those surveys where more turtles were sighted, presumably because of the inability to accurately assess turtle distribution when few turtles were seen, that is, when the number of turtles sighted increased, the relationship became tighter albeit there were fewer sampling dates that could then be included in the analysis. For example, selecting surveys where there were > eight turtle sightings (n = 21 surveys) showed that 73% of the variation in mean turtle distribution could be explained by wind direction ($F_{1,16} = 43{\cdot}6$, $r^2 = 0{\cdot}73$, $P < 0{\cdot}001$) (Fig. 5a). This strong correlation between wind direction and turtle location was supported by the data obtained from the three turtles tracked using GPS. For these GPS-tracked turtles, 65% of the variation in their daily mean position in the bay was explained by wind direction ($F^{1,57} = 106$, $r^2 = 0{\cdot}65$, $P < 0{\cdot}001$) (Fig. 5b,c).

When both mean wind direction and angular position of the warmest water in the bay each day were entered into a stepwise multiple regression (using minitab version 8·2) against mean daily turtle location (both with the transect data set and the GPS tracking data set), only wind direction entered the subsequent equation, that is wind direction seemed to have a stronger impact on turtle location than the location of the warmest water. However, analysis of individual GPS tracks showed that turtles were not simply always located directly downwind, but rather they made movements parallel to the shore moving across the wind direction (Fig. 6). This suggests that the turtles were not simply passively advected but rather actively controlled their position.

Sea temperature and turtle distribution

In total, we obtained 93 instances of TDR records where there was an accompanying temperature survey along the nearshore transects. The mean TDR temperature was significantly warmer than the near-shore temperature (mean difference +1·70ºC, t = 17·33, $P < 0{\cdot}001$) (Fig. 7). Furthermore, the mean TDR temperature was also warmer than the maximum near-shore temperature measured at the same time along the transects (mean difference +0·25ºC, t = 3·2, $P = 0{\cdot}002$). The elevation of the TDR temperatures above mean near-shore temperatures was significantly higher during afternoon surveys (mean difference +1·97ºC, n = 56) than during morning surveys (mean difference +1·28ºC, n= 37) ($t90 = 4{\cdot}0$, $P = 0{\cdot}0001$). Furthermore, the elevation of

TDR temperatures above mean near-shore temperatures tended to decline as the season progressed ($F_{1,54}$ = 23·8,r^2= 0·31, P< 0·0001) and ambient water temperatures approached 26ºC (Fig. 8). This suggests that turtle response to environmental conditions lessened as the season progressed and sea temperature increased.

Water temperature further from the shore

Turtles very rarely dived deep, with < 0·5% of their total time spent deeper than 6 m. However, for three of the six equipped turtles, we recorded a total of five dives to deeper than 10 m during May. We compared the temperature at depth versus the temperature experienced shallower than 5 m in the 30 mins before and after these deep dives. Water temperature measured when turtles were deeper than 10 m (i.e. > 1 km from the shore) was, on average, 2·34ºC less than water temperature when they were shallower than 5 m.

The potential energetic benefits of adopting thermal selection

We used empirical data on the relationship between inter-nesting intervals and water temperature to estimate the potential reduction in time to laying the first clutch caused by early season thermal selection by loggerhead turtles. In a comparative study across different nesting populations (Hays *et al.*, 2002a) it was shown that: log (internesting interval in days) = 2·25–0·043 temperature (ºC). At water temperatures of 22, 25, and 27ºC, the typical intervals between successive clutches are 20·1, 15·0 and 12·3 days. So at the start of the season when mean water temperatures are around 22ºC (or less in deeper water), if turtles select water that is 5ºC warmer than average, they might be expected to reduce their time to laying their first clutch by almost 8 days, and by 5 days if they select water 3ºC warmer than average.

DISCUSSION

Data loggers and transmitters are starting to transform our understanding of patterns of habitat utilization for hard-to study species. For example, acoustic tracking of dogfish has shown how individuals tend to rest in deeper cooler water and hunt in warmer shallower water to maximize their net energy gain (Sims *et al.*, 2006b).

Miniature dive loggers attached to American mink have revealed contrasting patterns of behaviour between individuals, with some being more terrestrial versus others that are more aquatic (Hays *et al.*, 2007). Similarly, high-resolution tracking with GPS loggers is allowing the detailed pattern movement for a range of terrestrial and aerial species to be determined (Hamer *et al.*, 2003; Wegge *et al.*, 2007), whereas technical constraints have, to date, largely limited the use of GPS tracking for species that spend most of their time submerged. We showed that the pattern of movement exhibited by GPS tracked turtles reflected the distribution of individuals revealed in boat surveys and that both of these patterns of distribution covaried with wind direction. As has been widely reported in lakes (Barnes & Mann, 1991), we found that wind direction influenced the location of warm water patches close to the shoreline. Furthermore, this link was tighter in the afternoon, presumably when the water had been subject to solar heating during the earlier part of the day (Hattori & Warburton, 2003; Pulgar *et al.*, 2005). The location of warm water patches provided the potential for thermal selection by loggerhead turtles and the consequence was that they experienced warmer water than if they were randomly distributed in the near-shore waters. Furthermore, while our information on the water temperature at greater depths within the bay was limited, the records from turtles equipped with temperature loggers suggested that the temperatures at depth further from shore were over 2ºC cooler than the shallower temperatures, that is, the actual water temperatures experienced by turtles at the end of May were probably around 5ºC above those they would have experienced if they rested at > 10 m, which is the typical resting depth of turtles in tropical nesting sites (Hays *et al.*, 2004c). While the important role of temperature in driving habitat selection is well established for a broad range of species, including a number of freshwater turtles (e.g. Tamplin, 2006), the novelty of our study is that we have shown how selection occurs even in a very dynamic thermal environment.

Several lines of evidence suggest that turtle repositioning is unlikely to be the result of passive drift. First, adult turtles are strong swimmers and therefore dictate their own position in the breeding season, even if currents or winds are strong. For example, at Ascension Island, breeding female green turtles position themselves around the 20-m isobath despite locally strong winds and currents (Hays *et al.*, 1999). Second, loggerhead turtles spend most of the time submerged, either in water or resting on the bottom (Houghton *et al.*, 2002), so they are unlikely to be strongly impacted by winds. Third, the thermal selection by the turtles seemed to change as the breeding season progresses, with the biggest elevation above mean bay temperature, that is, the strongest thermal selection, seeming to occur at the start of the season when water temperatures were coolest. Regardless of the exact mechanism at work, it was clear that the turtles repositioned themselves with respect to wind direction and this has not been reported at a breeding site previously. This finding poses two distinct types of question: what are the benefits of thermal selection by loggerhead turtles at this site and how is the thermal selection actually achieved?

Due to their large size, and resulting thermal inertia, adult loggerhead turtles may have a core temperature a few ºC above ambient, although their body temperature is still largely driven by the ambient water temperature (Spotila *et al.*, 1997). In general, $Q10$ values (the metabolic rate at T + 10ºC divided by the metabolic rate at T ºC) for loggerhead turtles are around 2·4 to 5·4 (Hochscheid *et al.*, 2004). So loggerhead turtles in warmer water will have increased metabolic rates and hence their production of clutches would be expected to be quicker, albeit that the instantaneous rate at which energy reserves are used will be faster. We used the empirical relationship between internesting intervals and water temperature to estimate that by selecting warm water, time to laying the first clutch might be reduced by as much as 5 days. Greece is near the latitudinal limit for loggerhead turtles and there is a marked seasonal variation in air temperature. The consequence of this variation is that there is a fairly tight window of optimal sand temperatures for egg development limited to between June and September (Margaritoulis, 2005). In more tropical nesting areas, this window of optimal conditions is much broader (Godley *et al.*, 2002), and hence, it is a female's energy reserves rather that the length of the available nesting season that constrains her reproductive output. Typical incubation durations for sea turtle eggs are around 50–60 days (Margaritoulis, 2005). Hence, clutches laid late in the season, (e.g. August) are at risk of being unable to complete development within the window of optimal conditions. By laying their first clutch of eggs as soon as possible in May, loggerhead turtles will thereby maximize the number of clutches they can lay within a season that experience optimum development temperatures even close to hatching.

Furthermore, reducing the time required to lay the first clutch will mean that turtles are able to minimize the time that they spend away from their foraging grounds.

It is well known that in many species, reproduction is timed seasonally to maximize offspring survival. For example, many species of mesozooplankton in temperate waters time egg production so that developing larvae are in the water when their phytoplankton prey is maximally abundant during the spring bloom (Irigoien *et al.*, 1998). Similar examples exist in other environments. For example, for birds migrating to high-latitude breeding sites, the chicks need to fledge and be ready for the return migration before local conditions or migration conditions deteriorate too much (Cooke *et al.*, 1984). Again, this situation may favour an early seasonal start for reproduction. The early season thermal selection shown by loggerhead turtles in Greece therefore seems to form part of a general strategy of animals to time their reproduction to those times when offspring survival is maximized.

Although we have demonstrated that turtles experience warmer water than expected by chance early in the breeding season in Greece, we have not established how this thermal selection is attained. The search strategies employed by animals is a hotly debated topic, particularly with reference to finding patches of prey (Edwards *et al.*, 2007). These same considerations apply equally to loggerhead turtles finding patches of warm water. Turtles might be able to perceive wind direction and use this as a cue to locate patches of warm water. In this case, experience would play a role in their ability to locate warm water patches. Alternatively, it might be that there is a component of more random search by turtles along the shore to find warm water patches. Tracking individuals in combination with simultaneous mapping of the thermal environment and wind direction might be used to disentangle these possibilities. Furthermore, various quantitative movement models (e.g. Sims *et al.*, 2000; Bailey & Thompson, 2006), primarily developed for objectively examining tracking data to infer where animals forage, might be usefully employed to examine tracking data to establish the search rule used by turtles to find warm water. In addition, biophysical models that integrate metabolic rate, body temperature, water temperature, and dive behaviour may shed further light on the benefits of thermal selection by sea turtles.

In summary, we have shown how an endangered ectotherm, the loggerhead sea turtle, near the limits of its breeding range, repositions itself daily to take advantage of thermal hotspots within a highly dynamic thermal environment. How turtles achieve this selection is not known, but it most probably contributes to the success of this species near its cold water range limits.

FIGURE & TABLE CAPTIONS

Figure 1. The 5-km survey area in Laganas Bay, Zakynthos island, Greece. Hatched lines comprise areas of human develop-ment. T1–T5 are the transect lines denoting the 1-, 3- and 5-m sampling stations. W1 and W2 are the beachfront and airport weather stations respectively. Bathymetry lines are set at 5-m sea depth intervals (i.e. –5, –10 etc.). M is the compass midpoint of the survey area for circular statistical analysis.

Figure 2. (a) The relationship between a sample of known loggerhead rookery (n = 121) nesting densities ($n.km^{-1}$*) and location (°N) in the Northern Hemisphere (data sources: SWOT; Bolten & Witherington, 2003); The black dot represents the relative position of the Zakynthos rookery. (b) Caretta caretta Loggerhead sea turtle. (c) The geographical position of Zakynthos; the black dots show the distribution of rookeries in the Northern Hemisphere; the arrows show the 5 rookeries of greatest nesting density.*

Figure 3. The relationships between mean wind direction per survey and warmest sea temperature location recorded on transects in the localized 5-km survey area; (a) all records ($F_{1,30} = 36{\cdot}3$, $r^2 = 0{\cdot}55$, $P < 0{\cdot}001$*) (b) afternoon records (*$F_{1,16} = 47{\cdot}7$, $r^2 = 0{\cdot}75$, $P < 0{\cdot}001$*).*

Fig. 4. Turtle distribution on days with different wind direction; (a) turtle distribution during a survey with north-east wind conditions with aggregations forming at transect 1 and (b) turtle distribution during a survey with south south-east wind conditions with aggregations forming between transects 3 and 4. Shaded bars show

number of turtles recorded along each transect. Arrow on each plot indicates mean turtle location.

Fig. 5. The relationships between the mean turtle location and mean wind direction for (a) surveys recording > eight turtle sightings in the 5-km study area ($F_{1,16}$ = 43·6, r^2 = 0·73, P < 0·001) with standard deviation bars and (b) mean derived GPS position per day of tracked turtles within Laganas Bay ($F_{1,57}$ = 106, r^2 = 0·65, P < 0·001); GPS1 black circles, GPS2 open circles, GPS3 triangles. In (c) the hourly GPS locations of the three tracked turtles are shown; GPS1 circles, GPS2 squares and GPS3 triangles.

Fig. 6. Movement of three turtle equipped with GPS loggers between 26 May 2006 and 29 May 2006. Each panel shows the movement of each turtle on 1 day and the mean wind direction measured using two independent weather stations (see methodology). The panels show how when the wind blew from the north-east on 26 May (panel a), the turtle aggregated further to the south-west of the bay, but note they were not located directly downwind indicating they were not simply passively advected but rather actively controlled their position. Between 27 May (panel b) and 28 May (panel c), the wind turned around to blow from the south-east and all three turtles moved to the north-east part of the bay. But note again that they did not simply aggregate directly downwind indicating that they were not simply passively advected but rather actively controlled their position.

Fig. 7. The differences recorded between the temperature experienced by tagged turtles (measured with a TDR) and the mean near-shore water temperature measured during each boat survey. Positive values indicate that the temperature experienced by a turtle was warmer than the mean near-shore water temperature.

Fig. 8. The elevation of temperatures (left axis, triangles) experienced by tagged turtles (measured with a TDR) above the mean near-shore water temperature during afternoon surveys versus the date. As the season progressed, this temperature elevation declined: temperature elevation (°C) = 3·8–0·0428 date (days since 30 April) ($F_{1,54}$ = 23·8, r^2 = 0·31, P < 0·0001). Also shown (right axis, circles) is the mean survey area temperature, showing the seasonal warming of the water.

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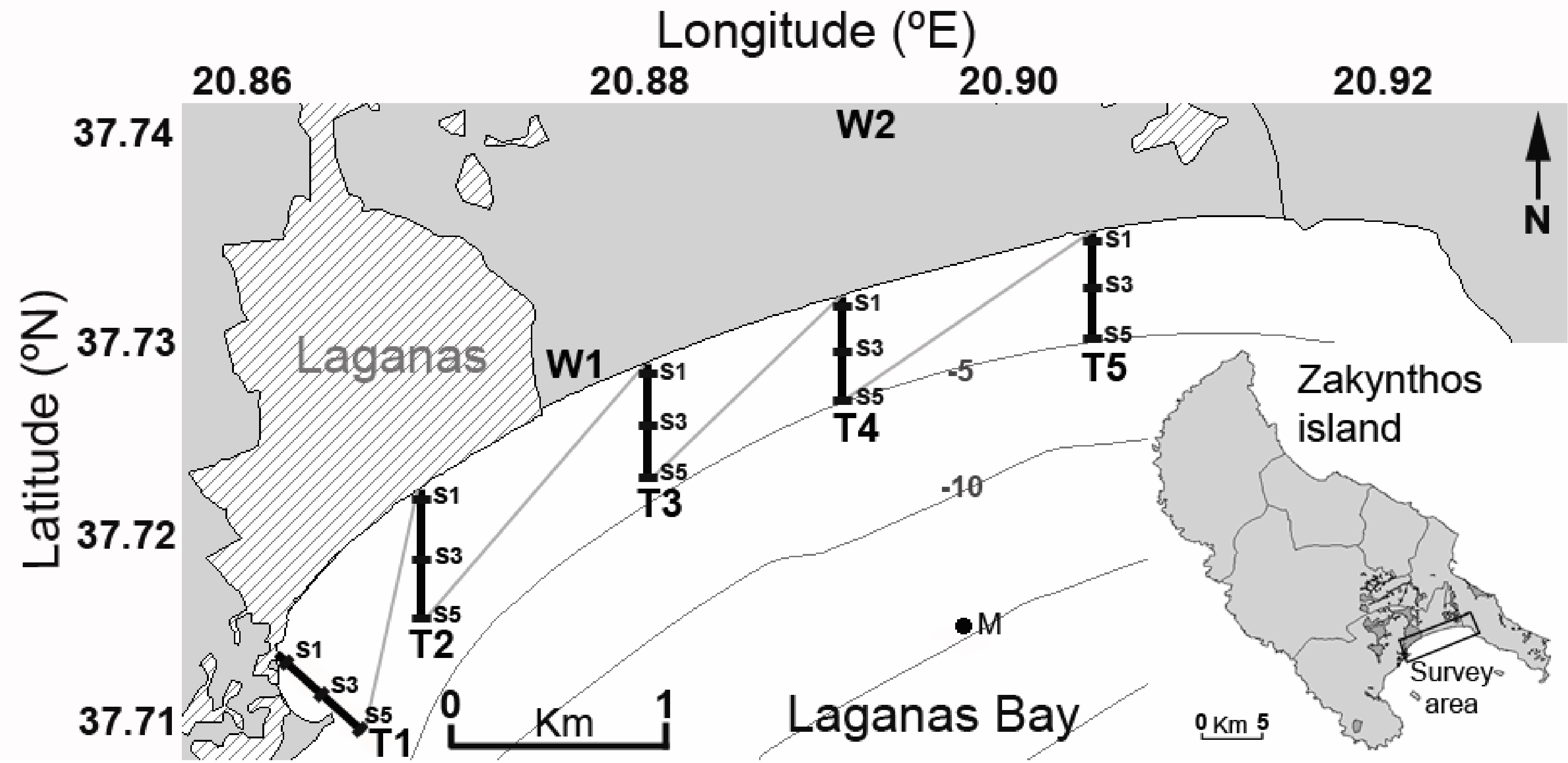

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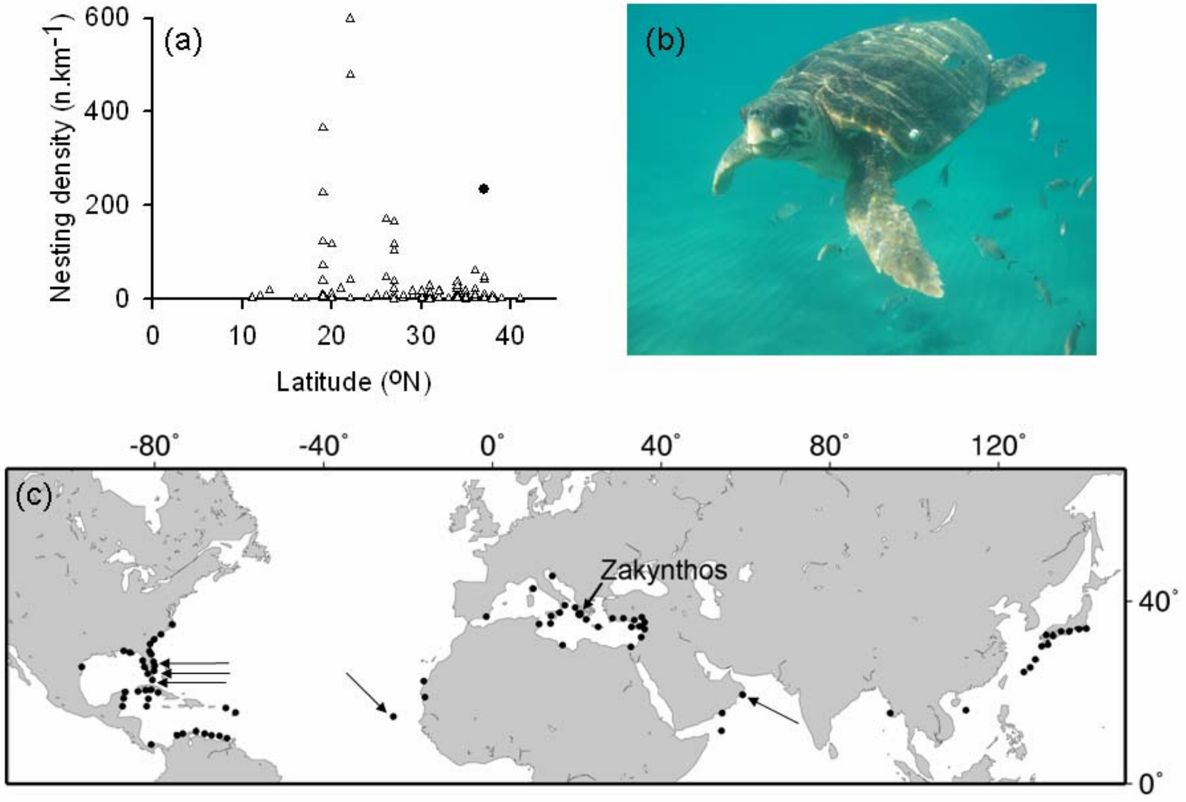

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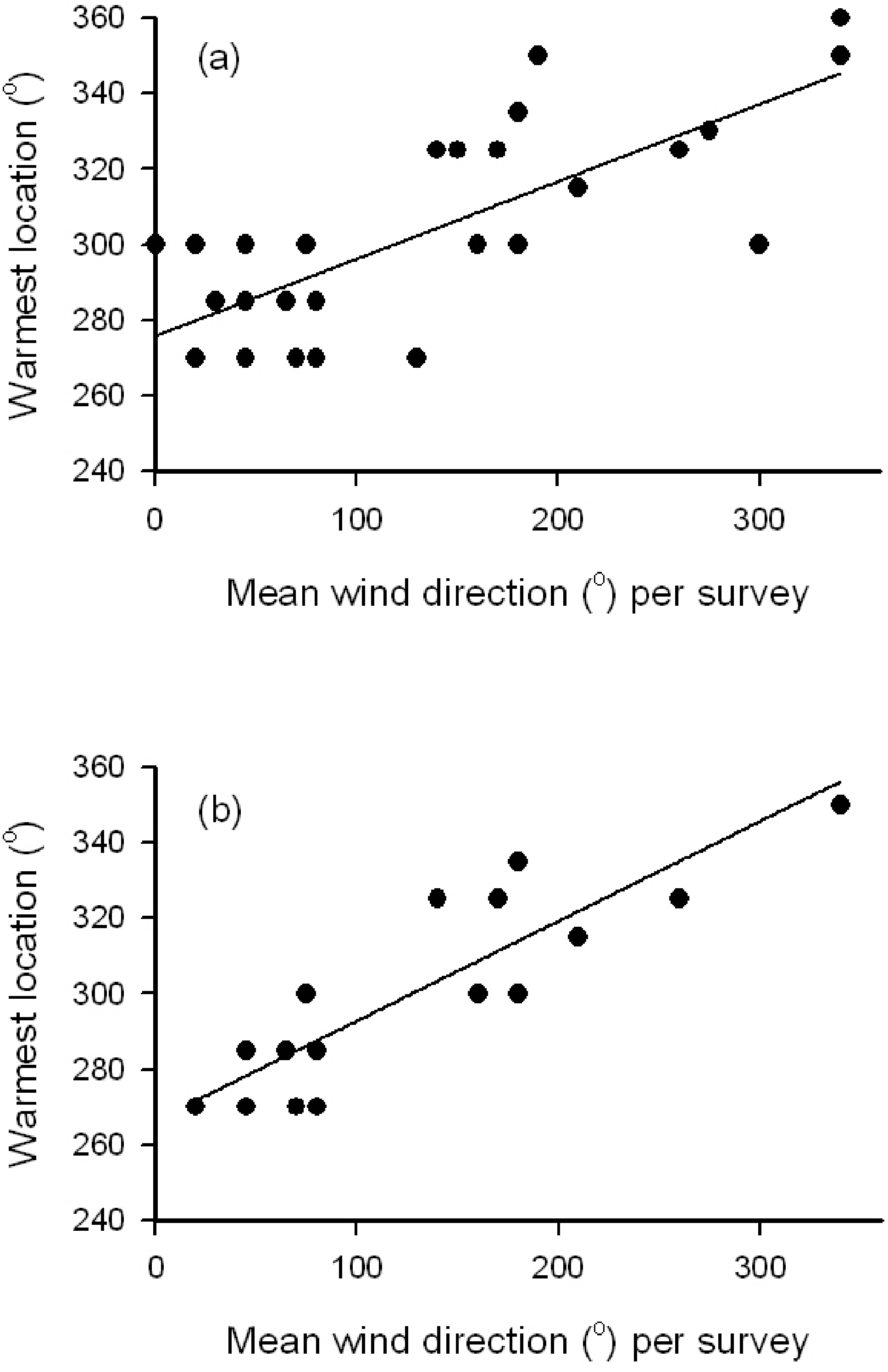

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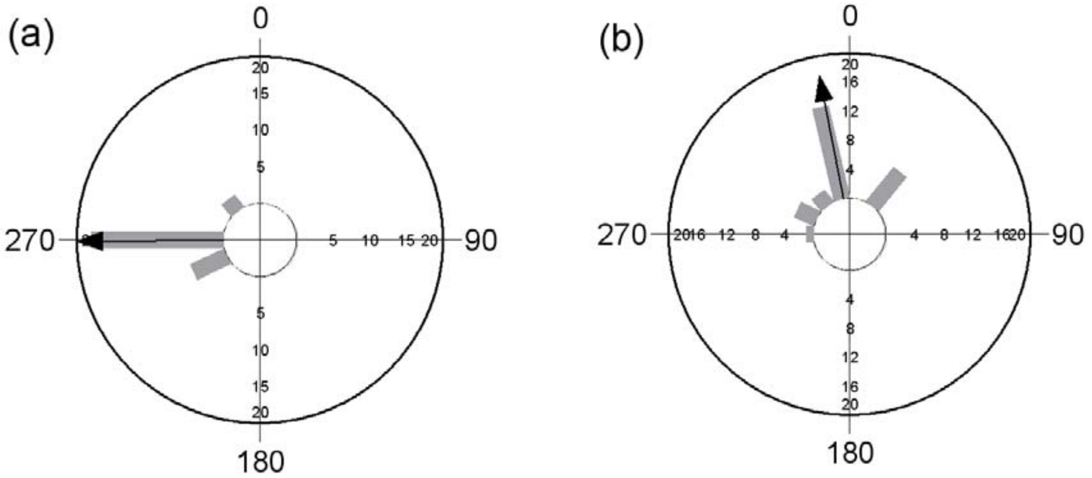

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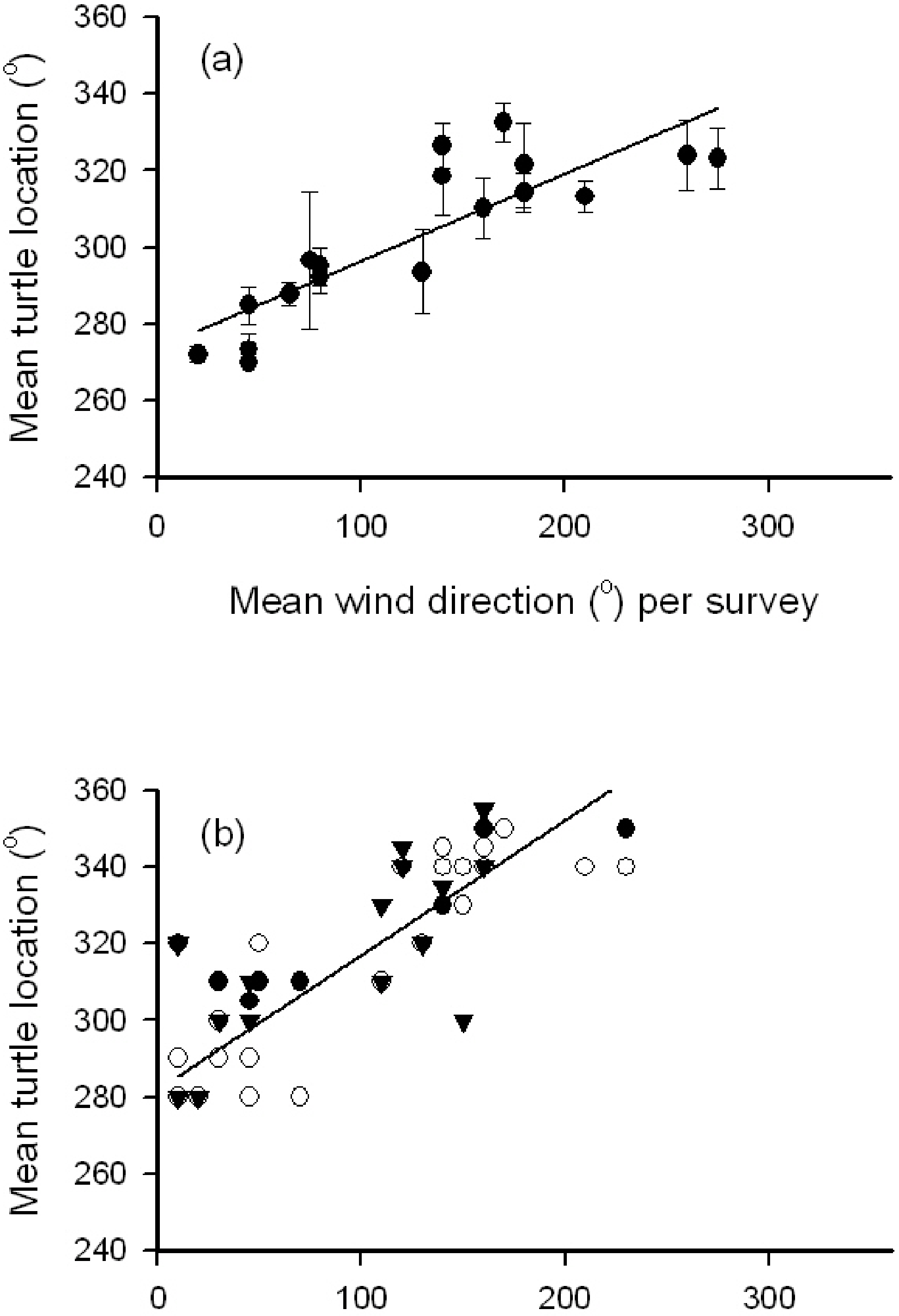

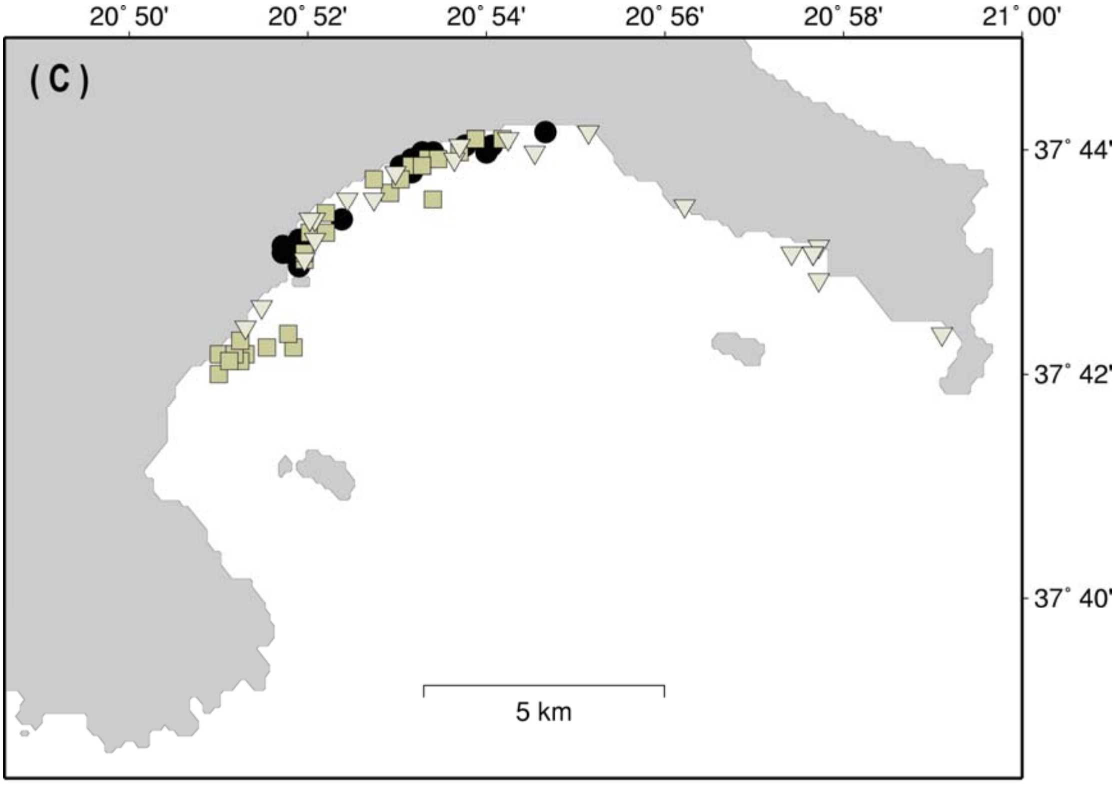
20° 50'
20° 52'
20° 54'
20° 56'
20° 58'
21° 00'
(C)
37° 44'
37° 42'
37° 40'
5 km

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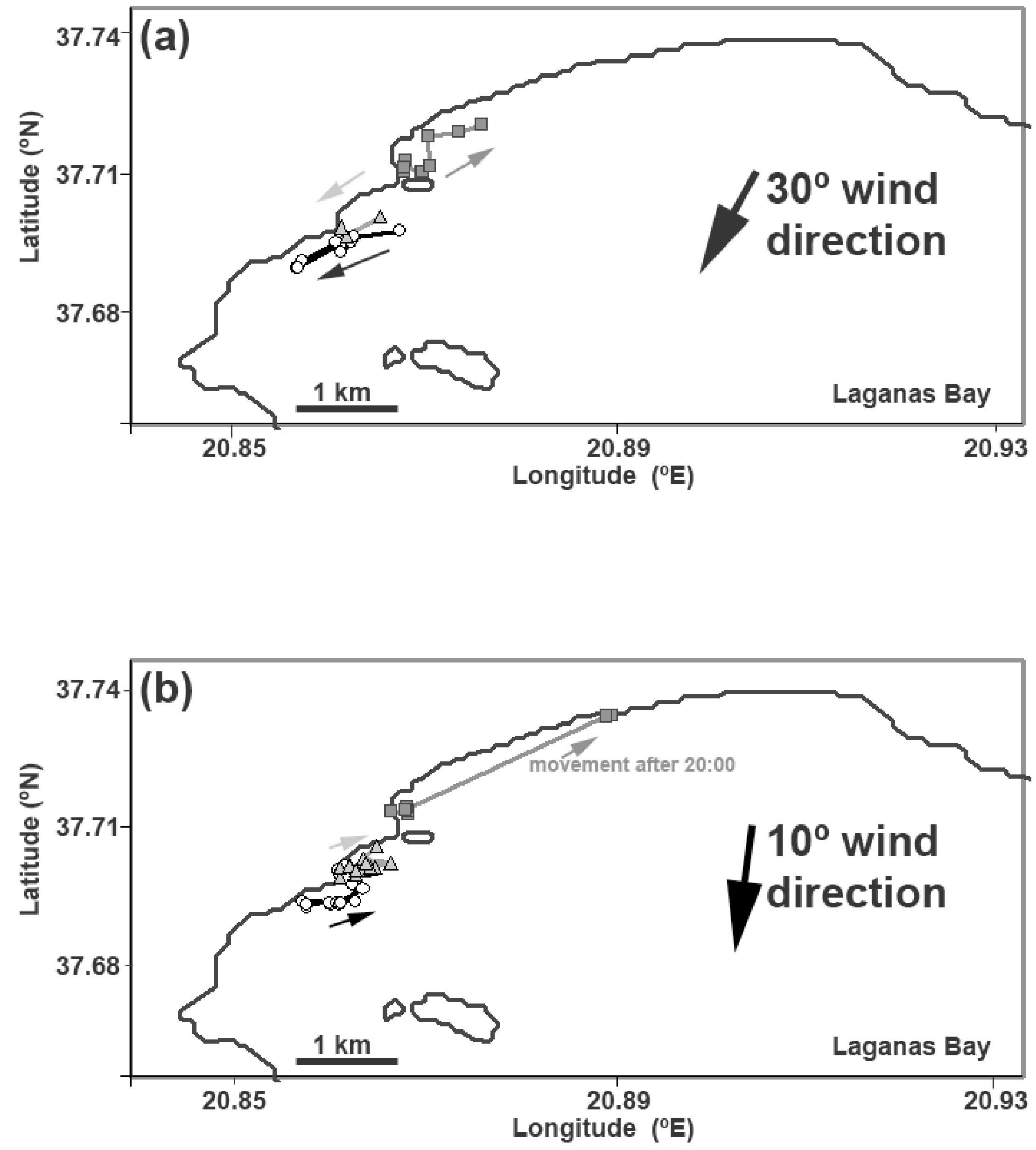
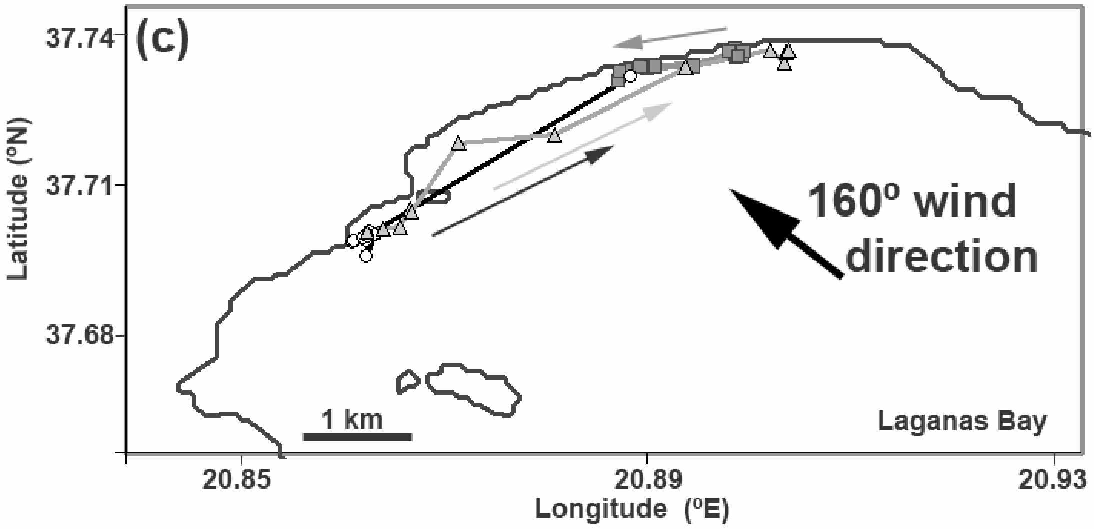
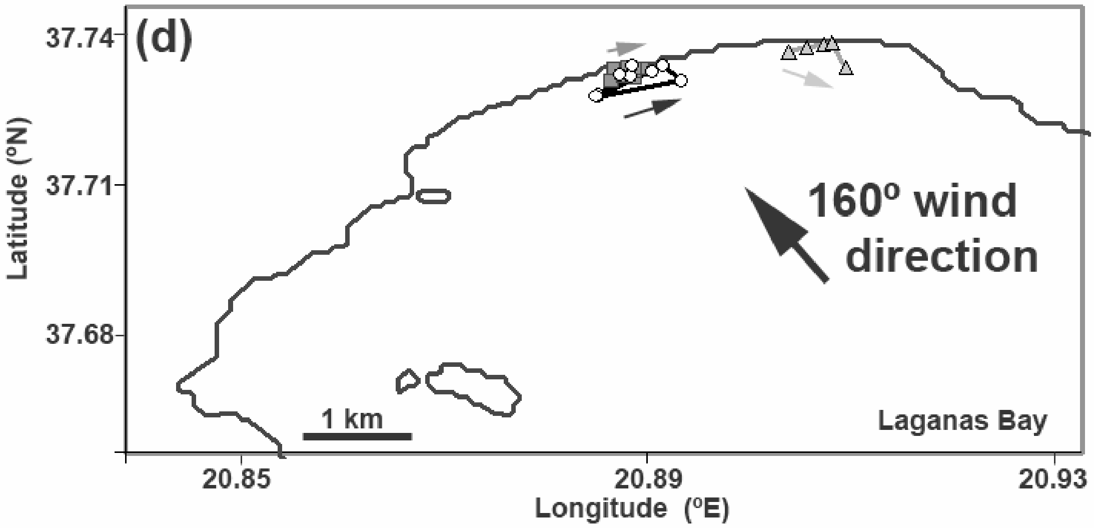



(c)
37.74
37.71
37.68
Latitude (°N)
160° wind direction
1 km
Laganas Bay
20.85
20.89
20.93
Longitude (°E)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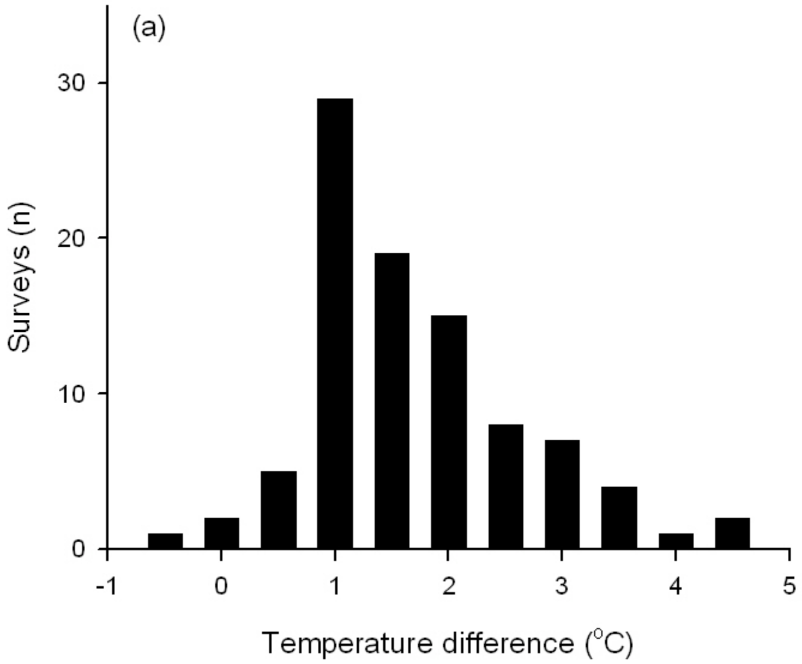

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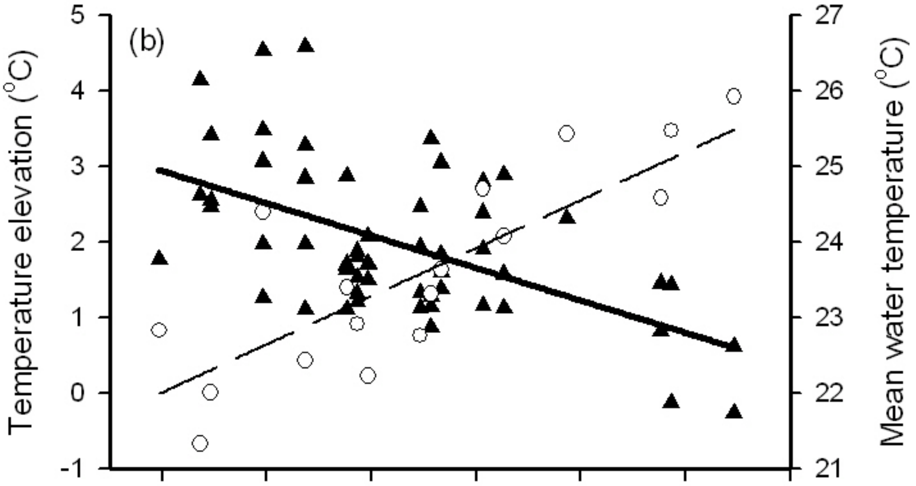

ΓΕΝΙΚΗ ΣΥΖΗΤΗΣΗ

Η παρούσα διδακτωρική διατριβή χρησιμοποιεί ένα εύρος άμμεσων και έμμεσων μεθολογιών για να προσφέρει νέες ιδέες σχετικά με την θαλάσσια οικολογία των θαλάσσιων χελωνών και την προστασία και διαχείρισή τους στο θαλάσσιο περιβάλλον, στον κόλπο του Λαγανά ο οποίος αποτελεί τον μεγαλύτερο βιότοπο αναπαραγωγής τους στη Μεσόγειο. Η έρευνα παρουσιάζει την πρώτη λεπτομερειακή αποτίμηση της δομής του πληθυσμού, της ηθολόγίας, των κινήσεων και της κατανομής των ενήλικων αρσενικών και θηλυκών θαλάσσιων χελωνών στον βιότοπο αναπαραγωγής τους. Καθώς ο βιότοπος βρίσκεται στα όρια της αναπαραγωγικής ακτίνας των θαλάσσιων χελωνών, οι οποίες είναι ερπετά και επομένως εξώθερμα ζώα, η έρευνά μας επεσήμανε ότι οι παράμετροι αναπαραγωγής δεν μπορούν να μελετηθούν ξεχωριστά από τις περιβαλλοντικές παραμέτρους, όπως η θερμοκρασία της θάλασσας.

Το πρώτο Κεφάλαιο είναι βασικό στην παρούσα έρευνα, καθώς η τεχνική της φωτο-αναγνώρισης επέτρεψε την ταυτοποίηση σε ξεχωριστά άτομα του πληθυσμού. Η φωτο-αναγνώριση έχει το πλεονέκτημα να είναι η κατάλληλη μέθοδος για τις αρσενικές θαλάσσιες χελώνες, οι οποίες δεν βγαίνουν στην ακτή (αλλά βλέπε Rice & Balazs, 2008), ώστε να είναι δυνατό να μαρκαριστούν με συμβατικές μεθόδους, αλλά απαιτείται η χρήση της δύσκολης τεχνικής της σύλληψης στη θάλλασα (π.χ. Hays *et al.*, 2001b; James *et al.*, 2005b), και έτσι δύσκολα ταυτοποιούνται. Τα φωτογραφικα δεδομένα παρέχουν την ευκαρία για τη διερεύνηση ενός εύρους παραμέτρων, οι οποίες μπορεί να επηρεάζουν τη διαχείριση και προστασία ενός είδους και την αποτίμηση οικολογικών κινδύνων, όπως η αφοσίωση σε μία περιοχή, τα πρότυπα αλληλεπίδρασης, τις φυσικές συνθήκες, τους δείκτες υγείας και την επίπτωση των ανθρωπογενών δραστηριοτήτων (Burger & Garber, 1995; Bennett *et al.*, 1999; Pettis *et al.*, 2004; Lusseau *et al.*, 2006). Το κεφάλαιο 1 καταδεικνύει, με τη χρήση δοκιμών, την εγκυρότητα, ή ακρίβεια, και την αξιοπιστία, ή πιστότητα, των φυσικών σημαδιών για την καταχώρηση ατόμων θαλάσσιων χελωνών σε ομάδες σύμφωνα με ένα απλό δένδρο αναγνώρισης, με τιν τρόπο αυτό όταν μια φωτογραφία έχει καταχωρηθεί σε μία ομάδα, τα σημάδια της μπορούν να χρησιμοποιηθούν για να την ταιριάξουν με ακρίβεια με άλλες φωτογραφίες του ίδιου ατόμου ανάμεσα σε πλήθος άλλες. Τα αποτελέσματα παρουσιάζουν μεγάλη ικανότητα στην ταξινόμηση των φωτογραφιών από όλες τις ομάδες των ερευνητών (68-100%), με τους άπειρους ερευνητές να μπορούν να αποκτήσουν τις απαραίτητες ικανότητες φωτο-ταξινόμησης με μια εικοσάλεπτη εκπαίδευση. Η δυσκολία της σύγκρισης και ταξινόμησης μεγάλου αριθμού φωτογραφιών (>400) ξεπεράστηκε με το διαχωρισμό των φωτογραφιών σε αρκετές ομάδες με λιγότερες από 100 φωτογραφίες, βασιζόμενοι στις διαφορές ενός μόνο σετ των χαρακτηριστικών του προσώπου. Ένα μικρό ποσοστό λάθους καταγράφηκε κατά τη διάρκεια των δοκιμών, από το οποίο οι λάθος θετικές περιπτώσεις (ταύτιση δύο φωτογραφιών από διαφορετικά άτομα, το οποίο οδηγεί σε υποεκτίμηση του πληθυσμού) ήταν λίγο περισσότερες από τις λάθος αρνητικές περιπτώσεις (μη ταύτιση, το οποίο οδηγεί σε υπερεκτίμηση του πληθυσμού). Επομένως, το σύνολο των λαθών κατά τη διάρκεια των χρόνου στη βάση δεδομένων, οδηγεί σε υπερεκτίμηση ή υποεκτίμηση του μεγέθους του πληθυσμού (Stevick *et al.*, 2001), είναι αμελητέο. Καθώς η βάση δεδομένων με φωτογρφίες συνεχώς μεγαλώνει, θα είναι απαραίτητο να αναπτυχθεί ένα πρόγραμμα ηλεκτρονικού υπολογιστή για τη σύγκριση και ταυτιση, όπως έχει αναπτυχθεί για διάφορα άλλα είδη σπονδυλωτών με τεράστιες βάσεις δεδομένων φωτογραφιών (Kelly, 2001; Hillman *et al.*, 2003; Beekmans *et al.*, 2005).

Στο δεύτερο Κεφάλαιο, η εντατική παρατήρηση των θαλάσσιων χελωνών μέσα στο νερό, διαφέρει από τις υπάρχουσες έρευνες σε περιοχές αναπαραγωγής στο ότι, αντί να καθορίζει ειδικά την συμπεριφορά κατά την ερωτοτροπία και το ζευγάρωμα (Booth & Peters, 1972; Dodd, 1988; Frick *et al.*, 2000), ή τα πρότυπα κινήσεων κατά τη διάρκεια της περιόδου φωλεοποίησης (Hopkins-Murphy *et al.*, 2003), διερευνά το σύνολο της συμπεριφοράς και ηθολογίας των θαλάσσιων χελωνών κατά την περίοδο αυτή. Οι έρευνες με απευθείας παρατηρήσεις στο θαλάσσιο περιβάλλον έχουν μεγάλη αξία για την ανάπτυξη της γνώσης μας σχετικά με τη συμπεριφορά των θαλάσσιων σπονδυλωτών, την επικύρωση των από απόσταση τεχνολογιών και συνεισφέρουν θετικά στη μελέτη και παρακολούθηση των οικοσυστημάτων. Οι δραστηριότητες που παρατηρήθηκαν ομαδοποιήθηκαν σε 4 μονήρει συμπεριφορές (ξεκούραση, κολύμπι, αναζήτηση τροφής, καθαρισμό) και 2 κοινωνικές συμπεριφορές (ανταγωνιστική αλληλεπίδραση, αναπαραγωγική δραστηριότητα), οι οποίες διαιρέθηκαν σε 14 υποκατηγορίες. Τα αποτελέσματα δείχνουν ότι, γενικά τα αρσενικά ήταν πιό δραστήρια και κοινωνικά από τα θηλυκά, το οποίο αποδίδεται στην ανάγκη για εύρεση περισσότερων ερωτικών συντρόφων για τη μεγιστοποίηση της αναπαραγωγικής ικανότητας, όταν στα θηλυκα αυτή μεγιστοποιείται με τη διατήρηση και την απόδοσή των ενεργειακών τους αποθεμάτων στην κατεύθυνση της ανάπτυξης των αυγών (Hays *et al.*, 2002a; Hopkins-Murphy *et al.*, 2003).

Οι έρευνα έδειξε ότι η συμπεριφορά των θαλάσσιων χελωνών *Caretta caretta* κατά την ερωτοτροπία και το ζευγάρωμα ακολούθησε παρόμοια πρότυπα με αυτά τα οποία έχουν τεκμηριωθεί σε άλλες έρευνες του ίδιου ή διαφορετικών ειδών θαλάσσιων χελωνών (Booth & Peters, 1972; Dodd, 1988; Frick *et al.*, 2000; Godley *et al.*, 2002; Rostal, 2005). Στους “γύρους” ερωτοτροπίας με μη δεκτικά θηλυκά, καταγράψαμε και τεκμηριώσαμε τη χρήση των ελλιγμών αποφυγής. Όπως και με άλλα είδη, παρατηρήσαμε ότι τα αρσενικά άτομα εντατικά αναζητούν δεκτικά θηλυκά (Jessop *et al.*, 1999) με το να περιπολούν την περιοχή, αλλά επίσης διαπιστώσαμε την ύπαρξη της διαμάχης μεταξύ αρσενικών, πιθανά για την κυριαρχία στην κατάσκτηση των θηλυκών. Περαιτέρω, ενώ η ύπαρξη ανταγωνισμού μετάξη των αρσενικών κατά τη διάρκεια του ζευγαρώματος έχει καταγραφεί σε άλλα είδη θαλάσσιων χελωνών (Booth & Peters, 1972), δεν είχε καταγραφεί για τις *Caretta caretta* (Frick *et al.*, 2000) έως την παρούσα έρευνα. Υψηλά επίπεδα, πολλαπλής πατρότητας στα αυγά μιας φωλιάς, έχει καταγραφεί στον πληθυσμό της *Caretta caretta* στη Ζάκυνθο (Zbinden *et al.*, 2007c), από το οποίο εξάγονται συμπεράσματα σχετικά με τα επίπεδα πολυανδρίας στον πληθυσμό της Ζακύνθου. Διατυπόθηκε η υπόθεση ότι μια μεγάλητερη αναλογια θηληκών στον πλυθησμό παράγει υψηλότερα επίπεδα πολλαπλής πατρότητας, καθώς μειώνει την ανταγωνιστικότητα μεταξύ των αρσενικών, καθώς επίσης και ότι οι μεγαλύτερες θηλυκες εμφανίζουν για υψηλότερα επίπεδα πολλαπλής πατρότητας (Zbinden *et al.*, 2007c). Ωστόσο, οι απευθείας παρατηρήσεις της συμπεριφοράς των αρσενικών χελωνών στην παρούσα έρευνα έδειξαν υψηλά επίπεδα ανταγωνισμού ανάμεσα στα αρσενικά, παρόλη την υψηλή αναλογία θηληκών ατόμα (βλέπε την εκτίμηση στο Κεφάλαιο 5). Για τη διερεύνηση αυτής την υπόθεσης θα χρειαστεί να υπολογιστεί η αφθονία του πληθυσμού, η πυκνότητά του, η λειτουργική αναλογία φύλων, τα πρότυπα κινήσεων, οι στρατηγικές ζευγαρώματος και οι κλάσεις μεγεθών των αρσενικών και θηλυκών ατόμων κατά την περίοδο της αναπαραγωγής. Αυτές οι πληροφορίες μπορούν να αποκτηθούν μέσω της απευθείας παρατήρησης της συμπεριφοράς, μιας εκτενούς βάσης δεδομένων ταυτοποίησης των ατόμων (π.χ. με φωτο-αναγνώριση) και λεπτομερούς ιχνηλάτησης ατόμων του πληθυσμού.

Στο Κεφάλαιο 2 παρουσιάζονται δεδομένα σχετικά με το ότι οι θαλάσσιες χελώνες επενδύουν σε ενεργές συμπεριφορές, οι οποίες δεν είχαν παρατηρηθεί στο παρελθόν, κατά τη διάρκεια της περιόδου αναπαραγωγής. Παράδειγμα τέτοιων συμπεροφορων είναι η εύρεση τροφής, ο καθαρισμός (αυτο-καθαρισμός και καθαρισμός από ψάρια) και ο συναγωνισμός ανάμεσα σε θηλυκές. Τα υψηλά ποσοστά επιβιωτών στο καβούκι (Frick *et al.*, 1988) και μια πρόσφατη επιστημονική έρευνα με τη χρήση ηλεκτρονικών οργάνων πάνω στο καβούκι χελωνών (Heithaus *et al.*, 2002b) οδήγησαν τους επιστήμονες να προτείνουν ότι οι *Caretta caretta* δεν επενδύουν τόσο πολύ στην συμπεριφορά καθαρισμού τους όσο άλλα είδη χελωνών (Bjorndal, 2003). Ωστόσο, αν και παρατηρήσαμε τις συμπεριφορές του αυτο-καθαρισμού και του καθαρισμού από ψάρια σε λίγες περιπτώσεις, τα φωτογραφικά δεδομένα παρουσιάζουν απτές αποδείξεις του αυτο-καθαρισμού, από τα χαρακτηριστικά σημάδια στο καβούκι, σε ένα μεγάλο μέρος του πληθυσμού που μελετήθηκε, δείχνοντας ότι οι *Caretta caretta* στον κόλπο Λαγανά επενδύουν στη δραστηριότητα του καθαρισμού. Σποραδικές προσπάθειες διατροφής με μαλάκια παρατηρήθηκαν τόσο σε αρσενικές όσο και σε θηλυκές *Caretta caretta* στον κόλπο Λαγανά. Ωστόσο, ο χρόνος εύρεσης τροφής ήταν μικρός, πιθανότατα επειδή υπήρχε η ανάγκη κατανάλωσης χρόνου και ενέργειας σε άλλες δραστηριότητες (π.χ. την εύρεση θηλυκών από τα αρσενικά), καθώς επίσης γιατί η πυκνότητα της λείας στην περιοχή ήταν τόσο χαμηλή ώστε ήταν περισσότερο επικερδές (π.χ. για τα θηλυκά) το να ξεκουραστούν από το να προσπαθήσουν να τραφούν. Παρότι ο ανταγωνισμός για την κυριαρχία χώρου ανάμεσα σε άτομα θαλάσσιων χελωνών έχει αναφερθεί χωρίς να περιγραφεί στη βιβλιογραφία (Limpus & Limpus, 2003), η έρευνά μας έδειξε ότι οι ανταγωνιστικές αλληλεπιδράσεις μεταξύ των θηλυκών *Caretta caretta*, είναι ένα σημαντικό στοιχείο της δραστηριότητάς τους κατά τη διάρκεια της αναπαραγωγικής περιόδου και γι'αυτό έγινε θέμα λεπτομερούς ανάλυσης στο Κεφάλαιο 3.

Ο τρόπος με τον οποίο τα άτομα του ίδιου είδους ανταγωνιζονται για τους φυσικούς πόρους επέτρεψε στους ερευνητές να μετρήσουν αντικειμενικά τη σημασία που έχει ένα ιδιαίτερο περιβάλλον, οικότοπος ή οικοσύστημα για ένα ζώο. Η ανάλυση του ενδοειδικού ανταγωνισμού ανάμεσα στα θηλυκά στο Κεφάλαιο 3 έδειξε ότι αυτή η αλληλεπίδραση εμπεριέχει κλιμάκωση της συμπεριφοράς από παθητικές απειλιτικές επιδείξεις (π.χ. να γυρίζουν γύρω-γύρω η μία από την άλλη), έως επιθετική συμπεριφορά (π.χ. αψιμαχίες), ο βαθμός των οποίων εμφανίζεται να διαφέρει ανάλογα με την κατάσταση της συμπεριφοράς τους. Η ανάλυση των ανταγωνιστικών δράσεων ανάμεσα στις θηλυκές *Caretta caretta* υποδεικνύει ότι με το να γυρίζουν η μία γύρω από την άλλη αξιολογούν το μέγεθος της αντιπάλου, ενώ με τις αψιμαχίες εκτιμούν τη δύναμη της αντιπάλου, καθώς επίσης και ότι η θέση της ουράς μεταδίδει την πρόθεση τους να κλιμακώσουν την πάλη ή να εγκαταλείψουν. Τα δεδομένα δείχνουν ότι ορισμένες περιοχές προτιμούνται και για αυτό οι χελώνες τις υπερασπίζονται. Το θαλάσσιο περιβάλλον δεν είναι ομοιογενές και η συμπεριφορά αυτή υποδεικνύει ότι οι χελώνες ανταγωνίζονται για τους σπάνιους υψηλής ποιότητας φυσικούς πόρους. Οι παρατηρήσεις υποστηρίζουν το υπόθεση της “ανάμειξης” του πληθυσμού, το οποίο προήλθε από την “Ιδανική Ελευθερή Κατανομή” (‘Ideal Free Distribution’) (Fretwell, 1972; Sutherland & Parker, 1986). Αυτή υποστηρίζει ότι οι θέσεις ξεκούρασης στον πυθμένα της θάλασσας αντιπροσωπεύουν βέλτιστους φυσικούς πόρους για τους οποίους οι θηλυκές θαλάσσιες χελώνες ανταγωνίζονται, ενώ η ξεκούραση στην επιφάνεια της θάλασσας γίνεται σε “μη βέλτιστες” θέσεις με συνέπεια να υπάρσει λιγότερος ανταγωνισμός.

Αυτή η συμπεριφορά μπορεί να προκύπτει από το γεγονός ότι ο ανταγωνισμός για μια θέση γίνεται για την απόκτηση καταφυγίου από ενεργοβόρες συναντήσεις, καθώς τα αρσενικά περιπολούν την περιοχή για την εύρεση δεκτικών θηλυκών (Booth & Peters, 1972; Whittow & Balazs, 1982; Lee & Hays, 2004). Σε αυτή την περίπτωση, ο χώρος μπορεί να είναι περιοριστικός παράγοντας, καθώς τα θηλυκά τα οποία ξεκουράζονται το ένα κοντά στο άλλο μπορεί να τραβήξουν την ανεπιθύμητη προσοχή των αρσενικών. Ωστόσο, τα θηλυκά που καταλαμβάνουν μια περιοχή ανταποκρίνονται στα αρσενικά τα οποία εισέρχονται στην ακτίνα όρασής τους με μία κάθετη “αρνητική” στάση (Booth & Peters, 1972), η οποία δεν παρατηρείται κατά την αλληλεπίδραση θηλυκού με θηλυκό παρά μόνο στην “επιθετική φάση”. Μια εναλλακτική θεωρία, η οποία αναπτύχθηκε προτείνει ότι, η διαμάχη ανάμεσα στις θηλυκές γίνεται για τις θερμοκρασιακά βέλτιστες οικοθέσεις ώστε να ενισχύσουν την ανάπτυξη των αυγών τους. Μελέτες έχουν αποδείξει ότι, στα ερπετά, η θερμοκρασία του περιβάλλοντος επηρεάζει την ανάπτυξη των αυγών και την βιωσιμότητα των νεοσσών, όπως επίσης την ανάπτυξη των ενήλικών και την επιβίωσή τους (π.χ. σαύρες: Wapstra, 2000; φίδια: Ladyman *et al.*, 2003). Είναι επομένως πιθανόν ότι οι θηλυκές θαλάσσιες χελώνες, ιδιαίτερα σε περιοχές με εύκρατο κλίμα όπως η Ζάκυνθος, ανταποκρίνονται σε θερμικά "σίνιαλα" και αναζητούν πιο θερμά νερά ώστε να επιταχύνουν την ανάπτηξη των αυγών τους. Η θεωρία αυτή ενισχύεται από συγκριτικές μελέτες της κατανομής των θαλάσσιων χελωνών αναμέσα σε εύκρατες και τροπικές περιοχές αναπαραγωγής όπου: στην πρώτη περίπτωση, που η θερμοκρασία της θάλασσας είναι πιο ψυχρή, οι θηλυκες χελώνες σχηματίζουν πυκνές συναθροίσεις κοντά στην ακτή, ενώ στη δεύτερη περίπτωση παραμένουν πιο διασκορπισμένες (π.χ. Hays *et al.*, 2002b). Με σκοπό να μελετήσουμε ιδιαίτερα τις πιθανές αιτίες των κοινωνικών αλληλεπιδράσεων ανάμεσα στις θηλυκες θαλάσσιες χελώνες, σύμφωνα με την παραπάνω θεωριά, η οποία βασίστηκε σε απ' ευθείας παρατήρησεις, οδηγηθήκαμε στη λεπτομερειακή διερεύνηση με τη χρήση απομακρυσμένων τεχνολογίων ώστε να βρούμε εάν η κατανομή των χελωνών αλλάζει σε συνάρτηση με τη μεταβολή της θερμοκρασίας στο θαλάσσιο περιβάλλον, (Κεφάλαιο 6).

Όπως δείξαμε στα Κεφάλαια 1 έως 3, οι απευθείας παρατηρήσεις της συμπεριφοράς των θαλάσσιων χελωνών είναι πολύ σημαντικές και ανοίγουν τη δυνατότητα σε νέους δρόμους σκέψεις, οι οποίοι είναι δύσκολο ή αδύνατο να αποκτηθούν με έμμεσες μεθόδους ή με τη χρήση καμερών τοπεθετημένων στο καβούκι των θαλάσσιων χελωνών. Ωστόσο, η απευθείας παρατήρηση ενός ζωντανού θαλάσσιου ζώου έχει περιορίσμούς. Για παράδειγμα η έρευνά μας είχε τους περιορισμούς της ώρας της ημέρας, τις συνθήκες και του βάθους της θάλασσας. Εξαιτίας τέτοιων περιορισμών, η χρήση απομακρυσμένης τεχνολογίας γίνεται συνεχώς πιο ευρεία. Παρόλα αυτά η χρήση αυτής της τεχνιξής χωρίς τη σύνδεσή της με απευθείας παρατηρήσεις, παράγει μόνο εικασίες σχετικά με τη συμπεριφορά και τις δραστηριότητες των ζώων. Μελέτες, οι οποίες συγκρίνουν άμεσες και έμμεσες μεθοδολογίες για τη συμπεριφορά ζώων, έχουν δείξει ότι οι απομακρυσμένες τεχνολογίες μπορούν να διαχωρίσουν τις ενεργές από τις μη ενεργές καταστάσεις των ζώων, δεν μπορούν όμως να ξεχωρίσουν με αξιοπιστία τα διαφορετικά πρότυπα συμπεριφοράς μέσα σε αυτές τις καταστάσεις

(Hansen *et al.*, 1992; Heithaus *et al.*, 2001). Τα αποτελέσματα στα Κεφάλαια 2 και 3 δείχνουν ότι οι *Caretta caretta* επιδεικνύουν πολύ μεγαλύτερο εύρος συμπεριφορών, στις περιοχές αναπαραγωγής, από ότι είχε έως τώρα τεκμηριωθεί. Είναι επομένως πιθανόν, ότι τα έμμεσα συμπεράσματα σχετικά με τα πρότυπα κινήσεων, τα οποία βασίζονται σε ανάλυση των δεδομένων από τους αισθητήρες, να υπόκεινται σε λάθος, όπως απέδειξε ο Houghton *et al.* (2002). Η ανάπτυξη των ηλεκτρονικών έχει κάνει τις υποβρύχιες βιντεοκάμερες εφικτές οικονομικά, δίνοντας έτσι τη δυνατότητα στους ερευνητές να παρατηρήσουν και να επιβεβαιώσουν τη συμπεριφορά των ζώων κάτω από το νερό (Davis *et al.*, 1999; Heithaus *et al.*, 2002b; Reina *et al.*, 2005; Hays *et al.*, 2006). Επομένως, η γνώση για τη συμπεριφορά των ζώων στο φυσικό τους περιβάλλον, η οποία αποκτήθηκε με άμεσες παρατηρήσεις, είναι απαραίτητη ώστε να βελτιωθεί η ακρίβεια της ερνηνείας των δεδομένων των απομακρυσμένων τεχνολογιών. Με τη συλλογή άμεσων δεδομένων σχετικά με τη συμπεριφορά των ζώων, οι ηλεκτρονικές συσκευές μπορούν να χρησιμοποιηθούν επιπλέον για την απόκτηση συγκεκριμένων πληροφοριών σε σχέση με τις τάσεις στην κοινωνική συμπεριφορά και τη χρήση των βιοτόπων από τα ζώα. Επομένως, η ανάλυση των πληροφοριών που αποκτήθηκαν από απευθείας παρατηρήσεις (Κεφάλαια 1 έως 3), έδωσε τη βασική γνώση από την οποία ερωτήσεις που γεννήθηκαν, απαντήθηκαν στα Κεφάλαια 4 έως 6 με τη χρήση απομακρυσμένης ιχνηλάτησης (remote tracking).

Στα Κεφάλαια 4 και 5 φαίνεται πως οι μονάδες ιχνηλάτησης GPS (καταγραφείς και μεταδότες), οι οποίοι τοποθετήθηκαν σε αρσενικά και θηλυκά άτομα θαλάσσιων χελωνών, μπορούν να χρησιμοποιηθούν για την απόκτηση χωρικών πληροφοριών σχετικά με τα λεπτομερειακά πρότυπα των κινήσεών των θαλασσιων χελωνών σε τοπικό και περιφερειακό επίπεδο, επιδεικνύοντας την αξία αυτής της τεχνικής σε σχέση με τη διαχείριση και προστασία. Για την αποτελεσματική διαχείριση, προστασία και βιώσιμη χρήση των θαλάσσιων περιοχών, είναι σημαντική η κατανόηση των σχέσεων ανάμεσα στους πληθυσμούς και στους βιότοπούς τους (Castilla, 2000; Canadas *et al.*, 2005), καθώς επίσης και η γνώση της επίδρασης των περιβαλλοντικών και ανθρωπογενών παραμέτρων (Thompson *et al.*, 2000; Tisdell & Wilson, 2002; Douglas-Hamilton *et al.*, 2005; Preisler *et al.*, 2006). Ο όγκος των δεδομένων και ο βαθμός ακρίβειας, σε σχέση με τα λεπτομερειακά πρότυπα κινήσεων, τα οποία αποκτήθηκαν με τη χρήση των μονάδων GPS, δεν θα μπορούσαν να αποκτηθούν με τη συμβατική τηλεμετρία (Hays *et al.*, 2001a; Hulbert & French, 2001; Tremblay *et al.*, 2006; Bradshaw *et al.*, 2007b). Τα δεδομένα που αποκτήθηκαν με τις μονάδες GPS στην περιοχή αναπαραγωγής δείχνουν ότι οι θαλάσσιες χελώνες, θηλυκές και αρσενικές, πριν την έναρξη της περιόδου ωοτοκίας χρησιμοποιούν κυρίως μια περιοχή σε απόσταση 500μ. από την ακτογραμμή (σε βάθος <5μ.) και με μήκος 9 χιλιόμετρα, από τα συνολικά 27.8 χιλιόμετρα της ακτογαρμμής. Οι παρατηρήσεις αυτές υποστηρίζουν υπάρχουσες εργασίες οι οποίες προτείνουν ότι οι θηλυκές χρησιμοποιούν θαλάσσια βάθη έως 15μ. στις περιοχές αναπαραγωγής (Hopkins-Murphy *et al.*, 2003), ωστόσο τα στοιχεία μας υποδεικνύουν τη χρήση από τα αρσενικά μιας πολύ στενότερης περιοχής βαθών, από τις έως σήμερα καταγραφές για χρήση θαλάσσιων βαθών έως 40μ. (Shaver *et al.*, 2005b). Ένα από τα αρσενικά τα οποία παρακολουθήσαμε, παρέμεινε στην περιοχή αναπαραγωγής, με μια αξιοπρόσεκτη αλλαγή στη χρήση βαθύτερων νερών μετά την έναρξη της ωοτοκίας. Η αλλαγή αυτή μπορεί να αντανακλά μια αλλαγή στην κατάσταση του ζώου, π.χ. από αναπαραγωγή σε διατροφή, και μπορεί να εξηγήσει τις καταγραφές χρήσης μεγαλυτερου εύρους βαθών από τις αρσενικές χελώνες, που έγιναν σε άλλες αναπαραγωγικές περιοχές (Shaver *et al.*, 2005b).

Η θέση της παραλίας ωοτοκίας και η σχετική πυκνότητα φωλεοποίησης χρησιμοποιήθηκαν στο παρελθόν για να προσδιοριστεί ο βαθμός προστασίας που θα πρέπει να έχουν οι γειτνιάζουσες θαλάσσιες ζώνες στον κόλπο του Λαγανά (Arapis & Margaritoulis, 1996). Η χρήση της ιχνηλάτησης των θηλυκών με GPS το 2006 και 2007 δείχνει επιπλέον την προτίμηση χρήσης της περιοχής, κοντά στην ακτογραμμή, η οποία βρίσκεται εκτός του πυρήνα προστασίας των θαλάσσιων περιοχών. Παρόμοια πρότυπα χρήσης θαλάσσιας περιοχής έχουν καταγραφεί και για τα αρσενικά. Παρότι οι θηλυκές θαλάσσιες χελώνες περνούν τον περισσότερο χρόνο τους εκτός της περιοχής όπου ισχύει απαγόρευση σκαφών, ένα σημαντικό ποσοστό του πληθυσμού ωοτοκεί σε κάποια από τις παραλίες ωοτοκίας που βρίσκονται εντός της περιοχής αυτής (Katselidis *et al.*, 2004), και τα δεδομένα μας υποδεικνύουν ότι οι χελώνες, λίγες ημέρες πριν την ωοτοκία, προτιμούν να συνχάζουν στη θαλάσσια περιοχή που γειτνιάζει με την παραλία ωοτοκίας που θα βγουν για να γεννήσουν. Αποτέλεσμα αυτού είναι ότι ο πυρήνας αυτός των θαλάσσιων περιοχών παραμένει πολύ σημαντικός για την προστασία και διαχείριση του βιοτόπου. Τα δεδομένα κινήσεων και βάθους δείχνουν ότι οι θηλυκές θαλάσσιες χελώνες προτιμούν να παραμένουν σε πολύ ρηχά νερά σε περιοχές με αμμώδη βυθό. Τα κριτήρια αυτά βρέθηκαν να ισχύουν μόνο για τη δύο λιγότερο προστατευόμενες θαλάσσιες περιοχές του κόλπου Λαγανά. Τα αποτελέσματα που παρουσιάζονται στα Κεφάλαια 4 και 5 παρέχουν αποδείξεις οι οποίες δείχνουν ότι ο σχεδιασμός των θαλάσσιων ζωνών, για να παρέχουν την απαραίτητη προστασία, θα πρέπει να βασίζεται στο κριτήριο της χρήσης της θαλάσσιας περιοχής από τις χελώνες (π.χ. βάθος, γειτνίαση με την ακτογραμμή και προτίμηση χρήσης), και όχι, όπως ισχύει, μόνο στη θέση των παραλιών ωοτοκίας. Τα δεδομένα μας υποστηρίζουν την οριοθέτηση το 2006 από το Φορέα Διαχείρισης Ε.Θ.Π.Ζ., της νέας πιλοτικής “οικοτουριστικής ζώνης” και την ισχυροποίηση των μέτρων σχετικά με τις δραστηριότητες των πλωτών μέσων στη ζώνη αυτή (Lusseau, 2004), και την επέκτασή της ώστε να περιλαμβάνει την κύρια περιοχή κοντα στην ακτογραμμή, η οποία χρησιμοποιείται και από τα δύο φύλα των θαλάσσιων χελωνών. Παρόλα αυτά χρειάζεται νομοθετική ρύθμιση για τον επανασχεδιασμό των θαλάσσιων ζωνών προστασίας, κάτι το οποίο είναι δύσκολο να πραγματοποιηθεί (Togridou *et al.*, 2006a; Campbell, 2007; Lawton, 2007). Καθώς τόσο τα αρεσενικά όσο και τα θηλυκά χρησιμοποιούν την περιοχή των θαλάσσιων ζωνών με τη μικρότερη προστασία για πάνω από το 50% του χρόνου τους, είναι πολύ σημαντικό να ποσοτικοποιηθεί η επίδραση όλων των παραθαλάσσιων ανθρώπινων δραστηριοτήτων (συμπεριλαμβανομένου της κολύμβισης, της ενοικίασης σκαφών και την παρατήρηση των θαλάσσιων χελωνών), όπως έχει γίνει και με άλλα θαλάσσια σπονδυλωτά τα οποία επηρεάζονται από ανθρώπινες δραστηριότητες (Lusseau, 2006). Περαιτέρω, η έρευνά μας έδειξε, την πιθανή παρουσία χελωνών όλο το χρόνο στον κόλπο Λαγανά. Επομένως θα πρέπει να πραγματοποιηθεί έρευνα σχετικά με τη χρήση της περιοχής κατα τη χειμερινή περίοδο, για τη βελτίωση των μέτρων προστασίας ειδικά σε σχέση με την τυχαία σύλληψη από αλιευτικά σκάφη (Martien *et al.*, 1999). Με τη διευκόλυνση που παρέχει η τεχνική της GPS ιχνηλάτησης στην λεπρομερή ανάλυση των προτύπων κινήσεων της άγριας ζωής, συνιστούμε τη χρήση της για την επανα-οριοθέτηση των ζωνών προστασίας στον κόλπο Λαγανά, Ζακύνθου, ώστε να διασφαλιστεί ότι ο βιότοπος καλύπτει τις ανάγκες προστασίας των θαλάσσιων χελωνών (Martien *et al.*, 1999; Sutherland *et al.*, 2004; James *et al.*, 2005b).

Τα δεδομένα που παρουσιάζονται στα Κεφάλαια 4 και 5 δείχνουν ότι αρκετές από τις χελώνες που παρακολουθούσαμε κινήθηκαν σε περιοχές εκτός της κύριας αναπαραγωγικής περιοχής, κάτα που συμφωνει με προηγούμενες προτάσεις ερευνητών, ότι οι *Caretta caretta* μπορεί να μην είναι τόσο σταθερής στην επιλογή μίας και μόνο παραλίας ωοτοκίας (Stoneburner, 1982; Hays & Sutherland, 1991; Katselidis *et al.*, 2004) όσο άλλα είδη θαλάσσιων χελωνών (Mortimer & Portier, 1989). Το επίπεδο των κινήσεων κατά την περίοδο ωοτοκίας μπορεί να εξαρτάται από τις ανάγκες που έχει κάθε είδος από το ενδιαίτημα, όπως αναζήτηση τροφής στις δερματοχελώνες (Georges *et al.*, 2007), ή πιθανά αναζήτηση ενναλλακτικών περιοχών ωοτοκίας στις *Caretta caretta*. Η υπόθεση αυτή υποστηρίζεται από το γεγονός ότι φωλεοποίηση πραγματοποιείται στις ανατολικές ακτές της Ζακύνθου και στην Πελοπόνησσο, όπου καταγράφηκε να πηγαίνουν χελώνες που συμμετείχαν στην έρευνά μας. Τα υψηλά επίπεδα πολλαπλής πατρότητας τα οποία έχουν καταγραφεί στον πληθυσμό της Ζακύνθου (Zbinden *et al.*, 2007c), θα μπορούσαν στην πραγματικότητα να προσδόσουν πλεονέκτημα στις θηλυκές, οι οποίες αναζητούν νέες παραλίες για να εποικίσουν, καθώς τα αυγά τους έχουν υψηλή γενετική ποικιλομορφία (Moore & Ball, 2002). Εάν αυτές οι κινήσεις εκτός της περιοχής αναπαραγωγής συμβαίνουν συχνά στο πληθυσμό, τότε τα παρόντα μέτρα προστασίας στη Ζάκυνθο θα πρέπει να επαναξεταστούν.

Το γεγονός ότι, τόσο οι αρσενικές όσο και οι θηλυκές θαλάσσιες χελώνες διανύουν τεράστιες αποστάσεις για να φτάσουν στις περιοχές αναπαραγωγής, όπου η αναζήτηση τροφής είναι ελάχιστη, έχει ως αποτέλεσμα τεράστιο ενεργειακό κόστος, το οποίο εξαρτάται από τα επίπεδα κινητικότητας και την περίοδο διαμονής (Jessop *et al.*, 1999; Luschi *et al.*, 2003). Όταν είναι στις περιοχές αναπαραγωγής τα αρσενικά, για αυξήσουν το αναπαραγωγικό τους αποτέλεσμα, πρέπει να επενδύσουν στη συνεχή αναζήτηση δεκτικών θηλυκών, στη διαμάχη με άλλα αρσενικά και στο ζευγάρωμα (Booth & Peters, 1972; Schofield *et al.*, 2006). Σύμφωνα με τη βιβλιογραφία, η “διαμάχη σπέρματος” σε άλλα είδη στα οποία συναντάται πολλαπλή πατρότητα, δείχνει ότι το πρώτο αρσενικό το οποίο θα ζευγαρώσει με ένα θηλυκό έχει τις περισσότερες πιθανότητες να γονιμοποιήσει τα περισσότερα ωάρια (Zamudio & Sinervo, 2000). Τα αρσενικά τα οποία παραμένουν μόνιμα στις περιοχές αναπαραγωγής, εξοικονομούν την ενέργεια που χρειάζεται για τη μετανάστευση και έχουν τη δυνατότητα να ζευγαρώσουν με περισσότερες θηλυκές, ειδικά σε πληθυσμούς όπου η άφιξη των θηλυκών είναι μεταβλητή. Ωστόσο, εάν δεν υπήρχαν περιοχές διατροφής κοντά στις περιοχές αναπαραγωγής, τότε λογικά, τα αρσενικά θα έπρεπε να φύγουν από τις περιοχές αναπαραγωγής όταν το αναπαραγωγικό κέρδος θα ήταν πλέον πολύ μικρό, π.χ. όταν οι περισσότερες θηλυκές έχουν ήδη ζευγαρώσει και δεν είναι πλέον δεκτικές (Plotkin *et al.*, 1996; Hays *et al.*, 2001b; Godley *et al.*, 2002; James *et al.*, 2005b). Η πλειονότητα των αρσενικών χελωνών (4 στις 5) που παρακολουθούσαμε μετανάστευσε εκτός της αναπαραγωγικής περιοχής πριν την έναρξη της ωοτοκίας. Τα αρσενικά παρουσίασαν γενικά παρόμοια διασπορά και πρότυπα μετανάστευσης με αυτά τα οποία καταγράφηκαν για τις θηλυκές μετά την ωοτοκία (Zbinden *et al.*, 2008), με διασκορπισμένες μακρινές περιοχές διατροφής. Δύο από τα αρσενικά της έρευνάς μας βρέθηκαν σε μακρινές περιοχές διατροφής ή διαχείμανσης, στην Τουρκία και στην Κροατία, οι οποίες αναγνωρίστηκαν έτσι γιατί οι τοποθεσίες που εμφάνιζαν τα GPS βρίσκονταν όλες συγκεντρωμένες σε αυτές τις περιοχές. Με το συνδυασμό των θέσεων από τα GPS, το φύλο και την κλάση ηλικίας με τοπικές εμπειρικές μελέτες ίσως είναι δυνατόν να αναγνωριστούν νέες περιοχές διατροφής, οι οποίες χρειάζονται εθνικά ή/και διασυνοριακά διαχειριστικά μέτρα και προστασία.

Η έρευνα του πληθυσμού των θαλάσσιων χελωνών πραγματοποιείται με την καταμέτρηση των ιχνών που αφήνουν οι θηλυκέσ θαλάσσιεσ χελωνές στις παραλίες ωοοτοκίας (Demetropoulols & Hadjichristophorou, 1995; Godley *et al.*, 2001a; Broderick *et al.*, 2002; Margaritoulis, 2005). Η μέθοδος αυτή αγνοεί το μέγεθος του αρσενικού "στοιχείου" στον ενήλικο πληθυσμό. Συνεπώς, ενώ υπάρχουν πληροφορίες σχετικά με την αναλογία φύλου στους νεοσσούς, μέσω της καταγραφής της θερμοκρασίας κατά την επώαση και τη διάρκειά της (Broderick *et al.*, 2001a; Zbinden *et al.*, 2007b), δεν είναι γνωστό το πως η αναλογία φύλου των νεοσσών επηρεάζει την αναλογία φύλου των ενηλίκων. Υψηλή αναλογία θηλυκών 60-99% έχει τεκμηριωθεί για τους νεοσσούς στη Μεσόγειο (βλέπε Zbinden *et al.*, 2007b), αλλά και σε άλλους πληθυσμούς στον κόσμο (Mrosovsky & Provancha, 1989; Marcovaldi *et al.*, 1997). Έρευνες σε νεαρά άτομα έδειξαν ότι παρόμοιες αναλογίες μπορεί να εξισορροπούνται με την είσοδο αρσενικών από άλλες περιοχές (Henwood, 1987), αν και αυτό μπορεί να οφείλεται σε μια διασπορά εξαρτώμενη από το φύλο (Casale *et* *al.*, 2006). Στο Κεφάλαιο 1, προτείναμε ότι ο συνδυασμός της φώτο-αναγνώρισης με τις πληροφορίες που συλλέγονται με τις έρευνες στο νερό μπορεί να χρησιμοποιηθεί για να υπολογιστεί ο αριθμός των αρσενικών στις περιοχές αναπαραγωγής και επομένως η λειτουργική αναλογία φύλου στα ενήλικα. Στη Ζάκυνθο, η χρήση των περιοχών κοντά στις ακτές από τα ενήλικα και των δύο φύλων, όπως παρουσιάστηκε στα Κεφάλαια 4 και 5 στη μελέτη με τη χρήση της τεχνικής της ιχνηλάτησης με GPS, έδειξε ότι η αναλογία θηλυκών 77% που καταγράφηκε κατά τη διάρκεια της έρευνας με τη χρήση της φωτο-αναγνώρισης το 2003 (Schofield *et al.*, 2006) μπορεί να μην είναι αποτέλεσμα της λήψης δειγμάτων πλησίον της ακτογραμμής. Ο υπολογισμός του συνολικού αριθμού και της αναλογίας φύλου εξαρτάται από την αναλογία επιστράτευσης (recruitment-rate) και την αναλογία επιστροφής (return-rate) και των δύο φύλων. Οι θηλυκές πιστεύεται ότι επιστρέφουν κάθε δύο χρόνια (Hays & Sutherland, 1991) και δεδομένα από την Αυστραλία υποστηρίζουν ότι τα αρσενικά επιστρέφουν κάθε χρόνο (Chaloupka & Limpus, 2001). Εάν συμβαίνει αυτό, τότε μια αναλογία 85% θηλυκών είναι πιθανή για το σύνολο του πληθυσμού των ενηλίκων, η οποία είναι πρεμφερής με την αναλογία 75% θηλυκών για την αναλογία φύλου των νεοσσών που προβλέφθηκε από τη Zbinden et al. (2007b) για τη Ζάκυνθο. Βρήκαμε ότι η πυκνότητα των θαλάσσιων χελωνών στην περιοχή αναπαραγωγής μπορεί να είναι δέκα φορές μεγαλύτερη από ότι περιμένουμε, γεγονός που βασίζεται στην εκτίμηση του μεγέθους του εποχικού πληθυσμού σε συνδυασμό με την αναλογία φύλου που παρατηρήσαμε. Η υψηλή αυτή πυκνότητα προκύπτει γιατί τα δεδομένα από το GPS δείχνουν ότι οι θαλάσσιες χελώνες κυρίως συγκεντρώνονται σε μια περιοχή 9km^2 πλησίον της ακτογραμμής, αντί να χρησιμοποιούν τη συνολική έκταση των 89km^2 του κόλπου Λαγανά. Επομένως, η περιοχή αυτή πρέπει να έχει προτεραιότητα για το διαχειριστικό σχέδιο και τις νομοθετικές ρυθμίσεις του Εθνικού Θαλάσσιου Πάρκου Ζακύνθου. Πρέπει να σημειωθεί ότι για τους παραπάνω υπολογισμούς χρησιμοποιήσαμαι συχνότητα ωοτοκίας 3, αν και ο αριθμός αυτός ποικίλλει πολύ στον πληθυσμό των *Caretta caretta* και χρειάζεται επιβεβαίωση (Dodd, 1988). Η υψηλή πυκνότητα, πιθανά, μπορεί επίσης να εξηγήσει τα ασυνήθιστα υψηλά ποσοστά πολλαπλής πατρότητας τα οποία έχουν καταγραφεί στο βιότοπο της Ζακύνθου (Zbinden *et al.*, 2007c), όπου αν και διαβιεί ένας μικρός πληθυσμός σε σύγκριση με άλλους βιοτόπους, παρουσιάζει υψηλά ποσοστά πολλαπλής πατρότητας (Jensen *et al.*, 2006; Lee, 2008).

Όπως υποδείχτηκε στο Κεφάλαιο 2, οι χελώνες δαπανούν το χρόνο τους στη θάλασσα κατά την αναπαραγωγική περίοδο σε μια ποικιλία δραστηριοτήτων όπως ζευγάρωμα, καθαρισμός και ανάπαυση (Booth & Peters, 1972; Schofield *et al.*, 2006). Η ανάπαυση στο βυθό έχει περιγραφεί ευρέως για τις θαλάσσιες χελώνες συμπεριλαμβανομένων των πράσινων χελωνών, των *Caretta caretta* και των hawksbills (Houghton *et al.*, 2002; Seminoff *et al.*, 2002; Hopkins-Murphy *et al.*, 2003; Houghton, 2003). Οι δημοσιεύσεις αναφέρουν ότι οι θηλυκές χελώνες αναπαύονται σε βάθη 15 μέτρων ή λιγότερο. Επομένως ήταν εξαιρετικά ενδιαφέρον (Κεφάλαια 4 και 5) ότι οι θηλυκές *Caretta caretta* τις οποίες εξοπλίσαμε με TDRs and GPS καταγραφείς στη Ζάκυνθο, σχεδόν ποτέ δεν βρέθηκαν σε βάθη μεγαλυτερα των 4 μέτρων κατά την περίοδο του Μαΐου και Ιουνίου. Τα δεδομένα δείχνουν ότι οι πλησίον της ακτής κινήσεις σε ρηχά νερά μπορεί να πραγματοποιώντας γενικά από τις θηλυκές *Caretta caretta* αυτή την περίοδο του χρόνου στο βιότοπο της Ζακύνθου. Με τον περιορισμό της περιοχής που χρησιμοποιούν, οι θηλυκές μπορεί να εξοικονομούν ενέργεια κατά την αναπαραγωγική περίοδο για όταν αυτές θα ωοτοκήσουν αρκετές φορές τους επόμενους μήνες (Hays *et al.*, 1999; Wallace *et al.*, 2005). Τα δεδομένα δείχνουν ότι οι θηλυκές δεν χρησιμοποιούν την περιοχή πλησίον της ακτής σαν καταφύγιο από τα αρσενικά μετά το ζευγάρωμα (Booth & Peters, 1972; Whittow & Balazs, 1982) καθώς διατηρούν το ίδιο πρότυπο χρήσης της περιοχής πλησίον της ακτής κατά τον πρώτο μήνα μετά την έναρξή της ωοτοκίας, παρότι τα περισσότερα αρσενικά πραγματοποιούν μεταναστέυση εκτός της περιόδου αναπαραγωγής αυτή την περίοδο. Περαιτέρω, η ποσοτική τυχαία ανάλυση (random crawl movement model analysis) των υψηλής ανάλυσης δεδομένων των GPS σε δύο από τις θηλυκές χελώνες που παρακολουθούσαμε (Κεφάλαιο 4), δείχνουν ότι κινήθκαν σύμφωνα με ένα παρόμοιο μη-τυχαίο πρότυπο, το οποίο υποδεικνύει ότι κοινές βιο-φυσικές διεργασίες μπορεί να καθορίζχουν τις κινήσεις τους. Συνεπώς, οι απευθείας παρατηρήσεις (Κεφάλαια 2 και 3) και η χρήση απομακρυσμένης τεχνολογλιας (Κεφάλαια 4 και 5) οδήγησαν στην συγκεκριμένη διερεύνηση των περιβαλλοντικών παραμέτρων σε συνδυασμό με τις κινήσεις των θηλυκών και την κατανομή τους (Κεφάλαιο 6).

Στο Κεφάλαιο 6, παρουσιάζουμε πρωτότυπα δεδομένα τα οποία δείχνούν πως οι θηλυκές θαλάσσιες χελώνες, κοντά στα όρια της αναπαραγωγικής τους ακτίνας, μετακινούνται καθημερινά, ώστε να εκμεταλλευτούν κατά τον καλύτερο τρόπο τη θερμότητα συγκεκριμένων σημείων, σε ένα πολύ δυναμικό, θερμικά, περιβάλλον. Δείξαμε ότι το πρότυπο κίνησης το οποίο βρέθηκε από τις με GPS παρακολουθούμενες χελώνες αντικατόπτριζε την κατανομή των ατόμων την οποία βρήκαμε με τις έρευνες με τη βάρκα και ότι και τα δύο αυτά πρότυπα ποικίλλαν ανάλογα με τη διεύθυνση του ανέμου, έτσι για παράδειγμα, όταν ο άνεμος φυσούσε από τα νότιο-ανατολικά τότε το θερμότερο νερό και η συγκέντρωση των χελωνών ήταν στο βόρειο-δυτικό τμήμα του κόλπου. Όπως συμβαίνει και στις λίμνες (Barnes & Mann, 1991), βρήκαμε ότι η διεύθυνση του ανέμου επηρεάζει την κατανομή του θερμού νερού πλησίον της ακτής. Επιπλέον, η σχέση αυτή ήταν ισχυρότερη το απόγευμα, όταν το νερό είχε ζεσταθεί από την ενέργεια του ήλιου νωρίτερα το πρωί (Hattori & Warburton, 2003; Pulgar *et al.*, 2005). Οι τοποθεσίες αυτών των “κηλίδων” θερμού νερού προσφέρουν τη δυνατότητα επιλογής στις χελώνες και το αποτέλεσμα ήταν η επιλογή θερμότερων περιοχών σε έυγκριση με την τυχαία στο νερό πλησίον της ακτής. Περαιτέρω, οι καταγραφές από τις χελώνες που τις είχαμε εξοπλίσει με θερμικούς καταγραφείς δείχνουν ότι οι θερμοκρασίες σε βάθη μακρύτερα από την ακτή ήταν κατά 2ºC χαμηλότερες από τις θερμοκρασίες στα ρηχά, το οποίο σημαίνει ότι η πραγματική θερμοκρασία του νερού που βίωναν οι χελώνες το Μάιο ήταν πιθανά 5ºC υψηλότερη από τη θερμοκρασία που θα βίωναν εάν αναπαύονταν σε βάθος >10 μέτρων, το οποίο έιναι το τυπικό βάθος για τις χελώνες στις τροπικές περιοχές αναπαραγωγής (Hays *et al.*, 2004c)

Οι ενήλικες *Caretta caretta* μπορεί να έχουν θερμοκρασία σώματος υψηλότερη κατά μερικούς βαθμούς ºC από το περιβάλλον, παρότι η θερμοκρασία τους εξαρτάται πολύ από τη θερμοκρασία τπυ περιβάλλοντος νερού (Spotila *et al.*, 1997). Γενικά, η τιμή του $Q10$ (ο μεταβολικός ρυθμός σε θερμοκρασία T + 10ºC διαιρούμενος με το μεταβολικό ρυθμό σε θερμοκρασία T ºC) για τις *Caretta caretta* είναι περίπου από 2·4 έως 5·4 (Hochscheid *et al.*, 2004). Επομένως οι *Caretta caretta* σε θερμότερα νερά θα έχουν αυξημένο μεταβολικό ρυθμό και συνεπώς η παραγωγή των αυγών τους θα είναι γρηγορότερη, αν και ο στιγμιαίος ρυθμός κατανάλωσης των ενεργειακών τους αποθεμάτων θα είναι ταχύτερος. Χρησιμοποιώντας τον βασικό κανόνα της σχέσης των διαστημάτων ανάμεσα στις φωλεοποιήσεις και της θερμοκρασίας του νερού, υπολογίσαμε ότι ο χρόνος της πρώης φωλεοποίησης μπορεί να μειωθεί έως και 5 ημέρες. Οι *Caretta caretta* με αυτόν τον τρόπο μπορούν να μεγιστοποιήσουν τον αριθμό των φορών που θα φωλεοποιήσουν σε μια περίοδο, παρότι η βέλτιστη θερμοκρασία για την ανάπτυξή των αυγών τους παρουσιάζεται κοντά στη περίοδο εκκόλαψης (Sato *et al.*, 1998; Hays *et al.*, 2002a). Επιπλέον, με τη μείωση του χρόνου της πρώτης φωλεοποίησης, οι χελώνες μειώνουν και το χρόνο που χρειάζεται να παραμείνιουν μακρυά από τις περιοχές διατροφής.

Τα ίχνη GPS έδειξαν ότι οι χελώνες δεν βρίσκονται πάντα στην προσήνεμη θέση (π.χ. λογώ παθητικής παράσυρσης), αλλά έκαναν κινήσεις παράλληλα με την ακτή, αντίθετα με τη διεύθυνση του ανέμου (π.χ. ενεργή επιλογή). Η παθητική μεταφορά δεν θεωρείται πιθανή αιτία καθώς οι ενήλικες χελώνες είναι δυνατοί κολυμβητές και έτσι καθορίζουν τη θέση τους κατά την αναπαραγωγική περίοδο, ακόμα και αν τα ρεύματα ή ο άνεμος είναι δυνατά. Για παράδειγμα στα Νησιά της Αναλήψεως, οι θηλυκές θαλάσσιες χελώνες παίρνουν θέση περίπου στην ισοβαθή των 20 μέτρων παρά τους τοπικούς δυνατούς ανέμους και ρεύματα (Hays *et al.*, 1999). Δεύτερον, οι *Caretta caretta* περνούν τον περισσότερο χρόνο τους κάτω από το νερό, είτε μέσα στο νερό είτε ξεκουράζονται στον πυθμένα (Houghton *et al.*, 2002), έτσι δεν είναι πιθανό να επηρεάζονται ιδιαίτερα από τους ανέμους. Τρίτον, η επιλογή θερμοκρασίας από τις χελώνες, φαίνεται να αλλάζει κατά τη διάρκεια της αναπαραγωγικής περιόδου, με τη μεγαλύτερη διαφορά από τη μέση θερμοκρασία του κόλπου να εμφανίζεται κατά την αρχή της περιόδου, όταν η θερμοκρασία του νερού είναι χαμηλότερη. Ανεξάρτητα με το πως πραγματικά λειτουργεί, ήταν ξεκάθαρο ότι οι χελώνες προσδιορίζουν τη θέση τους ανάλογα με τη διεύθυνση του ανέμου και αυτό δεν έχει αναφερθεί στο παρελθόν για μια αναπαραγωγική περιοχή.

Τα δεδομένα τα οποία χρησιμοποιήθηκαν στο Κεφάλαιο 6 δεν μπορούν να χρησιμοποιηθούν για τον καθορισμό του αν η επιλογή θερμοκρασίας επιτυγχάνεται διαμέσου (i) της αντίληψης της διεύθυνσης του ανέμου ως στοιχείο για την εύρεση τμημάτων θερμότερου νερού ή (ii) τυχαίας αναζήτησης. Η συνέχιση της ιχνηλάτησης των ατόμων σε συνδυασμό με τη συνεχή διερεύνηση του θερμοκρασιακού περιβάλλοντος, της διεύθυνσης του ανέμου και βιοφυσικών παραμέτρων μπορεί να δώσει τις απαραίτητες απαντήσεις. Παρόλα αυτά, τα αποτελέσματα της παρούσας μελέτης δίνουν πιθανές απαντήσεις (i) για τη διαμάχη των θηλυκών (Κεφάλαια 2 και 3), (ii) για τα παρόμοια πρότυπα κινήσεων τα οποία καταγράφηκαν σε διαφορετικές χελώνες (Κεφάλαιο 4) και (iii) για την κατανομή των θηλυκών χελωνών πλησίον της ακτής (και συνεπώς και των αρσενικών) η οποία καταγράφηκε στα Κεφάλαια 4 και 5.

Η μελέτη αυτή ασχολείται με τη διερεύνηση σημαντικών οικολογικών παραμέτρων των θαλάσσιων χελωνών στο σημαντικότερο βιότο αναπαραγωγής τους στη Μεσόγειο. Επιπλέον, τα στοιχεία τα οποία συλλέχθησαν κατά τη διάρκεια της έρευνας έδωσαν πρωτότυπες πληροφορίες για τη βελτίωση της προστασίας του είδους σε τοπικό και σε περιφερειακό επίπεδο. Στο Κεφάλαιο 1 η πιστοποίηση της τεχνικής της φωτο-αναγνώρισης και της σχετικής βάσης δεδομένων, έδωσε το μέσο για τη συλλογή ακριβέστερων πληροφοριών για τη δημογραφία του πληθυσμού, αλλά διαπιστώθηκε και ότι μπορεί να χρησιμοποιηθεί ως δείκτης της επιβίωσης των ενηλίκων μετά την αναχώρησή τους από την αναπαραγωγική περιοχή (Chaloupka & Limpus, 2002) και σε εφαρμοσμένες μελετες συμπεριφοράς για τη διερεύνηση της αλληλεπίδρασης ανάμεσα σε γνωστά άτομα του είδους. Στο Κεφάλαιο 2 τεκμηριώθηκε ένα πλήθος δραστηριοτήτων στην περιοχή αναπαραγωγής, αρκετές από τις οποίες δεν είχαν καταγραφεί ξανά στο παρελθόν, και μπορεί να οδηγούσαν στη λανθασμένη ερμηνεία των αποτελεσμάτων των απομακρυσμένων τεχνολογιών στα επόμενα κεφάλαια. Στην πραγματικότητα, η αναζήτηση της απάντησης για τη δομή και τη λειτουργικότητα της διαμάχης ανάμεσα στα θηλυκά, οδήγησε στη εκ βάθους διερεύνηση της κατανομής και των προτύπων κίνησεις των αρσενικών και θηλυκών (Κεφάλαια 4 και 5) υποδεικνύοντας την πολύ κοντά στην ακτή προτίμηση σε μια συγκεκριμένη περιοχή του κόλπου, και την ανάλυση των κινήσεων των χελωνών σε συνδυασμό με τη θερμοκρασία της θάλασσας και τις παραμέτρους του ανέμου (Κεφάλαιο 6).

Στο τελευταίο Κεφάλαιο διερευνήθηκει η σημασία που έχει η θερμοκρασία στη βιολογία των θαλάσσιων χελωνών, ειδικότερα λαμβάνοντας υπόψη το γεγονός ότι η Ζάκυνθος βρίσκεται στα όρια της αναπαραγωγικής ακτίνας της *Caretta caretta*. Όταν βρίσκονται στην περιοχή αναπαραγωγής, η διατήρηση της ενέργειας και η μεγιστοποίηση της ανάπτυξης των αυγών είναι εξαιρετικής σημασίας για τις θηλυκές χελώνες. Παρόλα αυτά, η περιοχή πλησίον της ακτής, όπου οι χελώνες μπορούν να βρουν τα επίπεδα θερμότητας τα οποία απαιτούνται για την ανάπτυξη των αυγών στις αρχές της περιόδου, βρίσκεται στη θαλάσσια περιοχή με τα λιγότερα μέτρα προστασίας όπου είναι συγκεντρωμένη η τουριστική ανάπτυξη. Επομένως, οι θαλάσσιες ζώνες προστασίας πρέπει να τροποποιηθούν, ώστε να συμπεριλαμβάνουν τις διάφορες οικοθέσεις οι οποίες σχετίζονται με τις δραστηριότητες των θαλάσσιων χελωνών και τη χωρική κατανομή τους που εξαρτάται από τις θερμοκρασιακές συνθήκες. Περαιτέρω, για να εκτιμηθεί η αποτελεσματικότητα των μέτρων προστασίας, είναι ανάγκη να προσδιοριστεί ο αντίκτυπος των ανθρώπινων θαλάσσιων δραστηριοτήτων (π.χ. παρατήρηση της χελώνας με ειδικά σκάφη, την ενοικίαση βαρκών, της κολύμβησης κ.λ.π.) στις θηλυκές θαλάσσιες χελώνες. Τελικά, η παραμονή στις περιοχές αναπαραγωγής αποτελεί ένα μικρό τμήμα της ζωής μιας ενήλικης χελώνας. Απαιτείται η γνώση των διαδρομών μετανάστευσης, των περιοχών διαχείμανσης/διατροφής όπου οι χελώνες περνούν παρατεταμένες περιόδους, ώστε να εφαρμοστούν αποτελεσματικά μέτρα διαχείρισης για την προστασία των αναπαραγωγικά ενεργών ενηλίκων. Συνεπώς, οι αρχικές πληροφορίες που λαμβάνονται σχετικά με τη μετανάστευση των αρσενικών, μπορούν να χρησιμοποιηθούν για τη βελτίωση της εθνικής και διεθνούς προσπάθειας για τον καθορισμό νέων αποτελεσματικών περιοχών προστασίας, στις οποίες θα περιλαμβάνονται οι περιοχές αναπαραγωγής, μετανάστασευσης και διατροφής. Αυτό είναι ιδιαίτερα σημαντικό, ειδικά αν ληφθεί υπόψη η πολύ χαμηλή αναλογία αρσενικών η οποία καταγράφηκε στον πληθυσμό της Ζακύνθου, βάση της έρευνας με φωτο-αναγνώριση στο Κεφάλαιο 1 σε συνδυασμό με την κατανομή των θηλυκών και αρσενικών χελωνών στα Κεφάλαια 4 και 5, και η οποία φαίνεται να συνεχίζεται καθόλη την ανάπτυξη.

Συμπερασματικά, η παρούσα μελέτη ανέδειξε την αξία της απευθείας παρατήρησης σε συνδυασμό με τη χρήση της απομακρυσμένης GPS ιχνηλάτησης στο θαλάσσιο περιβάλλον, ώστε να αναπτύξουμε τη γνώση μας σχετκά με την οικολογία της *Caretta caretta* και να εφαρμόσουμε αυτή τη γνώση για τη βελτίωση της προστασίας και διαχείρισης του είδους.

GENERAL DISCUSSION

The thesis research utilised a range of direct and indirect methodologies to provide new insights into sea turtle marine ecology and conservation management in the marine environment at the largest rookery in the Mediterranean. The study presented the first detailed assessment of adult male and female sea turtle in-water population structure, behavioural activity, movement and distribution patterns at a breeding area. Due to the rookery occurring at the limits of the breeding range for loggerheads, which are reptiles and hence ectothermic, our study highlighted that reproductive parameters could not be studied in isolation of environmental variables such as marine thermal conditions.

Chapter 1 was fundamental to the study, as the photo-identification technique provided a means of identifying both individual male and female loggerheads in the population. Photo-identification has the benefit of being suitable for male turtles, which do not come ashore (but see Rice & Balazs, 2008) to allow conventional tagging, requiring instead logistically challenging capture at sea (e.g. Hays *et al.*, 2001b; James *et al.*, 2005b), and so are rarely identified. The permanency of photographic data provides an opportunity to investigate a range of parameters that may influence species conservation management and ecological risk assessments such as site fidelity, patterns of interaction, physical condition, health indicators and the impact of anthropogenic activity (Burger & Garber, 1995; Bennett *et al.*, 1999; Pettis *et al.*, 2004; Lusseau *et al.*, 2006). Chapter 1 demonstrated, through the use of trials, the validity (i.e. accuracy) and reliability (i.e. precision) of natural markings for assignation of individual loggerhead sea turtles to groups according to a simple identification tree, and that once an image has been assigned to a group, its markings can be used to correctly match it to existing catalogue images of the same individual present in that group. The results indicated a high ability in photographic sorting and matching from all worker groups (range: 68-100%), with inexperienced workers rapidly acquiring photo-id skills in a a 20 minute training session. The difficulty of manually comparing and matching a large volume of photographic images (>400) was overcome by dividing turtles into several groups of <100 images based on variations in one set of facial features. A very low error rate was recorded during the course of the trials, with that of false positive errors (matching two photographs from different animals, resulting in population deflation) being slightly more frequent than false negative errors (failing to find a match, resulting in population inflation). Hence, the accumulation of errors over time in the database, leading to over or under estimations of population size (Stevick *et al.*, 2001), is likely to be negligible. As the photographic catalogue expands, it may become necessary to develop a computer-assisted matching programme, as has been designed for several other vertebrate species with large photographic population databases (Kelly, 2001; Hillman *et al.*, 2003; Beekmans *et al.*, 2005).

In Chapter 2, the intensive in-water observations of loggerheads differed from existing studies at breeding areas (courtship and internesting) in that, rather than specifically addressing courtship and mating behaviour (Booth & Peters, 1972; Dodd, 1988; Frick *et al.*, 2000), or inter-nesting movement patterns (Hopkins-Murphy *et al.*, 2003), we sought to investigate the complete behavioural ecology of sea turtles during this period. Direct observational studies in the marine environment are of great value in developing our knowledge of marine vertebrate behaviour, validating remote technologies and contributing towards ecosystem research and environmental monitoring. The observed activities were grouped into 4 solitary (resting, swimming, foraging, cleaning) and 2 social (antagonistic interactions, reproductive activity) behaviours, which were divided into 14 sub-categories. The results indicated that in general males were more active and social than females, which probably reflected the need to acquire multiple mates to maximise fitness, whereas female fitness would be maximised by energy conservation to divert resources towards egg development (Hays *et al.*, 2002a; Hopkins-Murphy *et al.*, 2003).

The research indicated that courtship and mating behaviour of loggerheads followed similar patterns to that documented in other studies of the same and different sea turtle species (Booth & Peters, 1972; Dodd, 1988; Frick *et al.*, 2000; Godley *et al.*, 2002; Rostal, 2005). In courtship bouts with unreceptive females, we corroborated and expanded on the use of avoidance manoeuvre sequences. As with other species, we observed that males competitively search for receptive females (Jessop *et al.*, 1999) in the form of patrolling but we also documented the presence of male–male combat, possibly for primary mate acquisition. Furthermore, while the presence of antagonistic attendant males in the company of copulating pairs has been recorded in other species of sea turtle (Booth & Peters, 1972), this was not documented in loggerheads (Frick *et al.*, 2000) until the current research. High levels of multiple paternity in clutches has been recorded in the Zakynthos loggerhead population (Zbinden *et al.*, 2007c), from which inferences about the levels of polyandry in the adult population have been made. It was hypothesised that a more female-biased sex-ratio may generate higher rates of multiple paternity due to decreased male-male competition, and that larger females were subject to higher levels of multiple paternity (Zbinden *et al.*, 2007c). However, direct observation of male behaviour during the current study indicated high levels of male-male competition, despite an apparently female-biased operational sex ratio (see Chapter 5 assessment below). To address this quandary, population abundance, density, operational sex-ratios and movement patterns, mating strategies and size classes of individual male and female turtles during the mating period would be required. Such information could potentially be obtained through direct observation of behaviour, a comprehensive identification database (i.e. photo-identification) and fine-scale tracking of all individuals in the population.

Chapter 2 presented records of female loggerheads investing in active behaviours previously unobserved in loggerheads during the breeding period, i.e. that of foraging, cleaning (self-cleaning and fish-cleaning symbiosis) and female–female contests. High carapace epibiont loads (Frick *et al.*, 1988) and a recent animal-borne sea turtle study (Heithaus *et al.*, 2002b) have led researchers to suggest that loggerheads do not invest as heavily in cleaning behaviour as other sea turtle species (Bjorndal, 2003). However, while we only observed self-cleaning and fish cleaning symbiosis on a few occasions, photographic records presented evidence of self-cleaning behaviour was apparent from the uniform scratch patterns on the carapaces of a large proportion of surveyed male and female turtles, indicating that loggerheads at Laganas Bay do invest in cleaning activity. Sporadic feeding attempts for molluscs by both female and male loggerheads at Laganas Bay were observed. However, time spent foraging was relatively short, presumably because of the need to spend time and energy on other activities (e.g. males searching for females), and possibly because prey densities were sufficiently low that sometimes it was more profitable (e.g. for females) to simply rest than attempt to feed. Contests between individuals over space has received anecdotal mention in sea turtle literature (Limpus & Limpus, 2003), yet our research indicated that antagonistic interactions are a noteworthy component of female loggerhead activity during the breeding period and was therefore subject to detailed assessment in Chapter 3.

The way in which individuals of a species compete over resources allows researchers to objectively measure the importance of a particular environment, habitat or ecosystem to animals. The assessment of female competition in Chapter 3 indicated that interactions involve ritualized escalation in behaviour from passive threat displays (e.g. head–tail circling) to aggressive combat (e.g. sparring), the degree of which appeared to differ with respect to behavioural state. The analysis of female loggerhead fight structure suggests that circling individuals evaluate opponent size, sparring individuals test opponent strength, and that the positioning of the prehensile tail signals motivational intent to either escalate or abort. The results suggest that certain sites may be preferentially sought after and defended by sea turtles. Marine environments are not homogeneous, and this behaviour indicates that turtles could be competing over a scarce high quality resource. These observations support the population ‘interference’ model derived from the ‘Ideal Free Distribution’ (Fretwell, 1972; Sutherland & Parker, 1986) in that seabed resting sites may represent an optimal resource over which individuals compete, whereas surface-basking occurs at suboptimal sites subject to less competition.

Such behaviour may arise in defence of space to obtain refuge from energy consuming encounters with males patrolling for receptive mates (Booth & Peters, 1972; Whittow & Balazs, 1982; Lee & Hays, 2004). In this instance, space may be the limiting factor, whereby females resting in close proximity to one another would attract unwanted male attention. However resident females initially respond to males entering their visual range by holding a vertical ‘refusal’ pose (Booth & Peters, 1972), which is not observed until the aggressive phase of female–female interactions. An alternative theory put forth by the researcher (GS) was the defence of thermally optimal sites to enhance egg development. Detailed research has shown that, in reptiles, environmental temperature affects the developmental rate of eggs and viability of offspring as well as adult growth and survival (e.g. lizards: Wapstra, 2000; snakes: Ladyman *et al.*, 2003). It is therefore possible that female turtles, particularly in temperate breeding areas such as Zakynthos, are responding to thermal cues in the environment by seeking out warmer water to accelerate egg development. This theory is further supported by comparative studies of sea turtle distribution in temperate and tropical breeding areas: in the former, where ambient sea temperatures are cooler, turtles form dense nearshore aggregations, whereas in the latter they remain more dispersed (e.g. Hays *et al.*, 2002b). In order to specifically investigate possible causes of social interactions between female turtles, this theory, based on direct observation, led to the detailed investigation using remote technology of whether female distribution alters in correlation to the dynamic thermal marine environment in Chapter 6.

As has been shown in Chapters 1-3, direct observations of turtle behaviour are of great value and provide many interesting insights that are difficult, or impossible, to gain from more indirect methods or animal-borne imaging. However, direct observation of free living marine animals is subject to a number of limitations; for instance, our study was limited by time of day, sea conditions and sea depth. Because of such limitations, the use of remote technology is becoming increasingly common. However, without corroborated observational research, such technology only produces informed guesswork of animal behavioural activities. Studies, comparing direct and indirect methodologies of animal behaviour, have shown that remote-sensing data can distinguish between active and inactive states, however it cannot reliably distinguish the different behaviour patterns within those states (Hansen *et al.*, 1992; Heithaus *et al.*, 2001). The findings in Chapter 2 and 3 have shown that loggerhead sea turtles exhibit a wider range of behaviour than has previously been documented at breeding areas. It is therefore likely that indirect inferences about movement patterns made from remote-sensing data analysis may be subject to error (as shown by Houghton *et al.*, 2002). Advances in electronics are making underwater video cameras economically viable, giving the researcher the opportunity to observe and confirm the underwater behaviour (Davis *et al.*, 1999; Heithaus *et al.*, 2002b; Reina *et al.*, 2005; Hays *et al.*, 2006). Hence, knowledge about free-living behaviour, obtained from direct observations, is essential towards improving the accuracy of remote-data interpretation of marine wildlife. By collecting direct baseline behavioural information, electronic devices could be subsequently used as a powerful tool to acquire specific information with respect to trends in marine animal social behaviour and habitat use. Therefore, the assimilated from direct observations in Chapters 1-3 provided a baseline from which questions were addressed in Chapters 4-6 through remote tracking.

Chapters 4 and 5 demonstrated how GPS tracking units (loggers and transmitters) attached to male and female loggerheads can be used to obtain accurate spatio-temporal information about the fine-scale movement patterns of at local and regional scales, illustrating the value of this technique for conservation management. To facilitate wildlife conservation and sustainable use of marine areas, it is essential to understand the relationship between populations and their habitats (Castilla, 2000; Canadas *et al.*, 2005), with knowledge about the impacts of environmental and anthropogenic parameters providing additional benefit (Thompson *et al.*, 2000; Tisdell & Wilson, 2002; Douglas-Hamilton *et al.*, 2005; Preisler *et al.*, 2006). The volume of data and degree of accuracy with respect to the fine-scale detail of movement patterns obtained using the GPS units could not have been replicated using conventional telemetry (Hays *et al.*, 2001a; Hulbert & French, 2001; Tremblay *et al.*, 2006; Bradshaw *et al.*, 2007b). GPS data obtained within the breeding area indicated that before the onset of the nesting season, both males and females primarily used an area within 500 m of shore (at sea bed depths < 5m) along a core 9 km stretch of the 27.8km length of coastline. These observations support existing work in which females use sea depths up to 15 m when in the breeding area (Hopkins-Murphy *et al.*, 2003), however our results indicate a much narrower area use by males than previously recorded sea depths of up to 40 m (Shaver *et al.*, 2005b). One of the tracked males remained in the breeding area, with a noticeable shift in sea depth use to deeper water following the onset of nesting. This shift may have reflected a change in the status of a resident, i.e. from breeding to foraging, and may explain the greater depth range recorded for males in other breeding areas (Shaver *et al.*, 2005b).

Nesting beach locations and relative nesting densities have been used to delineate the degree of protection offered by adjacent marine protection zones in Laganas Bay

(Arapis & Margaritoulis, 1996). GPS tracking of females in 2006 and 2007 indicated preferential nearshore area use outside of the core marine protected area, with similar patterns being recorded in tracked males. While female sea turtles spent the majority of time outside of the no-boating maritime protection zone, a significant proportion of the population nest on one or more of the beaches in this region (Katselidis *et al.*, 2004), and our data indicated that turtles are likely to preferentially frequent the region adjacent to the nesting beach in the days preceding nesting. As a result, this zone remains one of extreme conservation importance. The movement and depth data indicated that female turtles preferentially inhabit very shallow water in areas of submerged sand-banks - criteria only found in the two lesser protected boating zones. The findings presented in Chapters 4 and 5 provide quantitative evidence showing that for maritime zones to provide the necessary protection, they should be based on sea turtle key area use (i.e. sea depth, proximity to shore and habitat preference), and not only the location of nesting beaches as has been done until now. Our findings support the experimental introduction of the national park ‘ecotourism zone’ in 2006 to reduce disturbance to turtles through strengthened boating regulations (Lusseau, 2004), and expansion to include the prime section of coastline used by both sexes. However, governmental legislative action is required to reform existing zones, which is difficult to secure (Togridou *et al.*, 2006a; Campbell, 2007; Lawton, 2007). Since male and female turtles occupied the lesser protected zones for over 50% of time, it is important to quantify the impact of all near-shore human activities (including wading, swimming, private boat hire and turtle-watching), as has been done with other marine vertebrate species impacted by humans (Lusseau, 2006). Our study also indicated the possible presence of resident turtles, hence research to determine winter area use around Zakynthos is important to improve protection measures particularly with respect to the fishery industry bycatch (Martien *et al.*, 1999). With the advent of GPS tracking facilitating fine-scale analysis of wildlife movement patterns, we strongly recommend its use in the delineation of protection zones to ensure the habitat requirements of the species are met (Martien *et al.*, 1999; Sutherland *et al.*, 2004; James *et al.*, 2005b).

Chapters 4 and 5 data indicated that several of the tracked females moved at spatial scales beyond the main breeding, which is consistent with previous suggestions that loggerheads may show poorer beach fidelity (Stoneburner, 1982; Hays & Sutherland, 1991; Katselidis *et al.*, 2004) than other sea turtle species (Mortimer & Portier, 1989). The level of internesting movement may depend on the habitat needs of each species, such as foraging in leatherbacks (Georges *et al.*, 2007), or possibly prospecting alternative nesting sites in loggerheads. This suggestion is supported by the fact that nesting activity does occur on the east coast of Zakynthos and Peleponesse where the turtles in our study were recorded. The high level of multiple paternity recorded in the Zakynthos population (Zbinden *et al.*, 2007c) would in fact benefit females seeking to colonise new beaches as a single clutch carries a high genetic diversity (Moore & Ball, 2002). If these broad-scale movements occur regularly within the population, then current protective measures of the Zakynthos breeding area may require re-evaluation.

Both males and females undertake long migrations to breeding areas, where limited foraging is available, resulting in a massive energy cost depending on the level of activity and period of residency (Jessop *et al.*, 1999; Luschi *et al.*, 2003). Once at the breeding area, to maximise reproductive output, males must competitively search for receptive females, invest in male-male combat and mate (Booth & Peters, 1972; Schofield *et al.*, 2006). Literature on sperm competition of other species in which multiple paternity occurs have shown that the first male to mate with a female is more likely to sire the most offspring in a clutch (Zamudio & Sinervo, 2000). Males that remain at the breeding ground all year would save on the energetic cost of migration, and have the potential to mate with more females, especially in populations where female arrival is variable. However if foraging habitat was not available locally, logically, males should depart the breeding area when the reproductive benefit to the male is reduced, i.e. when most females have been mated and are no longer receptive (Plotkin *et al.*, 1996; Hays *et al.*, 2001b; Godley *et al.*, 2002; James *et al.*, 2005b). The majority of tracked males (four out of five) migrated out of the breeding area prior to the onset of nesting. The males showed broadly similar dispersal and migratory patterns to that recorded in post-nesting females (Zbinden *et al.*, 2008), with disparate distant foraging grounds. Two of the males in our study were tracked to distant foraging or wintering areas in Turkey and Croatia, identified due to the tracking locations being concentrated in one area. By combining tracking data of sex and age classes with local empirical studies it may be possible to identify other foraging sites in need of national and trans-boundary conservation management action.

The study of adult turtle populations is typically assessed by counting the tracks of females on nesting beaches (Demetropoulols & Hadjichristophorou, 1995; Godley *et al.*, 2001a; Broderick *et al.*, 2002; Margaritoulis, 2005) which ignores the size of the male component of the adult population. Consequently, while information is available on hatchling sex-ratios through records of incubation temperatures and durations (Broderick *et al.*, 2001a; Zbinden *et al.*, 2007b), how hatchling sex ratio projects through to adult sex-ratio is not known.. Highly skewed female sex-ratios of 60-99% have already been documented for loggerhead hatchlings in the Mediterranean (see Zbinden *et al.*, 2007b for overview) and other populations around the world (Mrosovsky & Provancha, 1989; Marcovaldi *et al.*, 1997). Studies of juveniles indicate that skewed ratios may be balanced by males originating elsewhere (Henwood, 1987), though this may be as a result of sex-related dispersal (Casale *et al.*, 2006). In Chapter 1 we suggested that combining photo-identification with in-water survey information could potentially be used to provide estimates of the number of males at breeding sites and hence adult operational sex ratios. At Zakynthos, the nearshore use by adults of both sexes shown in the GPS tracking study of Chapters 4 and 5, indicated that the 77% female bias recorded during in-water photo-identification surveys in 2003 (introduced in Chapter 1) (Schofield *et al.*, 2006) may not be the result of nearshore sampling bias. Estimates of total population numbers and sex-ratios depend on recruitment-rates and the return-rates of both males and females; females are believed to return bi-annually (Hays & Sutherland, 1991) and data from Australia suggest annual return-rates in males (Chaloupka & Limpus, 2001). If this is the case an 85% female bias may exist in the total adult population, which is similar to the 75% female bias in hatchling sex ratios predicted by Zbinden et al. (2007b) on Zakynthos. We found that sea turtle density in the breeding area may be ten-times greater than expected, based on an estimate of seasonal population size combined with our observed sex-ratio data. This high density arises because our GPS data show that sea turtles primarily aggregate along 9km^2 of coastline, rather than uniformly using the 89km^2 area of Laganas Bay. Hence, this area should be the first priority for the management plan and legislation of the National Marine Park of Zakynthos. It should be noted that for the purposes of these calculations we used a clutch-frequency of three, however this number is highly variable within loggerhead populations and requires confirmation (Dodd, 1988). The high density of turtles may also explain the unusually high multiple paternity recorded at the Zakynthos rookery (Zbinden *et al.*, 2007c) despite it being a small loggerhead population relative to other rookeries exhibiting high levels of multiple paternity (Jensen *et al.*, 2006; Lee, 2008).

As indicated in Chapter 2, turtles spend their time at sea during the breeding season engaged in a variety of activities such as mating, cleaning and resting (Booth & Peters, 1972; Schofield *et al.*, 2006). Resting on the sea bed has been widely reported for hard-shelled turtles including green, loggerhead and hawksbills turtles (Houghton *et al.*, 2002; Seminoff *et al.*, 2002; Hopkins-Murphy *et al.*, 2003; Houghton, 2003). Published literature reports that female turtles rest at depths of 15 m or less. Hence, in Chapter 4 and 5 it was interesting that female loggerhead turtles equipped with TDRs and GPS loggers at the Zakynthos rookery almost never dived to sea bed depths of more than 4 m during May and June. The data implies that the near-shore movements in shallow water might occur generally for female loggerhead turtles at this time of year at the Zakynthos rookery. By restricting area use, females may conserve energy expenditure during the reproductive season when they may lay several clutches across several months (Hays *et al.*, 1999; Wallace *et al.*, 2005). The data indicate it is unlikely that females are using the nearshore habitat as a refuge from males following mating (Booth & Peters, 1972; Whittow & Balazs, 1982) as they maintained the same pattern of nearshore habitat use in the first month following the onset of nesting, despite the fact that most males had migrated out of the breeding area by this time. Furthermore, quantitative random crawl movement model analysis of the high-resolution GPS data of two of the tracked female turtles in Chapter 4 indicated that they moved with a similar non-random pattern, suggesting common biophysical processes might be driving their movements. Hence, direct observations (Chapters 2 and 3) and remote technology (Chapters 4 and 5) led to the specific investigation of environmental parameters in correlation to female movement and distribution in Chapter 6.

In Chapter 6, we present novel data showing how female loggerheads, near the limits of their breeding range, reposition themselves daily to take advantage of thermal hotspots within a highly dynamic thermal environment. We showed that the pattern of movement exhibited by GPS tracked turtles reflected the distribution of individuals revealed in boat surveys and that both of these patterns of distribution covaried with wind direction, i.e. when the wind blew from the south-east the warmest water and turtle aggregations were in the north-west of the bay. As has been widely reported in lakes (Barnes & Mann, 1991), we found that wind direction influenced the location of warm water patches close to the shoreline. Furthermore, this link was tighter in the afternoon, presumably when the water had been subject to solar heating during the earlier part of the day (Hattori & Warburton, 2003; Pulgar *et al.*, 2005). The location of warm water patches provided the potential for thermal selection by loggerhead turtles and the consequence was that they experienced warmer water than if they were randomly distributed in the near-shore waters. Furthermore, the records from turtles equipped with temperature loggers suggested that the temperatures at depth further from shore were over 2ºC cooler than the shallower temperatures, that is, the actual water temperatures experienced by turtles at the end of May were probably around 5ºC above those they would have experienced if they rested at > 10 m, which is the typical resting depth of turtles in tropical nesting sites (Hays *et al.*, 2004c).

Adult loggerhead turtles may have a core temperature a few ºC above ambient, although their body temperature is still largely driven by the ambient water temperature (Spotila *et al.*, 1997). In general, $Q10$ values (the metabolic rate at T + 10ºC divided by the metabolic rate at T ºC) for loggerhead turtles are around 2·4 to 5·4 (Hochscheid *et al.*, 2004). So loggerhead turtles in warmer water will have increased metabolic rates and hence their production of clutches would be expected to be quicker, albeit that the instantaneous rate at which energy reserves are used will be faster. We used the empirical relationship between internesting intervals and water temperature to estimate that by selecting warm water, time to laying the first clutch might be reduced by as much as 5-days. Loggerheads will therefore maximize the number of clutches they can lay within a season that experience optimum development temperatures even close to hatching (Sato *et al.*, 1998; Hays *et al.*, 2002a). Furthermore, reducing the time required to lay the first clutch will mean that turtles are able to minimize the time spent away from foraging grounds.

The GPS-tracks showed that turtles were not simply always located directly downwind (i.e. passive advection), but rather made movements parallel to the shore moving across the wind direction (i.e. active selection). Passive drift is not likely to be responsible as adult turtles are strong swimmers and therefore dictate their own position in the breeding season, even if currents or winds are strong. For example, at Ascension Island, breeding female green turtles position themselves around the 20-m isobath despite locally strong winds and currents (Hays *et al.*, 1999). Second, loggerhead turtles spend most of the time submerged, either in water or resting on the bottom (Houghton *et al.*, 2002), so they are unlikely to be strongly impacted by winds. Third, the thermal selection by the turtles seemed to change as the breeding season progresses, with the biggest elevation above mean bay temperature, that is, the strongest thermal selection, seeming to occur at the start of the season when water temperatures were coolest. Regardless of the exact mechanism at work, it was clear that the turtles repositioned themselves with respect to wind direction and this has not been reported at a breeding site previously.

The data assimilated in Chapter 6 could not be used to establish whether thermal selection is attained through (i) perception of wind direction as a cue to locate patches of warm water or (ii) random search effort. Continued tracking of individuals in combination with tracking of the thermal environment, wind direction and biophysical parameters may provide answers. However, the results of this study, provide possible answers to (i) the female fights recorded in Chapters 2 and 3, (ii) the similar patterns of movement recorded in different turtles in Chapter 4 and (iii) the nearshore distribution of females (and consequently males) recorded in Chapter’s 4 and 5.

This thesis presented the first detailed documentation of sea turtle marine ecology at the Mediterranean’s largest loggerhead rookery. Furthermore, the information collected during the course of the study provided novel information towards improving protection of the species at both the local and regional level. In Chapter 1, the validation of the photo-identification database provided a means to acquire accurate information about population demographics, but could serve as an indicator of adult survival after departure from the breeding area (Chaloupka & Limpus, 2002) and in applied behavioural studies to assess interactions between known individuals. Chapter 2 documented a wide range of behavioural activities in the breeding area, several of which were previously unrecorded, and could have led to the mis-interpretation of results from remote technology in the later chapters. In fact, the question of structure and function of female fights in Chapter 3, led the the in-depth investigation of male and female distribution and movement patterns in Chapters 4 and 5 indicating the nearshore preference in a very specific area of the bay, and the analysis of turtle movement in correlation to marine thermal and wind parameters in Chapter 6.

The final chapter re-inforced the importance of temperature in sea turtle biology, particulary considering the fact that Zakynthos occurs at the limits of the breeding range for loggerheads. When at the breeding area energy conservation and maximisation of egg development are of extreme importance to female turtles. However, the nearshore area where turtles can potentially attain the thermal levels required for egg development in the early part of the season occur at the least protected maritime zones where the tourist industry is most concentrated. Hence, the protection zones should be amended to take into consideration the function of different habitats with respect to sea turtle behavioural activities and variable spatio-temporal distribution based on thermal conditions. Furthermore, in order to assess the effectiveness of introduced protection measures it will be necessity to obtain objective measures of the potential impact of marine based activities (i.e. turtle watching boats, private hire boats, snorkelling and swimming etc.) on female turtles. Ultimately breeding areas represent one segment of an adult’s life-history; knowledge about migratory routes and wintering/foraging grounds at which turtles spend protracted periods of time is required for effective conservation actions towards protecting reproductively active adults. Hence the preliminary information obtained on male migration has large scale application as it can be applied to towards enhancing national and international efforts to identify, delineate and develop of new and effective protected areas encompassing breeding, migratory and foraging areas. This is of particular importance due to the low male sex ratios recorded in the Zakynthos population, which based on the photo-identification research of Chapter 1 in combination with analysis of adult male and female distribution in Chapters 4 and 5 appears to continue throughout development.

In conclusion, the research conducted here illustrated the value of direct observational studies in combination with remote GPS tracking in the marine environment to develop our knowledge of loggerhead ecology and the application of this knowledge towards conservation management.

ΕΥΧΑΡΙΣΤΙΕΣ / ACKNOWLEDGEMENTS

I thank my PhD supervisors, Professor Giannis Pantis (Aristotle University of Thessaloniki, Greece), Professor Panayotis Dimopoulos (University of Ioannina, Greece) and Professor Graeme Hays (Swansea University, Wales, UK) who oversaw and asssisted the development of the proposed research into six published chapters. I thank Professor Giannis Pantis for giving me the opportunity to initiate the in-water research in 2003 which provided the basis on which the PhD has developed. I thank Professor Panayotis Dimopoulos for proposing the PhD. I thank Professor Graeme Hays for his suggestions and assistance to obtain funding for equipment to develop the research, and for covering the costs of my visits to Swansea University to process and produce the written research under his close supervision.

I thank Dr Charles Bishop and Peter Brown for use of their TrackTag GPS loggers, which formed a major component towards the development and realisation of this research.

I thank the Management Agency of the National Marine Park of Zakynthos, who gave permission for the presented research and who provided field assistance in the form of boat access and skilled personnel, without which the field study of the PhD would not have been possible.

I particularly thank Kostas Katselidis, Martin Lilley, Martyn Baker, Giorgos Mitrouskas and Mike Sheldon and Kostas Gounelis for their assistance in developing the method for turtle capture and participating in the capture of many turtles, without whom the field study of the PhD would not have been possible.

I express my gratitude to my father, David G. Schofield, who diligently proof read and made invaluable suggestions for every chapter prior to publication. I also thank Kostas Katselidis for assistance with the translation of sections of this thesis into Greek.

I sincerely thank the following people for all their assistance:

- Participation in photo-identification trials: including students of Swansea University, Aristotle University of Thessaloniki, colleagues, friends and family
- Contribution of photographs to the photo-identification database: Arnes Eide, Gerald Hau, Sheila Jack, Anna Proctor and Reinhard Kikinger
- Participation in in-water surveys: Martyn Baker, Amanda Banks, Kostas Gounelis, Valia Lianos, Charikleia Minotou, Karen Azodoh, Gabriele Dederer, Anna Proctor, Tim Proctor, Stephanie Hitchcock, Helena Herlitz, Marieka Hoecke, Katie Visvardi, Esa Eskelinen, Penny Gilmore, Tania Gilmore.
- Turtle capture team and skilled boat drivers: Kostas Katselidis, Martin K.S. Lilley, Kostas Gounelis, Martyn Baker, Giorgos Mitrouskas, Mike-Jen-Hannah Sheldon, David Oakley, Giannis Liveris, Giorgos Livanis, Nikos Margaris, Thomas Leonidis
- Beach retrieval of GPS units and other equipment from turtles: NMPZ personnel including Sofia Alexiou, Sakis Botos, TyAnn Lee, Ines Palomares, Veneranda Petta-Bika, Enrico Marcon; ARCHELON personnel including Mark Barrett, Philip Bradshaw, Chris Dean, Bronwen Gill, Alex Hogg, David Oakely, Emma Ransome, Bianca van Divendyk, Nick Walters, Judith Zbinden and others for invaluable assistancewith logger retrievals
- Tracktag equipment: Charles M. Bishop who was awarded a NERC Connect B Grant (NER/D/S/1999/00078); D.A. Davies and A. Jones for making the pressure proof logger housings
- Overseeing equipment placed in the field: Fanis Nikoloudakis of Divers Paradise Centre and Kostas Kollias
- GIS assistance: V. Hobson, L. Sourbes, K. Papadimitriou
- Statistics assistance : Professor Graeme C. Hays
- Logistical assistance: Professor A.D. Karagouni, Kostas Katselidis, Laurent Sourbes, Anastasia Kolokotsas, David G. Schofield, Marijke de Boer, Charlotte Sahlin.
- I acknowledge the use of the Maptool program for analysis and graphics in this paper (www.seaturtle.org).

- Symposium attendance financial support was provided by the National Marine Park of Zakynthos, the Sea Turtle Symposium Travel Grant supporters and my parents

Financial and logistical support towards the PhD was provided by:

- Boyd Lyon Sea Turtle Fund Scholarship & The Ocean Foundation
- The British Chelonia Group
- The Peoples Trust for Endangered Species
- TrackTag©
- The National Marine Park of Zakynthos
- Sirtrack
- Bangor University
- University of Ioannina
- Swansea University

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ΠΑΡΑΤΗΜΑ / APPENDIX 1: PHOTOGRAPHIC PLATES

Plate 1. West-East view: the wider area of Laganas Bay with Marathonisi islet (core 5km study area from small Cameo islet projecting from mainland to base of mountain)

Plate 2. East-West view: core 5km study area in Laganas Bay (from the initial promonotory - beneath mountain - to Cameo islet)

Plate 3. Loggerhead turtle breathing in the nearshore area fronted by the tourist development of Laganas village

Plate 4. TrackTag GPS logger before sealing

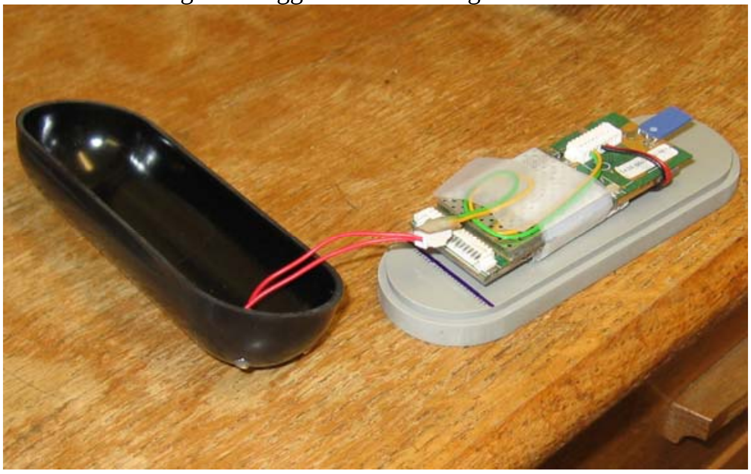


Plate 5. TrackTag GPS logger and Tinytag TDR on loggerhead turtle

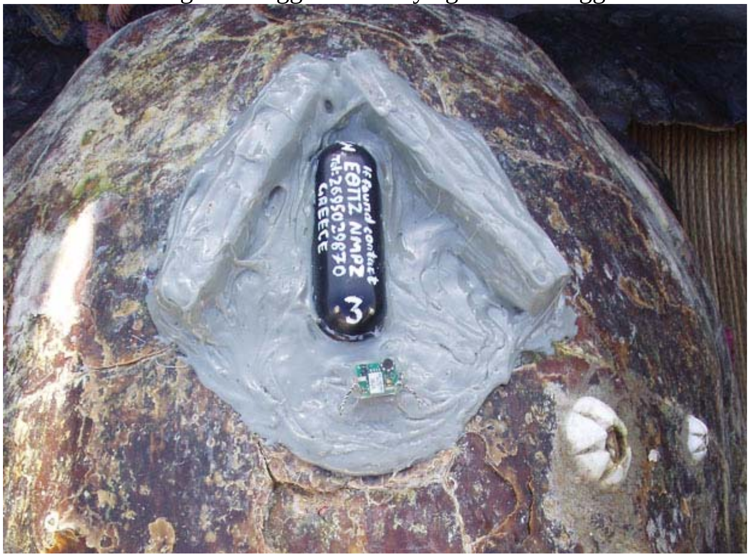


Plate 6. Tracktag GPS logger on female loggerhead turtle

Plate 7. Sirtrack GPS transmitter on male loggerhead turtle

Plate 8. Capturing a loggerhead turtle

Plate 9. Placing a loggerhead turtle in the semi-submerged containment box

Plate 10. Attaching the unit after cleaning the carapace

Plate 11. Turtle being released from containment box

Plate 12. Turtle swimming from containment box

ΠΑΡΑΤΗΜΑ / APPENDIX 2: SUPPLEMENTARY MATERIAL

Chapter 1

Photo identification trials 1 & 2

TRIAL 1 WORKSHEET:

SEPARATING TURTLE PHOTOGRAPHS INTO GROUPS

Contact: Gail Schofield g.schof@gmail.com

INSTRUCTIONS

This exercise investigates whether turtles can be separated into groups using natural markings.

A. The identification tree

1. You have been given an identification tree (Page 4) which is used to separate turtle images into groups for easier identification.
2. The identification tree is divided into four sequential steps (field 1 to field 4), and to place the images into the correct group you must follow the tree in the correct order.
3. Familiarise yourself with the identification tree, the four fields and 10 groups against which the turtle images are matched.
4. On a separate sheet you have **40** photographs of the right side of sea turtle heads (Page 5-6).

B. The trial

5. You are requested to complete the trial twice, with at least 1 day separating each run
6. **Before you begin** the 1st run of the trial, make a copy of this document to use in the 2nd run.
7. Record the time taken for both trial runs, from the moment you begin sorting the images to the moment you finish.
8. Allocate the 40 photos into the available groups on the identification tree.
9. Groups 4 to 10 are separated based on 'post-ocular' scale numbering and patterns (i.e. *scales outlined in red on the diagram*)

10. If an image appears to fit more than one group, you are allowed to allocate it to two or if necessary three groups. In such cases clarify which is your primary choice in the table provided.
11. For any images that do not match any group you can record them in the results table as 'could not allocate'.
12. Give each photograph a value of 1 (lowest) to 5 (highest) for (a) photograph image 'quality' (i.e. lighting, visibility, angle etc.) and (b) turtle scale pattern 'distinctiveness'.
13. You are allowed to re-order the photographs to assist with the allocation process and set aside images to return to at the end.
14. You can conduct the analysis directly on the worksheet by 'edit-copy-paste' or dragging each image into the empty cells beside the flow-chart for comparison, you can enlarge the images and/or chart for easier viewing, or if you have access to a good printer you can print out the document, cut up the photos and match them by hand
15. On completion of each trial run, please record which turtles (i.e. the turtle code number) you placed into each group(s) in the 'results tables' on pages 2-3.
16. As you conduct each trial, make sure the previous run results are NOT visible.
17. On completion of the two tables, please return them as soon as possible to Gail at g.schof@gmail.com as a separate document.

Thank you

Trial 1 Results Worksheets

TRIAL 1 : SEPARATING TURTLE PHOTOGRAPHS INTO GROUPS

1st RUN

OBSERVER	
Time start:	
Time end:	

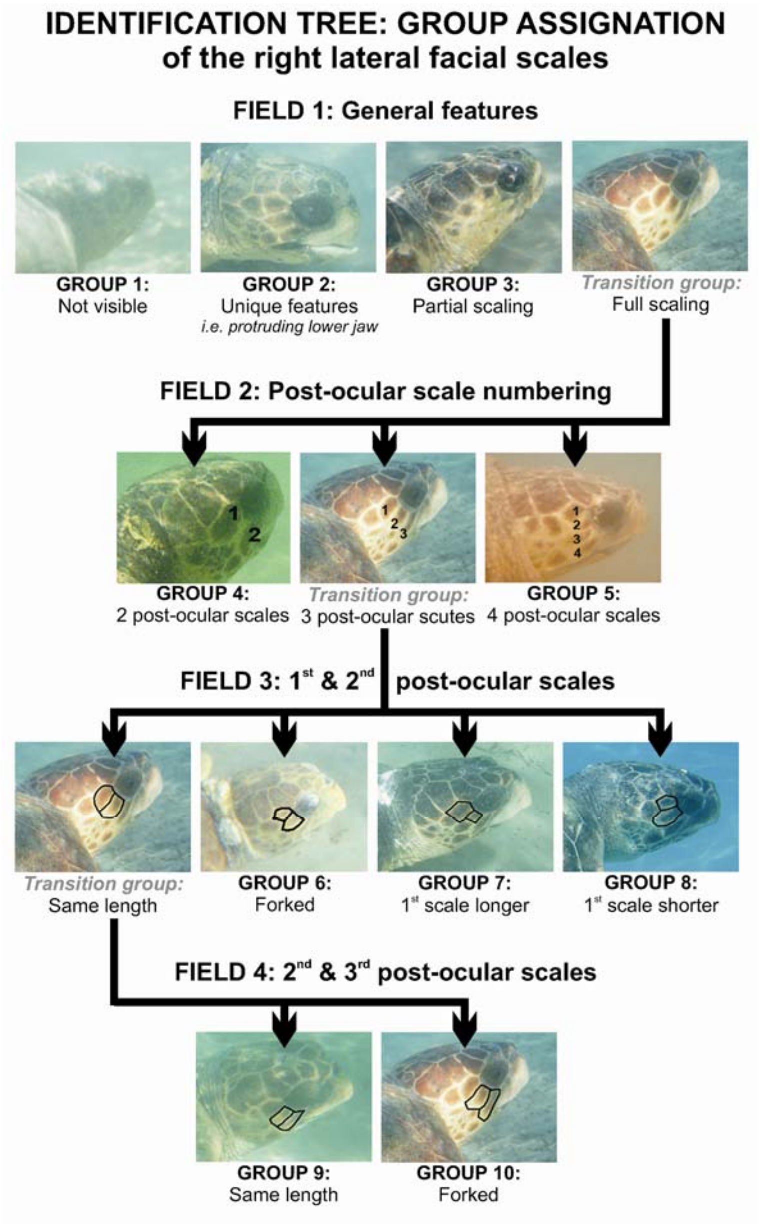
Turtle Photo-code	**Primary group**	**Secondary groups**	**Photograph quality (Score 1-5)**	**Turtle scale distinctiveness (Score 1-5)**
Turtle image 3				
Turtle image 7				
Turtle image 8				
Turtle image 12				
Turtle image 15				
Turtle image 18				
Turtle image 23				
Turtle image 24				
Turtle image 31				
Turtle image 34				
Turtle image 35				
Turtle image 36				
Turtle image 37				
Turtle image 52				
Turtle image 59				
Turtle image 74				
Turtle image 84				
Turtle image 87				
Turtle image 97				
Turtle image 98				
Turtle image 99				
Turtle image 102				
Turtle image 108				
Turtle image 113				
Turtle image 125				
Turtle image 127				
Turtle image 132				
Turtle image 138				
Turtle image 143				
Turtle image 154				
Turtle image 162				
Turtle image 167				
Turtle image 171				
Turtle image 186				
Turtle image 187				
Turtle image 190				
Turtle image 195				
Turtle image 199				
Turtle image 200				
Turtle image 205				

TRIAL 1 : SEPARATING TURTLE PHOTOGRAPHS INTO GROUPS

2nd RUN

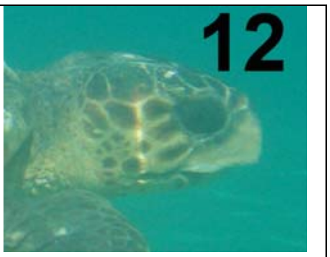
OBSERVER	
Time start:	
Time end:	

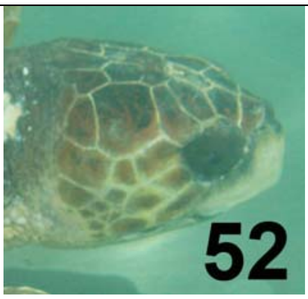
Turtle Photo-code	**Primary group**	**Secondary groups**	**Photograph quality (Score 1-5)**	**Turtle scale distinctiveness (Score 1-5)**
Turtle image 3				
Turtle image 7				
Turtle image 8				
Turtle image 12				
Turtle image 15				
Turtle image 18				
Turtle image 23				
Turtle image 24				
Turtle image 31				
Turtle image 34				
Turtle image 35				
Turtle image 36				
Turtle image 37				
Turtle image 52				
Turtle image 59				
Turtle image 74				
Turtle image 84				
Turtle image 87				
Turtle image 97				
Turtle image 98				
Turtle image 99				
Turtle image 102				
Turtle image 108				
Turtle image 113				
Turtle image 125				
Turtle image 127				
Turtle image 132				
Turtle image 138				
Turtle image 143				
Turtle image 154				
Turtle image 162				
Turtle image 167				
Turtle image 171				
Turtle image 186				
Turtle image 187				
Turtle image 190				
Turtle image 195				
Turtle image 199				
Turtle image 200				
Turtle image 205				

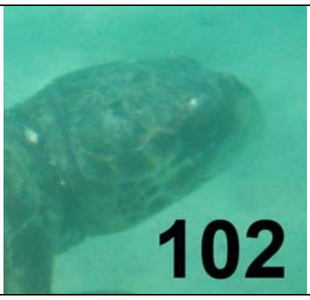

IDENTIFICATION TREE: GROUP ASSIGNATION of the right lateral facial scales
FIELD 1: General features
GROUP 1: Not visible
GROUP 2: Unique features
i.e. protruding lower jaw
GROUP 3: Partial scaling
Transition group: Full scaling
FIELD 2: Post-ocular scale numbering
1
2
1
2
3
1
2
3
4
GROUP 4: 2 post-ocular scales
Transition group: 3 post-ocular scutes
GROUP 5: 4 post-ocular scales
FIELD 3: 1st & 2nd post-ocular scales
Transition group: Same length
GROUP 6: Forked
GROUP 7: 1st scale longer
GROUP 8: 1st scale shorter
FIELD 4: 2nd & 3rd post-ocular scales
GROUP 9: Same length
GROUP 10: Forked

NOTES:

Photographic images







 125	 127	 132	 138
 143	 154	 162	 167
 171	 186	 187	 190
 195	 199	 200	 205

TRIAL 2 WORKSHEET:

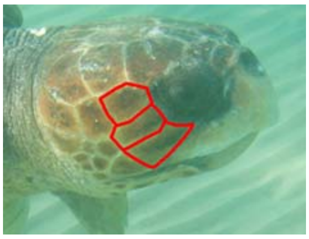
USING NATURAL MARKINGS TO RECOGNISE INDIVIDUAL TURTLES

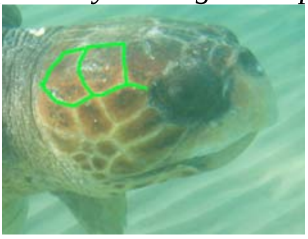
Contact: Gail Schofield g.schof@gmail.com

INSTRUCTIONS

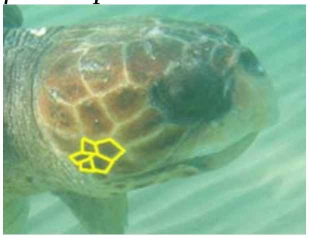
This exercise investigates if individual loggerheads can be recognised by their natural scale markings on the lateral side of the head.

1. You have been given two documents:
    a. A ‘database’ (pages 4-6) that contains 15 images of ‘primary capture’ turtles that have already been observed and are known to be different from each other.
    b. A ‘new records’ table (page 7) that contains 20 new turtle photographs (captures)
2. Your task is to compare the new photographs with those on the existing database.
3. You are requested to complete the trial twice, with at least 1 day separating each run
4. **Before you begin** the 1st run of the trial, make a copy of this document to use in the 2nd run.
5. Record the time taken for both trial runs, from the moment you begin sorting the images to the moment you finish.
6. Take each photo, one at a time, from the ‘new records table’ (page 7), and compare the turtle scale patterns against the ‘primary captures’ provided in the database (pages 4-6)
7. This is done by placing the first new photo in the empty column, beside ‘primary capture’ ‘turtle 1’ (*by dragging the image with the mouse, or by using the cut-paste options*). If the scale patterns of the two images do not match, then move the image you are trying to match into the next row, and compare it with ‘turtle 2’ etc.
   i.e. turtles are compared by looking at the patterns of different groups of scale patterns


Post-ocular


Temporal


Sub-temporal


Tympanic & central

8. If you do not find a match, place it at the end of the first column of ‘primary captures’ as a new unique individual – *and remember to include them in future comparisons…*
9. Repeat the same process with the rest of the images.
10. *Keep in mind*, the photos have been acquired across a 4 year timeframe and barnacle presence (white objects) changes annually, some of the turtles may be new captures that may not match your existing records, some may be single, double or even triple recaptures.
11. Give each photograph a value of 1 (lowest) to 5 (highest) for (a) photograph image ‘quality’ (i.e. lighting, visibility, angle etc.) and (b) turtle scale pattern ‘distinctiveness’.
12. You are allowed to re-order the photographs to assist with the allocation process and set aside images to return to at the end.
13. You can conduct the analysis directly on the worksheet, you can enlarge the images for easier viewing, or if you have a good printer you can print out the document, cut up the photos and match them by hand.
14. **During** each trial run, please record which turtles (i.e. the turtle code number) you matched with each ‘primary capture’ turtle from the database on the table on pages 2-3. If you are completing the ‘results table’ as you conduct the exercise, make sure the previous run results are NOT visible.
15. On completion of the table, please return the table as soon as possible to Gail at g.schof@gmail.com as a separate document.

Thank you

Trial 2 Results Worksheet

TRIAL 2: USING NATURAL MARKINGS TO RECOGNISE INDIVIDUAL TURTLES			
1st RUN			
OBSERVER:			
Time start:			
Time end:			
Database of 'primary captures'	Matched 'new' turtle captures	**Photograph quality (Score 1-5)**	**Turtle scale distinctiveness (Score 1-5)**
Turtle 1			
Turtle 2			
Turtle 3			
Turtle 4			
Turtle 5			
Turtle 6			
Turtle 7			
Turtle 8			
Turtle 9			
Turtle 10			
Turtle 11			
Turtle 12			
Turtle 13			
Turtle 14			
Turtle 15			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			

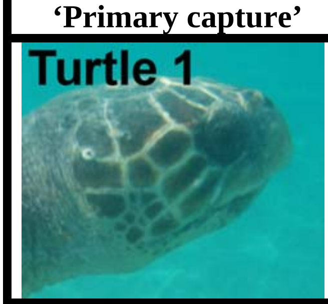
TRIAL 2: USING NATURAL MARKINGS TO RECOGNISE INDIVIDUAL TURTLES

2nd RUN

OBSERVER:	
Time start:	
Time end:	

Database of ‘primary captures’	Matched ‘new’ turtle captures	**Photograph quality (Score 1-5)**	**Turtle scale distinctiveness (Score 1-5)**
Turtle 1			
Turtle 2			
Turtle 3			
Turtle 4			
Turtle 5			
Turtle 6			
Turtle 7			
Turtle 8			
Turtle 9			
Turtle 10			
Turtle 11			
Turtle 12			
Turtle 13			
Turtle 14			
Turtle 15			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			
New Turtle __			

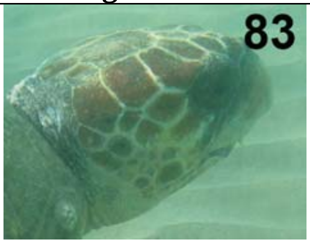
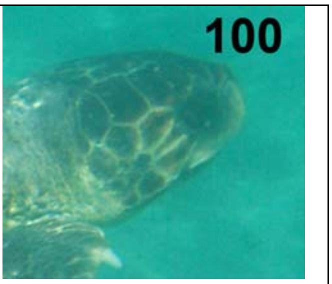
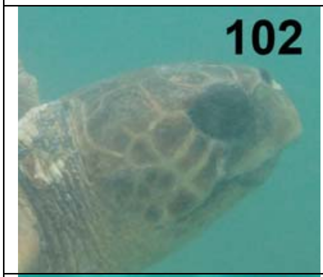
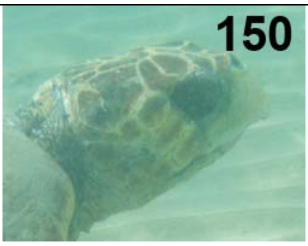
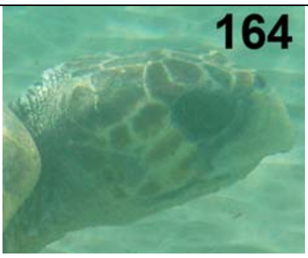
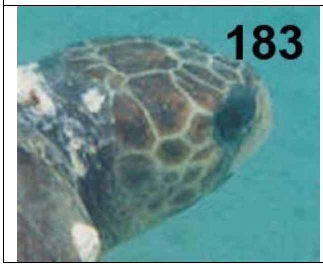
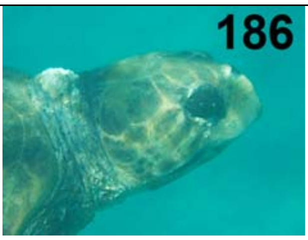
Trial 2 Turtle Database

TURTLE DATABASE: ‘*Group 10*’ sample			
‘Primary capture’	**New match**	**New match**	**New match**
			
			
			
			
			
			

 Turtle 7			
 Turtle 8			
 Turtle 9			
 Turtle 10			
 Turtle 11			
 Turtle 12			
 Turtle 13			

Turtle 14			
Turtle 15			

Trial 2 New turtle ‘capture’ photographs for matching

 52	 74	 83	 100
 102	 109	 115	 124
 142	 150	 153	 154
 162	 164	 171	 175
 183	 186	 200	 208

ΠΑΡΑΤΗΜΑ / APPENDIX 3: JOURNAL PUBLICATIONS

Κεφάλαιο / Chapter 1

Schofield, G., K.A. Katselidis, P. Dimopoulos, J.D. Pantis. 2008. Investigating the viability of photo-identification as an objective tool to study endangered sea turtle populations. Journal of Experimental Marine Biology & Ecology 360:103-108

Κεφάλαιο / Chapter 2

Schofield, G., K.A. Katselidis, J.D. Pantis, P. Dimopoulos, G.C. Hays. 2006. Behaviour analysis of the loggerhead sea turtle *(Caretta caretta*) from direct in-water observation. Endangered Species Research 2:71-79

Κεφάλαιο / Chapter 3

Schofield, G., K.A. Katselidis, J.D. Pantis, P. Dimopoulos, G.C. Hays. 2007. Female-female aggression: structure of interaction and outcome in loggerhead sea turtles. Marine Ecology Progress Series 336: 267-274

Κεφάλαιο / Chapter 4

Schofield, G., C.M. Bishop, G. MacLean, P. Brown, M. Baker, K.A. Katselidis, P. Dimopoulos, J.D. Pantis, G.C. Hays. 2007. GPS tracking of sea turtles as a tool for conservation management. Journal of Experimental Marine Biology and Ecology. 347: 58-68

Κεφάλαιο / Chapter 5

Schofield, G., M.K.S. Lilley, C.M. Bishop, P. Brown, K.A. Katselidis, P. Dimopoulos, J.D. Pantis, G.C. Hays. 2009. Conservation hotspots: intense space use by breeding male and female loggerheads at the Mediterranean's largest rookery. Endangered Species Research. doi: 10.1111/j.1365-2656.2008.01454.x

Κεφάλαιο / Chapter 6

Schofield, G., C.M. Bishop, K.A. Katselidis, P. Dimopoulos, J.D. Pantis, G.C. Hays. 2009. Microhabitat selection by sea turtles in a dynamic thermal environment. Journal of Animal Ecology 78 (1):14-21

Journal of Experimental Marine Biology and Ecology 360 (2008) 103–108

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Investigating the viability of photo-identification as an objective tool to study endangered sea turtle populations

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ARTICLE INFO

Article history:
Received 18 March 2008
Received in revised form 1 April 2008
Accepted 2 April 2008

Keywords:
Bio-monitoring
Conservation management
Ecology
Individual recognition
Population

ABSTRACT

We assessed the potential of using natural facial markings to identify individuals in an endangered breeding population of loggerhead sea turtles (*Caretta caretta*). We divided individual turtles into ten groups based on facial (post-ocular) scale patterns to facilitate rapid comparison of new images in a large photographic catalogue of known turtles (exceeding 400 unique individuals). The matching process was validated by using turtles marked with external flipper tags. An experienced observer achieved a mean 99% success in identifying individuals using photo-id. The reliability and wider utility of the technique was assessed through testing the ability of naïve and trained observers to (1) consistently allocate known (i.e. flipper tagged) individuals into the correct groups (2) correctly match known individuals within one group. In all trials the mean success rate in photographic sorting and matching ranged from 68-100%. A 20 minute training session was found to significantly improve observer ability, i.e the photo-id skills were rapidly acquired by inexperienced workers. Photo-id has the benefit of being suitable for male turtles, which do not come ashore to allow conventional tagging, and so are rarely identified. Photo-id may facilitate the assessment of the numbers of male and female turtles at breeding areas and allow adult sex ratios to be measured.

1. Introduction

The ability to identify individuals within a population is often a starting point for ecological and conservation studies (Thompson et al., 2000; Sibly et al., 2005; Lusseau et al., 2006; Bradshaw et al., 2007; McMahon et al., 2007). Realistic estimates of population size and life history parameters are central to effective wildlife management, but are often difficult to measure in long-lived and elusive migratory marine vertebrates (Caughley, 1994). Most studies with free-ranging animal populations rely on the physical capture of animals and the placement of artificial tags, brands or other objects to allow their subsequent identification (Wilson and Wilson, 1989; McMahon et al., 2007). Such approaches have often been used successfully although there are sometimes problems such as stress to the animals through capture, handling and tag attachment and impacts of the marker itself. For example flipper bands have been shown to increase mortality in penguins as have some flipper tags used in sea turtle research (Nichols and Seminoff, 1998; Dugger et al., 2006). Furthermore, the inevitable loss of identification markers (i.e. from incorrect attachment or being knocked/bitten off) (Limpus, 1992) can become problematic in some species, interrupting the continuity of long-term studies of long-lived species of conservation concern (Sibly et al., 2005).

An alternative to attaching markers to wildlife, is to use visual identification of individuals. The ability to recognize individuals from naturally occurring features has many advantages over conventional marking techniques including: animals are not physically captured, identifiable characteristics are stable over time, and the behaviour of the animal is less likely to be affected by the identification system (Hammond, 1990; Blackmer et al., 2000). Photographic identification, in which researchers photographically capture these natural markings to identify and re-identify individuals, has proven to be a useful tool in long-term monitoring of wild animal populations (Thompson et al., 2000; Forcada and Aguilar, 2003; Bradshaw et al., 2007). For example, whisker patterns are used in lions, facial scale patterns in sea turtles, pelage spot patterns in whale-sharks, fin shape and scarring in dolphins (Richardson et al., 2000; Thompson et al., 2000; Arzoumanian et al., 2005; Ogutu et al., 2006).

Many sea turtle research programmes use some form of conventional tagging method (i.e. plastic, monel, titanium) to obtain life history information about nesting females at breeding areas or of different age classes at foraging areas (Chaloupka and Limpus, 2001;

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doi:10.1016/j.jembe.2008.04.005

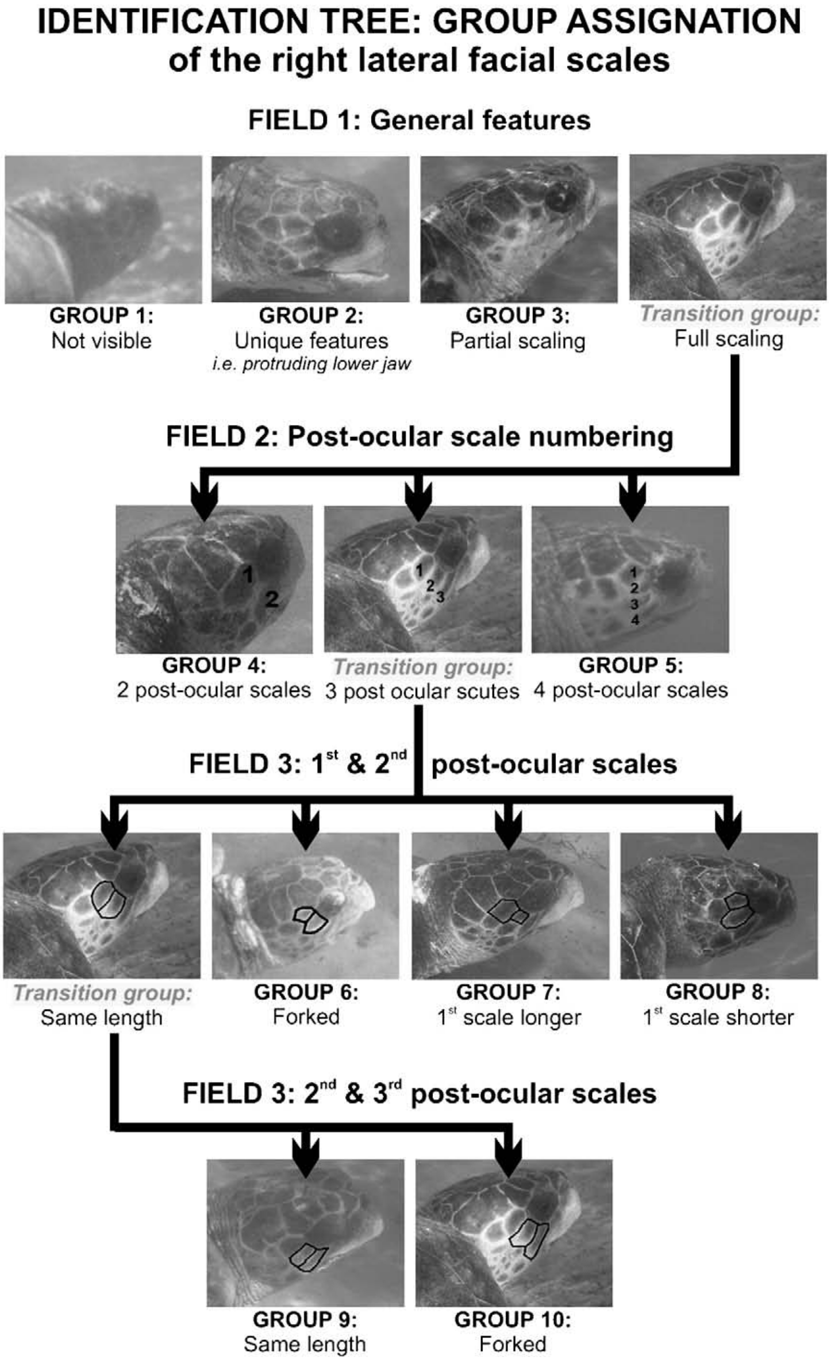

Fig. 1. Identification tree separating the turtle images into ten groups based on the relative shapes of the post-ocular scales.

Balazs and Chaloupka, 2004). Flipper tagging studies tend to preferentially target adult female turtles due to their accessibility on the nesting beaches, resulting in a skewed picture of the adult population structure. Furthermore, significant levels of tag loss often reduce the reliability and scientific value of data collected (Mrosovsky, 1976; Limpus, 1992; Witzell, 1998; Broderick and Godley, 1999). Alternative more endurable methods have recently been used, including passive integral transponders (PIT) (McDonald and Dutton, 1996), natural genetic markers (Bowen, 1995) and photo-identification using head scalation patterns (Richardson et al., 2000).

While photo-identification has been explored in several sea turtle species (Bennett et al., 1999; Richardson et al., 2000; Rodriguez and Sarti, 2000; Schofield et al., 2004; White, 2006; Wood, 2006), the utility of this approach as a bio-monitoring tool when population sizes are large has not been established. Furthermore while experienced workers may have a good ability to visually discriminate individuals (Douglas-Hamilton and Douglas-Hamilton, 1975), a photographic data base can potentially be used more widely, and have longevity beyond the career of the originator, if other users can be trained to reliably use the data-base. The aim of this work is to construct an objective tool based on photo-identification which is easy to use for experienced and non-experienced personnel and is credible and effective for individual recognition of male and female turtles for application in population bio-monitoring, behaviour studies and conservation. We therefore set out with two objectives; first to establish the utility of photo-identification in a large population by testing the technique at the Mediterranean's largest loggerhead turtle rookery, where several hundred turtles aggregate each summer; second to establish whether naïve users could easily and reliably learn to use photo-identification to recognise individual sea turtles.

2. Materials and methods

2.1. Study area and turtle population

Our study was conducted at Laganas Bay, Zakynthos island, Greece (37 °43'N 20 °53'E). Several hundred loggerhead sea turtles (*Caretta caretta*) annually aggregate in the near-shore waters of Laganas Bay to breed from late April to early August (Schofield et al., 2006; Schofield et al., 2007a).

2.2. Data source

Still photographs were taken of male and female loggerheads in the sea. An Olympus Digital 500 (5.0 megapixel) camera with underwater housing was used, while snorkeling at a distance of 2-7 m from the target animal. Images were collected between late April and early August during five years of surveying, 2003-2007. Animal gender was determined based on tail length dimorphism (Casale et al., 2005).

For the purpose of the trials, between one and five digital photographs were selected for each of 170 'confirmed' individuals, validated by the presence of external plastic flipper tags (attached within the framework of the NGO Archelon beach monitoring programme). The tags were attached prior to the onset of the study and the selected turtles retained the same tag(s) in all subsequent sightings as confirmation of their identity. All photographs were of the right lateral head region of the turtle, and were selected based on two criteria (1) all images of the same turtle were from different sighting events separated by at least 1 day, (2) only high digital photographs (300-pixel resolution) were used in which all facial scales were visible. Before use, each image was assigned a unique identification number.

2.3. Group-assignation and photographic matching

Using an identification tree split into four sequential fields, we divided individuals into ten groups based on the relative shapes of the post-ocular scales (Fig. 1). Each group contained < 100 individuals.

We used the lateral facial scale patterns to differentiate between different individuals within each group (Fig. 2a & b). Comparison and matching of photographs within each group was made by subjective observation of three different sets of facial scale groups: (1) the numbering and pattern of tympanic and central scales (2) the relative shapes of the sub-temporal scales, and (3) the relative shapes of the temporal scales. Within each group turtles are separated into 'male', 'female' and 'unknown' categories. This means that if the sex is not determined when the animal is photographed, the individual can be matched following separation into one of the groups.

2.4. Expert observer validation against flipper tagged turtles

The lead author (GS) who has observed turtles in the water for many years conducted a trial to validate her ability to consistently sort and match 200 photographs from known turtles identified with flipper tags. This trial was conducted twice with two different sets of 200 images (i) without and (ii) with the aid of the identification tree. In both versions, the observer was given a catalogue containing 50 unique turtle images. A separate set of 150 unsorted images was provided, each of which could be assigned as a 'new capture' or a 're-capture' when compared to the images in the primary catalogue (Table 1a). The average number of images per individual was 2.7 (range 1-5) for both data sets respectively. In both versions, the trial was repeated on three different occasions separated by an interval of at least one day. The time taken to complete each trial run was recorded.

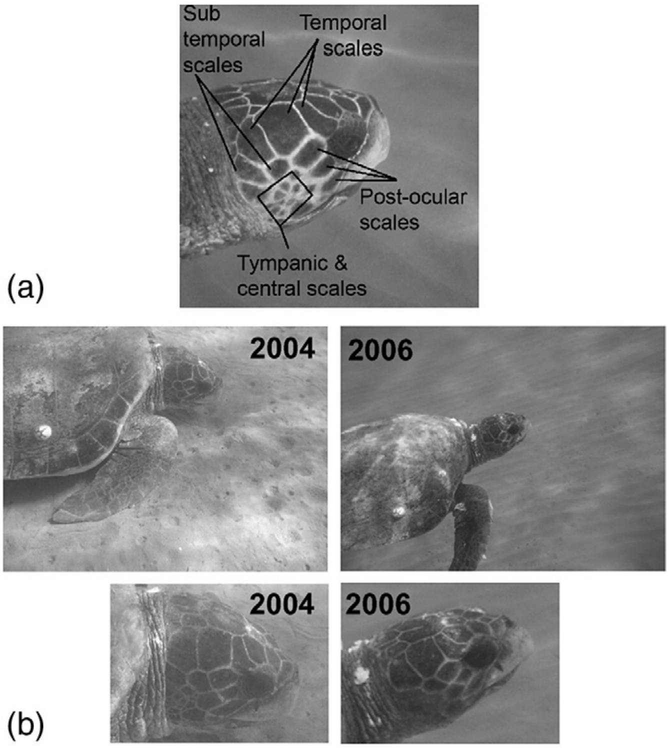

Fig. 2. (a) Lateral head scales of loggerhead turtle used for matching images in this study. (b) Sample lateral facial scale data sets from the photo-identification database. Raw images (top row) from newly submitted (right) and catalogued (left) encounters are processed by comparison of different sets of scale groups (bottom row).

2.5. Naïve observer trials

2.5.1. Trial 1: separating turtles into groups

A trial was conducted to assess observer ability to allocate turtles into the correct groups when a reasonably large number of captures is involved (Supplementary Fig. 1). Each observer was given instructions on how to use the 'identification tree' and was asked to allocate 40 images into one or more groups (Table 1b), or state if unable to place the image. The average number of images per individual turtle was 1.3 (range 1- 2). The trial was conducted twice, separated by an interval of at least one day. In the first run of the trial, all observers (n=44) were inexperienced. Before the second run of the trial, part of the group (n=24) received training. The time taken to complete each trial was recorded.

2.5.2. Trial 2: matching turtles within groups

A trial was conducted to assess observer ability to correctly match turtles within one group when a reasonably large number of captures is involved (Supplementary Fig. 2). Each observer was given a catalogue containing 15 unique images. A separate set of 20 unsorted images was provided, each of which could be assigned as a 'new capture' or 're-capture' when matching against the provided catalogue (Table 1c). The average number of images per individual turtle was 1.8 (range 1-4). The trial was conducted twice, separated by an interval of at least one day. In the first run of the trial, all observers (n=49) were inexperienced. Before the second run of the trial, part of the group (n=23) received training. The time taken to complete each trial was recorded.

In all trials, the observers were permitted to re-order the displayed 'capture' images to assist with the sorting/matching process, and were allowed to set aside images given during sequential identification to return to at the end.

Table 1
The photographic image categories for each trial (a) expert observer validation (b) naïve observers separating images into groups (c) naïve observers matching turtles within groups

Table 1a

Trial type	Total Images	Database Images	Images to Match	Catalogue image matches					New catalogue Images	New catalogue image matches				
				0	1	2	3	4		0	1	2	3	4
Matching not Using groups	200	50	150	15	8	11	9	7	31	9	2	9	8	3
Matching by Using groups	200	50	150	12	12	17	6	3	35	5	7	11	8	4

Table 1b

Total Images	Database Images	Images to Match	Group matches										Singles	Duplicates
			1	2	3	4	5	6	7	8	9	10		
50	10	40	1	2	5	1	1	4	6	7	8	5	22	9

Table 1c

Total Images	Database Images	Images to Match	Catalogue image matches					New catalogue Images	New image matches				
			0	1	2	3	4		0	1	2	3	4
35	15	20	6	6	2	1	0	4	2	1	1	0	0

2.6. Trial analyses

To quantify observer ability, five photo-matching categories were defined; 1) a Match-Match (MM) indicates that the observer correctly matched the photograph to the correct group or individual, 2) the New-New (NN) category indicates that the observer correctly placed the photograph as a new group/individual not found in the existing database, 3) a New-Match (NM) category indicates that the observer correctly matched a new photograph to another newly added image to the database, 4) a False-Match (FM) was determined when an observer incorrectly matched a photograph to a different group/individual in the photographic database (false positive error), 5) a False-New (FN) category was defined as when an observer incorrectly classified a photograph as a new image but it was already in the photographic database (false negative error). We demonstrated the consistency and reproducibility of observer judgement within trials by providing multiple photographs of single individuals.

We used paired Students *t*-tests to examine the relative improvement in skill and time requirement within and between observer groups.

3. Results

3.1. Expert observer validation against flipper tagged turtles

The accuracy and consistency of photographic matching of turtles validated from flipper tags was extremely high; without use of identification tree (98%), with use of identification tree (100%). Incorrect matching occurred for the same three images in all three runs of the first version of the trial (without identification tree), with turtles being incorrectly specified as new captures (i.e. inflation of the population). The use of the identification tree to group turtles before matching resulted in turtles being matched at a significantly faster rate (paired Student's *t*-test, t=33.1, *df*=4, $P<0.001$) with a 50% reduction in matching time required; from 2.26 to 1.14 minutes per image (Table 2).

3.2. Naïve observer trials

3.2.1. Trial 1: separating turtles into groups

In the first run of the trials when all observers were naïve, a mean accuracy of 69% was obtained with observers taking 42 minutes on average to complete the trial. Student t-tests indicated no significant difference in ability in the first run of the trial between those that did and did not receive subsequent training (Student's *t*-test, t=0.18, *df*=42, *P*=0.8). Repetition of the trials, indicated a slightly significant improvement in the untrained group (mean 76%, paired Student's *t*-test, t=2.11, *df*=38, *P*=0.04) and a highly significant improvement in the trained group (mean 83%, paired Student's *t*-test, t=4.27, *df*=46, $P<0.0001$). Trial repetitions took an average 30 minutes in both trained and untrained groups and were not found to be significant in either group.

3.2.2. Trial 2: matching turtles within groups

In the first run of the trials when all observers were naïve, a mean accuracy of 71% was obtained with observers taking 47 minutes on average to complete the trial. Student t-tests indicated no significant difference in ability in the first run of the trial between those that did and did not receive training (Student's *t*-test, t=0.07, *df*=47, *P*=0.07). Repetition of the trials, indicated no significant improvement in the untrained group (mean 78%, Student's *t*-test, t=1.57, *df*=50, *P*=0.1) and a highly significant improvement in the trained group (mean 87%, Student's *t*-test, t=3.74, *df*=44, $P<0.0001$). Trial repetitions took an average 37 minutes in both trained and untrained groups and were not found to be significant in either group.

Table 2
Expert observer validation of photo-identificationt technique using confirmed turtle images

Task	Run	Time to Complete / min	Matching time per image / min	Images to match / trial	Average correct photo-matches	Average false matches (false positive errors)	Average failed matches (false negative errors)	Per trial group percentage success
Matching	1	346	2.3	150	146	0	4	97
Without	2	333	2.2	150	147	0	3	98
Grouping	3	345	2.3	150	147	0	3	98
Matching	1	178	1.18	150	150	0	0	100
With	2	168	1.12	150	150	0	0	100
Grouping	3	172	1.14	150	150	0	0	100

In the first run of the trials when all observers were naïve, 32% of the images matched incorrectly, of which 16% were false negative (no match found), 28% were false positives (new images matched with existing) and 56% of the images were mis-matched existing images. In the second run of the trials, there was no significant difference in the untrained group, whereas in the trained group a significant decline in false positive (Student's *t*-test, t=3.04, *df*=44, *P*=0.004) and mis-matching (Student's *t*-test, t=2.62, *df*=44, *P*<0.001) was found.

4. Discussion

Photo-identification of natural markings is increasingly being used to collect data on individual animals for application to demographic studies (Thompson et al., 2000; Lusseau et al., 2006; Bradshaw et al., 2007). Although information obtained from photo-identification is highly valuable (Hammond, 1990; Blackmer et al., 2000), processing data in large catalogues can be labour-intensive and subject to human error (Kelly, 2001). Through the use of trials, our study demonstrated the validity (i.e. accuracy) and reliability (i.e. precision) of natural markings for assignation of individual loggerhead sea turtles to groups according to a simple identification tree, and that once an image has been assigned to a group, its markings can be used to correctly match it to existing catalogue images of the same individual present in that group.

The size of sea turtle populations is typically assessed by counting tracks of females on nesting beaches (Demetropoulos and Hadjichristophorou, 1995; Godley et al., 2001; Broderick et al., 2002; Margaritoulis, 2005). However this ignores the size of the male component of the adult population. Yet, identifying male turtles is also important to assess population size and sex ratio. It relatively easy to estimate hatchling sex ratios by, for example, recording incubation temperatures or incubation durations (Broderick et al., 2001a; Zbinden et al., 2007). Furthermore it is possible to reconstruct long-term trends in hatchling sex ratios from environmental proxies such as air temperature (Hays et al., 2003). However, how hatchling sex ratio projects through to adult sex ratio is not known. Hence nothing is known about long-term trends in adult sex ratios for sea turtles and implications of climate change for this important demographic parameter. Photo-id, when combined with in-water surveys, clearly has the potential to start providing estimates of the number of males at breeding sites and hence also adult sex ratios.

As well as a lack of information on adult sex ratios, there is also very little known in general about the ecology of male turtles. Direct observations have been used to infer mating seasonality and the departure time of male turtles from breeding areas (e.g. Godley et al., 2002), while paternity in clutches can be assessed without sampling adult males themselves from which inferences about male-female encounters and male movements (Lee et al., 2007; Lee, 2008) can be made. However, very few male turtles are identified by tagging because this requires logistically challenging capture at sea (e.g. Hays et al., 2001; James et al., 2005) as males very rarely emerge onto land (but see Rice & Balazs, 2008). Photo identification will allow a new era of experimental and ecological studies of male turtles, allowing, for example, the behaviours of known individuals to be assessed (Schofield et al., 2006; Schofield et al., 2007b). In addition, photo-identification will allow the interval between successive breeding seasons (the remigration interval) to be established. For female turtles, remigration intervals may be several years, presumably because it takes a long time for individuals to attain a threshold body condition before they embark on breeding migrations (e.g. Broderick et al., 2001b; Hays, 2000; Chaloupka et al., 2008). However, the remigration interval of male turtles are poorly understood, although it is possible that they may be appreciably shorter that for females (Chaloupka and Limpus, 2001), since males do not invest resources in egg production and hence they may lose less condition during breeding seasons.

The accuracy and reliability of photographic matching may be impeded by image quality (i.e. light intensity and sea clarity in underwater photographs) and/or database size (Whitehead et al., 1997; Forcada and Aguilar, 2003; Beekmans et al., 2005). As a consequence, mistakes may result in the wrong inferences being made about the biology of animals. For example, false negative errors (failing to find a match) inflate population estimates, while false positive errors (matching new individuals to an existing database image) deflate population estimates. We recorded a very low error rate during the course of the trials, with that of false positive errors (matching two photographs from different animals) being slightly more frequent than false negative errors. Hence, the accumulation of errors over time in our database, leading to over or under estimations of population size (Stevick *et al.*, 2001), is likely to be negligible.

Our results showed that while in all trials the success rate in photographic matching was very high, experience and training improved the reliability to match individuals (Douglas-Hamilton and Douglas-Hamilton, 1975). Furthermore, at present we have overcome the difficulty of manually comparing and matching a large volume of photographic images (>400) by dividing turtles into several groups of <100 based on variations in one set of facial features. As our photographic catalogue expands, it may become necessary to developed a computer-assisted matching programme, as has been designed for several other vertebrate species with large photographic population databases (Kelly, 2001; Hillman et al., 2003; Beekmans et al., 2005). However, confirmation is required of the stability of the natural features (i.e. colouration and relative scale sizes) being used (Forcada and Aguilar, 2003; Arzoumanian et al., 2005).

Accurate information about the population structure and ecology is not only vital to address the conservation needs of the Zakynthos sea turtle rookery, but could serve as an indicator of adult survival after departure from the breeding area (Chaloupka and Limpus, 2002). Such insights could provide a quantitative foundation for the re-evaluation of the regional, national and global conservation status of this species, thus strengthening international maritime protection policies amongst Mediterranean countries (Thompson et al., 2000; Sibly et al., 2005; Fagan and Holmes, 2006). For example, the creation of photo-libraries at local, national and regional scales, within which individual life-histories of individuals could be developed as well as knowledge about small and large scale migrations of male and female turtles, e.g. between islands or across the Mediterranean basin and how this impacts micro and macro population dynamics. The permanency of photographic data not only permits retrospective analyses as research objectives evolve, but also provides an opportunity to investigate other parameters that may also influence species conservation management and ecological risk assessments such as site fidelity, patterns of interaction, physical condition, health indicators and the impact of anthropogenic activity (Burger and Garber, 1995; Bennett et al., 1999; Pettis et al., 2004; Lusseau et al., 2006).

In conclusion, our study has validated the accuracy, reliability and ease of training of using natural facial markings to identify individuals in a breeding population of loggerhead sea turtles. Within the framework of a long-term monitoring programme, our photographic matching technique could potentially be used to obtain new insights about sea turtle population trends, behaviour, ecology and conservation status. Ultimately, appropriate wildlife management depends on the acquisition of realistic life history information, and photo-identification is a proven technique, facilitating the continuity of long-term studies for long-lived species of conservation concern.

Acknowledgements

The authors thank the National Marine Park of Zakynthos and Greek Ministry of Agriculture for permission to conduct this research activity. We thank G.C. Hays for his valuable comments and contribution to the manuscript. We especially thank all who participated in the trials. We thank A. Eide, G. Hau, S. Jack, A. Proctor and R. Kikinger for contributing photographs to the database. We thank the NMPZ for financial assistance in the form of boat access and skilled drivers. Special thanks to all who participated in the fieldwork, especially M. Baker, A. Banks, V. Lianos, C. Minotou and K. Visvardi. **[SS]**

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jembe.2008.04.005.

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Vol. 2: 71–79, 2006

ENDANGERED SPECIES RESEARCH
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Printed December 2006

Behaviour analysis of the loggerhead sea turtle *Caretta caretta* from direct in-water observation

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ABSTRACT: Direct observation of animal behaviour is essential for the effective conservation of endangered species in their natural habitat, understanding their function within ecosystems and validating inferences made using remote technology. The aim of this study was to document the daytime behavioural activity of loggerhead sea turtles *Caretta caretta* at a temperate breeding area through direct observations. Between April and July of 2003 to 2005, turtle behaviour on initial sighting was recorded during 287 h of observation, comprising 1534 sighting events of solitary (n = 80 male, n = 1335 female) and social (n = 65 same sex, n = 54 mixed sex) activity. We grouped observed activities into 4 solitary and 2 social behaviours, which were divided into 14 sub-categories. Solitary behaviour included resting, swimming, foraging and cleaning. Social behaviour included antagonistic interactions and reproductive activity. Foraging, cleaning and female–female contests are not documented in published literature for loggerhead sea turtles at breeding areas. Our results suggest that during the breeding period (1) male behaviour was primarily social and active (2) female behaviour was primarily solitary and inactive.

KEY WORDS: Sea turtle · Behaviour · Solitary · Social · Activity · Interaction

INTRODUCTION

Direct observation of animals in their natural environment contributes important information about how species adapt to a particular environment. Information about behaviour and interactions at the level of individuals is key to understanding how an animal may impact the surrounding community as well as ecosystem function, organisation and response to disturbance (Piraino et al. 2002). Hence, studies of behaviour in the field are fundamental for the effective conservation of animals in their natural habitats (Mills et al. 2005).

Direct observations in the marine realm are often restricted due to sea depth and state, underwater visibility, natural light availability, physical danger and adequate access to the study animal (Hooker & Baird 2001). Due to the difficulties of studying large marine vertebrates in their natural habitats, most studies of their behaviour have relied on inferences from animal-borne devices. For example, in sea turtle research devices such as data-loggers, radio and satellite telemetry are used (Hopkins-Murphy et al. 2003, Hochscheid et al. 2005, Myers et al. 2006). While useful, these techniques cannot describe the full range of behavioural patterns of wild animals that direct first-person observations can (Houghton et al. 2002). To date, there have been few quantitative observational studies of sea turtles (Booth & Peters 1972, Whittow &

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Balazs 1982, Dodd 1988, Losey et al. 1994, Frick et al. 2000); however, the development of animal-borne cameras has provided the opportunity to observe and confirm the underwater behaviour of these and other marine vertebrates (Davis et al. 1999, Heithaus et al. 2002, Reina et al. 2005, Hays et al. 2006).

Sea turtles are endangered worldwide, therefore a detailed understanding of their behaviour is a key factor to be considered when drawing up effective conservation management policies. This is particularly important in coastal areas where marine oriented tourism is focused on sea turtles (Meadows 2004). On Zakynthos island in Greece, high densities of reproductively active loggerhead sea turtles and turtle-watching enterprises co-exist in a very restricted area each summer. Currently turtle watching protocols and permitted observation zones are evolving under the guidance of the National Marine Park of Zakynthos. However, due to the lack of knowledge about sea turtle behaviour and habitat use in this and similar coastal reproductive areas, decisions are not currently scientifically based.

Laganas Bay, in the National Marine Park of Zakynthos, is an ideal location for investigating the behaviour of loggerhead sea turtles *Caretta caretta* at a temperate breeding area. Several hundred adult turtles are found at nearshore aggregations for about 4 mo following migration into the bay each spring (Margaritoulis 2005). In sea turtles, mating and first nesting occur up to 6 wk apart (Wood & Wood 1980, Miller et al. 2003), with females storing sperm to fertilize several clutches laid during the season at intervals of around 14 d (Hays et al. 2002a).

The aim of this study was to gather information about the behaviour of male and female loggerhead sea turtles in the marine environment during the breeding period. In this paper we (1) document the solitary and social behaviour of loggerhead sea turtles, and (2) discuss how differences in the proportions of observed male and female behaviour may reflect gender-specific strategies.

MATERIALS AND METHODS

Laganas Bay is situated at the southeastern part of the Greek island of Zakynthos (37° 43′ N, 20° 52′ E) (Fig. 1). The bay is generally shallow, reaching a depth of about 50 m, with sea surface temperatures of 15°C in March rising to 28°C in August (Comprehensive Ocean Atmosphere Data Sets (COADS) database, www.cdc.noaa.gov/coads/). In-water surveys have been conducted annually since 2003 to collect information about loggerhead sea turtle marine ecology from April to July during the breeding season. The nesting season runs from approximately late-May to early September (Margaritoulis et al. 2003). Hence, our surveys spanned the time during which there was still some mating activity, but many females had started nesting.

Surveys were conducted in Laganas Bay along a 5.5 km stretch of nearshore water, extending 1 km into the sea to depths of up to 10 m (Fig. 1). Surveys were conducted over a total of 287 h on 104 d across 3 yr (2003 to 2005). Surveys were primarily concentrated in the afternoons between 12:00 and 18:00 h, lasting an average of 3 h (minimum 1 , maximum 7 h). Observers entered the water from a boat, a kayak or directly from the shore.

Boat surveys (405 km, 137 h) were conducted by 2 to 3 observers in April and May of 2003 on a 4 m boat with an outboard engine. Sessions lasted an average of 5 h (minimum 4, maximum 7 h) at a maximum boat speed of 4 knots km^{-1}. Line transects across the entire survey area were performed during each survey session that ran parallel to shore at sea depths of 10, 7, 5 and 3 m.

Kayak surveys (77 km, 33 h) were conducted by 2 observers in May and June of 2004 on 2 sea-kayaks at

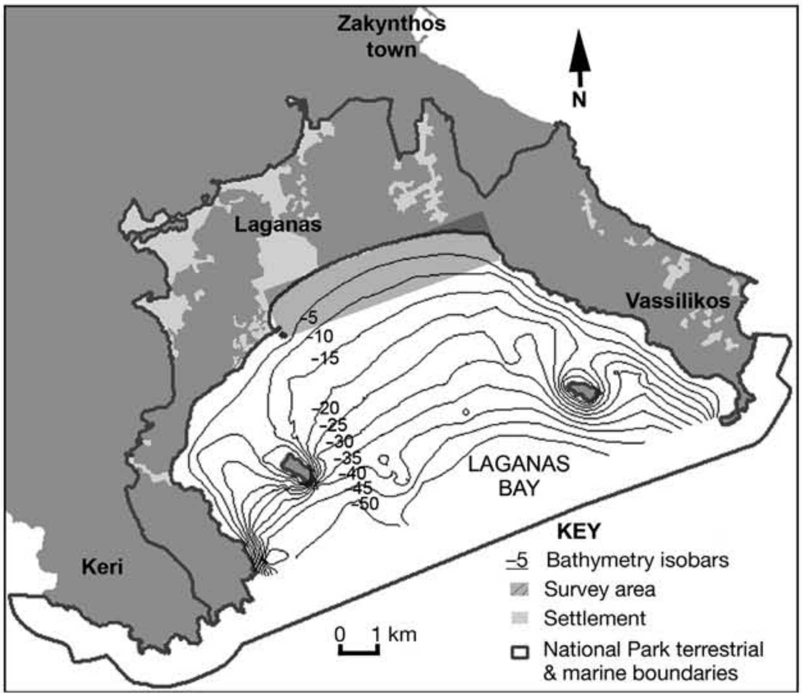

Fig. 1. Laganas Bay situated on the southern part of Zakynthos Island, showing the survey area

randomly selected sites within the survey area. Sessions lasted an average of 2 h (minimum 1, maximum 3 h). A 2 km line transect was conducted at a sea depth of 5 m and returning at a sea depth of 3 m during each session.

Snorkel-swim surveys (163 km, 117 h) were conducted by 1 to 2 observers in May and June of 2004 and 2005 at randomly selected sites within the survey area. Sessions lasted an average of 1.7 h (minimum 1, maximum 3 h). A 1 km line transect was conducted with the observer swimming parallel to shore at a sea depth of 3 m and returning by wading at a sea depth of 1 m.

On sighting a sea turtle, the GPS location was recorded (using a GARMIN Etrex-legend) while the observer entered the water from the boat/kayak at a distance of at least 5 to 10 m from the target animal(s) and approached until within underwater visual range (subject to daily variations in underwater visibility, approx. average 4, minimum 0.5, maximum 8 m), to minimize disturbance of ongoing behaviour. On encountering the animal(s), photographic records were collected in addition to biological, environmental and behavioural observations (including response to underwater observer presence). Photographs were taken using an Olympus Digital 500 (5.0 megapixel) with underwater housing. Video footage, using a Sony DCR-HC32E Handycam with housing, was collected to classify observed behaviours and inter-specific interactions. Sex was estimated using tail length (Casale et al. 2005).

Analyses included only the initial behaviour observed at each sighting event. Non-parametric Chi-square statistics were used for comparative analysis of the behaviour sighting data. We regarded the results to be significant when $p < 0.05$.

RESULTS

General survey information

The behaviour of loggerhead sea turtles at initial sighting was recorded at 1534 sighting events of solitary (n = 80 male, n = 1335 female) and social (n = 65 same sex, n = 54 mixed sex) activity. This bias towards female turtles partly reflects their location closer to shore where surveys were concentrated. However this ratio may also reflect the highly skewed bias towards females found in hatchling loggerhead turtles in Mediterranean populations (Godley et al. 2001, Mrosovsky et al. 2002).

On average, 1.5 sightings km^{-1} were made by boat (n = 615), 3 sightings km^{-1} were made by kayak (n = 237) and 4 sightings km^{-1} were made by snorkel-swim surveys. Sightings lasted 2.7 min on average (SD = 4 min, minimum 1 , maximum 65 min).

We grouped observed behaviour into 4 solitary and 2 social behaviours (Fig. 2) comprising 14 sub-categories (Table 1).

Solitary behaviour descriptions

Resting. This incorporates both resting on the sea bed and surface-basking (Table 1, Fig. 3A,B, Video clips 1 to 3, see www.int-res.com/articles/suppl/n002p071_videos/). When resting on the seabed the head, body and flippers were lowered on the substrate. Females never rested within visual range of one another. At 4 sightings large fish (>0.5 m body length) were sighted in close proximity to resting females. At 34 sightings, juvenile saddled bream *Oblanda melanura* (2 to 4 cm body length) were observed feeding opportunistically on resting turtles that neither solicited nor appeared to respond to this activity. Surface-basking turtles rested at the sea surface or up to 1 m beneath the sea surface with the head and flippers lowered.

Swimming. This includes along the seabed, in the water column and near the sea surface as well as patrolling by males (Table 1, Fig. 3C,D, Video clips 4 to 6, see www.int-res.com/articles/suppl/n002p071_videos/). At 29 sighting events, 6 different fish species

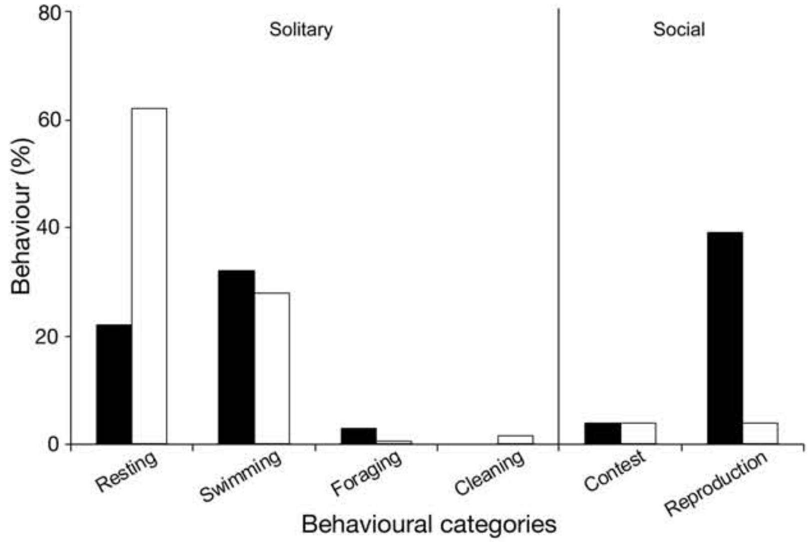

Fig. 2. *Caretta caretta*. Relative proportions of behaviour exhibited by male (black, n = 139) and female (white, n = 1449) loggerhead sea turtles at initial sighting

Table 1. *Caretta caretta*. Summary table of the breakdown of loggerhead sea turtle behaviour at each sighting event during surveying

Status	Behaviour category	Behaviour sub-category	Sex	Number of sighting events
Solitary	Resting	Resting on seabed	M	27
			F	676
		Surface-basking	M	4
			F	226
	Swimming	Along seabed	M	8
			F	89
		In water column	M	12
			F	197
		Near surface	M	21
			F	121
		Patrolling	M	4
			F	0
	Foraging	Infaunal mining	M	4
			F	5
	Cleaning	Self-cleaning	M	0
			F	6
		Fish cleaning symbiosis	M	0
			F	15
Social	Contest	Male-male	M+M	5
		Female-female	F+F	60
	Reproduction	Courtship	M+F	34
		Copulation	M+F	15
		Copulation with interference by attendant(s)	(M+F)+M	5

(adult and juvenile) were recorded swimming in close proximity to turtles (in the folds of the hind flipper-body join, or above or beneath the carapace or head).

Four males patrolling for females were each followed at close proximity by the in-water observer for an average of 43 min (SD = 17 min). The males all appeared to swim parallel to shore at sea depths of 0.5 to 3 m. On detecting a female the male swam faster, generally approaching the female side on and nudging/biting at her carapace initiating courtship behaviour. By combining all data sets, we estimated that patrolling males encountered a female every 9 min on average (SD = 3).

Foraging. Both males and females were observed mining for bivalves (Table 1, Fig. 3E, Video clips 7 & 8, see www.int-res.com/articles/suppl/n002p071_videos/). Females made sporadic attempts, but none were observed to be successful. Males foraged close to shore in areas where females also aggregate to rest. Bouts lasted a minimum of 30 min, which was defined as periods when turtles dug in the sand and ended when no digging was reported for 5 min. The males swam along the seabed, and on detecting bivalves in the sand they dug in the sand with their beak using the flippers for momentum. Successful attempts were recognised by the expulsion of segments of crushed mollusc shell from both the nares and oral cavity. By combining all data sets, we estimated that males made digging attempts about twice a minute (mean 38 s, SD = 7) with a 45% foraging success rate (n = 148 attempts).

Cleaning. This includes both self-cleaning and fish cleaning symbiosis (Table 1, Fig. 3F,G, Video clips 9 & 10, see www.int-res.com/articles/suppl/n002p071_videos/). When self cleaning, turtles repetitively rubbed their heads, flippers and carapace against submerged rocks or anchors. Algae, barnacles and limpets were visibly removed, and distinctive parallel markings were created running the length of the carapace. Based on this uniformity of scratch patterns (different to that created by claw/carapace scratches during mating/ fighting), we were able to detect if this behaviour had been performed recently in all sighted turtles. We found that 55% of females and 19% of males sighted had performed this activity at least once during the survey period.

Female turtles were observed visiting a specific cleaning station and actively soliciting cleaning by juvenile sheepshead bream *Diplodus puntazzo* (12 to 14 cm body length). The solicitation posture was held until fish approached; the turtle extended her head, with her hind limbs sprawled and the forelimbs stretched forward, and the body slightly raised above the seabed. Turtles were cleaned by an average of 13 fish (SD = 4.8) at any one time. Bream are omnivorous, and were assumed to be primarily feeding on micro-organisms on the turtles soft and hard body surfaces; however, epidermal skin lesions were also targeted. This caused turtles to react by flicking the head, twisting the body, swimming fast, biting at their own flippers or fish or on rocks, or to depart the cleaning zone altogether. Within an hour of departure 2 turtles returned for repeat cleaning.

Social behaviour descriptions

Contest. This included female–female and male–male interactions (Table 1, Fig. 3H,I, Video clips 11 to 13, see www.int-res.com/articles/suppl/n002p071_videos/). Female contests lasted on average 3.4 min (SD = 1.02 min) and involved ritualized escalation in behaviour from passive threat displays (e.g. head–tail circling) to aggressive combat (e.g. sparring, biting and chasing). The presence of intruder females triggered a response in 76% of observed cases. Contests were usually initiated when the intruder entered the visual range of the resident; however, for 12% of instances, contests were initiated by tactile advances (nuzzling/biting of carapace) from the intruder. Male contests followed the same pattern of escalation as that of female competition. During fights males would bite, spar, lock flippers while plastron to plastron, attempt to mount, and repeatedly swim to and from each other at speed, until one opponent retreated. In all instances, the retreating male curled its tail under the carapace while the winner held its tail straight.

Reproduction. This includes courtship and copulation with and without male attendants (Table 1, Fig. 3J–L, Video clips 14 to 19, see www.int-res.com/articles/suppl/ n002p071_videos/). Courtship was initiated by a male entering the visual range of a female, advancing quickly and biting at the carapace (Video clip 14). The male would attempt to get behind the female and mount; however, if the female was not receptive, she would counter his actions by attempting to (1) take a vertical position in the water with the plastron facing the male, which sometimes led to the male locking plastrons with the female (Video clips 15 & 16), (2) maintain head–head position preventing the male from circling around, often trying to obtain a higher horizontal position in the water than the male (Video clip 17), (3) spin out from under a male attempting to mount (Video clip 18), (4) attempt to get behind the male and bite at his tail (Video clip 19). Males attempting to court females during the inter-nesting period were never observed to successfully mount and mate.

Mating was observed on 20 occasions during the pre-nesting period, both on the sea surface and on the seabed. Copulation had already begun when the turtles were initially observed, and males were mounted for periods of at least 40 min (the total duration was not recorded). Mounted males hooked their fore-flipper claws over the anterior rim of the female carapace and were observed repeatedly biting at the necks of females. Mating appeared to occur more frequently (1) during rough sea conditions when underwater visibility was low (90%, 18 pairs) and (2) during April (70%, 14 pairs). Copulation with interference by attendant males was recorded on 5 occasions. Only one attendant was recorded at any one time with mating pairs. One mounted male was successfully dislodged by attendant interference. Attendant behaviour included fast swimming to and from the mating pair and aggressive biting of the mounted male's (and on occasion female's) fore and hind flippers, neck, tail and carapace. During attacks mounted females would attempt to evade the attendant by diving to the seabed and swimming along it, ceasing all movement between attacks.

Female behaviour

At 1449 female sightings (Fig. 2), significantly more were observed in solitary (92%) than social (8%) behaviour ($\chi^2_1 = 1020$, $p < 0.001$). Solitary females were more likely to be found inactive (68%) than active (32%) ($\chi^2_1 = 164$, $p < 0.001$). While cleaning behaviour only accounted for 1.5% of observations, very similar uniform scratch patterns on the carapace (different to that of mating scratches) were documented at over 50% of female sighting events.

Male behaviour

At sighting events with male loggerheads present (Fig. 2, n = 139), analysis of initial behaviour observations indicated that they were just as likely to be found in solitary (57%) as social states (43%; $\chi^2_1 = 2.33$, $p = 0.1$). There was no significant difference in the occurrence of active (61%) and inactive (39%) solitary states ($\chi^2_1 = 3.24$, $p = 0.07$). Uniform scratch patterns, identical to that of females observed performing self cleaning, were found on the carapace of males at 19% sighting events. The proportion of social behaviour observed in males (43%) was 5 times greater than that of females (8%). Furthermore, the proportion of active solitary behaviour observed in males (62%) was double that of females.

DISCUSSION

Through intensive in-water observations of loggerhead sea turtles during the breeding season, we found that a broad range of behavioural activities were exhibited. Our research differed from existing studies at breeding areas (courtship and internesting) in that, rather than specifically addressing courtship and mating behaviour (Booth & Peters 1972, Dodd 1988, Frick et al. 2000), or inter-nesting movement patterns (Hopkins-Murphy et al. 2003), we sought to investigate the behavioural ecology of sea turtles during this period.

Our results indicated that in general males were more active and social than females, which probably reflected the need to acquire multiple mates to maximise fitness, whereas female fitness would be maximised by energy conservation to divert resources towards egg development (Hays et al. 2002a, Hopkins-Murphy et al. 2003). However, we observed female loggerheads investing in active behaviours previously unobserved in loggerheads during the breeding period, i.e. that of foraging, cleaning (self-cleaning and fish-cleaning symbiosis) and female–female contests.

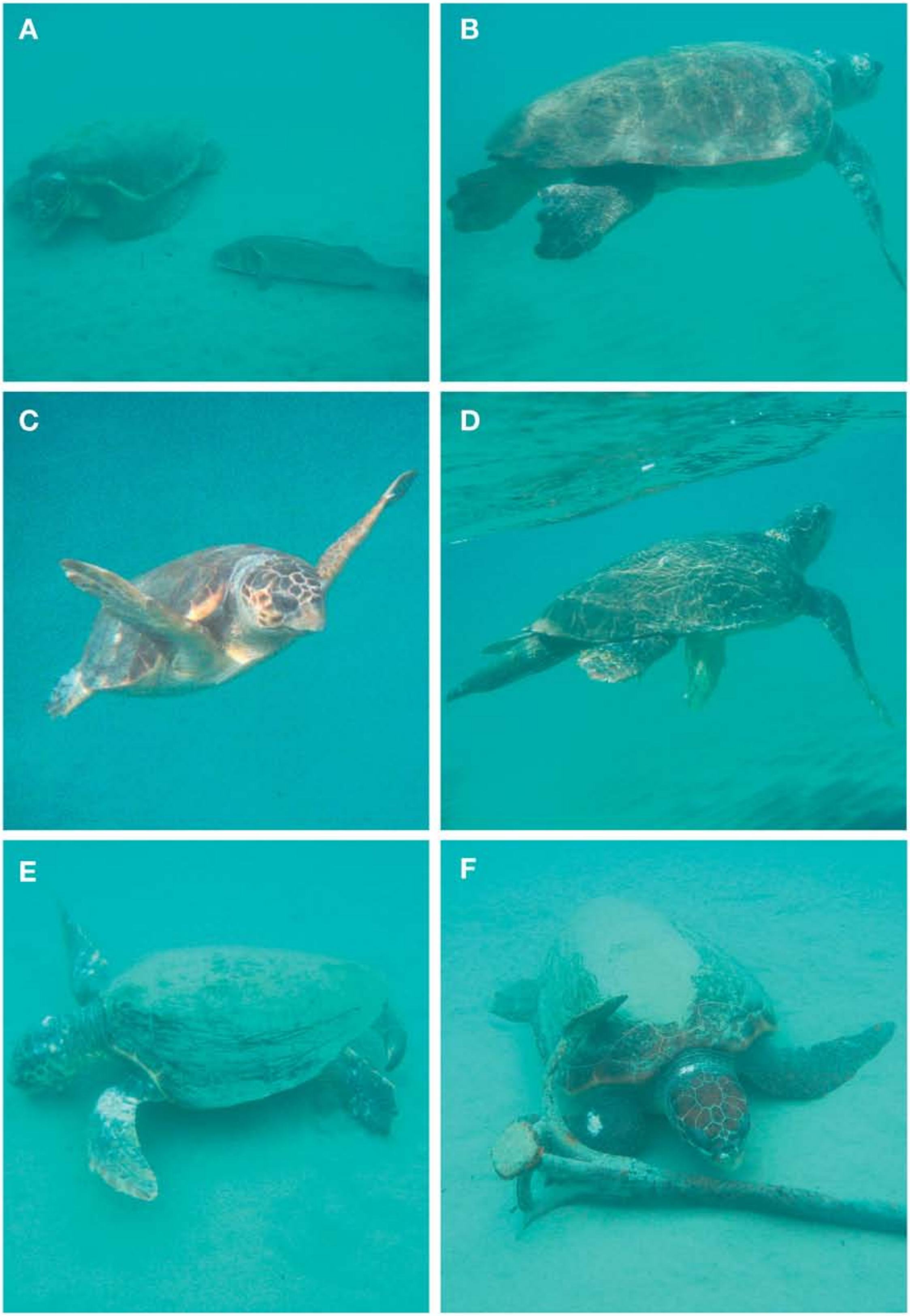

Fig. 3. *Caretta caretta.* (A) Female loggerhead resting on the seabed; (B) female surface-basking; (C) female swimming; (D) male patrolling for females; (E) male foraging for molluscs; (F) female rubbing against an anchor; (G) female posing at a fish cleaning station manned by sheepshead bream *Diplodus puntazzo*; (H) antagonistic female interaction; (I) antagonistic male interaction; (J) loggerhead courtship activity; (K) loggerheads copulating; (L) loggerheads copulating with antagonistic attendant male

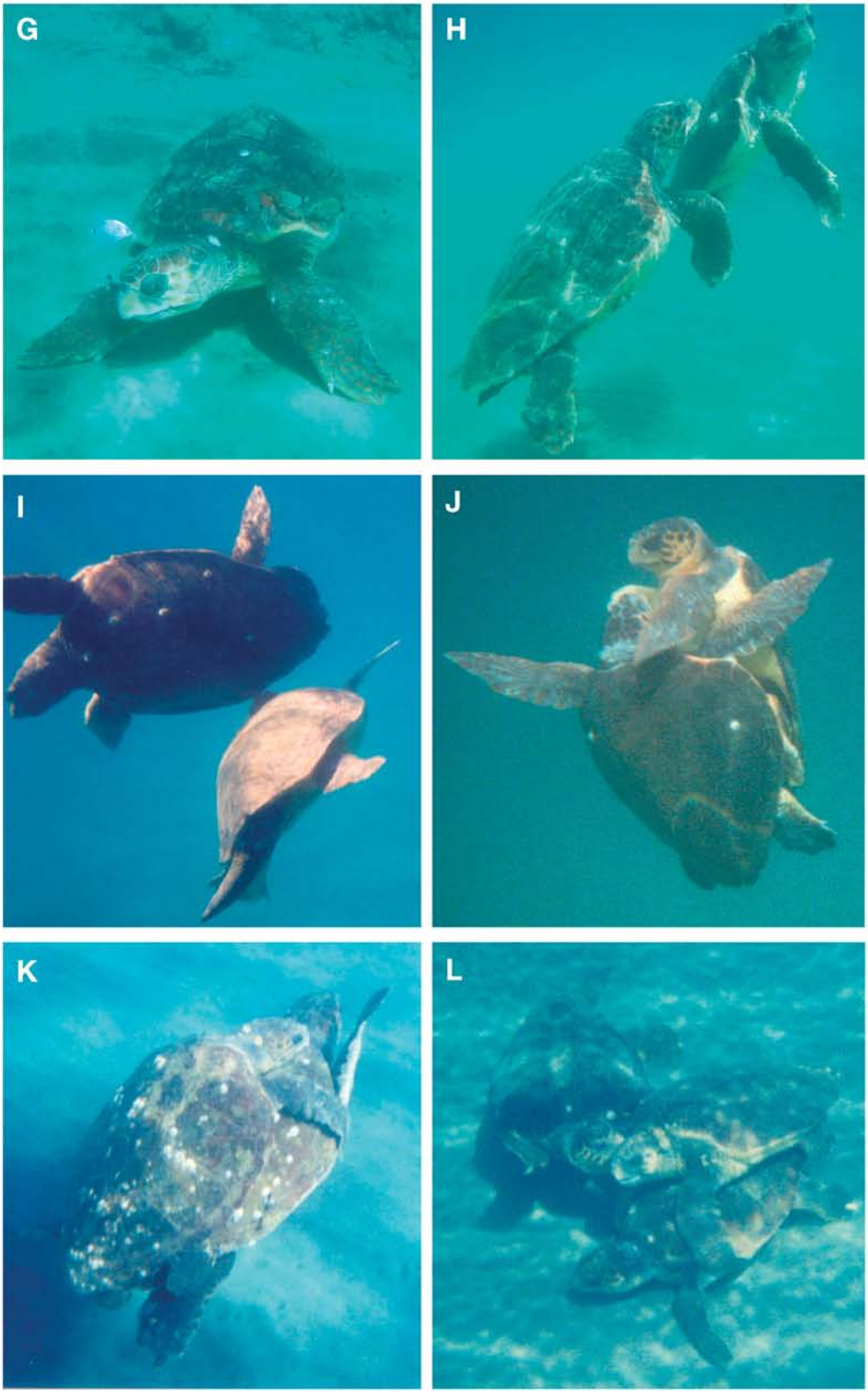

Fig. 3 (continued)

Contests between individuals over space has received anecdotal mention in sea turtle literature (Limpus & Limpus 2003), yet our research indicated that antagonistic interactions are a noteworthy component of female loggerhead activity during the breeding period. It is possible that females may be benefiting from (1) thermally optimal sites to enhance egg development, or (2) space to obtain refuge from energy consuming encounters with males patrolling for receptive mates (Booth & Peters 1972, Whittow & Balazs 1982, Lee & Hays 2004).

Both self-cleaning (e.g. green turtles *Chelonia mydas*: Heithaus et al. 2002) and cleaning symbioses have been recorded in other sea turtle species at foraging and breeding grounds (e.g. green turtles: Losey et al. 1994, hawksbill turtles *Eretmochelys imbricata*: Sazima et al. 2004). However, high carapace epibiont loads (Frick et al. 1998) and a recent animal-borne sea turtle study (Heithaus et al. 2002) have led researchers to suggest that loggerheads do not invest as heavily in cleaning behaviour as other sea turtle species (Bjorndal 2003). Yet, while we only observed self-cleaning and fish cleaning symbiosis on a few occasions, evidence of self-cleaning behaviour was apparent from the uniform scratch patterns on the carapaces of a large proportion of surveyed male and female turtles, indicating that loggerheads at Laganas Bay do invest in cleaning activity.

Herbivorous foraging behaviour has been documented in one Mediterranean population of female green turtles at a breeding area (Hays et al. 2002b). Similarly, we observed sporadic feeding attempts for molluscs by both female and male loggerheads at Laganas Bay. However, time spent foraging was relatively short, presumably because of the need to spend time and energy on other activities (e.g. males searching for females), and possibly because prey densities were sufficiently low that sometimes it was more profitable (e.g. for females) to simply rest than attempt to feed.

Direct observations of loggerhead sea turtle mating systems in the wild remain rudimentary (Dodd 1988, Frick et al. 2000). Courtship and mating behaviour of loggerheads have been found to follow similar patterns to that documented in other sea turtle species (Booth & Peters 1972, Rostal et al. 1998). In courtship bouts with unreceptive females we corroborated and expanded on the use of avoidance manoeuvre sequences. Furthermore, we recorded that females would attempt to circle behind persistent males to make offensive advances biting at their tails. As with other species, we observed that males competitively search for receptive females (Jessop et al. 1999) in the form of patrolling but we also documented the presence of male–male combat, possibly for primary mate acquisition. Furthermore, while the presence of antagonistic attendant males in the company of copulating pairs has been recorded in other species of sea turtle (Booth & Peters 1972), this was not documented in loggerheads (Frick et al. 2000) until the current research.

Direct observations of turtle behaviour are of great value and provide many interesting insights that are difficult, or impossible, to gain from more indirect methods or animal-borne imaging. Studies, comparing direct and indirect methodologies of animal behaviour, have shown that remote-sensing data can distinguish between active and inactive states, however it cannot reliably distinguish the different behaviour patterns within those states (Hansen et al. 1992, Heithaus et al. 2001). Our findings have shown that loggerhead sea turtles exhibit a wider range of behaviour than has previously been documented at breeding areas. It is therefore likely that indirect inferences about movement patterns made from remote-sensing data analysis may be subject to error (as shown by Houghton et al. 2002). It is also possible that jaw activity patterns may be subject to misclassification (Hochscheid et al. 2005) due to the failure to document activities such as sparring and biting in contests and courtship, biting at cleaner fish during cleaning, or biting themselves during self cleaning. The recent development of animal-borne cameras has given researchers of marine vertebrates, such as sea turtles, the opportunity to observe and confirm the underwater behaviour (Davis et al. 1999, Heithaus et al. 2002, Reina et al. 2005, Hays et al. 2006). Hence, knowledge about free-living behaviour, obtained from direct observations, is essential towards improving the accuracy of remote-data interpretation of marine wildlife.

To implement effective wildlife management and conservation plans, accurate information about animal behaviour, habitat use and population dynamics are essential. On Zakynthos, our data may be used to improve the existing national park conservation policies. The protection zones should be amended to take into consideration the function of different habitats with respect to sea turtle activities. Furthermore, sea turtle watching protocols should be refined, limiting in-water watching activities to regions where behaviour is minimally impacted.

In conclusion, direct observational studies in the marine environment are of great value in developing our knowledge of marine vertebrate behaviour, validating remote technologies and contributing towards ecosystem research and environmental monitoring.

Acknowledgements. We especially thank the National Marine Park of Zakynthos for allowing us to conduct this study. We thank the many people who contributed to this research, in particular Martyn Baker, Amanda Banks, Kostas Gounelis, Valia Lianos, Charikleia Minotou, Fanis Nikoloudakis, Charlotte Sahlin and David G. Schofield.

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Editorial responsibility: Brendan Godley (Editor-in-Chief), Penryn, UK

Submitted: June 17, 2006; Accepted: October 5, 2006
Proofs received from author(s): November 24, 2006

Vol. 336: 267–274, 2007

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 27

Female–female aggression: structure of interaction and outcome in loggerhead sea turtles

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ABSTRACT: Aggressive behaviour between females of the same species is not widely documented, particularly in marine vertebrates. During a 3 yr in-water survey at the temperate loggerhead sea turtle *Caretta caretta* breeding area of Zakynthos, Greece, female–female interactions comprised 4% of all female loggerhead sighting events (n = 60 out of 1449 events). Male–female interactions comprised an additional 4% of sighting events, while 92% were of solitary females. The structure of interactions was analysed for 58 of these sighting events, each lasting an average of 3.4 min (SD ± 1) and comprising a total of 3.1 h observation time. We found that interactions involved ritualized escalation in behaviour from passive threat displays (e.g. head–tail circling) to aggressive combat (e.g. sparring). We suggest that circling individuals evaluate opponent size, sparring individuals test opponent strength, and that the positioning of the prehensile tail signals motivational intent to either escalate or abort. The presence of intruder females triggered a passive response in 100% of events involving basking and swimming turtles (n = 19); although residents resting on the seabed only responded on 69% of occasions (n = 27), their response was almost 4 times more likely to escalate to one of aggression. Our results suggest that certain sites may be preferentially sought after and defended by sea turtles.

KEY WORDS: *Caretta caretta* · Sequential assessment · Evolutionary stable strategy · Territory · Marine · Vertebrate · Reptile

INTRODUCTION

Although aggression between males is a widespread phenomenon, the same behaviour between females is less frequently documented (Liker & Szekely 1997). Aggressive behaviour primarily arises to exclude intruders from defended areas in order to avoid competition for resources (Petrie 1984). Intra-specific aggression usually serves to establish hierarchy among individuals for access to resources. In the case of females, aggression is usually related to factors that affect their own and/or their offspring's survival: for instance food, mates, gestation sites, nest sites and sites to evade predators (Gowaty & Wagner 1988, Liker & Szekely 1997, Woodley & Moore 1999). Such behaviour requires an individual to invest in defence (e.g. to expend energy and/or time) so that some kind of benefit can be obtained (e.g. improved ranking or exclusive access to a limited resource). Because the relative importance of each defended resource can vary in space and time, it is often difficult to explain the origin of aggression. However, the degree of aggression is usually correlated with opponent capability and/or resource availability (Brown 1964).

Confrontations between 2 individuals are usually characterised by specific stereotypical behaviour that is divided into stages of escalating aggression (Ruby 1978) in which individuals evaluate and test the ability of the opponent (Parker 1974, Maynard Smith 1994). Contests are usually resolved through low cost dis-

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plays of physical attributes (Ruby 1978), and only escalate into costly aggressive (agonistic) interaction if neither competitor retreats (Enquist & Leimar 1983). The outcome of escalated contests depends on a range of parameters such as competitive ability (resource holding power) and occupancy of a territory or hierarchical rank (prior residency effect). The residing individual is usually expected to win because, over time, the optimal sites/ranks are occupied by superior competitors (evolutionary stable strategies; Maynard Smith & Price 1973, Parker 1974). However, a range of factors associated with individual fitness and/or resource value may also affect competitor motivation and hence contest outcome (pay-off asymmetries such as contest duration and previous encounters; Kotiaho et al. 1999, Cressman et al. 2004).

Although aggressive behaviour and contest escalation is widely documented for many vertebrates and invertebrates, direct observations of the aggressive behaviour of free-living animals in the marine environment is primarily limited to captive studies, usually of fish (Bisazza & Pilastro 1997). Most research on large free-living marine animals relies on the attachment of electronic devices, such as data-loggers and satellite transmitters, to elucidate animal behaviour (e.g. of fish, seabirds, seals, whales, dolphins and sea turtles) related to diving and migratory activity. Although electronic devices have the capacity to record a range of animal movements, physiological processes and environmentally related parameters, at present they cannot—with the exception of camera systems—be used to infer intra- and inter-species interactions. Yet such interactions may be key to establishing how individuals utilise habitats and function within larger marine ecosystems.

Sea turtles are deep–diving migratory marine vertebrates; hence, remote technology has played an important role in understanding their aquatic activity (Hays et al. 2002a, Myers et al. 2006). However, without reliable comparative direct behavioural observations (Booth & Peters 1972, Whittow & Balazs 1982, Houghton et al. 2003) there is a risk of misinterpreting or even overlooking aspects of sea turtle biology (as shown by Houghton et al. 2002). For instance, telemetry studies have shown that sea turtles are solitary, even when individuals of a particular species share overlapping home ranges at foraging or breeding site aggregations (Hays et al. 2002b, Murphy-Hopkins et al. 2003). Nevertheless, there is anecdotal evidence of aggressive interactions between individuals when in close proximity to one another (Herbst & Jacobson 2000, Limpus & Limpus 2003).

Laganas Bay on the island of Zakynthos (Greece) is a major breeding area for loggerhead sea turtles *Caretta caretta* (Margaritoulis 2005). Several hundred turtles seasonally aggregate nearshore, making it relatively easy to acquire quantitative information on their aquatic behaviour through direct observation. As part of an ongoing in-water survey, we recorded repeated instances of female–female interactions. In the present study, we describe the stages of contest escalation from passive displays to aggressive combat. Based on existing theoretical game models of competition, we suggest how opponents communicate information on capability and motivation, and we discuss possible reasons for aggressive behaviour among female loggerhead sea turtles.

MATERIALS AND METHODS

Laganas Bay is about 12 km long by 8 km wide, and is situated on the Greek island of Zakynthos (study area: 37° 66′–37° 73′ N, 20° 84′–20° 99′ E). Since 2003, in-water surveys have been conducted there annually between April and July, thus encompassing the loggerhead sea turtle breeding season (courtship and inter-nesting periods). Surveys were organised to cover a range of daylight hours between 08:00 and 20:00 h. They lasted 2 to 6 h depending on the method used (e.g. boat, kayak or snorkelling) and weather conditions. Boat, kayak and snorkel surveys were concentrated along a 5.5 km stretch of nearshore area at sea depths of up to 10 m, depths at which large numbers of female loggerhead sea turtles tend to aggregate during the breeding season (Fig. 1).

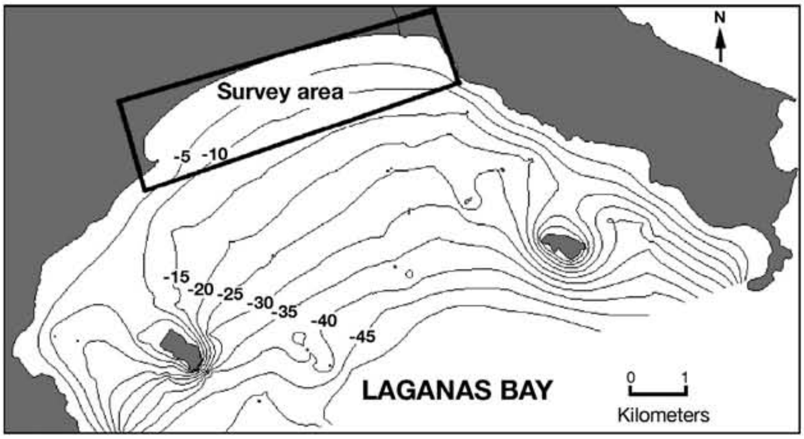

Fig. 1. Survey area (37° 66′–37° 73′ N, 20° 84′–20° 99′ E) in Laganas Bay on the Ionian island of Zakynthos, Greece. Bathymetry contours (m) indicated

On sighting a sea turtle from the boat or kayak, the distance to the individual and the GPS location were recorded. The observer then entered the water at a distance of at least 5 m from the target animal(s) and approached until within underwater visual range. Surveys were only conducted when the underwater visual range (which varied according to sea state) exceeded 2 m, in order to minimize disturbance of ongoing behaviour. On encountering the animal(s), photographs were taken, and biological, environmental and behaviour observations (ongoing behaviour and behavioural response to the presence of the underwater observer) were recorded. Written records were made of all behavioural observations. In events involving social interactions, the start and end times were recorded and the position in which the tail was held at the beginning and end of interactions was documented in writing. During 2005, video footage was collected to classify all observed solitary and social behaviour as well as inter-species interactions. Sex was estimated using previously documented tail-length dichotomies for mature adult male and female turtles (Casale et al. 2005).

We calculated mean and standard deviation for normally distributed metric data. We used non-parametric chi-square statistical analysis to assess the correlation between behavioural states and confrontation data (passive versus aggressive). We regarded results to be significantly different from H_0 when $p < 0.05$.

RESULTS

Female–female interactions comprised 4% of all female loggerhead sea turtle sighting events (n = 60 out of 1449 events) during the 3 yr survey. Male–female interactions comprised an additional 4% of sighting events while 92% of sighting events were of solitary females. We recorded the structure of 60 contests each lasting an average of 3.4 min (SD ± 1; range 1–6 min), comprising a total of 3.1 h of observations.

Prior to contests, the behaviour of the resident turtle was always solitary and consisted of resting on the seabed, 65% (n = 39); surface-basking, 13.5% (n = 8); swimming, 18.5% (n = 11); or fish cleaning symbiosis, 3% (n = 2). Female interactions during fish cleaning symbiosis were excluded from the data set owing to the small sample size and because fish cleaning was only observed in the survey area during 1 season.

Confrontation structure

Turtles displayed a stereotyped sequence of escalating behaviour during contests. We divided contest escalation into 4 stages that could be concluded at any stage by the retreat of 1 opponent. The stages were (1) initial contact, stimulated by visual or tactile cues, (2) passive confrontation, comprising wide head–tail circling, with individuals maintaining a distance of 1.5 m from one another (3) aggressive confrontation, involving violent physical contact, (4) separation, with both turtles leaving or one fleeing and the other chasing. The confrontation structure and the outcomes of confrontations are presented in Fig. 2.

Initial contact

Initial contact occurred when intruders entered the visual range of residents. In all encounters of intruders with basking or swimming residents (100%, n = 19) both turtles responded. However, while contact was made in the majority of encounters of intruders with residents resting on the seabed (82%, n = 32), it was not always by both individuals.

Three scenarios were presented by resident turtles resting on the seabed (n = 39) when an intruder entered their occupied space: (1) in 18% (n = 7) of encounters the intruder passed by, either unnoticed or ignored, (2) in 54% (n = 21) of encounters the intruder advanced on the resident turtle, obtaining visual contact and a defensive response by 91% (n = 19) of resting site residents (Fig. 3) in which the anterior body and head were raised with mouth gaping (as observed by Limpus & Limpus 2003), (3) in 28% (n = 11) of encounters the intruder advanced on the resident, obtaining no visual contact or defensive response, and proceeded to attack the resting turtle by nuzzling or biting the carapace (Fig. 4), thus stimulating a response in 73% (n = 8) of interactions.

Passive phase

Once visual contact was made with the left or right eye (depending on which side the intruder entered visual range), it was not broken until separation. At this point, passive confrontation was initiated in the form of wide head–tail circling, with individuals maintaining a distance of 1.5 m. All intruder interactions with basking and swimming turtles (n = 19) led to a passive response, whereas residents resting on the seabed responded on only 69% of occasions (n = 27).

The majority of confrontations that progressed to the passive phase were actually resolved in that phase, i.e. 88% (n = 7) of surface-basking, 91% (n = 10) of swimming confrontations (89.5% combined) and 63% (n = 17) of seabed resting site confrontations. A significantly higher proportion of confrontations with resting site residents developed into aggressive confrontation than did those with surface-basking/swimming residents ($\chi_1^2 = 4.92$, $p < 0.02$; 37% [n = 10] and 10.5% [n = 2] respectively).

Aggressive phase

Aggressive confrontation was triggered when one turtle stopped circling to face the other head-on. A sequence of physically violent interactions was initiated, starting with sparring, in which the turtles snapped at each others' jaws (Fig. 5), with one or both turtles holding offensive 'horizontal' or defensive 'vertical' positions in the water column. This progressed to close circling in which the turtles snapped at the opponent's posterior carapace and/or flippers, followed by chasing and snapping at the neck and/or central cara-

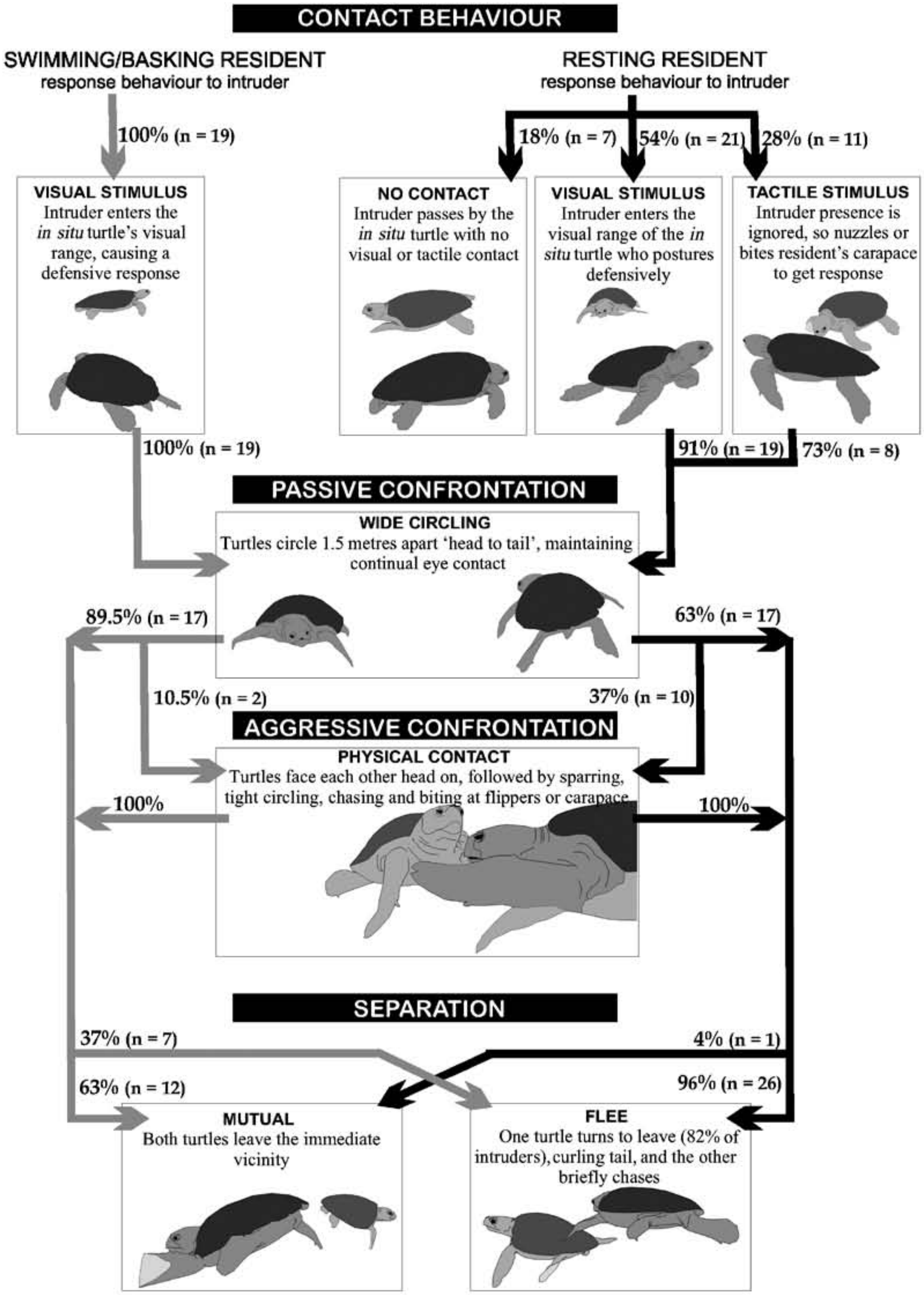

Fig. 2. *Caretta caretta*. Stages of female–female loggerhead competition; % values on arrows indicate outcomes from different interactions

Fig. 3. *Caretta caretta.* Resident's visually provoked response to intruder

Fig. 4. *Caretta caretta.* Tactile stimulus by intruder to provoke resident response

pace. All aggressive confrontations involved sparring and 36 % (n = 4) progressed to close circling; of these 75 % (n = 3) progressed to chasing and biting before separation.

Separation

Separation was either mutual, with both turtles initially swimming away in generally opposite directions, or involved one opponent briefly chasing the other out of the immediate vicinity. Although the prehensile tail of adult male sea turtles has been documented to serve the primary function of curling under the female carapace for penile penetration (Miller et al. 2003), the present study noted that the prehensile tails of females used significantly often during confrontations ($\chi_1^2 = 3.89$, $p < 0.04$), possibly as a signal of the opponent's intention. In 70 % (n = 21) of passive and 80 % (n = 12) of aggressive interactions, the first turtle to depart visibly curled its tail immediately prior to separation.

Fig. 5. *Caretta caretta.* Aggressive sparring between females

Separation of intruders and resident surface-basking or swimming turtles was generally mutual (62.5 % [n = 5] and 63.5 % [n = 7] respectively; 63 % combined), with no significant difference observed between the frequency of capitulation (i.e. departure) of intruders and residents ($\chi_1^2 = 0.6$, $p < 0.4$). In confrontations with resting site residents, there was a 96 % (n = 26) probability that one of the opponents would flee rather than both depart mutually. Intruders were significantly more likely to depart first during passive and aggressive confrontations with resting site residents ($\chi_1^2 = 19.18$, $p < 0.001$), with an intruder win rate of 15 % (n = 5) that was reduced by a further 5 % during aggressive confrontations.

DISCUSSION

Our research illustrates that interactions between female loggerhead sea turtles are subject to escalation, the degree of which appears to differ with respect to behavioural state. Aggressive behaviour between females may arise (1) as a side-effect of elevated reproductive hormones (Woodley & Moore 1999) or (2) as a side-effect of fending off male advances once receptivity has passed. However, resident females initially respond to males entering their visual range by holding a vertical 'refusal' pose (Booth & Peters 1972), which is not observed until the aggressive phase of female–female interactions. Although heightened olfactory senses (Bartol & Musick 2000) may enable residents to identify and respond to intruders accordingly, prior to their entrance into residents' visual range, this does not account for the incidence of aggressive behaviour also observed in foraging individuals and captive juveniles (Herbst & Jacobson 2000, Limpus & Limpus 2003).

Our observations indicate that interactions were more aggressive when they involved resting site locations than when basking and swimming turtles were concerned, and that these locations were noticeably sought after by intruders. Marine environments are not homogeneous, and this behaviour indicates that turtles could be competing over a scarce high quality resource. These observations support the population 'interference' model derived from the 'Ideal Free Distribution' (Fretwell 1972, Sutherland & Parker 1986) in that seabed resting sites may represent an optimal resource over which individuals compete, whereas surface-basking and swimming states occur at sub-optimal sites subject to less competition.

In some breeding areas, female turtles have been observed to take refuge from energetically costly interactions with reproductively active patrolling males by occupying nearshore waters (Booth & Peters 1972, Lee & Hays 2004). In this instance, space may be the limiting factor, whereby females resting in close proximity to one another would attract unwanted male attention. This may also account for the incidence of beach-basking behaviour of green turtles *Chelonia mydas* at Hawaii (Whittow & Balazs 1982). Therefore, the size of the defended aquatic sites may correlate with the visual range of the resident, which is controlled by dynamic physical parameters such as light or sea clarity (Valdimarsson & Metcalfe 2001).

Alternatively, detailed research has shown that, in gestating reptiles, environmental temperature affects the developmental rate and viability of offspring as well as adult growth and survival (e.g. lizards: Wapstra 2000, snakes: Ladyman et al. 2003). It is therefore possible that female turtles, particularly in temperate breeding areas, are responding to thermal cues in the environment by seeking out warmer water to accelerate gestation. Temperature regulation may also serve as an alternative explanation for Hawaiian green turtle beach-basking behaviour (Whittow & Balazs 1982). This theory is further supported by comparative studies of sea turtle distribution in temperate and tropical breeding areas: in the former, where ambient sea temperatures are cooler, turtles form dense nearshore aggregations, whereas in the latter they remain more dispersed (e.g. Hays et al. 2002b).

In contests between female loggerhead sea turtles, we observed that established residents at seabed resting sites were more likely to win both passive (73%) and escalated aggressive (68%) contests, supporting established evolutionary ecology competition models (e.g. Parker 1974, Maynard Smith 1982, Enquist & Leimar 1983). Competition escalation models predict that differences in opponent fighting ability should determine the outcome, usually favouring the stronger opponent. It is likely that initial resident status depends on time of arrival, whereas the length of residency depends on how rested the individuals are prior to each encounter combined with individual competitive ability.

Motivation to fight is influenced by many parameters related to individual fitness and resource value, and is subject to regular re-evaluation by each opponent, with respect to confrontation frequency, intensity and duration (e.g. Kotiaho et al. 1999, Cressman et al. 2004). We found that confrontations at surface-basking or swimming locations were more likely to mutually terminate at the passive stage; hence, resource value may also play an important role in determining fight duration and escalation (e.g. Kotiaho et al. 1999).

We suggest that a combination of size assessment and resource value could account for the 3 initial contact categories observed between occupants and intruders at resting sites. In cases with 'no contact', the intruder passes over an occupant with superior competitive ability or at a site of low resource value. In instances with a 'visual response', the intruder establishes visual contact, initiating a confrontation sequence with an equally matched resting site occupant. Finally, in interactions provoked by a 'tactile response', high resource value may motivate some intruders to provoke confrontations with opponents of superior competitive ability, although they have little chance of winning. Intruders that select the right opponent may have more to gain or less to lose than the established resident, resulting in the resident giving way to the intruder (Kotiaho et al. 1999), independent of the resident's holding power and strength.

When confronted with an opponent, competitors must acquire appropriate information about each other prior to initiating a fight. Such information is usually obtained through a set of passive threat displays (Ruby 1978). In sea turtles, passive head–tail circling behaviour may represent a 'cheap' way to determine opponent strength through size evaluation, while the position in which the prehensile tail is held may be an energetically inexpensive signal for motivational intent (with no correlation with animal strength). We suggest that tail position may be used to obtain information about the opponent's willingness to escalate or abort conflict at any stage of the combat sequence. An extended tail signals willingness to proceed, whereas tail curling at any part of conflict escalation indicates a competitor's decision to abort. Hence, when a contestant's decision to continue beyond passive head–tail circling is 'borderline', just a quick visual assessment of the opponent's tail position could determine intent.

Although cheap signals invite cheating (e.g. Parker 1974, Maynard Smith 1994), use of the tail to signal intent may be evolutionarily stable as long as both opponents benefit. While the costs of circling are low (in terms of energy and lost time), the expense of escalation to physical contact are high (risk of injury) and may keep cheating under control. Therefore, while sparring is not potentially dangerous, it may present an honest indicator of opponent strength and motivation (e.g. Kotiaho et al. 1999).

The way in which individuals of a species compete over resources allows researchers to objectively measure the importance of a particular environment, habitat or ecosystem to animals. Direct observation of free living marine animals is subject to a number of limitations; for instance, our study was limited by time of day, sea conditions and sea depth. Because of such limitations, use of remote technology is becoming increasingly common. However, without corroborated observational research, such technology only produces informed guesswork of animal behavioural activities. Advances in electronics are making underwater video cameras economically viable, giving the researcher the opportunity to obtain direct observational information within a wide range of marine settings (e.g. cameras may be hand-held or attached to the seabed, boat, remote-vehicle or study animal). By collecting direct baseline behavioural information, electronic devices could be subsequently used as a powerful tool to acquire specific information with respect to trends in marine animal social behaviour and habitat use. A useful goal for future studies would be to attempt to quantify the competitive abilities of fighting sea turtles and assess how their ability impacts the outcome of encounters. For example, it might be that competitive ability is related to body size or length of residency, as is the case in some other vertebrates (Downes & Shine 1998, Gray et al. 2002). Our study can be considered a first step towards application of remote technology in order to specifically investigate possible causes of social interactions between sea turtles.

Acknowledgements. This research was permitted and financially supported by the National Marine Park of Zakynthos. We thank the many people who contributed to this research, especially A. Banks, K. Gounelis, V. Lianos, C. Sahlin and D. G. Schofield.

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Editorial responsibility: Rory Wilson (Contributing Editor), Swansea, UK

Submitted: March 22, 2006; Accepted: July 28, 2006
Proofs received from author(s): February 22, 2007

Journal of Experimental Marine Biology and Ecology 347 (2007) 58 – 68

Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY

www.elsevier.com/locate/jembe

Novel GPS tracking of sea turtles as a tool for conservation management

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Received 11 January 2007; received in revised form 22 February 2007; accepted 8 March 2007

Abstract

We used recently developed, low-powered, TrackTag™ GPS loggers to track the movements of female loggerhead sea turtles (*Caretta caretta*) at the largest breeding population in the Mediterranean (Zakynthos, Greece). Three turtles were tracked for a total of 73 days in May and June 2006, during which time 3753 GPS locations were obtained after filtering outliers (51 per day per turtle). The diving behaviour of these three turtles and three others was also monitored using time–depth recorders (TDR). The GPS data revealed that all three turtles spent most of their time in shallow water (< 4 m sea bed depth) very close to the shore (< 200 m), primarily ranging along an 18.5 km section of coastline. These observations were corroborated by TDR data acquired from all six turtles and frequent first-hand sightings of turtles close to shore during the breeding period. Comparison with random crawl movement models indicated that two of the tracked turtles moved with a similar non-random pattern, suggesting common biophysical processes might be driving their movements. The movement and depth data that we collected both suggest that existing legislation to safeguard sea turtles within this protected region may not include the most critical habitats for female loggerhead sea turtles during the breeding period. Our study demonstrated the feasibility of using GPS tracking to investigate fine-scale movements of a marine vertebrate, illustrating the value of GPS tracking for wildlife conservation management.

Keywords: Behaviour ecology; Biotelemetry; Coastal management; Habitat use; Marine animals; Validation

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1. Introduction

Understanding movement patterns and the factors that affect animal distribution are integral components of behavioural ecology, conservation and protected area management. Conventional animal biotelemetry systems,

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0022-0981/$ - see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.jembe.2007.03.009

such as radio and satellite transmitters, have revolutionised the ability to track wildlife movement over vast spatial and temporal scales (Maehr et al., 2002; Luschi et al., 2003; Sale et al., 2006; Sims et al., 2006). Despite this, variable accuracies and infrequent intervals between fixes (Hays et al., 2001; Hulbert and French, 2001) limit their application at finer spatial resolutions, and when quantifying movement patterns in relation to biophysical parameters at small scales (Wilson et al., 2002; Bradshaw et al., 2007). However, the acquisition of high resolution tracking information may be important in formulating rational, adaptive and dynamic management decisions for nature reserves, endangered species and related conservation policies (Argardy, 1994; Castilla, 2000; Thompson et al., 2000; Parra et al., 2006).

Loggers based on the Global Positioning System (GPS) are an important new technology allowing wildlife to be studied with unparalleled accuracy, often to within ranges of 10 m (Moen et al., 1997; Hulbert and French, 2001). However the level of accuracy has been found to vary among animals depending on terrain, habitat and behaviour (Moen et al., 1997; Friar et al., 2004). While GPS loggers, some linked to transmitters to relay the positional data, are routinely used for terrestrial and aerial animals (Douglas-Hamilton et al., 2005; Biro et al., 2006), tracking marine vertebrates with GPS loggers has proved more problematic. This is because infrequent surfacing behaviour limits the time when loggers are available for acquiring satellite signals. For marine species therefore, the current challenge is, in as short a time possible, to acquire sufficient information in order to calculate GPS positions when an animal surfaces. There are several initiatives underway to achieve this goal and some limited success has been achieved, depending on species and surfacing interval (Sisak, 1998; Jay and Garner, 2002; Ryan et al., 2004; Yasuda and Arai, 2005; Petersen et al., 2006; Sheppard et al., 2006).

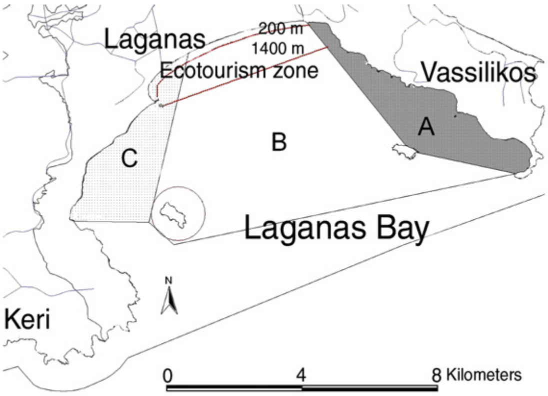

Fig. 1. Map of Laganas Bay containing National Marine Park of Zakynthos (NMPZ) marine protection and ecotourism zones. Zone A = no-boating zone, zone B = boating permitted at 6 km h^{-1} but no mooring, zone C = boating permitted at 6 km h^{-1} and mooring, Ecotourism zone = including a swim zone 0–200 m from shore and an NMPZ endorsed turtle-watching business zone 200–1400 m from shore (adapted from map of NMPZ www.nmp-zak.org).

Fig. 2. Loggerhead sea turtle following TrackTag™ GPS logger attachment.

While satellite and VHF telemetry studies have been effectively used to investigate sea turtle oceanic migratory routes (Luschi et al., 2003; Hays et al., 2004b; Sale et al., 2006) to coastal foraging or breeding grounds, details about behaviour and habitat use at these regions of seasonal residency remain limited (Heithaus et al., 2002a, b; Houghton et al., 2002; Seminoff et al., 2002; Hopkins-Murphy et al., 2003; Yasuda and Arai, 2005). Existing studies of female sea turtles at breeding areas using remote technology have been primarily conducted following the onset of nesting (Hays et al., 1991; Hays et al., 2002; Houghton et al., 2002; Hays et al., 2003a; Hopkins-Murphy et al., 2003). These studies indicate that inter-nesting females tend to inhabit sea depths of 15 m or less, and may be found as much as 10 km from the nesting beaches, often exhibiting movements parallel to the coast.

Laganas Bay, on the island of Zakynthos in Greece, is the largest loggerhead sea turtle (*Caretta caretta*) rookery in the Mediterranean (Margaritoulis, 2005). It is visited by several hundred sea turtles and several hundred thousand tourists each summer (Arianoutsou, 1988). Sea turtles often begin residency in Laganas Bay as early as April, before nesting starts in late May, and are frequently observed in close proximity to shore (Schofield et al., 2006). Nesting beach locations and relative nesting densities were used to delineate the degree of protection offered by marine protection zones in Laganas Bay (Arapis and Margaritoulis, 1994). The no-boating zone encompassing three nesting beaches (out of a total of six), which account for about 70% of nesting activity (Margaritoulis, 2005). Since establishment of the National Marine Park of Zakynthos (NMPZ) in 1999, stricter regulation of near-shore tourism and turtle-watching activities in the two boating zones has been introduced, however empirical data about in-water sea turtle movement is necessary to validate and improve existing management actions.

Many coastal regions are subject to anthropogenic pressure, in the form of fisheries, coastal development and tourism (Arianoutsou, 1988; Hays et al., 2003b; Parra et al., 2006). It is therefore important to obtain information about where, when and why endangered species, such as sea turtles, use these areas, in order to implement rational and effective protective legislation and management of human activities (Argardy, 1994; Thompson et al., 2000). The aim of this study was to investigate sea turtle movement and habitat use at the internationally important rookery of Zakynthos. We used recently developed, low-powered, TrackTag™ GPS loggers to follow individual sea turtle movements and evaluate the effectiveness of existing marine protection zones.

2. Methods

2.1. Study animal

TrackTag™ GPS loggers were deployed onto four adult female loggerhead sea turtles (curved carapace lengths 81–89 cm) in Laganas Bay, Zakynthos, Greece (Fig. 1, 37°43′N 20°53′E), during the pre-nesting period in May 2006 and removed during the inter-nesting period in June 2006. In one case, deployment problems caused the logger to malfunction so that no data were collected. Hence data were collected from three turtles. In addition, six time–depth recorders (TDR) were deployed and retrieved from all four turtles plus another two female turtles. The attachment of all devices was conducted under licenses from the Greek Ministry of Agriculture. A 4 m research boat was used to find turtles resting on the seabed at depths less than 1.5 m. The turtles were captured using the turtle-rodeo technique (Ehrhart and Ogren, 1999) and lifted onto the boat. Following capture, the curved carapace length was measured and then a GPS logger and/or TDR attached using a standard method we have widely employed before with various transmitters and loggers (Hays et al., 2003a). In brief, the carapace was cleaned and then the logger embedded in quick setting two-part epoxy resin (Powerfastners Inc., New Rochelle, NY, USA) with wooden baffles positioned at the anterior to help prevent impacts to the equipment (see Fig. 2). Loggers and TDRs were removed from the animals by one of two methods,

Table 1
Presentation of TrackTag™ GPS logger locations acquired and those remaining following filtration

GPS logger	Turtle parameters		Date GPS attached	Date GPS retrieved	Date of nesting	Full no. days attached	All GPS locations		Locations removed	In-water GPS locations		Filtering processes of in-water locations									
	CCL*/ cm	CCW*/ cm										Visually erroneous		Speed		SV		DOP		Hourly	
							Total	Av. fix / day	Nesting beach	Total	Av. fix/ day	Total	Av. fix/ day	Total	Av fix/ day	Total	Av. fix/ day	Total	Av. fix/ day	Total	Av. fix/ day
GPS2	81	73.5	19/5/2006	6/6/2006	31/5/2006	17	1076	63	214	862	51	734	43	519	31	721	34	437	21	181	10
GPS3	89	76	23/5/2006	26/6/2006	25/6/2006	31	3077	99	817	2260	73	2007	65	2189	69	1761	57	1160	37	479	15
GPS4	87	72	24/5/2006	18/6/2006	7/6/2006	25	1335	53	247	1088	44	1012	40	818	33	907	36	588	24	266	11
						73	5488	75	1278	4210	58	3753	51	3526	48	3389	46	2185	30	926	13

(CCL* = curved carapace length of turtle, CCW* = curved carapace width of turtle).

(i) using the rodeo capture technique, or (ii) by recovery on the beach immediately following nesting.

2.2. GPS loggers

We used recently developed, low-powered, archival Navsys Ltd. TrackTag™ GPS devices (http://www.navsys.com). Battery-life is saved due to TrackTag requiring < 60 ms to be powered up and acquire enough data for a navigational fix. This speed of acquisition is made possible because the positions are calculated during post-processing. Our devices had a memory capacity of 32,750 positions. The logger was housed in a stream-lined, pressure tight, ABS plastic casing measuring 101–34–26 mm ($L \times W \times H$). The mass of the device, including battery and housing, was 55 g (c. 0.001% of estimated sea turtle mass). Loggers had a saltwater switch so that they only attempted to acquire information from the GPS satellites when the turtle was at the surface. This system helps to extend memory capacity along with battery life. Navsys estimates accuracy of locations to be around 30 m (2dRMS) 95% of the time using a horizontal and stationary receiver in the UK. Prior to deployment, the GPS loggers were charged and programmed using Navsys TrackTag™ software to record in continuous mode at 30 s intervals when the saltwater switch indicated the units were not submerged. The housing was sealed using ABS water-resistant glue requiring a 6 h drying period. GPS co-ordinates were recorded with a spatial resolution of 0.0001° (11 m for latitude and 8.8 m for longitude at 37°N).

On retrieval, all GPS locations were plotted to examine the turtles' movements. Data when the turtles were ashore (nesting or on aborted nesting attempts) were removed from all analysis and were confirmed by direct field observation, GPS onshore location and/or by TDR analysis of depth and temperature values. Due to the surfeit of data we also explored various filters to remove potentially erroneous locations. These methods included (1) removal of visually erroneous locations, such as those that fell well on land or were completely spatially different to previous and successive fixes within the same timeframe, (2) using a maximum rate of travel of 5 km h^{-1} between successive locations (Hays et al., 2004a; Tremblay et al., 2006) which was selected based on calculations from 3 or more consecutive fixes occurring at 10–20 min intervals, (3) using the 'dilution of precision' (DOP), measuring the quality of satellite geometry, in which values below 10 are retained (Adrados et al., 2002) and (4) using the 'satellite visibility' (SV) with a threshold of > 4 satellites following previous work (Sea Mammal Research Unit SMRU, http://smub.st-and.ac.uk).

2.3. TDR devices

To record the diving behaviour of turtles we used time–depth recorders (TDRs); LOTEK LTD_1100 model TDRs (LOTEK Marine Technologies, St. John's, Newfoundland). The TDRs weighed 5 g in air, sampled depth with a precision of 2 cm, temperature with a precision of 0.2 °C and stored up to 16,384 readings for each parameter (http://www.lotek.com/ltd1100.htm). The TDRs employed "time-extension" sampling whereby the sampling interval was adjusted so that data continued to be collected regardless of the length of deployments. Hence, the sampling frequency was approximately the length of the deployment divided by 16,384, which, in our study, equated to a sampling interval of < 1 min to around 4 min. For each data set we conducted a zero point offset, whereby we determined the shallowest depth recorded every 4 h. We would expect this depth to be the surface (0 m) and so all the raw depth values from the loggers were adjusted accordingly, typically by a maximum of a few 10 s of cm. This process of zero point calibration is standard within TDR studies (see for example, Hays et al., 2007).

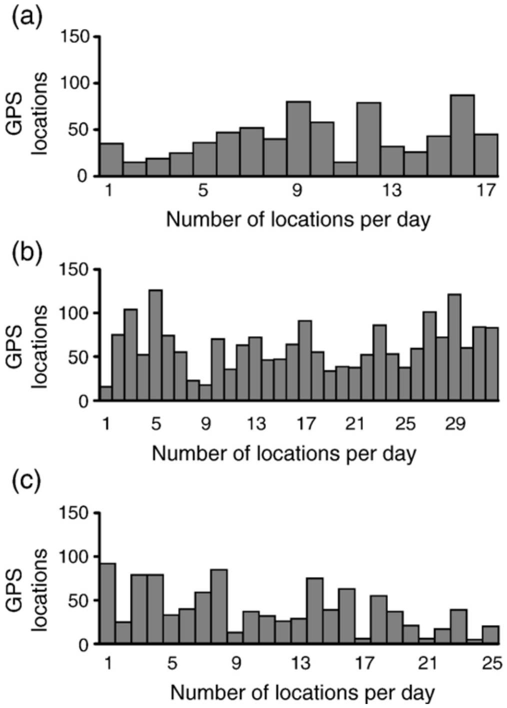

Fig. 3. Histograms of the number of daily GPS locations for each turtle. (a) GPS2. (b) GPS3. (c) GPS4.

Data when the turtles were ashore (nesting or on aborted nesting attempts) were removed from further analysis. These events were confirmed by direct field observation and/or by analysis of depth and temperature values indicating that the turtle was ashore.

2.4. Turtle spatial area use

Using the Geographic Information Systems (GIS) package ArcView 3.1 we identified key area use by overlaying the turtle GPS fixes on existing features, including (i) sea depth parameters, (ii) Natura 2000 marine habitats and (iii) National Marine Park of Zakynthos maritime zones. To obtain an objective measure of sea turtle key area use in relation to the selected features, we initially filtered the GPS fixes by selecting one fix per hour for each turtle (Tremblay et al., 2006). The GIS programme provided the attributes of the polygons for each feature within the maps. The location of turtle GPS fixes was analysed (using the "query" and "summarise" tools) with respect to the chosen features, to indicate areas that are in need of increased protection.

2.5. Turtle movement model simulations

Two turtles that were tracked moving around Laganas Bay at the same time (GPS2 and GPS3) seemed to show broadly the same pattern of movement rather than moving randomly with respect to each other. We therefore compared their movements against two random walk models. First we calculated the distance separating these two turtles every 3 h between 24/5/2006 and 6/6/2006, excluding days on which turtles nested (31/5/2006). In model 1 we assumed that each turtle moved randomly within Laganas Bay (defined by latitudes 37°70′–37°74′ N and longitudes 20°84′-20°96′E). Given that the bay at its widest point is about 12 km, we assumed that within 3 h a turtle could travel anywhere in the bay. We therefore divided the bay into grid squares (178 m in latitude by 211 m longitude) and randomly selected grid squares for each modelled turtle at 3 h intervals. At each time we calculated the distance apart between the two modelled turtles. In model 2, we constrained the movements of the modelled turtles so that they moved randomly but only within 900 m of the shore in Laganas Bay. For both models, 1000 movement steps were generated. The

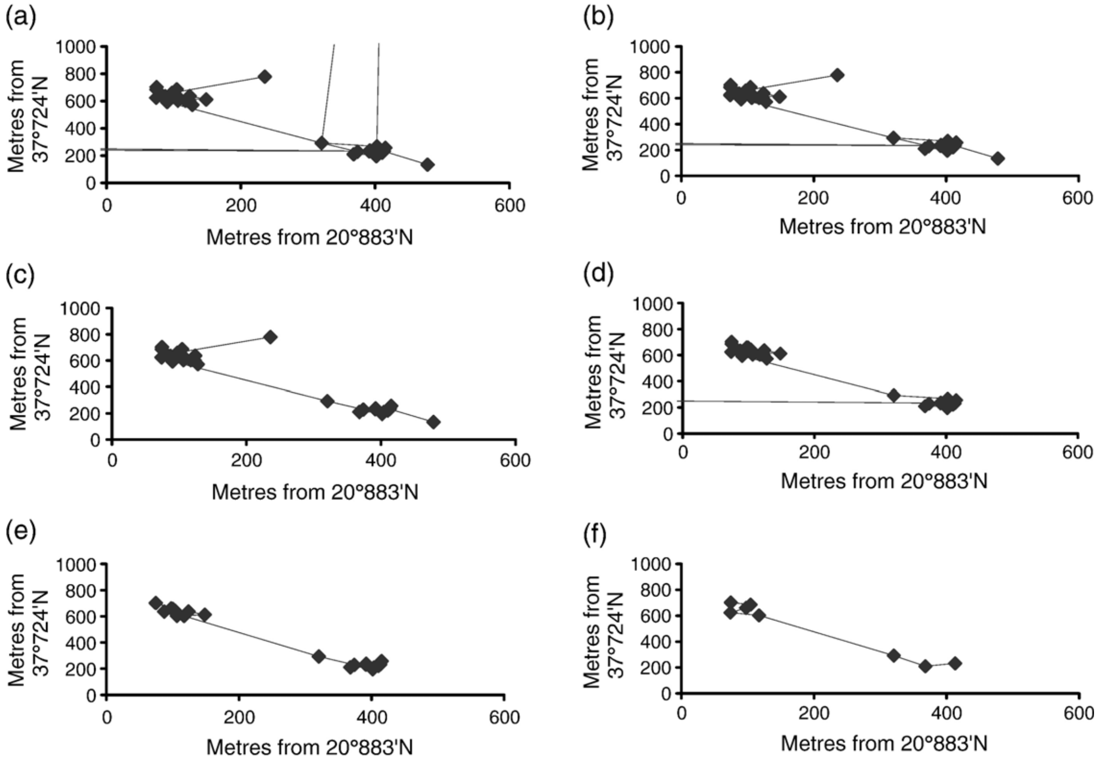

Fig. 4. Graph showing the difference between GPS logger locations retained with the different filtration methods. (a) All GPS in-water locations. (b) Visually erroneous locations filter. (c) Speed filter 5 km h^{-1}. (d) Satellite visibility filter >4. (e) Dilution of precision filter <10. (f) Hourly positional locations.

differences in observed distribution of actual and random walks were calculated using Kolmogorov–Smirnov tests.

3. Results

3.1. TrackTag™ GPS loggers

Excluding deployment and retrieval days, the three turtles equipped with GPS loggers were tracked for a total of 73 complete days (17, 31 and 25 days respectively) between 20 May and 23 June 2006. All three turtles nested at the same beach (Sekania, in maritime zone A) during the period of GPS logger attachment.

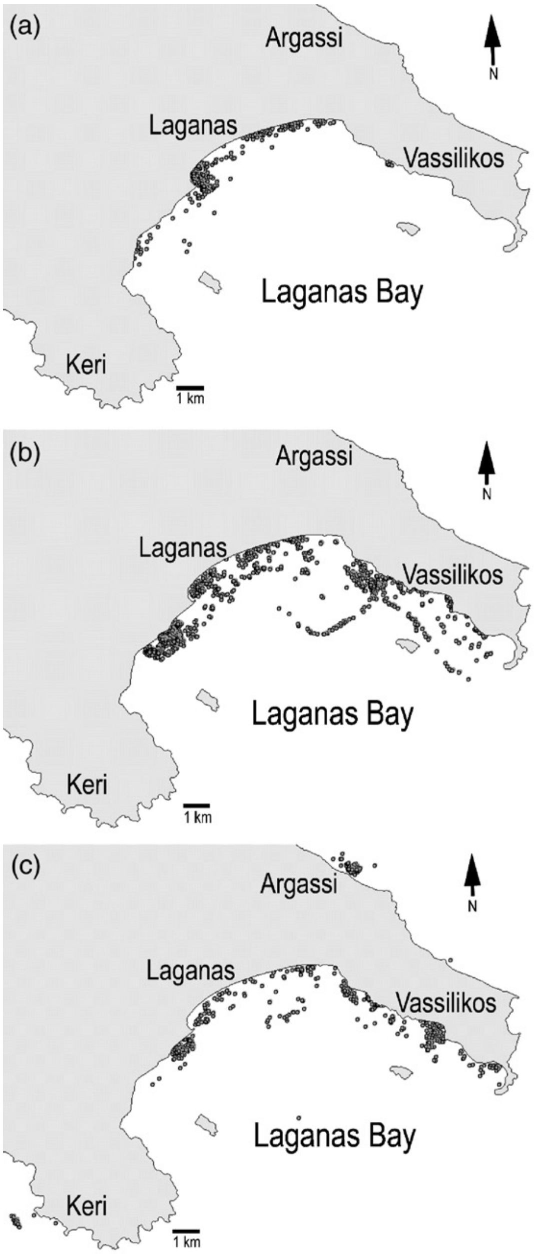

Fig. 5. GPS logger tracks including nesting beach emergence fixes. (a) GPS2. (b) GPS3. (c) GPS4.

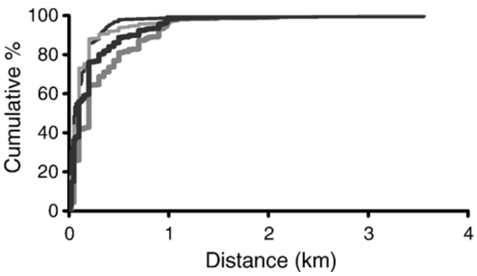

Fig. 6. The cumulative frequency distribution for the distances from shore using hourly GPS logger locations of all three GPS turtles combined (thick solid black line) and each turtle separately. GPS2 fine black line, GPS3 thick grey line, and GPS4 thick dashed grey line.

A total of 5488 GPS fixes were obtained, of which 1278 were from when the turtles were making nesting attempts, leaving 4210 in-water locations. On filtering the data for visually erroneous locations, 457 fixes were removed, leaving 3753 GPS fixes (89%), with an average daily fix rate of 51 locations (Table 1, Fig. 3a–c). Alternative filtration methods of the in-water locations, using the speed filter left 64% of locations, while 40% and 62% of locations were retained respectively using the DOP and SV based filtration methods (Table 1). In all cases the tracks, either with raw or filtered locations, were very similar and the high number of daily locations allowed accurate assessment of each turtle's movement (Fig. 4a–f) (Hays et al., 2004a). Hence, we selected to base subsequent data analysis on GPS locations that remained following the removal of 'visually erroneous' locations.

The GPS loggers indicated that all three turtles primarily used an 18.5 km section of the 27.8 km coastline of Laganas Bay; with 100%, 100% and 84% of in-water GPS locations for each turtle respectively (Fig. 5a–c and Appendix A). Only GPS4 left the breeding area during the survey period. Analysis of hourly turtle locations against bathymetry, corroborated this coastal preference, suggesting that 79% of time was spent at sea bed depths < 5 m. Analysis of turtle distance from shore at hourly intervals indicated that 89% of hourly locations occurred within 0.5 km of shore, 76% within 0.2 km of shore and 56% within 0.1 km of shore (Figs. 6 and 7a). Analysis of our dataset using GIS overlays of Natura 2000 habitats suggested that the turtles do not uniformly inhabit shallow waters, but prefer habitats comprising submerged sandbanks (63% fixes) over other near-shore habitats, such as shallow rocky reefs (37% fixes) (Fig. 7b).

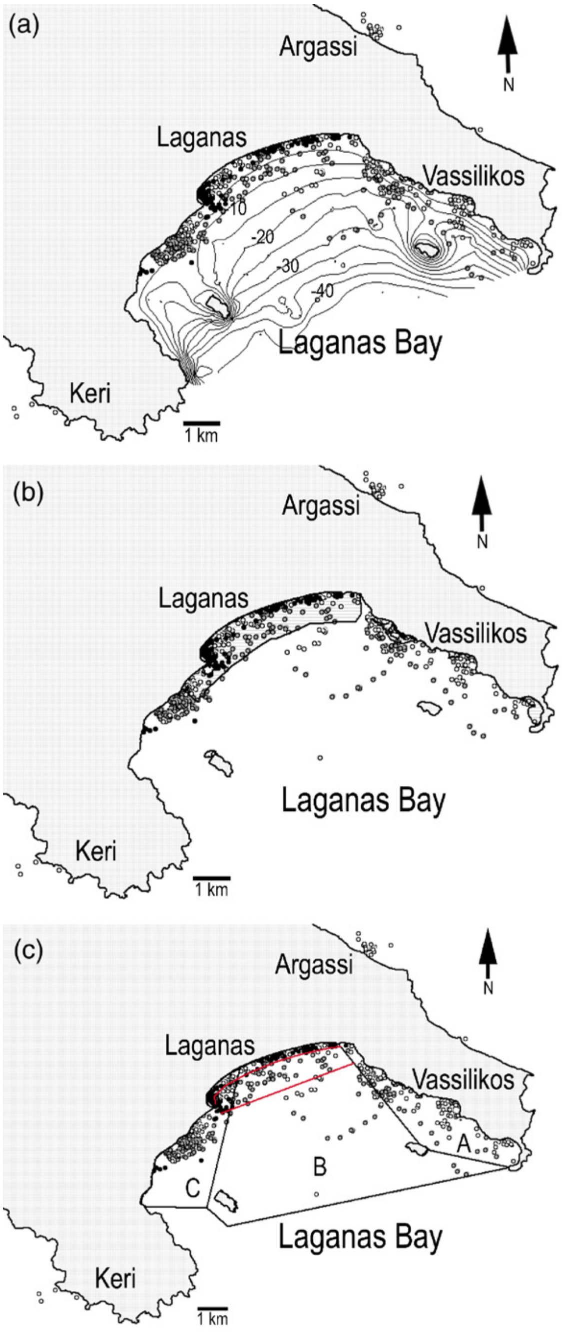

Fig. 7. GIS maps showing the hourly GPS logger locations of all three turtles with respect to (a) bathymetry, (b) Natura 2000 habitat of submerged sand-banks, (c) NMPZ maritime protection zones and ecotourism zone (swim 0–200 m from shore, turtle-watching 200–1400 m from shore).

Table 2
Table of TDR data from six sea turtles showing the percentage of shallow pattern of depth utilization

Animal ID	Percent of time at mid-point depth bin/metres				
	1	3	5	7	11
GPS2	89.92	7.12	2.05	0.74	0.01
GPS3	95.34	3.42	1.21	0.02	0
GPS4	80.75	16.03	3.05	0.15	0.01
TDR1	79.69	16.68	2.80	0.46	0.12
TDR2	89.23	7.99	2.61	0.12	0.02
TDR3	91.89	7.39	0.57	0.14	0

Analysis of hourly GPS locations with respect to the National Park maritime zones indicated that turtles spent on average 25%, 29% and 42% GPS of time in maritime protection zones A, B and C respectively. The turtles spent on average 56% (range 34%–94%) of time within the ecotourism zone straddling maritime zones B–C. GPS4 spent 4% of the survey period outside of the three protection zones (Fig 7c).

3.2. TDR devices

The near-shore movements of the three turtles equipped with GPS loggers was reflected in their patterns of depth utilisation with the vast majority of their time spent at very shallow depths. For example, all three turtles spent > 95% of their time at sea depths shallower than 4 m (Table 2). Similarly for a further three turtles equipped with TDR loggers only, for a total of 67 days (31, 12 and 21 days respectively) between 16 May and 27 June, their patterns of depth utilisation were also very shallow (Table 2) with all these turtles similarly spending > 95% of their time shallower than 4 m.

3.3. Turtle movement and simulations

Analysis of comparative locations of actual GPS2 and GPS3 turtles at three-hourly intervals indicated that

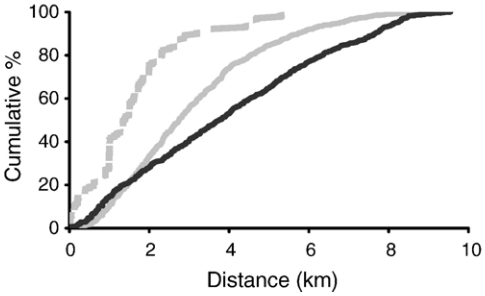

Fig. 8. The cumulative frequency distribution for the distances apart of GPS2 and GPS3 turtles measured every 3 h between 24/5/2006 and 6/6/2006 (dashed line) and modelled turtles moving within the bay following random walk models. Thick solid grey line = random walk model 1, thick black solid line = random walk model 2. The observed distribution differed significantly from both random walk models (Kolmogorov–Smirnov tests, $D = 0.4245$, $P < 0.001$ and $D = 0.5031$, $P < 0.001$ respectively).

they occurred at distances of ≤ 1.5 km apart on 55% of occasions (average 1.6 km, range 0.01–5.44). Analysis of comparative locations of GPS4 with GPS2 and GPS3 indicated that they occurred at ≤ 1.5 km of both GPS2 and GPS3 on 38% of occasions (average 2.6 km, range 0.01–8.3).

In both models the frequency distribution for the distances apart between the two modelled turtles was different to that in the observed data (Fig. 8), with GPS2 and GPS3 generally being more closely associated than that predicted by both random walk models (Kolmogorov–Smirnov tests, $D=0.4245$, $P<0.001$ and $D=0.5031$, $P<0.001$ respectively). In other words, this evidence suggests that turtles 2 and 3 were moving in the same manner within the bay.

4. Discussion

Increasing development and settlement of human populations in coastal locations has become an important issue worldwide, threatening the sustainability of many marine and coastal resources (Arianoutsou, 1988; Argardy, 1994; Parra et al., 2006). To facilitate wildlife conservation and sustainable use of marine areas, it is essential to understand the relationship between populations and their habitats (Castilla, 2000; Canadas et al., 2005), with knowledge about the impacts of environmental and anthropogenic parameters providing additional benefit (Thompson et al., 2000; Tisdell and Wilson, 2002; Douglas-Hamilton et al., 2005; Preisler et al., 2006). However, quantification of such parameters is often difficult hence the ‘precautionary approach’ to protect wildlife is applied in many areas, whereby measures are introduced, such as the regulation of boating activity, to minimise disturbance across general regions (Thompson et al., 2000; Wilson et al., 2004; Lusseau, 2006; Sorice et al., 2006). In the case of sea turtles, nesting beach locations and relative nesting densities have been used to delineate the degree of protection offered by adjacent marine protection zones (Arapis and Margaritoulis, 1994). While this approach has shown relatively good success in general, core protection areas may not reflect actual areas of wildlife habitat use, as we have demonstrated in our study at the largest sea turtle rookery in the Mediterranean.

The fine-scale detail of movement patterns obtained using the GPS loggers during this study, could not have been replicated using conventional telemetry (Hays et al., 2001; Hulbert and French, 2001; Tremblay et al., 2006; Bradshaw et al., 2007). This has been made possible because the TrackTag™ GPS system calculates the position during post-processing rather than in real time (http://www.navsys.com). We have shown here how TrackTag™ GPS loggers can now obtain large numbers of locations for marine species. The volume of data and degree of accuracy obtained using the TrackTag™ system are greatly improved in comparison to that obtained in previous GPS studies of marine wildlife (Sisak, 1998; Arai and Ono, 2002; Jay and Garner, 2002; Yasuda and Arai, 2005; Petersen et al., 2006), facilitating fine-scale analysis and application to protected area management.

While the movement models we have used in this study are very basic, a number of more refined models could potentially be explored. For example, correlated random walk models, which randomly draw step lengths from the measured step-length frequency distribution, may provide a more refined test of whether animals are moving randomly (e.g. Heithaus et al., 2002a). Similarly techniques such as fractal analysis and first passage time analysis provide mathematical approaches for exploring the details of habitat use by tracked animals, so that habitat preferences can be identified (e.g. Pinaud and Weimerskirch, 2005; Bailey and Thompson, 2006). One of the great advantages of the high resolution tracks provided by GPS loggers (high accuracy of locations combined with very frequent locations) is that a range of quantitative movement analysis can be performed on the data, with the biological signal not being compromised by artefacts introduced by measurement errors (Bradshaw et al., 2007). Hence the technology we have introduced here has great utility for tracking a wide range of marine vertebrates that surface to breathe including mammals and birds (C.M. Bishop unpublished). Furthermore, tethered GPS data-loggers may work for those non air-breathing animals (e.g. some fish) that do not surface to breathe but nevertheless come close to the surface.

During our study, while female sea turtles spent the majority of time outside of the no-boating maritime protection zone, a significant proportion of the population nest on one or more of the beaches in this region (Katselidis et al., 2004), and our data indicated that turtles are likely to preferentially frequent the region adjacent to the nesting beach in the days preceding nesting. As a result, this zone remains one of extreme conservation importance. The movement and depth data indicated that female turtles preferentially inhabit very shallow water in areas of submerged sand-banks. These criteria are only found in the two lesser protected boating zones. Our findings clarify that for maritime zones to provide the necessary protection, they should be based on sea turtle key area use (i.e. sea depth, proximity to shore and habitat preference), and not only the location of nesting beaches as has been done until now. While the national park has acted on an existing transect based survey (Schofield et al., 2004) to form an 'ecotourism zone' to improve regulation of turtle-watching activities, our data suggest that this zone needs to be extended by about another 4 km, with the implementation of stronger regulations on marine area use within this region. Since female turtles occupied this zone for over 50% of time, it is important to quantify the impact of all near-shore human activities (including wading, swimming, private boat hire and turtle-watching), as has been done with other marine vertebrate species impacted by humans (Lusseau, 2006).

Turtles spend their time at sea during the breeding season engaged in a variety of activities such as mating, cleaning and resting (Booth and Peters, 1972; Schofield et al., 2006). Resting on the sea bed has been widely reported for hard-shelled turtles including green, loggerhead and hawksbills turtles (Houghton et al., 2002; Seminoff et al., 2002; Hopkins-Murphy et al., 2003; Houghton et al., 2003). Often female turtles are reported resting at depths of 15 m or less, and this relatively deep resting is reflected in the data provided from TDR deployments. However, in this study it was striking that female loggerhead turtles at the Zakynthos rookery almost never dived to sea bed depths of more than 4 m during May and June. This pattern of shallow diving was seen both in the turtles equipped with GPS loggers and TDRs ($n=3$) and those carrying only TDRs ($n=3$). The fact that both groups showed similar patterns of depth utilisation implies that the near-shore movements in shallow water we saw for the three GPS-equipped individuals might occur generally for female loggerhead turtles at this time of year at the Zakynthos rookery. The turtles may be inhabiting regions close to shore to avoid males (Booth and Peters, 1972). However, since turtles appear to selectively change sites on a daily basis and individuals had similar movement patterns, this suggests other processes may drive these near-shore movements. Our study has demonstrated how GPS tracking can be used to obtain accurate spatio-temporal information about the fine-scale movement patterns of a marine vertebrate, illustrating the value of this technique for wildlife conservation management and improvement of protection measures.

Acknowledgements

The authors thank the National Marine Park of Zakynthos and Greek Ministry of Agriculture for permission to conduct this research activity. We thank the NMPZ for boat access and skilled drivers, especially K. Gounelis. Special thanks to V. Hobson, L. Sourbes, K. Papadimitriou and D.G. Schofield with GIS assistance and advice. We also thank D.A. Davies and A. Jones for making the pressure proof logger housings; and NMPZ and Archelon volunteers including S. Botos, C. Dean, D. Oakely, B. Gill, P. Bradshaw, E. Ransome, M. Barrett and others for invaluable assistance with logger retrievals. The authors wish to acknowledge the use of the Maptool program for analysis and graphics in this paper (www.seaturtle.org). Support for TrackTag GPS dataloggers was provided by a grant from NERC (NER/D/S/1999/00078) awarded to C.M.B. **[SS]**

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jembe.2007.03.009.

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Preprint, 2009
doi: 10.3354/esr00137

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Contribution to the Theme Section 'Biologging technologies: new tools for conservation'

Conservation hotspots: implications of intense spatial area use by breeding male and female loggerheads at the Mediterranean's largest rookery

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ABSTRACT: The implementation of appropriate protection measures for endangered species in protected areas requires knowledge of their fine-scale habitat use. In May and June of 2006 and 2007, we used GPS loggers (some linked to the Argos system) and a conventional Argos transmitter to track male and female loggerhead turtles *Caretta caretta* in the vicinity of the breeding area of Laganas Bay within the National Marine Park of Zakynthos, Greece. We obtained (1) 9681 useable locations (mean: 1383 locations ind.$^{-1}$; range: 519 to 2198 locations) from Tracktag GPS loggers attached to 7 females for a mean duration of 34 d (range: 17 to 52 d); (2) 1245 useable locations (mean: 311 locations ind.$^{-1}$; range: 38 to 1110 locations) from 4 males fitted with Fastloc Argos tags for a mean duration of 29 d (range: 3 to 51 d) and (3) 100 locations from 1 male fitted with a conventional Argos satellite tag tracked for 128 d. GPS data indicated that before the onset of nesting, both males and females primarily used an area within 500 m of the shore along a core 9 km stretch of coastline, where existing protective legislation requires strengthening. Our observations suggest that a 76.7 % female-biased operational sex ratio, measured previously from in-water surveys, may represent a realistic sex ratio estimate in the period before nesting starts. In the first month following the onset of nesting, female spatial distribution remained similar, whereas most males departed for distant areas presumably to forage. Our study provides quantitative evidence of the need to improve the management planning and conservation measures to protect sea turtles in a coastal breeding area, and new insights on male turtle migration.

KEY WORDS: Conservation management · Endangered species · Population density · Marine vertebrate · Migratory species · Multiple paternity · Wildlife telemetry

INTRODUCTION

Effective conservation management of wide-ranging marine vertebrates requires quantitative information at both local and regional levels (Hyrenbach et al. 2000). In recent decades, satellite telemetry has facilitated the tracking of wildlife movement over thousands of km. Invaluable information has been provided on migratory corridors and the essential resources that they link, such as reproductive and foraging grounds (Morreale et al. 1996, Sheppard et al. 2006, Rasmussen et al. 2007, Zbinden et al. 2008). While such corridors are rarely protected, partly due to the fact that they often traverse political borders, the prime resource sites they connect

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may meet 'siting' criteria for inclusion within national protected area management schemes (Gardenfors 2001, Campbell 2007, Lawton 2007, Wood & Dragicevic 2007). To formulate effective protective zoning and associated conservation legislation and policies, objective and quantitative evidence is required with respect to habitat preferences of key species and core area use within such sites (Sutherland et al. 2004, Togridou et al. 2006). This is of particular consequence in coastal zones where increasing levels of human settlement, leisure and fishing activities may already be placing pressure on endangered species populations and the natural resources on which they depend (Martien et al. 1999, Zbinden et al. 2007a). However, conventional satellite transmitters provide only fairly coarse spatial resolution and are primarily useful in documenting broad-scale movements (Hays et al. 2001a). Recently, tracking units based on GPS technology have become available to wildlife researchers, with an accuracy of metres (Hulbert & French 2001). For this reason, GPS technology is an increasingly important tool to quantitatively address the conservation management requirements of wide ranging terrestrial and marine species both within and between the reserves designated to protect them (Ryan et al. 2004, Douglas-Hamilton et al. 2005, Schofield et al. 2007).

For the globally endangered sea turtle species, much information is now available on the periodic broad-scale movements of adult females as they migrate between nesting and foraging areas, which is usually derived from Argos satellite transmitters (e.g. Luschi et al. 2003, James et al. 2005b, Broderick et al. 2007, Zbinden et al. 2008). Habitat use within breeding and foraging areas has been inferred using mark-recapture, radio, sonic and/or satellite telemetry (van Dam & Diez 1998, Hopkins-Murphy et al. 2003, Zbinden et al. 2007a), and more recently GPS units (Yasuda & Arai 2005, Schofield et al. 2007). However, there remains a bias towards female-oriented research because they come ashore to nest, providing an easy opportunity to attach tracking equipment. At temperate breeding areas, satellite and sonic telemetry studies of female loggerheads indicate use of areas <15 m deep (Hopkins-Murphy et al. 2003, Zbinden et al. 2007a), and recent GPS tracking indicates possible use of areas as shallow as <4 m (Schofield et al. 2007).

Compared to females, far less is known about male turtle movements (but see Limpus 1993, Plotkin et al. 1996, Hays et al. 2001b, James et al. 2005a, Shaver et al. 2005), due to the necessity, and difficulties, of in-water capture (Ehrhart & Ogren 1999). Existing research indicates that males may occupy areas of up to 40 m depth at breeding grounds (Shaver et al. 2005) and, following a protracted mating period, appear to exhibit similar migration patterns to adult female conspecifics (for overview see Sakamoto et al. 1997, Godley et al. 2008). To objectively determine whether existing or suggested protection measures at local (i.e. within a national park or reserve), national and regional level is appropriate, high-resolution tracking of all segments of the population actively using the area is needed (Seminoff et al. 2002). Furthermore, in the Mediterranean, sea turtle foraging areas remain largely lacking in protective legislation (Zbinden et al. 2008), hence confirmation of the use of certain areas by both adult males and females following migration from breeding areas may provide evidence supporting the establishment of much needed protection sites.

The island of Zakynthos, Greece, hosts the largest known breeding population of loggerheads in the Mediterranean (Margaritoulis 2005). Several hundred loggerhead turtles enter Laganas Bay at the southern part of Zakynthos to breed from mid April onwards (Schofield et al. 2006), and female turtles generally nest from late May until early August, with an average of 1300 clutches per season (Margaritoulis 2005). Existing marine protection zones were delineated based on nesting beach locations and relative nesting densities (Arapis & Margaritoulis 1996). Since the formation of the National Marine Park of Zakynthos (NMPZ) in 2000, regulation of recreational nearshore activities (particularly organised and incidental turtle watching activities) has been strengthened; however, for new legislation to be passed, accurate information on marine area use by adult male and female turtles is essential. During in-water surveys to assess turtle distribution and behaviour between 2003 and 2005 (Schofield et al. 2006, 2008), we noted a strong bias towards female sightings (n = 80 male, n = 1335 female), and accredited this at the time to differential spatial use by males and females in Laganas Bay. Preliminary research using highly accurate GPS TrackTag loggers indicates that female turtles primarily utilise 18.5 km of nearshore coastline at seabed depths of <5 m (or up to 1 km distance from shore; Schofield et al. 2007). However, it was not known whether males exhibit similar patterns.

The aim of our study was to investigate the fine scale movement of male and female loggerhead turtles *Caretta caretta* within a major breeding rookery using GPS tracking units. We also assess the departure of males from the breeding grounds and identify the location of distant post-breeding, presumably foraging, sites. We consider how our data might be used to contribute to sea turtle conservation measures, policies and legislation at a local and regional scale. At the local scale, we evaluate the status of protection measures in the NMPZ, while at the regional scale we contribute information for protection across international borders of male sea turtles through linking of breeding and foraging areas.

MATERIALS AND METHODS

Study area. Laganas Bay is situated at the south-eastern part of Zakynthos island, Greece (37° 43′ N, 20° 52′ E). The bay is generally shallow, reaching a depth of about 50 m and a marine area of 89.2 km^2, which forms the Marine Protection Area of the NMPZ. Laganas Bay has a coastline of 27.8 km in length (Fig. 1). Within the bay are 6 discrete nesting beaches (Fig. 1) with a total length of 6.16 km (Margaritoulis 2005).

Tracking units and turtle capture technique. During 2006 and 2007, GPS tracking units were placed on adult male and female loggerheads; GPS transmitters were placed on males due to the low likelihood of re-sighting for unit retrieval (and hence the need to remotely relay data), while GPS loggers were placed on females, since units could be removed when individuals subsequently nested. In 2006 and 2007, TrackTag™ GPS loggers (Navsys, www.navsys.com) were deployed onto 4 and 5 adult female loggerhead turtles (curved carapace lengths 77 to 89 cm), respectively. The units were attached during the pre-nesting period in May and removed in June (see Schofield et al. 2007 for detailed logger information). In 2 cases (one in each year), loggers malfunctioned due to deployment problems so that no data were collected. In 2007, 4 Fastloc GPS-Argos tags (Sirtrack, www.sirtrack.com) and 1 conventional Kiwisat 101 PTT Argos unit (Sirtrack) were deployed onto males (curved carapace lengths 79 to 91 cm). The Fastloc GPS-Argos transmitters relayed GPS information remotely via the Argos system. The Fastloc tags were on continuously but included a salt-water switch to suppress attempts to transmit or acquire data when the units were submerged. In addition, the Fastloc data was stored on-board, so that all the acquired Fastloc-GPS data could be downloaded directly to a computer in the event of instrument recovery. One coat of antifoulant was painted on all Sirtrack units.

Navsys estimates the accuracy of TrackTag locations to be around 30 m (2dRMS) for 95% of locations recorded using a horizontal and stationary receiver in the UK. Fastloc units have an accuracy of 55 m in 95% of locations recorded and 20 m in 50% of locations recorded (see www.sirtrack.com). The conventional Argos unit accuracy is categorised by location classes (LC): LC 3, LC 2, LC 1 or LC 0 locations, which are classified as within 150, >150 to 350, >350 to 1000 or >1000 m. Locations classified as Classes A and B have been ill defined, but probably indicate poor accuracy (particularly LC B) (Hays et al. 2001a).

A 4 m research boat was used to find turtles at water depths of 1 to 7 m. Turtles were captured at random along the central 12 km stretch of coastal waters over submerged sandbanks only (for safety reasons) using the turtle-rodeo technique (Ehrhart & Ogren 1999), and were swum into a semi-submerged wooden box attached to the side of the boat (Fig. 2a). Following capture, curved carapace length was measured and a GPS logger or transmitter was attached using a standard method previously employed with various transmitters/loggers (Hays et al. 2003). In brief, the carapace was cleaned and then the logger, embedded in quick setting 2-part epoxy resin (Powerfastners) with wooden baffles, was positioned at the anterior to help prevent impacts to the equipment (Fig. 2b,c). The reproductively active status of captured individuals was determined through in-water observation of courtship and mating activity. The attachment of all devices was conducted under licenses from the Greek Ministry of Agriculture. All GPS loggers and one GPS transmitter were retrieved from the animals by 1 of 2 methods: (1) using the rodeo capture technique or (2) by recovery on the beach immediately following nesting.

Data analysis. All GPS transmitter and logger locations were first plotted to allow a quick initial visual inspection. The data were filtered by (1) subjectively removing visually erroneous locations (i.e. on land or spatially different fixes to previous and successive fixes

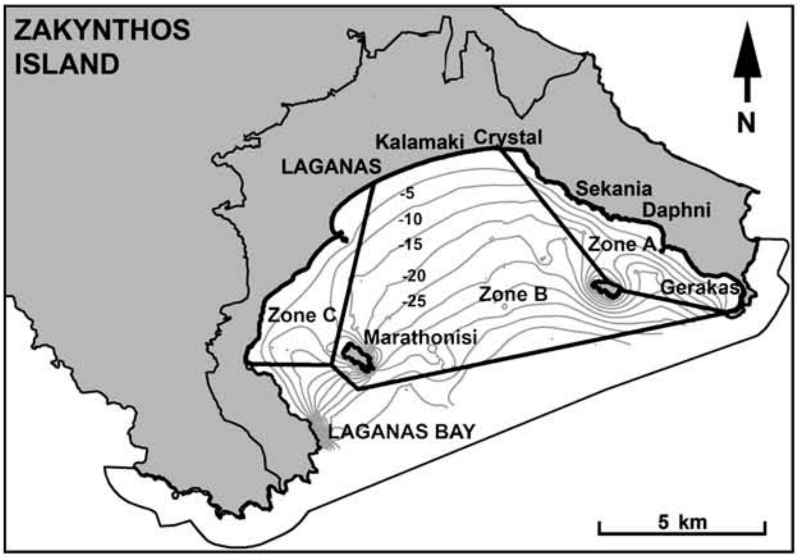

Fig. 1. Area of the National Marine Park of Zakynthos (NMPZ) encompassing the 6 loggerhead nesting beaches of Laganas Bay (Marathonisi, Kalamaki, Crystal, Sekania, Daphni, Gerakas). Bathymetry (isobars at 5 m sea depth intervals) and the 3 NMPZ protection zones are shown; Zone A (no boating activity), Zone B (boating speed up to 6 kn permitted and no mooring), Zone C (boating up to 6 kn permitted and mooring)

within the same timeframe), (2) using a maximum rate of travel of 5 km h^{-1} between successive locations (Hays et al. 2004), which was selected based on calculations from 3 or more consecutive fixes occurring at 10 to 20 min intervals, and (3) removing data from when the turtles were onshore (nesting and/or aborted nesting attempts). We then calculated the mean GPS location h^{-1} for each turtle (Tremblay et al. 2006). We calculated the daily mean location of each turtle from the hourly datasets, from which the daily distance from shore of different turtles was calculated. We divided the 27.8 km coastline of Laganas Bay into 3 equal sections of coastline, each 9 km long (the eastern, central and western sections), and used hourly datasets to determine general area use. Note that the eastern section of coastline falls in the highly protected no-boating park zone,while the eastern and central sections fall in the low protected zones where boating is permitted. An estimate of migratory distance for the males was calculated by summing up distance travelled between daily locations. For the data from the conventional Argos PTT unit, locations were filtered using a maximum rate of travel of 5 km h^{-1} between successive locations (Hays et al. 2004).

In order to correlate male departure times with respect to the onset of nesting, information on the daily nest number in 2007 was obtained from the NMPZ for all beaches in Laganas Bay. The number of new nests from the previous night was assessed from tracks. The mean date of nesting for 2007, 3 July, was determined by:

$$\text{Mean date of nesting} = \frac{\sum xf}{\sum f}$$

where x is the day of year (i.e. 1 January = Day 1 and 31 December = Day 365) and f is the number of nests. The nesting 'peak' is the date on which the greatest number of nests was recorded (27 June, Day 178).

The mean date on which the transition between the pre-nesting (phase prior to the first nesting event) and internesting (phase between first and last nesting events) period occurred was calculated from the first nesting event for each female from the GPS datasets (Table 1). This was identified when locations were being consistently recorded at 30 s intervals for a minimum of 30 min, indicating that the turtle was on land. If more than one nesting event was recorded in a 5 d period, the last event was selected as the successful event, with the preceding events being recorded as non-nesting emergences. Subsequent nesting events were also identified in 5 of the tracked turtles, and this information was used to calculate internesting intervals. For correlation with the dataset of the male that remained in the breeding area, we also separated the 2 periods by identifying the date from which nests were recorded daily thereafter. In 2006 and 2007, the first nest was laid on 29 May (Day 149) and 17 May (Day 137), respectively, with regular daily nesting being recorded from 29 May (Day 149) and 1 June (Day 152) onwards, respectively.

Nearshore surveys. For the current study, we revisited the in-water sea turtle distribution and behaviour datasets from 2003, when the most robust surveys were conducted by boat (Schofield et al. 2006, 2008). On 27 fair weather days from 14 April to 31 May 2003, daily line transects were made at seabed depths of 3, 5, 7 and 10 m (i.e. up to 1 km from shore) along a 5.5 km stretch of nearshore coastline within Laganas Bay (for map see Schofield et al. 2006). Boat surveys (405 km total distance, 137 h total duration) were conducted by 2 to 3 observers on a 4 m boat with an outboard engine. Sessions lasted an average of 5 h (minimum 4, maxi-

Table 1. GPS logger and transmitter locations acquired and those remaining after filtration. Dates given as dd/mm/yyyy. CCL: curved carapace length of turtle; CCW: curved carapace width of turtle. No. of operational days and mean points per day are highlighted in bold

Year	Turtle ID	Device	CCL	CCW	Date GPS attached	Date GPS stopped	Date of first nesting	Date of departure	No. days operational	Post-filtering locations	
			(cm)							Total	Mean d^{-1}
2006	Female_1	TrackTag GPS	81	73.5	19/5/2006	6/6/2006	21/5/2006		**17**	519	**31**
2006	Female_2	TrackTag GPS	89	76	23/5/2006	26/6/2006	25/6/2006		**31**	2198	**69**
2006	Female_3	TrackTag GPS	87	72	24/5/2006	18/6/2006	7/6/2006		**25**	818	**33**
2007	Female_4	TrackTag GPS	83	75	4/5/2007	25/6/2007	5/6/2007		**52**	2081	**25**
2007	Female_5	TrackTag GPS	84	77	8/5/2007	11/6/2007	3/6/2007		**34**	909	**27**
2007	Female_6	TrackTag GPS	81	74	9/5/2007	26/6/2007	23/5/2007		**48**	1779	**37**
2007	Female_7	TrackTag GPS	77	66	11/5/2007	12/6/2007	21/5/2007		**35**	1377	**39**
2007	Male_1	Sirtrack GPS	81	72	8/5/2007	26/6/2007		n/a	**49**	1110	**23**
2007	Male_2	Sirtrack GPS	91	81	10/5/2007	30/6/2007		20/5/2007	**51**	53	**1**
2007	Male_3	Sirtrack GPS	81	74	14/5/2007	17/5/2007		14/5/2007	**3**	38	**13**
2007	Male_4	Sirtrack GPS	79	70	10/5/2007	25/5/2007		22/5/2007	**15**	44	**1**
2007	Male_5	Sirtrack satellite	90	83	7/5/2007	12/9/2007		23/5/2007	**128**	100	**0.8**
					Total				**488**	**11026**	**22.5**

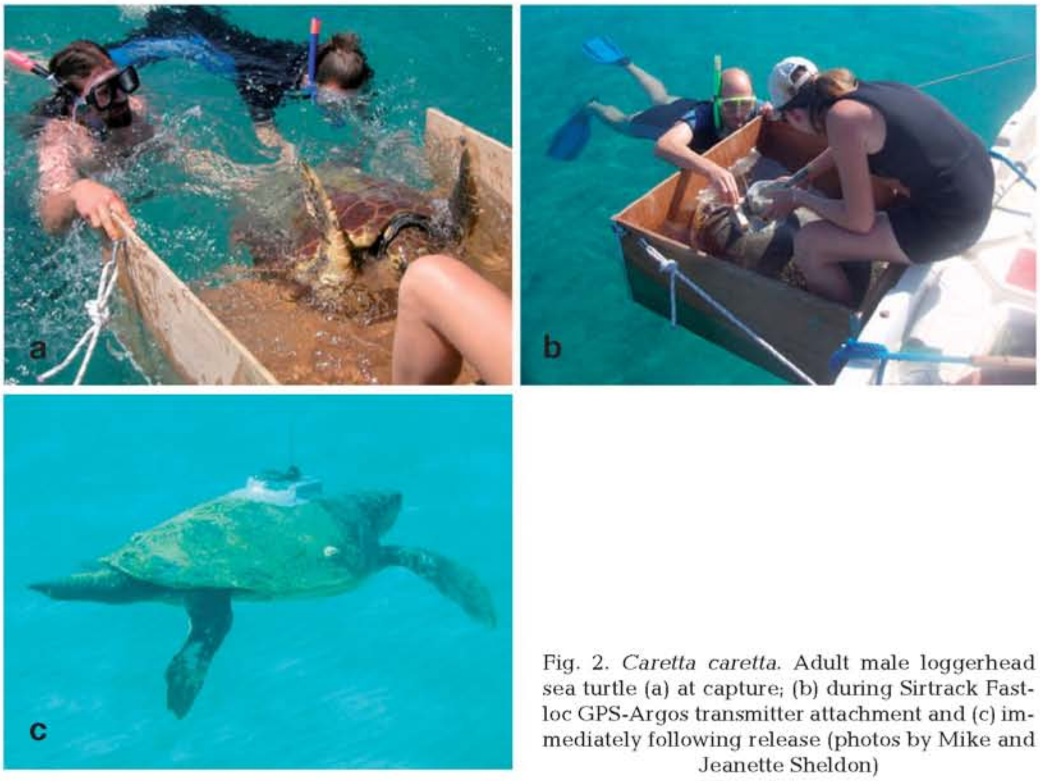

Fig. 2. *Caretta caretta.* Adult male loggerhead sea turtle (a) at capture; (b) during Sirtrack Fastloc GPS-Argos transmitter attachment and (c) immediately following release (photos by Mike and Jeanette Sheldon)

mum 7 h) at a maximum boat speed of 4 knots. The survey period covered a range of daylight hours between 09:30 and 19:30 h. GPS locations of turtle sightings were recorded using Garmin E-Trex hand-held units and still photographs were taken underwater when snorkelling at a distance of 2 to 7 m from the target animal, using an Olympus Digital 500 (5.0 megapixel) camera with underwater housing. Animal gender was determined based on tail-length dimorphism (Casale et al. 2005) and presence/absence of external identification-tags (only females are tagged).

We used the natural scalation patterns on the lateral facial region to identify individual turtles with high accuracy (see Schofield et al. 2008).

RESULTS

Tracking data

Excluding deployment and retrieval days, we tracked 3 female turtles equipped with TrackTag GPS loggers in 2006 and 2007 for a mean 34 d each (range 17 to 52 d). The 4 males equipped with Fastloc GPS-Argos transmitters were tracked for a mean 29 d each (range 3 to 51 d). The 1 male equipped with a conventional Argos transmitter was tracked for 128 d (Table 1). The volume of useable locations obtained from the different devices (TrackTag GPS loggers, unretrieved Fastloc GPS-Argos transmitters, retrieved Fastloc GPS-Argos transmitter and conventional Argos satellite transmitter) are presented in Table 1. The retrieved TrackTag loggers and Fastloc transmitter provided a much greater volume of data compared to that relayed via Argos. As expected, given their greater accuracy, all GPS units provided very detailed information on sea turtle area use, in contrast to the conventional Argos unit from which only the general location of the turtle could be inferred (Fig. 3).

Male and female area use in the breeding area

The data from the GPS units (loggers and transmitters) indicated that both male and female turtles primarily used the marine area close to shore (from hourly positional datasets) (Fig. 3a & video animation in electronic supplement at www.int-res.com/articles/suppl/esr00137_app/). Before and after the onset of nesting, 82 % of all 7 female GPS locations in Laganas Bay occurred within 500 m of the shore (Fig. 4a) (approx. depth <5 m). In the pre-nesting period, 92 % of all 4 male GPS locations also occurred within 500 m of the shore in Laganas Bay (Fig. 4b).

The GPS units not only indicated this nearshore preference, but also that the tracked males and females appear to prefer certain stretches of coastline within Laganas Bay. We found that, before the onset of nest-

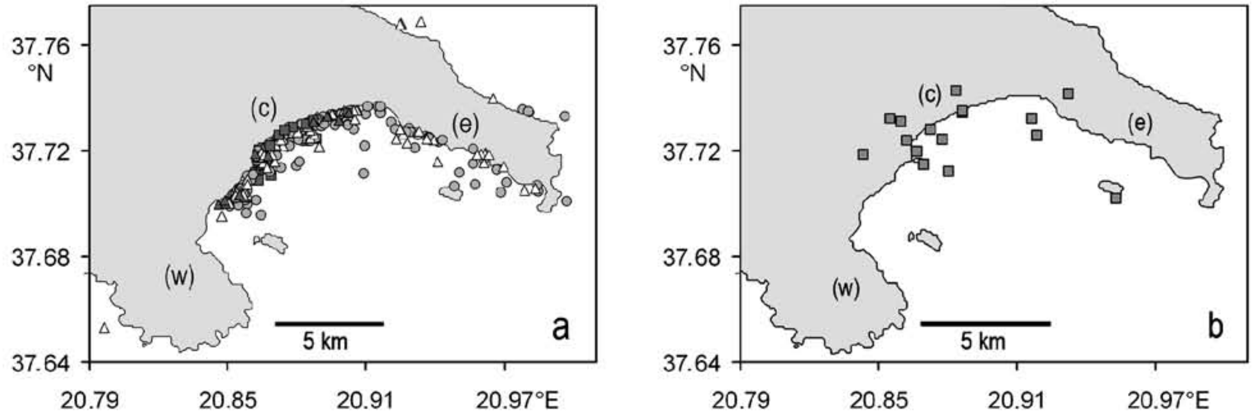

Fig. 3. *Caretta caretta*. Daily mean (a) GPS locations for males (n = 4, 72 locations, squares) and females (2006: n = 3, 109 locations, triangles; 2007: n = 4, 124 locations, circles) in Laganas Bay and (b) male Argos locations (n = 1, 16 locations). We considered Argos fixes falling on land as belonging to the closest point off the coast. Bay divisions: (w) western (c) central, (e) eastern

ing, 100% of male GPS locations and 77% of female GPS locations occurred along the central section of coastline. Only one GPS-tracked male remained in Laganas Bay following the onset of the nesting season and appeared to restrict all its activity to the central section of coastline before and after the onset of nesting. Of the 7 tracked females, activity was confined within Laganas Bay before the onset of nesting (99% of GPS locations), with some movement out of Laganas Bay occurring after the nesting season had started in June (79% of GPS locations in Laganas Bay).

After the onset of nesting, females continued to preferentially frequent the central section of coastline (54% of GPS locations). Before and after the onset of nesting, 21% of female GPS locations occurred along the eastern section of coastline (containing 3 nesting beaches together representing 70% of rookery nesting effort), which appeared to be associated with nesting activity, with turtles in general moving to this section of coastline 3 to 5 d before nesting. Just 0.2% of female GPS locations occurred along the western section of the coastline.

Female movement in the vicinity of the breeding area

Of the 7 females tracked using GPS loggers, 4 remained in Laganas Bay before and after the onset of nesting. Three turtles exited Laganas Bay on 6 occasions. In 2006, one turtle exited Laganas Bay on 2 occasions, frequenting the island's west coast for one day during the pre-nesting period and the east coast for 4 d following the first nesting event. In 2007, 1 turtle exited Laganas Bay on one occasion during the internesting period and occupied the east coast for 4 d. One turtle exited Laganas Bay on 3 occasions prior to the first nesting and swam to the east coast for 1 d on each occasion. The day following the first nesting (indicated by the GPS data), the same turtle travelled 96 km to Kyparissia Bay in the Peloponnese over a 15 d period (Fig. 5); travelling for 4 d directly to the Peloponnese, remaining there for 8 d and returning over 3 d. The turtle nested again on Zakynthos 5 d later, with an internesting interval of 20 d. It is unlikely that the turtle nested when in Kyparissia, as no locations were continuously recorded at 30 s intervals to indicate the

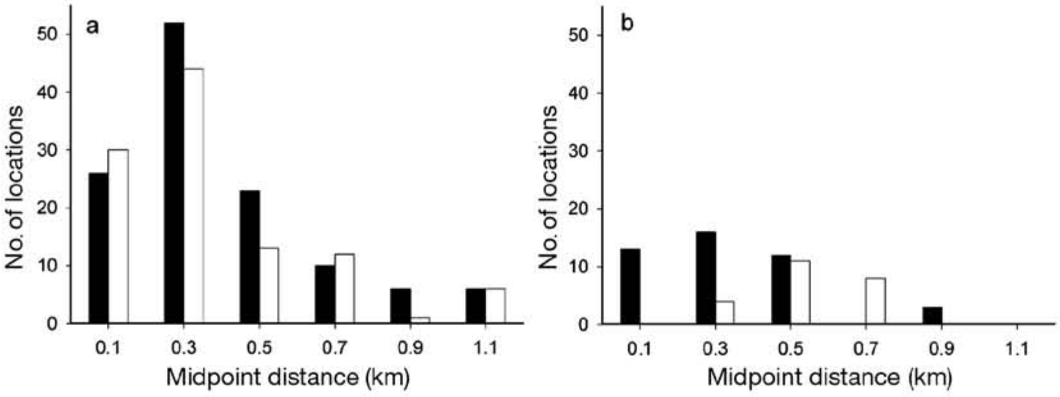

Fig. 4. *Caretta caretta*. Distance from shore before (black bars) and after (white bars) the onset of the nesting season for (a) females (n = 7) and (b) males (n = 4 before and n = 1 after) obtained from hourly positional datasets

turtle was out of the water, and we also documented a mean internesting interval of 17 d (SD ± 3.3) in 5 of the tracked turtles.

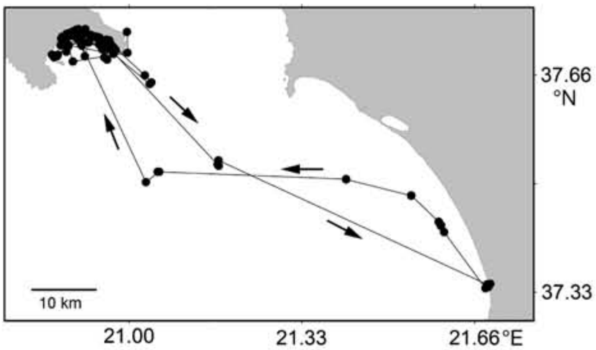

Fig. 5. *Caretta caretta*. Internesting migration from Zakynthos to the Peloponnese by 1 female during 2007

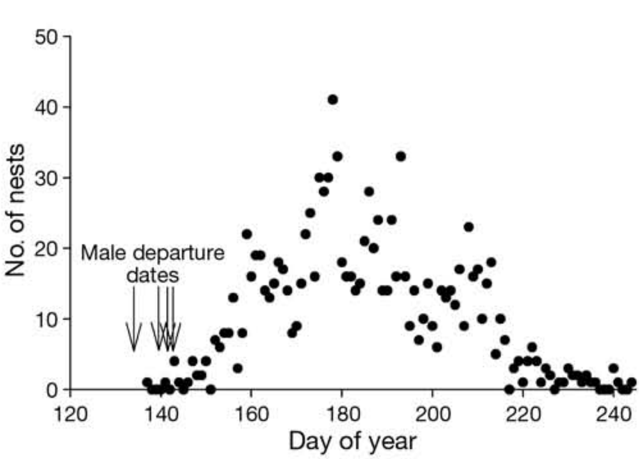

Fig. 6. *Caretta caretta*. Number of nests each day of year 2007. Days of departure of the 4 tracked male turtles are indicated with arrows (nesting data obtained from NMPZ archives)

Male movement following the onset of the nesting season

Males departed from the breeding grounds of Laganas Bay between 14 and 23 May (Table 1), which averaged 3 d after the first recorded nest (17 May, Day 137), 12 d before the start of regular nesting activity (1 June, Day 152), 38 d before the nesting peak (27 June, Day 178) and 44 d before the mean date of peak nesting (3 July, Day 183) (Fig. 6).

Four of the males departed in different directions; 2 departed in a south-easterly direction, one in a south-westerly direction and one in a north-westerly direction (Fig. 7a). One male remained in Laganas Bay and was last sighted on 27 August (when the Fastloc GPS-Argos transmitter was retrieved), still inhabiting the same nearshore section.

Two males were tracked to their presumed foraging areas (Fig. 7b). The male with the Fastloc GPS-Argos transmitter swam to a foraging area between the islands of Olib and Silba in Croatia, 721 km north of the nesting area. It travelled a total distance of 762 km over 21 d and was recorded to arrive at the presumed foraging grounds on 12 June, remaining there until 30 June when transmissions terminated. The male equipped with the conventional Argos transmitter swam to a foraging area in the Bay of Izmir in Turkey, 597 km north east of the nesting area. The turtle travelled a

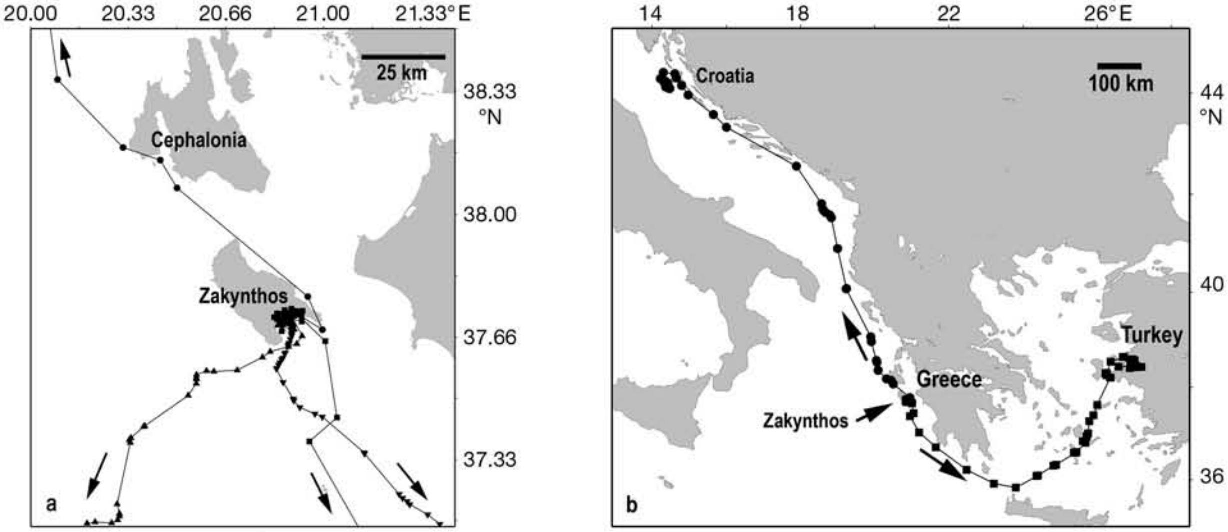

Fig. 7. (a) Disparate departure directions of the 4 males that migrated away from Zakynthos. (b) Long distance migration of 2 male turtles from the breeding area of Zakynthos; 1 GPS transmitter track to the islands of Olib and Silba in Croatia and 1 satellite transmitter track to the Bay of Izmir in Turkey

total distance of 927 km (calculated from daily mean locations) to reach the presumed foraging area over an 18 d period, was recorded to arrive on 10 June and was still transmitting from the same vicinity on 12 September.

Interestingly, the male that remained in Laganas Bay changed its spatial area use in the periods before and after the onset of nesting activity from mainly within 500 m to more than 500 m from shore (Fig. 4b).

Population parameters

In the current study, we combine the results of the in-water surveys with turtle GPS locations information to calculate an operational sex ratio for the breeding area. We crudely estimated the mean female seasonal breeding population size to be 463 individuals by dividing the mean number of nests recorded between 1984 and 2002 (1293.7 nests; Margaritoulis 2005) with an estimated mean clutch frequency of 3 (based on information from Jensen et al. 2006, Zbinden et al. 2007a).

In 2003, photographic records were collected from a total of 460 loggerhead sightings during 27 surveys in April and May. From these records, we identified 38 unique males and 127 unique females, with an average resighting rate of 3 times per individual across surveys. From this information, we calculated a 76.7% female bias (1 male to 3.3 females) in the operational sex ratio. We also recorded the average sex ratio in each field survey and found a significant temporal change across the survey period, from 66.7% male bias (2 males to 1 female) in April to a 90% female bias (1 male to 9 females) in late May ($F_{1,22} = 71.3$, $r^2 = 0.75$, $p < 0.001$) (Fig. 8).

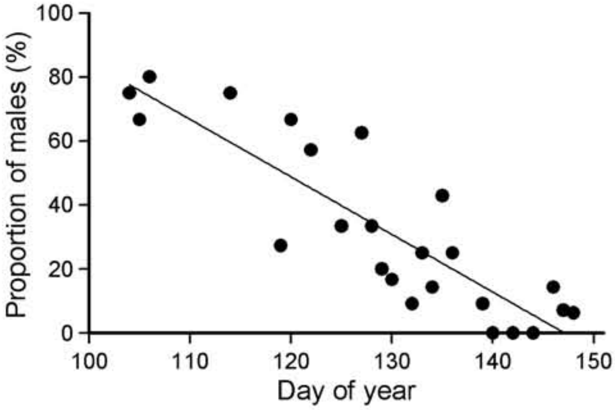

Fig. 8. *Caretta caretta*. Proportion of males present in the nearshore waters of Laganas Bay, showing a significant decline between 14 April and 31 May in 2003 ($F_{1,22} = 71.3$, $r^2 = 0.75$, $p < 0.001$)

DISCUSSION

The fine-scale movements recorded for both male and female loggerhead turtles in the present study provide information on critical habitat use to guide management decisions fundamental to their conservation. Our data strongly suggest that, before the onset of nesting, both males and females use the same nearshore area, along a specific 9 km stretch of coastline and primarily within 500 m of shore (or within 5 m sea depths) in Laganas Bay. This supports previous observations that females use sea depths up to 15 m when in the breeding area (Hopkins-Murphy et al. 2003); however, our results indicate a much narrower area use by males than the previously recorded sea depths of up to 40 m (Shaver et al. 2005). One of the tracked males remained in the breeding area, with a noticeable shift in sea depth use to deeper water following the onset of nesting. This shift may have reflected a change in the status of a resident, i.e. from breeding to foraging, and may explain the greater depth range recorded for males in other breeding areas (see Shaver et al. 2005).

Our observations suggest that it is unlikely that females are successfully using the nearshore habitat as a refuge from males following mating (Booth & Peters 1972, Whittow & Balazs 1982). For example, females maintained the same pattern of nearshore habitat use in the first month following the onset of nesting, despite the fact that most males had migrated out of the breeding area by this time. Males may be found close to shore because they follow the females to maximise their mating opportunities. By restricting their area use, females may conserve energy expenditure during the reproductive season, when they may lay several clutches over several months (Hays et al. 1999, Wallace et al. 2005). Furthermore, turtles utilising the nearshore area of Laganas Bay have been found to experience water temperatures around 5°C above that in waters >10 m depth (Schofield et al. 2009), which would decrease the duration between nesting events (Sato et al. 1998, Hays et al. 2002), thereby allowing a greater number of clutches to be laid when incubation conditions are optimal. Future studies might examine the behaviour of females later in the season to see if their interesting behaviour changes, for example with seasonally increasing water temperatures (Hays et al. 2002).

In 2006, one of the 3 tracked female turtles utilised waters outside of Laganas Bay (Schofield et al. 2007). The behaviour of this individual was not discussed due to the small sample size and the probability of this being anomalous for this population (see Zbinden et al. 2007a). However, the results of the 2006 and 2007 tracking data combined indicated that several of the tracked females moved at spatial scales beyond the main breeding area, which is consistent with previous suggestions that loggerheads may show poorer beach fidelity (Stoneburner 1982, Hays & Sutherland 1991, Katselidis et al. 2004) than some other sea turtle species (Mortimer & Portier 1989). The discrepancy in observations between Zbinden et al. (2007a) and our study, both in the same breeding area, may be attributed to the former recording movement in late June to August and the latter recording movement in May to late June, possibly indicating a change in behavioural patterns across the nesting period. The level of internesting movement may depend on the habitat needs of each species, such as foraging in leatherbacks (Georges et al. 2007) or possibly prospecting alternative nesting sites in loggerheads. This suggestion is supported by the fact that nesting activity does occur on the east coast of Zakynthos and Peloponnese where the turtles were recorded in our study. If these broad-scale movements occur regularly within the population, then current protective measures of the Zakynthos breeding area may require re-evaluation.

The use of GPS tracking in the present study defined the fine-scale habitat use by both males and females of the sea turtle breeding population and, therefore, the critical site at which heightened protection measures are required (Sutherland et al. 2004, Wood & Dragicevic 2007). Our research was conducted in collaboration with the NMPZ to evaluate the effectiveness of existing protective zoning. Of management interest, GPS tracking of females in 2006 and 2007 indicated preferential nearshore area use outside of the core marine protected area, with similar patterns being recorded in tracked males. Our findings support the experimental introduction of the national park 'ecotourism zone' in 2006 to reduce disturbance to turtles through stricter boating regulations (Lusseau 2004) and expansion to include the prime section of coastline used by both sexes. However, governmental legislative action is required to reform existing zones, which is difficult to secure (Togridou et al. 2006, Campbell 2007, Lawton 2007). Our study also indicated the possible presence of resident turtles, hence research to determine winter area use around Zakynthos is important to improve protection measures, particularly with respect to the fishery industry bycatch (Martien et al. 1999). GPS tracking facilitates the fine-scale analysis of wildlife movement patterns and we strongly recommend its use in the delineation of protection zones to ensure that the habitat requirements of the species in question are met (Martien et al. 1999, Sutherland et al. 2004, James et al. 2005b).

Establishing the number of adult males and females is important, as empirical evidence for highly skewed female adult sex ratios may necessitate an increased conservation focus on males. Furthermore, climate change may impact turtle population dynamics, hence an understanding of sex ratios at different life stages is vital to ensure effective protection. At the Zakynthos rookery, we inferred a highly female-biased adult sex ratio using our photo-identification and GPS tracking information. The GPS tracks from our 11 male and female turtles indicated that 100% of male and 77% of female hourly locations occurred along the central 9 km of coastline during May. The consistency of nearshore use by tracked individuals in this study strongly suggests that this is a general feature of the population as a whole, therefore the Zakynthos operational sex ratio recorded in 2003 may be representative of the population. However, as with many biotelemetry studies, our sample sizes were fairly small and further tracking with larger sample sizes would clearly be useful. To obtain a preliminary estimate of population size, we crudely combined the 2003 sex ratios with the mean female operational population size. We predicted an operational population size of about 593 individuals: 130 males and 463 females. This calculation clearly contains a number of assumptions—further work is needed to refine estimates of relative males and female numbers as well as to establish the variance of these estimates.

Highly skewed female sex ratios of 60 to 99% have already been documented for loggerhead hatchlings in the Mediterranean (see Zbinden et al. 2007b) and other populations around the world (Mrosovsky & Provancha 1989, Marcovaldi et al. 1997). Studies of juveniles indicate that skewed ratios may be balanced by males originating from elsewhere (Henwood 1987), though this may be a result of sex-related dispersal (Casale et al. 2006). Estimates of total population numbers and sex ratios depend on recruitment rates and the return rates of both males and females; females are believed to return biannually (Hays & Sutherland 1991) and data from Australia suggest annual return rates in males (Chaloupka & Limpus 2001). If this is the case, an 85% female bias may exist in the total adult population, which is similar to the 75% female bias in hatchling sex ratios on Zakynthos predicted by Zbinden et al. (2007b). However, robust measurements of remigration intervals for both males and females from a single population are scant, and this topic needs further study. If the difference in remigration intervals between males and females is even more marked than the 1 and 2 yr, respectively, that we have assumed, then the consequences are that the female bias in the adult sex ratio may be even more extreme than 85%. Laganas Bay is not thought to contain large numbers of juvenile turtles. Certainly no small juveniles were seen during surveys. In theory, very large juveniles might be assigned as females, but the lack of smaller juveniles suggests that this possibility is unlikely and therefore would not impact our conclusions in any important way.

We found that sea turtle density in the breeding area may be high, since our GPS data show that sea turtles primarily aggregate along 9 km^2 (9 km long by 1 km out to sea) of coastline, rather than uniformly using the 89 km^2 area of Laganas Bay. Based on our preliminary population estimate we calculated that, if sea turtle densities were uniform across Laganas Bay, there would be 5.3 ind. km^{-2}. However, our GPS data suggested that, if 100% males and 77% females utilise 9 km^2 nearshore area during May, we may have densities of 54 ind. km^{-2}. Hence, this high use area should be the first priority for the management plan and legislation of the NMPZ. It should be noted that, for the purposes of these calculations, we used a clutch frequency of 3; however, this number is highly variable within loggerhead populations and requires confirmation (Dodd 1988). Estimating the number of turtles from the total number of clutches laid each year is crucially dependent on the estimate used for the mean number of clutches per individual. Establishing the number of adult males and females is important, as empirical evidence for highly skewed female adult sex ratios may necessitate an increased conservation focus on males. However, estimates of mean clutch frequency for sea turtles are problematic because of the logistic difficulties of observing females every time they nest. Hence, estimates of mean clutch frequency may need to be refined in the future as better data become available using new methods (e.g. Cronin & McConnell 2008). The high density of turtles at Zakynthos may explain the unusually high multiple paternity recorded at the Zakynthos rookery (Zbinden et al. 2007c) despite it being a small loggerhead population relative to other rookeries exhibiting high levels of multiple paternity (Jensen et al. 2006, Lee 2008).

In support of the literature, we observed a male bias in the adult population at the start of the nesting season, yet most tracked males departed prior to the onset of nesting (Plotkin et al. 1996, Godley et al. 2002, James et al. 2005a). Both males and females undertake long migrations to breeding areas. Female turtles only need to mate once as they have the capacity to store sperm to fertilise subsequent clutches and so may resist multiple mating (Booth & Peters 1972, Lee & Hays 2004). Therefore, there is a trade-off for male turtles when away from the foraging area; to maximise paternity rates, they must arrive at the breeding area early enough to mate with unmated females, but not so early that they waste energy waiting for females to arrive. Males that remain at the breeding ground all year would save on the energetic cost of migration and have the potential to mate with more females, especially in populations where female arrival is variable. While some individuals may forage year-round on Zakynthos, prey availability may not be adequate to sustain the population, resulting in different adult dispersal strategies as indicated by Shaver et al. (2005), with most males migrating out of the breeding area prior to the onset of nesting. Presumably, these males were departing from the breeding area when most females had mated and were no longer receptive (Plotkin et al. 1996, Hays et al. 2001b, Godley et al. 2002, James et al. 2005b).

Adult male turtles monitored by satellite have been recorded to travel large distances from breeding grounds (Sakamoto et al. 1997, Hays et al. 2001b, James et al. 2005a). One of the few studies to follow both sexes tracked adult leatherbacks in the North Atlantic, where similar long-distance movements for the sexes were seen (James et al. 2005b). Our results suggest that males have broadly similar dispersal and migratory patterns to those recorded in post-nesting females (Zbinden et al. 2008), with disparate distant (presumed foraging) grounds. Two of the males in our study were tracked to distant presumed foraging areas in Turkey and Croatia, identified due to the tracking locations being concentrated in one area. Following the widely held paradigm for the life history of loggerhead turtles, we assume these distant areas were foraging and/or overwintering areas (see Lohmann et al. 2008). By combining tracking data of sex and age classes with local empirical studies it may be possible to identify other foraging sites in need of national and trans-boundary conservation management action (Gardenfors 2001, Campbell 2007, Wood & Dragicevic 2007).

Our study supports the value of GPS tracking for the understanding of spatial area use of marine vertebrates such as sea turtles at both local and regional scales. At the local scale, GPS tracking contributes to the evaluation of conservation measures, policies and legislation, while at the large scale, it can be applied to create integrated networks of protected areas encompassing breeding, migratory and foraging areas at national, trans-boundary and global levels. Our study indicated that, while retrievable GPS units produce a much larger volume of data, GPS transmitters provide the opportunity to track the fine-scale movement of more elusive components of the population (i.e. males) within the protected area and at post-migratory foraging grounds. This is of particular importance because of the low male sex ratios recorded in the Zakynthos population, which appears to continue throughout development. In conclusion, fine-scale GPS tracking of wildlife movement patterns may contribute towards enhancing national and international efforts to identify, delineate and develop new and effective protected areas.

Acknowledgements. The authors thank the National Marine Park of Zakynthos (NMPZ) and Greek Ministry of Agriculture for permission to conduct this research. Financial and logistical support was provided by the Peoples Trust for Endangered Species, the British Chelonia Group, TrackTagConservation management, Endangered species, Population density, Marine vertebrate, Migratory species, Multiple paternity, Wildlife telemetry™, NERC Connect B Grant NERC/D/S/1999/00078 (award to C.M.B.), Swansea University and the NMPZ. We thank M. Baker, K. Gounelis, K. Katselidis, N. Margaris, G. Mitrouskas and M., J. and H. Sheldon for in-water capture assistance. We thank NMPZ and Archelon personnel for logger retrieval assistance: T. Lee, I. Palomares, V. Petta-Bika, D. E. Marcon, M. Barrett, P. Bradshaw, C. Dean, B. Gill, A. Hogg, D. Oakely, E. Ransome, B. van Divendyk, N. Walters and J. Zbinden. We acknowledge use of the Maptool program (www.seaturtle.org).

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Editorial responsibility: Jeffrey Seminoff,
La Jolla, California, USA

Submitted: May 9, 2008; Accepted: August 30, 2008
Proofs received from author(s): January 23, 2009

Journal of Animal Ecology
British Ecological Society

Journal of Animal Ecology 2009, **78**, 14–21 doi: 10.1111/j.1365-2656.2008.01454.x

Microhabitat selection by sea turtles in a dynamic thermal marine environment

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Summary

1. Reproductive fitness is often compromised at the margins of a species' range due to sub-optimal conditions.

2. Set against this backdrop, the Mediterranean's largest loggerhead sea turtle (*Caretta caretta*) rookery at Zakynthos (Greece) presents a conundrum, being at a very high latitude for this species, yet hosting a high concentration of nesting.

3. We used visual surveys combined with global positioning system (GPS) tracking to show that at the start of the breeding season, individuals showed microhabitat selection, with females residing in transient patches of warm water. As the sea warmed in the summer, this selection was no longer evident.

4. As loggerhead turtles are ectothermic, this early season warm-water selection presumably speeds up egg maturation rates before oviposition, thereby allowing more clutches to be incubated when sand conditions are optimal during the summer.

5. Active selection of warm waters may allow turtles to initiate nesting at an earlier date.

Key-words: climate change, distribution, ectotherm, micro-habitat, remote technology

Introduction

Habitat selection, and its impact on reproductive fitness, has long been one of the cornerstones of ecological research (e.g. Loe *et al*. 2006; Parra 2006). Moreover, recent concern over the implications of climate change has heightened interest in how patterns of habitat selection might change in the future (e.g. Braschler & Hill 2007). From the suite of possible environmental parameters, temperature often plays a key role in influencing habitat preferences over a range of spatial scales. For example, over the broad scale (e.g. across ocean basins), temperature may influence the distribution of species and their seasonal movements (McMahon & Hays 2006), while on smaller scales of metres or kilometres, temperature may drive the specific microhabitat selected by individuals. For example, features such as rocks or scrub are used to make adjustments in body temperature for terrestrial species (e.g. frogs, Hamer, Lane & Mahony 2003; baboons, Hill 2004; snakes, Shine *et al*. 2005). Similarly, some aquatic species have been shown to preferentially select sites near water outflows from power stations where the water is warmer (e.g. manatees, Laist 2005; sea turtles, Lyon *et al*. 2006; alligators, Murphy & Brisbin 1974). Thermal selection has also been demonstrated for freshwater turtles (e.g. Parmenter 1980).

We can liken this ecological problem of thermal selection to animals searching for patchily distributed prey, where individuals are constantly having to make decisions on where to reposition themselves to maximize resource acquisition. For animals searching for prey, the pattern of movement may be fundamentally impacted by whether animals have a good knowledge of what drives the prey distribution within their environment (Sims *et al*. 2005, 2006a). Likewise, when the resource of interest is temperature, rather than prey, we might predict different search patterns depending on the animal's knowledge of its environment as well as its physiological state and ecological needs.

The importance of thermal selection in a dynamic environment may be particularly acute at the limits of species distributions where environmental conditions may be at the margins of suitability, and hence, the implications of thermal habitat selection are greater. Such situations might, therefore, be ideal for testing the existence of fine-scale thermal selection in a dynamic thermal environment.

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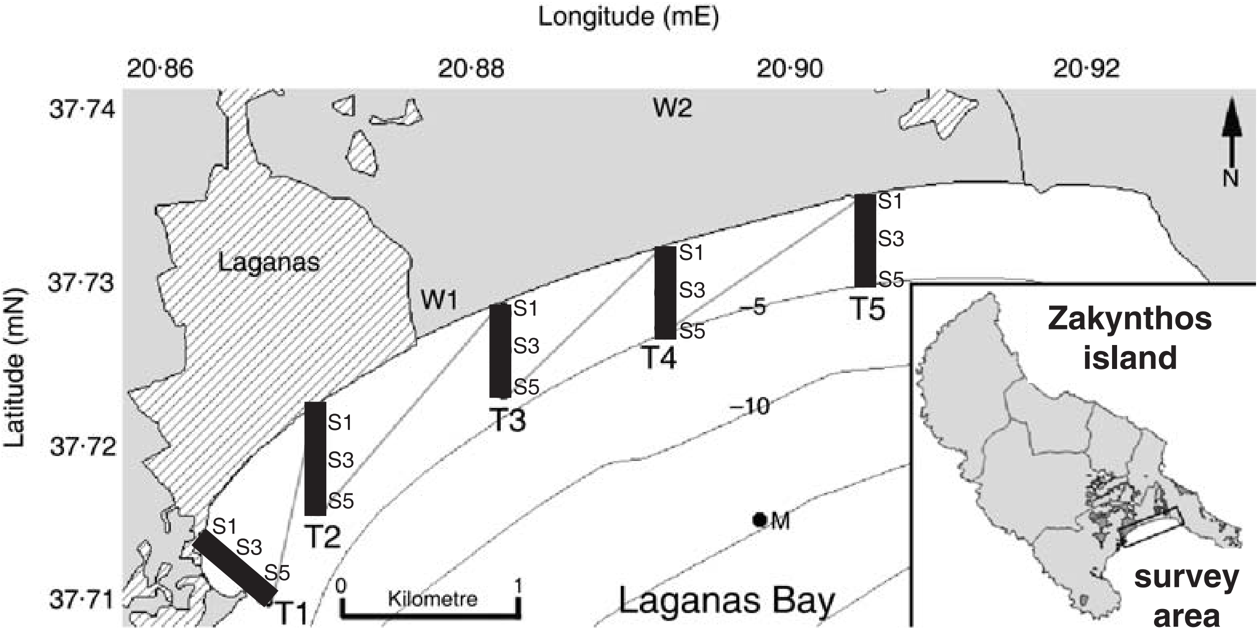

Fig. 1. The 5-km survey area in Laganas Bay, Zakynthos island, Greece. Hatched lines comprise areas of human development. T1–T5 are the transect lines denoting the 1-, 3- and 5-m sampling stations. W1 and W2 are the beachfront and airport weather stations respectively. Bathymetry lines are set at 5-m sea depth intervals (i.e. –5, –10 etc.). M is the compass midpoint of the survey area for circular statistical analysis.

Loggerhead sea turtles (*Caretta caretta*) are fairly widely distributed across subtropical and temperate latitudes (Dodd 1988). The rookery on Zakynthos island (Greece) in the semi-enclosed Laganas Bay is unusual in that it is relatively large (Margaritoulis 2005) despite being situated at the latitudinal margins of the species' breeding range. When turtles migrate to Zakynthos to mate in March–May, sea surface temperatures are generally cool (*c.* 13–22 °C) before increasing towards mid-summer. Therefore, the size of the breeding population at Zakynthos, despite these cold conditions, is a conundrum. It might be predicted that turtles display thermal selection to overcome cold conditions, although such thermal selection has not been demonstrated before in sea turtles. Certainly it is widely known that in lakes and semi-enclosed water bodies, the wind direction may cause warm near-surface water to accumulate at the down-wind end of the water mass (e.g. Barnes & Mann 1991). Hence, it is possible that there may be heterogeneous water temperatures at Zakynthos, offering the possibility of thermal selection by sea turtles at this site. Here we examine if sea turtles at this site show thermal selection and consider the possible benefits in terms of increasing egg maturation rates before oviposition, thereby allowing the seasons' first clutch to be laid earlier which may enhance reproductive fitness.

Material and methods

STUDY AREA

Fieldwork took place in Laganas Bay (37·7°N, 20·9°E) on the Greek island of Zakynthos. Ad-hoc surveys at sea using boats and snorkellers conducted between April and July in 2003, 2004 and 2005 indicated that female turtles tended to aggregate along a 5-km section of coast within the bay (Schofield *et al.* 2007), so we focused our effort on this area.

TRANSECT SURVEYS

Transect surveys were conducted to obtain information on (i) sea surface and seabed temperature, and (ii) sea turtle distribution across Laganas Bay. Five transect lines (T1–T5), each with three temperature stations at 1-, 3- and 5-m sea depths were delineated along a pre-selected 5-km section of near-shore water (Fig. 1). We used a 4-m boat with an outboard engine, with travel speeds of four knots between stations. Each transect line was 0·75 km in length, at a minimum distance of 1 km from adjacent station start points, set on a north–south line, except for the first transect which was set on a northeast–southeast line (due to land form characteristics). The global positioning system (GPS) location of each transect station was recorded using GARMIN eTrex-legend (Olathe, KS, USA). Between 9 May and 13 July 2006, 34 morning and afternoon line transects were conducted, each spanning a 2-h period. Forty-five per cent of transects were conducted between 09·00 and 11·00 h and 55% of transects were conducted between 15·00 and 17·00 h. Seventy-five per cent of transects were conducted in a west–east order, while 25% were conducted in an east–west order to allow for time-dependent variations in temperature/turtle records. At each temperature station, the sea surface and seabed temperatures were recorded for a 3-min interval using Tinytag TGP-4204 (Gemini Data Loggers, Chichester, West Sussex, UK) external probe (rapid response) and TGP-4017 (Gemini Data Loggers, Chichester, West Sussex, UK) internal probe (slower response) loggers respectively. Between stations, the loggers were placed in a bucket of seawater to reduce the time required to adjust to ambient water temperature. Validation experiments showed both types of instrument consistently recorded the temperature to within 0·01 °C of one another. The 3-min measurement period was selected on the basis of the thermal response time of the TGP-4017 logger, that is, after this time there was no change in the measured temperature.

All turtle sightings, whether at the surface or submerged and within 20 m of the boat, were recorded by two observers (i) at each temperature station, (ii) between temperature stations, (iii) on the outgoing (east–west transect order) or return (west–east transect order) journey from port. On sighting a turtle, the time, sea depth, turtle depth and turtle behaviour were recorded. All surveys were conducted in a good sea state, to reduce the impact of conditions on sighting probability.

ENVIRONMENTAL DATA

Weather data were recorded in three independent ways to try and remove any impact of very local weather conditions on land impacting our interpretation of the weather in Laganas Bay. (i) Wind direction, cloud cover and sea state were recorded approximately at the start and end of each survey by direct observation, (ii) a WS-2300 weather station (La Crosse Technology Ltd, La Crosse , WI, USA) positioned 100 m in land (Fig. 1) was set to record a range of parameters (including air temperature, wind direction and speed) at 30-min intervals (and downloaded bi-weekly onto computer) between 8 May and 31 July 2006, and (iii) hourly data sets were provided by the Zakynthos Airport weather station located 1 km inland from Laganas Bay (Fig. 1) for the period of 1 May to 31 July 2006. Where readings from the WS-2300 and airport weather stations were in agreement, we took the mean of these observations. When they differed appreciably (e.g. due to local topography influencing wind direction), then the weather station record was selected which showed a wind direction that most closely matched that observed visually during the surveys at sea.

ANIMAL-BORNE LOGGERS

Navsys Ltd. TrackTag^{TM} GPS loggers (Colorado Springs, CO, USA; http://www.navsys.com) were attached to three female loggerhead sea turtles for a total of 73 complete days (17, 31 and 25 days respectively) between 20 May and 23 June 2006. In addition, we used time-depth recorders (TDRs) that recorded ambient temperature and depth; LOTEK LTD_1100 model TDRs (LOTEK Marine Technologies, St. John's, NF, Canada). These were attached to the three females fitted with GPS loggers plus three others for a total of 140 days (17, 31, 25 and 31, 12, 21 days respectively) between 16 May and 27 June. For GPS and TDR system parameters and attachment-retrieval methodology, see Schofield *et al.* (2007).

Validation trials were conducted to confirm the equivalence of temperature readings made by the different temperature devices. In a controlled experiment, we compared the sea temperature readings of the Tinytag TGP-4204 external probe ($n = 1$), Tinytag TGP-4017 internal probe ($n = 1$) and Lotek TDRs ($n = 6$) used during the research. All equipment readings were simultaneously taken for 10 min at 30-s intervals at the surface, 1-, 3-, 5- and 7-m sea depths. We found that the two Tinytag loggers consistently recorded temperature to within 0·01 °C of one another at the sea surface (the external probe was not used at lower depths). The TDRs recorded temperature on average 0·09 °C lower than the Tinytag TGP-4017 internal probes (range –0·01 to –0·16, SD ± 0·04). These small differences were corrected in the data analysis.

WATER TEMPERATURE FURTHER FROM THE SHORE

We were unable to conduct our own surveys of water temperature far from the shore for logistic reasons. Therefore, we used the *in-situ* temperature readings made by equipped turtles to assess water temperature further from the shore, since water depth increased in the middle of the bay (Fig. 1).

TURTLE DISTRIBUTION ANALYSES

We investigated whether turtle distribution, recorded both on transect surveys and with GPS tracked turtles, was linked to wind direction. For the surveys in Laganas Bay, we calculated the mean turtle position on transects by assessing their angular distribution around the bay from a central reference point and then applying circular statistics (Fig. 1, ORIANA version 2·00).

To obtain an objective measure of area use for GPS tracked turtles, we initially filtered the GPS fixes (average of 51 fixes turtle^{-1} day^{-1}) by selecting the central location for each hour for each turtle (Tremblay *et al.* 2006). Subsequently, we calculated the daily mean GPS derived position for each tracked turtle. All GPS locations occurring outside of the Laganas Bay area were removed. All GPS locations in the 3 days before egg laying were removed, as existing literature indicates a pattern of increasing activity as a nesing event approaches (Hays *et al.* 1991; Hays *et al.* 1999) that may be driven by active nesting beach selection rather than immediate environmental parameters.

TURTLE TEMPERATURE ANALYSES

We investigated if individual turtles fitted with TDRs ($n = 6$) experienced warmer water than expected by chance. To do this, we examined the water temperatures measured on transects in Laganas Bay. For each survey (either morning or afternoon), we determined the mean and maximum water temperature measured by the Tinytag temperature devices. During the same sampling period at which each survey was conducted, we determined the mean temperature measured by the TDRs attached to individual turtles.

Results

WIND DIRECTION VERSUS SEA TEMPERATURE

Within the 5-km transect area, there was variability in the sea temperature between different transects, and we found that this variability was strongly correlated with wind direction. For example, when the wind blew from the south-east, the warmest water was found in the north-west part of the bay. Overall, the mean wind direction explained 55% of the variation in the location of the warmest sea temperature recorded on each transect survey ($F_{1,30} = 36·3$, $r^2 = 0·55$, $P < 0·001$) (Fig. 2a). This wind–temperature relationship was even stronger during afternoon surveys ($F_{1,16} = 47·7$, $r^2 = 0·75$, $P < 0·001$) (Fig. 2b).

TURTLE DISTRIBUTION

A total of 351 turtle sightings were made during 34 surveys in the 5-km study area. On average, 10 individuals were sighted per survey (range 0–38 sightings survey^{-1}). There was strong link between turtle distribution and wind direction. For example, Fig. 3 shows the distribution of turtles on 2 days of contrasting wind direction and shows how when the wind blew from the east, turtles were concentrated in the western

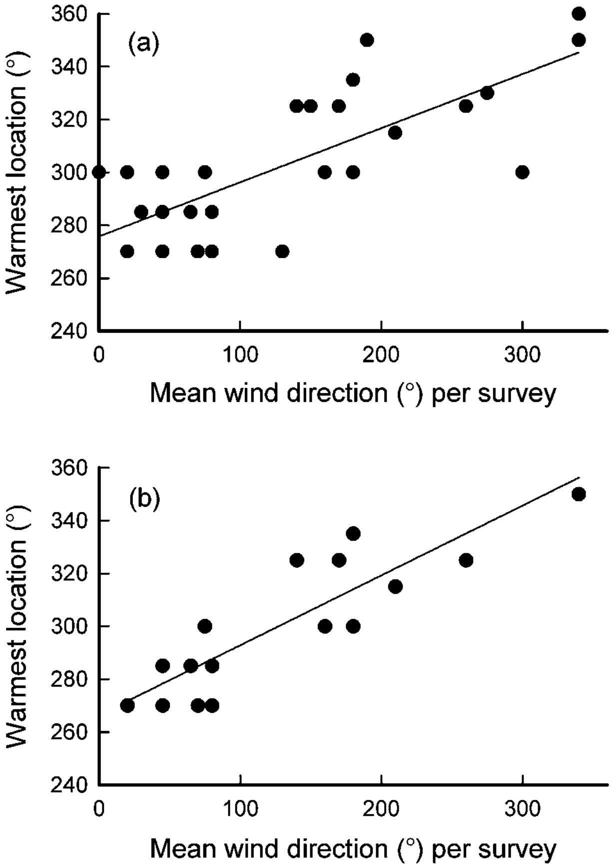

Fig. 2. The relationships between mean wind direction per survey and warmest sea temperature location recorded on transects in the localized 5-km survey area; (a) all records ($F_{1,30} = 36{\cdot}3$, $r^2 = 0{\cdot}55$, $P < 0{\cdot}001$) (b) afternoon records ($F_{1,16} = 47{\cdot}7$, $r^2 = 0{\cdot}75$, $P < 0{\cdot}001$).

part of the bay, while when the wind blew from the south the turtles were seen in the northern part of the bay.

This relationship between wind direction and turtle distribution was always significant but improved when we selected those surveys where more turtles were sighted, presumably because of the inability to accurately assess turtle distribution when few turtles were seen, that is, when the number of turtles sighted increased, the relationship became tighter albeit there were fewer sampling dates that could then be included in the analysis. For example, selecting surveys where there were > eight turtle sightings ($n = 21$ surveys) showed that 73% of the variation in mean turtle distribution could be explained by wind direction ($F_{1,16} = 43{\cdot}6$, $r^2 = 0{\cdot}73$, $P < 0{\cdot}001$) (Fig. 4a).

This strong correlation between wind direction and turtle location was supported by the data obtained from the three turtles tracked using GPS. For these GPS-tracked turtles, 65% of the variation in their daily mean position in the bay was explained by wind direction ($F_{1,57} = 106$, $r^2 = 0{\cdot}65$, $P < 0{\cdot}001$) (Fig. 4b,c).

When both mean wind direction and angular position of the warmest water in the bay each day were entered into a stepwise multiple regression (using MINITAB version 8·2) against mean daily turtle location (both with the transect data set and the GPS tracking data set), only wind direction entered the subsequent equation, that is wind direction seemed to have a stronger impact on turtle location than the location of the warmest water.

However, analysis of individual GPS tracks showed that turtles were not simply always located directly downwind, but rather they made movements parallel to the shore moving across the wind direction (Fig. 5). This suggests that the turtles were not simply passively advected but rather actively controlled their position.

SEA TEMPERATURE AND TURTLE DISTRIBUTION

In total, we obtained 93 instances of TDR records where there was an accompanying temperature survey along the near-shore transects. The mean TDR temperature was significantly warmer than the near-shore temperature (mean difference +1·70 °C, $t = 17{\cdot}33$, $P < 0{\cdot}001$) (Fig. 6). Furthermore, the mean TDR temperature was also warmer than the maximum near-shore temperature measured at the same time along the transects (mean difference +0·25 °C, $t = 3{\cdot}2$, $P = 0{\cdot}002$). The elevation of the TDR temperatures above mean near-shore temperatures was significantly higher during afternoon surveys (mean difference +1·97 °C, $n = 56$) than during morning surveys (mean difference +1·28 °C, $n = 37$) ($t_{90} = 4{\cdot}0$, $P = 0{\cdot}0001$). Furthermore, the elevation of TDR temperatures above mean near-shore temperatures tended to decline as the season progressed ($F_{1,54} = 23{\cdot}8$, $r^2 = 0{\cdot}31$, $P < 0{\cdot}0001$) and ambient water temperatures approached 26 °C (Fig. 7). This suggests that turtle response to environmental

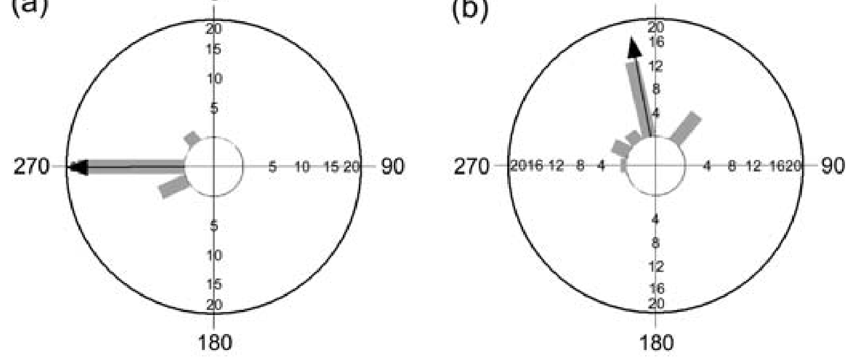

Fig. 3. Turtle distribution on days with different wind direction; (a) turtle distribution during a survey with north-east wind conditions with aggregations forming at transect 1 and (b) turtle distribution during a survey with south south-east wind conditions with aggregations forming between transects 3 and 4. Shaded bars show number of turtles recorded along each transect. Arrow on each plot indicates mean turtle location.

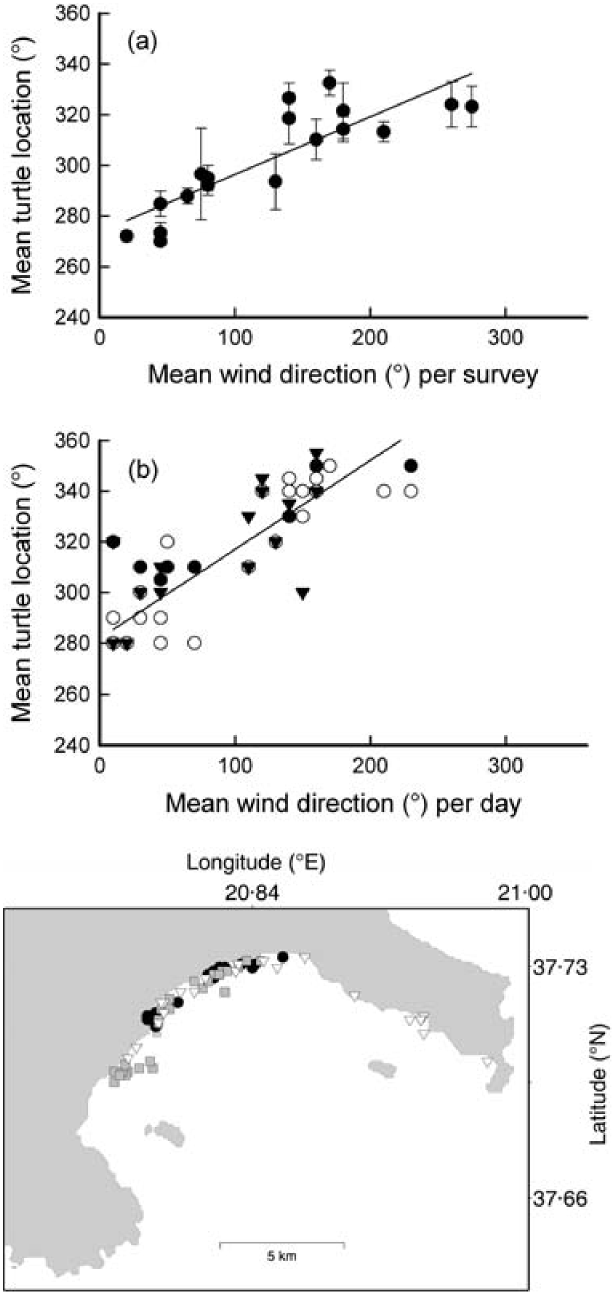

Fig. 4. The relationships between the mean turtle location and mean wind direction for (a) surveys recording > eight turtle sightings in the 5-km study area ($F_{1,16} = 43{\cdot}6$, $r^2 = 0{\cdot}73$, $P < 0{\cdot}001$) with standard deviation bars and (b) mean derived GPS position per day of tracked turtles within Laganas Bay ($F_{1,57} = 106$, $r^2 = 0{\cdot}65$, $P < 0{\cdot}001$); GPS1 black circles, GPS2 open circles, GPS3 triangles. In (c) the hourly GPS locations of the three tracked turtles are shown; GPS1 circles, GPS2 squares and GPS3 triangles.

conditions lessened as the season progressed and sea temperature increased.

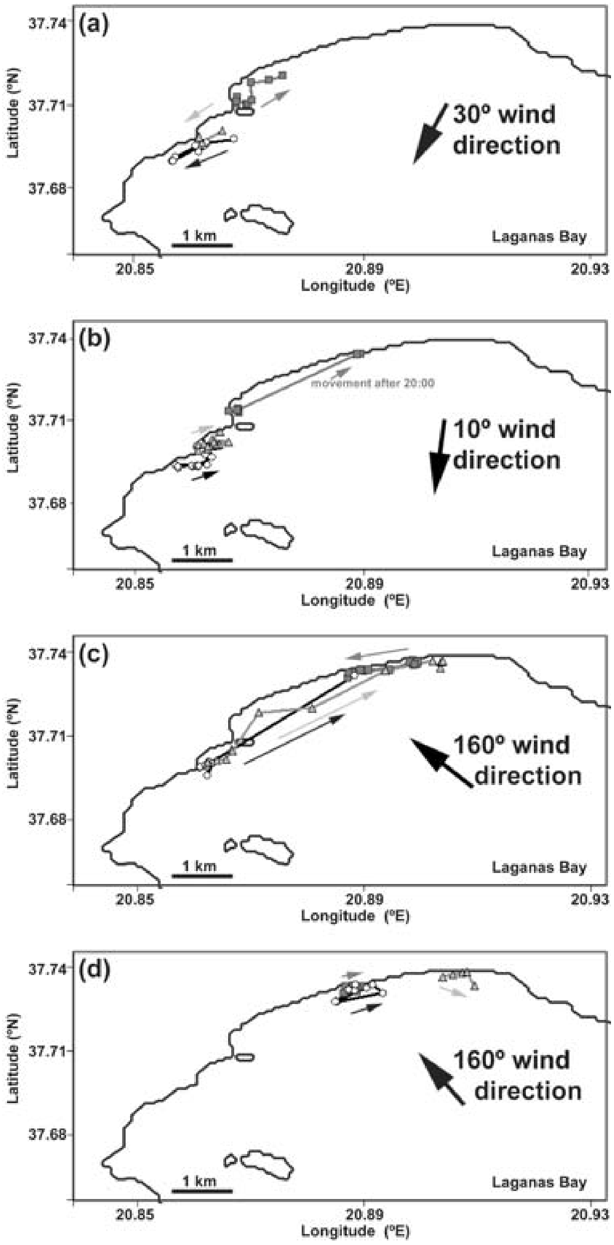

Fig. 5. Movement of three turtle equipped with GPS loggers between 26 May 2006 and 29 May 2006. Each panel shows the movement of each turtle on 1 day and the mean wind direction measured using two independent weather stations (see methodology). The panels show how when the wind blew from the north-east on 26 May (panel a), the turtle aggregated further to the south-west of the bay, but note they were not located directly downwind indicating they were not simply passively advected but rather actively controlled their position. Between 27 May (panel b) and 28 May (panel c), the wind turned around to blow from the south-east and all three turtles moved to the north-east part of the bay. But note again that they did not simply aggregate directly downwind indicating that they were not simply passively advected but rather actively controlled their position.

WATER TEMPERATURE FURTHER FROM THE SHORE

Turtles very rarely dived deep, with < 0·5% of their total time spent deeper than 6 m. However, for three of the six equipped turtles, we recorded a total of five dives to deeper than 10 m during May. We compared the temperature at depth versus the temperature experienced shallower than 5 m in the 30 mins before and after these deep dives. Water temperature

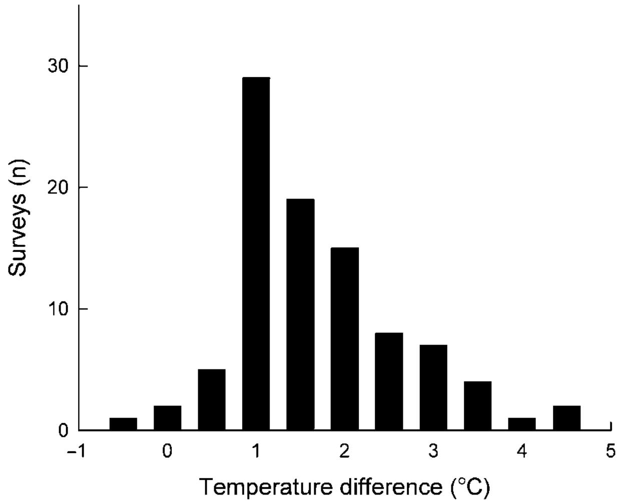

Fig. 6. The differences recorded between the temperature experienced by tagged turtles (measured with a TDR) and the mean near-shore water temperature measured during each boat survey. Positive values indicate that the temperature experienced by a turtle was warmer than the mean near-shore water temperature.

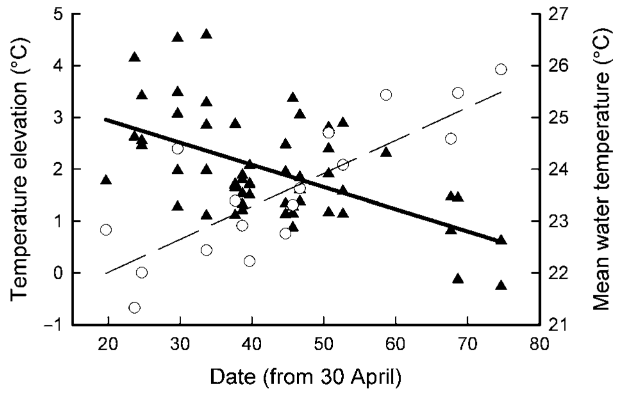

Fig. 7. The elevation of temperatures (left axis, triangles) experienced by tagged turtles (measured with a TDR) above the mean near-shore water temperature during afternoon surveys versus the date. As the season progressed, this temperature elevation declined: temperature elevation (°C) = 3·8–0·0428 date (days since 30 April) ($F_{1,54}$ = 23·8, r^2 = 0·31, P < 0·0001). Also shown (right axis, circles) is the mean survey area temperature, showing the seasonal warming of the water.

measured when turtles were deeper than 10 m (i.e. > 1 km from the shore) was, on average, 2·34 °C less than water temperature when they were shallower than 5 m.

THE POTENTIAL ENERGETIC BENEFITS OF ADOPTING THERMAL SELECTION

We used empirical data on the relationship between inter-nesting intervals and water temperature to estimate the potential reduction in time to laying the first clutch caused by early season thermal selection by loggerhead turtles. In a comparative study across different nesting populations (Hays *et al.* 2002) it was shown that: log (internesting interval in days) = 2·25–0·043 temperature (°C). At water temperatures of 22, 25, and 27 °C, the typical intervals between successive clutches are 20·1, 15·0 and 12·3 days. So at the start of the season when mean water temperatures are around 22 °C (or less in deeper water), if turtles select water that is 5 °C warmer than average, they might be expected to reduce their time to laying their first clutch by almost 8 days, and by 5 days if they select water 3 °C warmer than average.

Discussion

Data loggers and transmitters are starting to transform our understanding of patterns of habitat utilization for hard-to-study species. For example, acoustic tracking of dogfish has shown how individuals tend to rest in deeper cooler water and hunt in warmer shallower water to maximize their net energy gain (Sims *et al.* 2006b). Miniature dive loggers attached to American mink have revealed contrasting patterns of behaviour between individuals, with some being more terrestrial versus others that are more aquatic (Hays *et al.* 2007). Similarly, high-resolution tracking with GPS loggers is allowing the detailed pattern movement for a range of terrestrial and aerial species to be determined (Hamer *et al.* 2007; Wegge, Finne & Rolstad 2007), whereas technical constraints have, to date, largely limited the use of GPS tracking for species that spend most of their time submerged. We showed that the pattern of movement exhibited by GPS tracked turtles reflected the distribution of individuals revealed in boat surveys and that both of these patterns of distribution covaried with wind direction. As has been widely reported in lakes (Barnes & Mann 1991), we found that wind direction influenced the location of warm water patches close to the shoreline. Furthermore, this link was tighter in the afternoon, presumably when the water had been subject to solar heating during the earlier part of the day (Hattori & Warburton 2003; Pulgar, Bozinovic & Ojeda 2005). The location of warm water patches provided the potential for thermal selection by loggerhead turtles and the consequence was that they experienced warmer water than if they were randomly distributed in the near-shore waters. Furthermore, while our information on the water temperature at greater depths within the bay was limited, the records from turtles equipped with temperature loggers suggested that the temperatures at depth further from shore were over 2 °C cooler than the shallower temperatures, that is, the actual water temperatures experienced by turtles at the end of May were probably around 5 °C above those they would have experienced if they rested at > 10 m, which is the typical resting depth of turtles in tropical nesting sites (Hays, Metcalfe & Walne 2004). While the important role of temperature in driving habitat selection is well established for a broad range of species, including a number of freshwater turtles (e.g. Tamplin 2006), the novelty of our study is that we have shown how selection occurs even in a very dynamic thermal environment.

Several lines of evidence suggest that turtle repositioning is unlikely to be the result of passive drift. First, adult turtles are strong swimmers and therefore dictate their own position in the breeding season, even if currents or winds are strong. For example, at Ascension Island, breeding female green turtles position themselves around the 20-m isobath despite locally strong winds and currents (Hays *et al.* 1999). Second, loggerhead turtles spend most of the time submerged, either in water or resting on the bottom (Houghton *et al.* 2002), so they are unlikely to be strongly impacted by winds. Third, the thermal selection by the turtles seemed to change as the breeding season progresses, with the biggest elevation above mean bay temperature, that is, the strongest thermal selection, seeming to occur at the start of the season when water temperatures were coolest. Regardless of the exact mechanism at work, it was clear that the turtles repositioned themselves with respect to wind direction and this has not been reported at a breeding site previously. This finding poses two distinct types of question: what are the benefits of thermal selection by loggerhead turtles at this site and how is the thermal selection actually achieved?

Due to their large size, and resulting thermal inertia, adult loggerhead turtles may have a core temperature a few °C above ambient, although their body temperature is still largely driven by the ambient water temperature (Spotila, O'Connor & Paladino 1997). In general, Q_{10} values (the metabolic rate at $T + 10$ °C divided by the metabolic rate at T °C) for loggerhead turtles are around 2·4 to 5·4 (Hochscheid, Bentivegna & Speakman 2004). So loggerhead turtles in warmer water will have increased metabolic rates and hence their production of clutches would be expected to be quicker, albeit that the instantaneous rate at which energy reserves are used will be faster. We used the empirical relationship between internesting intervals and water temperature to estimate that by selecting warm water, time to laying the first clutch might be reduced by as much as 5 days. Greece is near the latitudinal limit for loggerhead turtles and there is a marked seasonal variation in air temperature. The consequence of this variation is that there is a fairly tight window of optimal sand temperatures for egg development limited to between June and September (Margaritoulis 2005). In more tropical nesting areas, this window of optimal conditions is much broader (Godley *et al.* 2002), and hence, it is a female's energy reserves rather that the length of the available nesting season that constrains her reproductive output. Typical incubation durations for sea turtle eggs are around 50–60 days (Margaritoulis 2005). Hence, clutches laid late in the season, (e.g. August) are at risk of being unable to complete development within the window of optimal conditions. By laying their first clutch of eggs as soon as possible in May, loggerhead turtles will thereby maximize the number of clutches they can lay within a season that experience optimum development temperatures even close to hatching. Furthermore, reducing the time required to lay the first clutch will mean that turtles are able to minimize the time that they spend away from their foraging grounds.

It is well known that in many species, reproduction is timed seasonally to maximize offspring survival. For example, many species of mesozooplankton in temperate waters time egg production so that developing larvae are in the water when their phytoplankton prey is maximally abundant during the spring bloom (Irigoien *et al.* 1998). Similar examples exist in other environments. For example, for birds migrating to high-latitude breeding sites, the chicks need to fledge and be ready for the return migration before local conditions or migration conditions deteriorate too much (Cooke, Findlay & Rockwell 1984). Again, this situation may favour an early seasonal start for reproduction. The early season thermal selection shown by loggerhead turtles in Greece therefore seems to form part of a general strategy of animals to time their reproduction to those times when offspring survival is maximized.

Although we have demonstrated that turtles experience warmer water than expected by chance early in the breeding season in Greece, we have not established how this thermal selection is attained. The search strategies employed by animals is a hotly debated topic, particularly with reference to finding patches of prey (Edwards *et al.* 2007; Sims, Righton & Pitchford 2007). These same considerations apply equally to loggerhead turtles finding patches of warm water. Turtles might be able to perceive wind direction and use this as a cue to locate patches of warm water. In this case, experience would play a role in their ability to locate warm water patches. Alternatively, it might be that there is a component of more random search by turtles along the shore to find warm water patches. Tracking individuals in combination with simultaneous mapping of the thermal environment and wind direction might be used to disentangle these possibilities. Furthermore, various quantitative movement models (e.g. Sims *et al.* 2000; Bailey & Thompson 2006), primarily developed for objectively examining tracking data to infer where animals forage, might be usefully employed to examine tracking data to establish the search rule used by turtles to find warm water. In addition, biophysical models that integrate metabolic rate, body temperature, water temperature, and dive behaviour may shed further light on the benefits of thermal selection by sea turtles.

In summary, we have shown how an endangered ectotherm, the loggerhead sea turtle, near the limits of its breeding range, repositions itself daily to take advantage of thermal hotspots within a highly dynamic thermal environment. How turtles achieve this selection is not known, but it most probably contributes to the success of this species near its cold water range limits.

Acknowledgements

We thank the National Marine Park of Zakynthos (NMPZ) and Greek Ministry of Agriculture for permission to conduct this research. Support for TrackTag GPS data loggers was provided by a grant from NERC awarded to CMB. G. MacLean, P. Brown, D.A. Davies and A. Jones for constructing and donating the TrackTag GPS loggers and enclosures. V. Hobson, A. Kolokotsas and D.G. Schofield for logistical assistance. NMPZ for boats and drivers for fieldwork, including K. Gounelis and M. Baker. F. Nikoloudakis of Divers Paradise Centre. K. Kollias for equipment assistance. NMPZ and Archelon volunteers, including S. Botos, C. Dean, D. Oakley, B. Gill, P. Bradshaw, E. Ransome, M. Barrett and many others for field and transmitter retrieval assistance. We acknowledge the use of Maptool (a product of SEATURTLE.ORG, http://www.seaturtle.org) in the creation of certain graphics.

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Received 7 November 2007; accepted 25 June 2008
Handling Editor: David Sims

ΠΑΡΑΤΗΜΑ / APPENDIX 4: CONFERENCE PRESENTATIONS

Κεφάλαιο / Chapter 1

Schofield, G., K. Katselidis, & J. Pantis. 2008. Assessment of photo-identification and GIS as a technique to collect in-water information about loggerhead sea turtles in Laganas Bay, Zakynthos Greece (poster presentation). Proceedings of the Twenty-fourth Annual Symposium on Sea Turtle Biology & Conservation U.S. Dept. Commerce. NOAA Tech. Memo. NMFS-SEFSC. Pp152-153

Κεφάλαιο / Chapter 2

Schofield, G., K.A. Katselidis, J.D. Pantis, P. Dimopoulos & G.C. Hays. 2006. Preliminary documentation of loggerhead solitary and social behaviour in the maritime breeding area of Laganas Bay, Zakynthos, Greece (poster & DVD presentation). Twenty-Sixth International Symposium on Sea Turtle Biology and Conservation. Pp110-112

Κεφάλαιο / Chapter 3

Schofield, G., K.A. Katselidis, J.D. Pantis, P. Dimopoulos & G.C. Hays. 2007. Female-female aggression in loggerhead sea turtles: structure of interaction and outcome. (Poster presentation) Twenty-Seventh International Symposium on Sea Turtle Biology and Conservation. Myrtle Beach, South Carolina. Pp59

Κεφάλαιο / Chapter 4

Schofield, G., C.M. Bishop, G. MacLean, P. Brown, M. Baker, K.A. Katselidis, P. Dimopoulos, J.D. Pantis, G.C. Hays. 2007. GPS tracking for fine-scale conservation management: following sea turtles within a marine protected area. (Poster presentation). Presented at the Twenty-Eighth International Symposium on Sea Turtle Biology and Conservation. Loreto, Baja California Sur, Mexico**.** Pp59

Κεφάλαιο / Chapter 6

***Schofield, G**., C.M. Bishop, K.A. Katselidis, P. Dimopoulos, J.D. Pantis, G.C. Hays .No time to chill out: GPS tracking reveals micro-habitat selection by breeding loggerhead turtles. Full oral presentation (12 minute) at the Twenty-Ninth International Symposium on Sea Turtle Biology and Conservation. Brisbane, Australia, February 2009*

NOAA Technical Memorandum NMFS-SEFSC-567

PROCEEDINGS
OF THE TWENTY-FOURTH
ANNUAL SYMPOSIUM ON SEA TURTLE
BIOLOGY AND CONSERVATION

22 to 29 February 2004
San Jose, Costa Rica

Compiled by:
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U.S. DEPARTMENT OF COMMERCE
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January 2008

Assessment of photo-identification and GIS as a technique to collect in-water information about loggerhead sea turtles in Laganas Bay, Zakynthos, Greece

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Laganas Bay, on the island of Zakynthos, is a protected area with one of the densest nesting rookeries for loggerheads in the Mediterranean. Nesting females have been studied extensively on these beaches, but little information is available about population dynamics. Until 2003, sea based studies of sea turtles were not attempted due to National Marine Park of Zakynthos (NMPZ) policy to minimize harassment of sea turtles. In 2003, the NMPZ conducted a non-invasive in-water survey gathering preliminary information about the sea turtle population. The natural marking technique of photo-identification was used in combination with a global positioning system (GPS) to identify individual turtles and record sighting locations during daily surveys. In one month, multiple identifications of 161 sea turtle individuals were acquired from 460 sight-mark-resight records. About one-third of all reproductive females in the 2003 nesting season were identified. The findings of this study are used in this presentation to assess:

- The importance of selecting reliable physical features for photo-identification for repeated recognition in a long-term database.
- The uses of photo-identification to investigate population size, sex ratio, reproductive activity, return rates and residency.
- The potential of photo-identification combined with geographic information system (GIS) technology to identify trends in turtle distribution with biological, environmental and geographical parameters.
- The behavior response of the turtles to photo-identification oriented research activity.

In conclusion, this presentation will consider the potential future applications of photo-identification as a technique to study sea turtle populations on a national and international scale.

The threats on sea turtles in Togo

Gabriel H. Segniagbeto[1], E. J. Bowessidjaou [2], J. Fretey [3], H. Segniagbeto [2], F. K. Akpamou[4], and A. Formia [5]

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Togo is a coastal country situated in the Gulf of Guinea whose sandy beaches represent potential sea turtle nesting sites. Four species of sea turtles have been identified along the Togolese coast: the green turtle (*Chelonia mydas*), the hawksbill (*Eretmochelys imbricata*), the olive ridley (*Lepidochelys olivacea*) and the leatherback (*Dermochelys coriacea*). The females of *C. mydas*,

26th Annual Symposium on Sea Turtle Biology and Conservation

Island of Crete, Greece, 3-8 April 2006

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second approach to evaluate the association of sea turtles with seamounts employed satellite telemetry. The results support the hypothesis that distribution patterns of loggerheads are related to local topographic characteristics and that seamounts appear to be important habitats for juvenile oceanic loggerhead sea turtles.

Acknowledgements: MS gratefully acknowledges travel support from UNEP's RAC/SPA (Regional Activity Centre for Specially Protected Areas) and other donors through the Symposium Travel Committee.

Order: 99 **Abstract ID:** 1541 **Type:** Poster **Subject:** Behavior and Movements

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MOVEMENT AND BEHAVIOR OF FLORIDA NESTING LEATHERBACKS

Christopher R. Sasso[1], Chris Johnson[2], Kelly Stewart[3], and Sheryan P. Epperly[1]

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Two archival satellite tags were deployed in May 2005 on leatherback turtles nesting on Juno Beach, Florida. One tag was deployed for the programmed 90 days, and one was recovered on a beach 20 km away 9 days after deployment with the tether cut. Data on movement and dive behavior during the inter-nesting and post-nesting periods are presented.

Order: 100 **Abstract ID:** 1725 **Type:** Poster **Subject:** Behavior and Movements

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PRELIMINARY DOCUMENTATION OF LOGGERHEAD SOLITARY AND SOCIAL BEHAVIOUR IN THE MARITIME BREEDING AREA OF LAGANAS BAY, ZAKYNTHOS, GREECE

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Knowledge about animal behaviour is essential to determine how individuals may prolong survival and/or maximise reproductive fitness by the differential partitioning of energy stores to meet the metabolic demands of reproduction, body maintenance, locomotion, and food-processing (Hays,2000). Information describing loggerhead sea turtle behaviour in marine breeding areas (courtship and inter-nesting) remains rudimentary, with recent studies deducing behaviour from data collected by aerial surveys, data-loggers, tracking-devices and genetics studies. Laganas Bay, on Zakynthos Island, is one of the most important breeding rookeries for endangered loggerhead sea turtles in the Mediterranean (Margaritoulis, 2005). The National Marine Park of Zakynthos was established to protect all habitats utilised by this population during the breeding period. Therefore, the NMPZ developed a sea-based research programme, complementing an ongoing ARCHELON nesting-beach project, to investigate loggerhead population dynamics and behaviour ecology in the protected maritime area. Due to NMPZ policy to minimise harassment of sea turtles and because Zakynthos attracts over five-hundred thousand visitors each summer, traditional invasive 'mark-recapture' methods were avoided. Instead, the low-stress and promising data-rich technique of photo-identification was selected, whereby individual turtles are recognised based on natural facial-markings. Information about environmental conditions, turtle location (GPS), biology and behaviour was also collected. Surveys were performed

at Laganas Bay across three years, during both the courtship (April-May) and inter-nesting (June-July) periods. 1658 behavioural observations were compiled across 287 hours of day-time surveys. In total, 149 observations of 45 unique males and 1509 observations of 402 unique females were made, this bias partly reflecting females being found closer to shore where surveys were concentrated. A total of twelve behavioural states were recorded, comprising of seven solitary and five social behaviours. Solitary behaviour includes resting (18%male, 46%female), surface-basking (3%male, 15%female), swimming including patrolling males (30%males, 27%females), foraging (3%males, 0.3%females), self-cleaning (0.4%females), symbiotic fish cleaning (1%females). Social associations include female-female defence (8%females), male-male conflicts (7%males), courtship (23%males, 2%females), copulation (13%males, 1.5%females) and copulatory male attendants (3%). Chi-squared statistical analysis indicated a highly significant difference between the diurnal solitary and social behavioural states for male and female loggerheads ($P<0.001$), with males being four times more likely to be encountered in a social situation. When solitary, males performed significantly more active behaviours than females ($P<0.001$). Animal behaviour carries energy costs, hence activities that maximise reproductive fitness should be selected (Hays, 2000). Female turtles should therefore primarily invest in inactive behaviours to channel energy reserves towards increasing the rate of egg gestation. In contrast, males should expend energy through active mate search and acquisition techniques, to increase their chances of copulating with more females. Our findings support these basic assumptions however more research is required to improve our knowledge about sea turtle strategies and implications to reproductive fitness, by obtaining complete activity energy budgets and documenting changes in behavioural state across the breeding period.

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Order: 101 **Abstract ID:** 1387 **Type:** Oral **Subject:** Behavior and Movements

MOVEMENTS OF IMMATURE AND POST-NESTING KEMP'S RIDLEY SEA TURTLES IN THE NORTHWESTERN GULF OF MEXICO

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The Kemp's ridley sea turtle, *Lepidochelys kempii*, is exhibiting a modest recovery from devastating declines that reduced its nesting activity from a single-day estimate of 40,000 in 1947 to 702 nests during all of 1985. Increased ridley nesting at Rancho Nuevo, Mexico has been complemented by commencement and growth of nesting on the Texas (USA) coast. This activity has grown from 1−2 nests annually prior to 1995 to a record 51 in 2005 (D. Shaver, pers. comm.), with most of these occurring on the lower Texas coast. Five nests laid on the upper Texas coast in 2004 and eight in 2005 suggest a northern expansion of the nesting range and increased survival among immature and adult conspecifics. Although beach monitoring is crucial to estimating nesting population size and activity, at-sea data are essential for evaluating management strategies and understanding in-water dynamics of all life history stages. The Kemp's Ridley Recovery Plan lists determining "seasonal use of nearshore habitat by juveniles/subadults" and determining "migratory paths and foraging areas" as necessary components of a strategy to achieve this species' recovery, but such data are currently sparse. Eight Kemp's ridleys were outfitted with satellite transmitters and

NOAA Technical Memorandum NMFS-SEFSC-569

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April 2008

(1%), Virginia (2%), North Carolina (7%), South Carolina (3%), Georgia (2%), and Florida (78%). Species specific and size specific movements were also examined in this study.

FEMALE-FEMALE AGGRESSION IN LOGGERHEAD SEA TURTLES: STRUCTURE OF INTERACTION AND OUTCOME

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Aggressive behaviour between females of the same species is not widely documented, particularly in marine vertebrates. Between 2003 and 2006, in-water surveys were conducted to collect information about loggerhead sea turtle (*Caretta caretta*) marine ecology at the temperate breeding area of Zakynthos in Greece. Between April and July, along a 5.5 km stretch of nearshore area, 92% (n = 1333) of sighting events were of solitary females, 4% (n = 60) were of male-female interactions and 4% (n = 60) comprised female-female interactions. The structure of female-female loggerhead sea turtle interactions was analysed for 58 sighting events, each lasting an average of 3.4 minutes (SD ± 1), comprising a total of 3.1 hours observation time. We found that female interactions involved ritualized escalation in behaviour from passive displays (e.g. head-tail circling) to aggressive combat (e.g. sparring). We suggest that circling individuals evaluate opponent size, sparring individuals test opponent strength, and the positioning of the prehensile tail signals motivational intent to either escalate or abort. The presence of intruder females triggered basking and swimming turtles to respond in 100% of events (n = 19), whereas, while residents resting on the seabed responded on 69% occasions (n = 27), they were almost four times more likely to escalate to aggression. While contests were usually initiated when the intruder entered the visual range of the resident, in 12% of instances contests were initiated by tactile advances (nuzzling or biting of carapace) from the intruder. Our results suggest that certain sites may be preferentially sought after and defended by female loggerhead sea turtles.

MIGRATORY ROUTES AND RESIDENT AREAS OF ADULT FEMALE AND MALE FLORIDA GREEN TURTLES

Barbara Schroeder[1], Llewellyn Ehrhart[2], Dean Bagley[2], Michael Coyne[3], Allen Foley[4], George Balazs[5], and Blair Witherington[6]
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Green turtles, *Chelonia mydas*, are the second most abundant sea turtle in Florida waters - juveniles and adults inhabit nearshore and inshore waters, with adults found primarily in the

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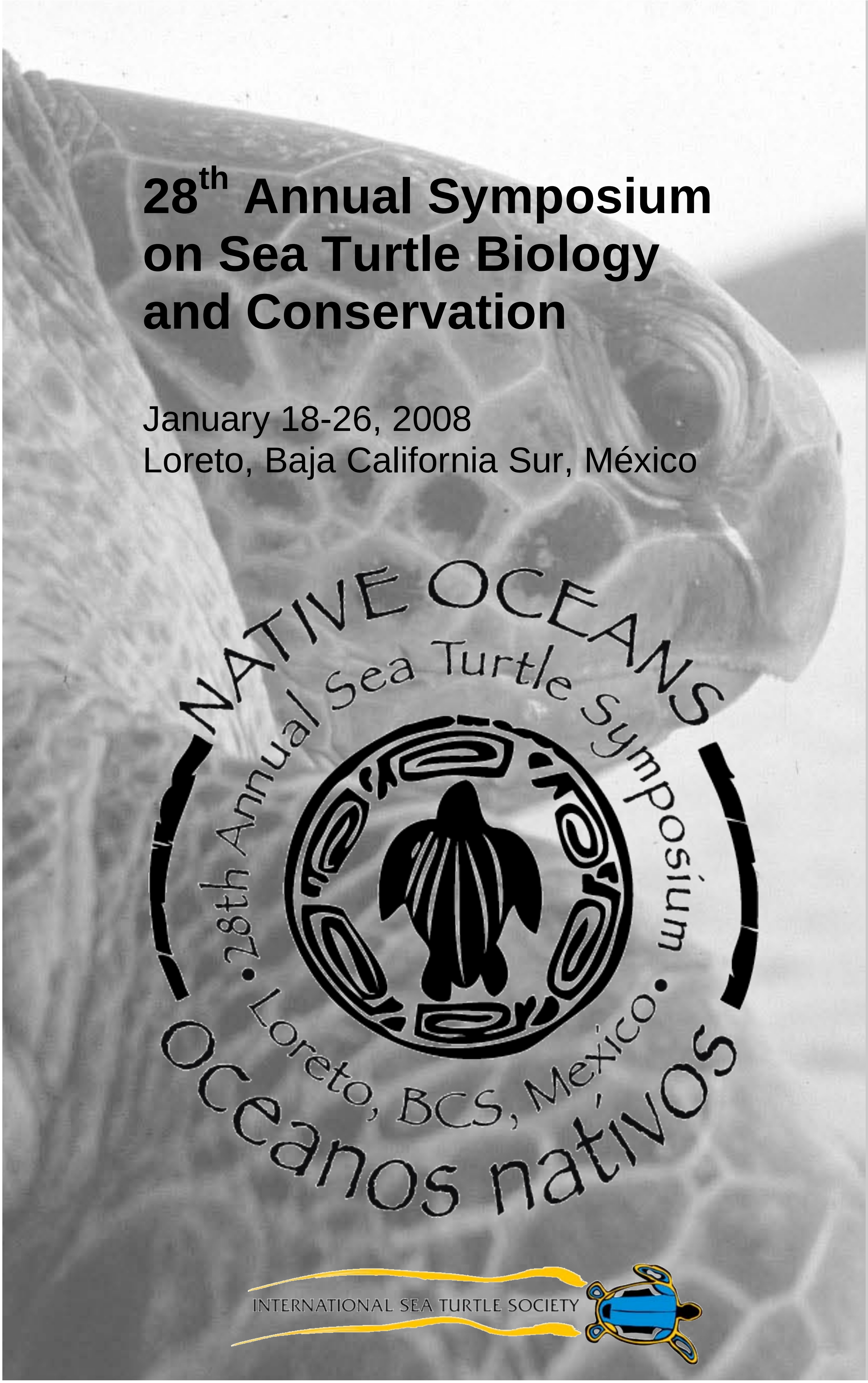

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GPS TRACKING FOR FINE-SCALE CONSERVATION MANAGEMENT: SEA TURTLE MOVEMENT PATTERNS IN A MARINE PROTECTED AREA

Gail Schofield[1], Charles M. Bishop[2], Grant MacLean[3], Peter Brown[3], Martyn Baker[4], Kostas A. Katselidis[5], Panayotis Dimopoulos[6], John D. Pantis[7], and Graeme C. Hays[8]

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Worldwide, coastal regions are subject to anthropogenic pressure, in the form of fisheries, coastal development and tourism. Therefore the ability to track wildlife at high resolution within a nature reserve may be important in formulating rational, adaptive and dynamic management decisions for endangered species and related conservation policies. It is important to obtain information about where, when and why endangered species, such as sea turtles, use these areas, in order to implement rational and effective protective legislation and management of human activities. While conventional radio and satellite transmitters have revolutionised the ability to track wildlife movement over vast spatial and temporal scales, recently developed loggers based on the Global Positioning System (GPS) allow wildlife to be studied with unparalleled accuracy. Laganas Bay, on the island of Zakynthos in Greece, is the largest loggerhead sea turtle (*Caretta caretta*) breeding area in the Mediterranean. Around 400 sea turtles migrate to Zakynthos each summer to breed, along with over 700,000 tourists. Sea turtles arrive in Laganas Bay as early as April, before nesting starts in late May, and are frequently observed close to shore. In this study we investigated the movement and habitat use of female loggerhead sea turtles in Laganas Bay during the breeding and inter-nesting period. Using recently developed, low-powered, TrackTagTM GPS loggers, we tracked three female turtles for a total of 73 days in May and June 2006. A total of 3,753 GPS locations were obtained, with an average of 51 fixes per day per turtle (min: 40, max: 65). We also monitored the diving behaviour of these three turtles and three other females using time-depth recorders (TDR). The information obtained from our GPS loggers indicated that all three turtles spent most of their time in shallow water (

Order: 74 **Abstract ID:** 2441 **Type:** Oral **Subject:** Behavior and Movements

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KEMP'S RIDLEY MIGRATORY PATHS AND FORAGING AREAS IN THE NORTHWESTERN GULF OF MEXICO

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The northwestern Gulf of Mexico is considered developmental habitat for the critically-endangered Kemp's ridley sea turtle, *Lepidochelys kempii*, and of growing importance to adult females as evidenced by annual nesting increases on the Texas coast since 1995. Although beach monitoring is crucial to estimating nesting population size and activity, in-water data are essential for evaluating management strategies and understanding population dynamics. In fact, the Kemp's Ridley Recovery Plan lists examining "seasonal use of nearshore habitat by juveniles/subadults" and determining "migratory paths and foraging areas" as necessary components of a strategy to achieve the recovery of this species, but such data are currently sparse. Fifteen immature Kemp's ridleys averaging 36.3 cm (SD=4.7 cm) straight carapace length (SCL) and seven adult females averaging 63.8 cm SCL (SD=2.0 cm)

To: g.schof@freemail.gr
From: abstracts@seaturtle.org
Date: 16/11/2008 22:26
Subject: ISTS 29 - Presentation Acceptance Notification - ORAL

This is an auto-generated e-mail. Please do not respond to this message.

Abstract Number: 2926
Title: NO TIME TO CHILL OUT: GPS TRACKING REVEALS MICRO-HABITAT SELECTION BY BREEDING LOGGERHEAD TURTLES
Type: Oral Presentation
Presenting Author: Gail Schofield
Session: Migration and Movement

Dear Gail Schofield:

I am writing to inform you that your abstract has been accepted for oral presentation at the 29th Annual Symposium on Sea Turtle Biology and Conservation, in Brisbane, Australia (January 17 - 19, 2009). You are scheduled to present your paper in the Migration and Movement Session. Please notify us immediately if there is any change in your planned attendance or the presentation of your paper.

You will be informed by December 15, 2008 via electronic mail of the exact time and location of your presentation. This email will also include instructions for meeting with your Session Chairs. At this meeting, scheduled for the day prior to your presentation, your Session Chair will collect your presentation media (see "Special Instructions", below).

If you cannot attend the symposium, please inform DuBose Griffin, Program Coordinator (griffind@dnr.sc.gov), by January 10, 2009. Failure to do so may disqualify you from submitting abstracts in subsequent years.

Authors will be able to edit their abstracts online until November 29, 2008. This editing period is your opportunity to thank funding sources and make light edits. Please note that substantial changes or additions to the abstract are not allowed.

You can click on the link below to be automatically logged in to your abstract. Or log in to the Symposium web site as usual, visit the "Registration Desk" and click on "Abstracts" to view your accepted abstracts. When you have completed your edits please click the "FINISHED" link next to each abstract so that your abstract can be compiled.

http://iconferences.seaturtle.org/cgi-bin/autologin.pl?code=xx2vAz90oCH7I&abstract_id=2926

SPECIAL INSTRUCTIONS FOR COMPUTER PRESENTATIONS: All computer presentations must be made using Microsoft Power Point. Your presentation will be loaded onto an IBM compatible laptop computer for your session. Please ensure that you have a CD or USB memory stick with you to give to your Session Chair the night before your presentation. Please ensure that your computer presentation is scanned for viruses before handing it in. We also strongly recommend that you bring a back-up copy, either a duplicate CD or a USB memory stick. We CANNOT hook up your laptop to the projector, so you must have a portable copy of your presentation! If you are using Microsoft PowerPoint 2007 to create your presentation, please save your presentation so that it is compatible with all prior versions of PowerPoint.

All oral presentations will be given in English. There will be no simultaneous translation. It is requested you complete your talk in 12 minutes to allow 2 minutes for questions and 1 minute for transition time. (This is especially important for oral presentations made by Student Award candidates, as performance on questions and answers is an integral part of the student presentation assessment process.) You will be asked to step down from the podium at 15 minutes, whether or not you have completed your presentation. There will be no exceptions to this time limit. Support for the use of 35 mm slides will not be provided as experience dictates that, nowadays, more technical problems arise with this medium.

We look forward to your presentation and to seeing you at the Symposium. If you have any questions, please respond by e-mail. Thank you!

Sincerely,

Mark Hamann, Tony Tucker, Bill Irwin, Jason Van De Merwe and DuBose Griffin
Program Committee, 29th ISTS
Contact E-mail: abstracts@seaturtle.org

Κεφάλαιο / Chapter 6. Accepted oral presentation (12 minutes)

NO TIME TO CHILL OUT: GPS TRACKING REVEALS MICRO-HABITAT SELECTION BY BREEDING LOGGERHEAD TURTLES

Gail Schofield, Charles M. Bishop, Kostas A. Katselidis, Panayotis Dimopoulos,
John D. Pantis & Graeme C. Hays

University of Ioannina, Greece
National Marine Park of Zakynthos, Greece
Bangor University, Wales
University of Thessaloniki, Greece
Swansea University, Wales

Loggerhead sea turtle breeding areas (*Caretta caretta*) are distributed across subtropical and temperate latitudes. The rookery on Zakynthos island (Greece) in the semi-enclosed Laganas Bay is unusual in that it is relatively large despite being situated at the latitudinal margins of the species' breeding range. When turtles migrate to Zakynthos to mate in March–May, sea surface temperatures are generally cool (*c.*13–22°C) before increasing towards mid-summer. It might be predicted that turtles display thermal selection to overcome cold conditions, although such thermal selection has not been demonstrated before in sea turtles. We examined if turtles on Zakynthos show thermal selection, and considered the possible benefits in terms of enhancing reproductive fitness. Ad-hoc surveys at sea conducted between April and July in 2003, 2004 and 2005 indicated that female turtles tended to aggregate along a 5-km section of coastline within the bay, so we focused our research in this area. In 2006, morning and afternoon transect surveys (along five transect lines) were conducted to obtain information on (i) sea-surface and seabed temperature at 15 stations (using Tinytag loggers), and (ii) sea turtle distribution. Weather data were recorded at two land-based stations. Navsys Ltd TrackTag GPS-loggers and LOTEK Ltd_1100 time-depth recorders (TDRs) were attached to three female loggerheads for 17, 31 and 25 days between 20/05/2006-23/06/2006. We also attached TDRs to three other females for 31, 12, 21 days between 16/05/2006-27/06/2006. We found a strong correlation for wind direction with both sea-temperature and turtle distribution, i.e. when the wind blew from the south-east the warmest water and turtle aggregations were in the north-west of the bay. These observations were supported by the GPS-tracked turtles, with 65% of variation in daily mean position being explained by wind direction. Analysis of individual GPS-tracks showed that turtles were not simply always located directly downwind (i.e. passive advection), but rather made movements parallel to the shore moving across the wind direction (i.e. active selection). The temperature loggers suggested that the temperatures at depth further from shore were over 2°C cooler than shallower temperatures, implying the actual water temperatures experienced by turtles in late May were probably around 5°C above those they would have experienced if they rested at >10 m. We used the empirical relationship between internesting intervals and water temperature to estimate that by selecting warm water, time to laying the first clutch might be reduced by as much as 5-days. Loggerheads will therefore maximize the number of clutches they can lay within a season that experience optimum development temperatures even

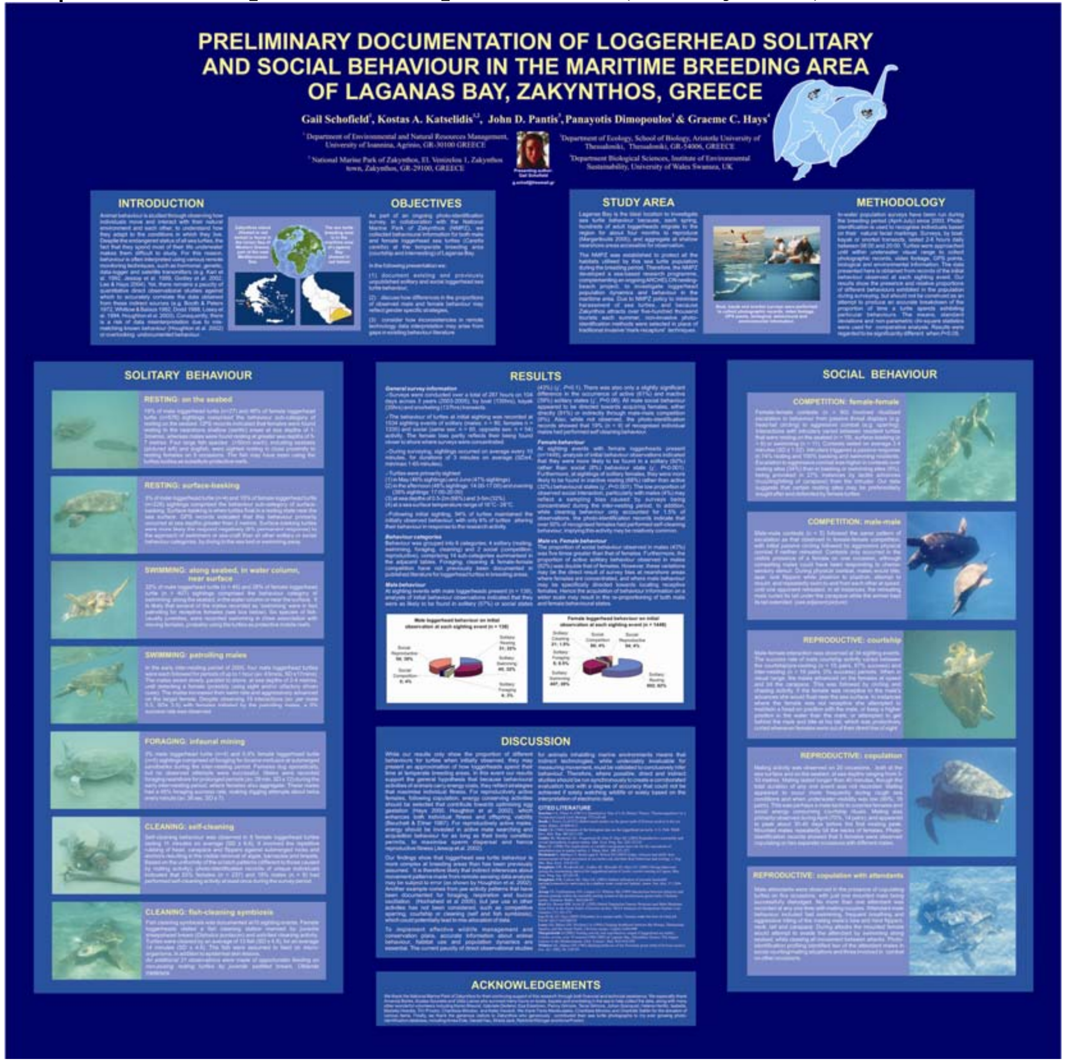
close to hatching. Furthermore, reducing the time required to lay the first clutch will mean that turtles are able to minimize the time spent away from foraging grounds. In summary, we have shown how female loggerheads, near the limits of its breeding range, repositions themselves daily to take advantage of thermal hotspots within a highly dynamic thermal environment. How turtles achieve this selection is not known, but it most probably contributes to the success of this species near its cold water range limits.

Κεφάλαιο / Chapter 1. Poster presentation (1.2m by 1.2m)

ASSESSMENT OF PHOTO-IDENTIFICATION & GIS AS A TECHNIQUE TO COLLECT IN-WATER INFORMATION ABOUT LOGGERHEAD SEA TURTLES IN LAGANAS BAY, ZAKYNTHOS, GREECE

Gail Schofield, Kostas A. Katselidis & John D. Pantis.
National Marine Park of Zakynthos
Website: http://www.nmp-zak.org.

Κεφάλαιο / Chapter 2. Poster presentation (1.2m by 1.2m)



PRELIMINARY DOCUMENTATION OF LOGGERHEAD SOLITARY AND SOCIAL BEHAVIOUR IN THE MARITIME BREEDING AREA OF LAGANAS BAY, ZAKYNTHOS, GREECE

Gail Schofield[1], Kostas A. Katselidis[1,2], John D. Pantis[3], Panayotis Dimopoulos[1] & Graeme C. Hays[4]

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INTRODUCTION

OBJECTIVES

STUDY AREA

METHODOLOGY

SOLITARY BEHAVIOUR

RESTING: on the seabed

RESTING: surface-basking

SWIMMING: along seabed, in water column, near surface

SWIMMING: patrolling males

FORAGING: infaunal mining

CLEANING: self-cleaning

CLEANING: fish-cleaning symbiosis

RESULTS

Male loggerhead behaviour on initial observation at each sighting event (n = 130)

Female loggerhead behaviour on initial observation at each sighting event (n = 1448)

DISCUSSION

ACKNOWLEDGEMENTS

SOCIAL BEHAVIOUR

COMPETITION: female-female

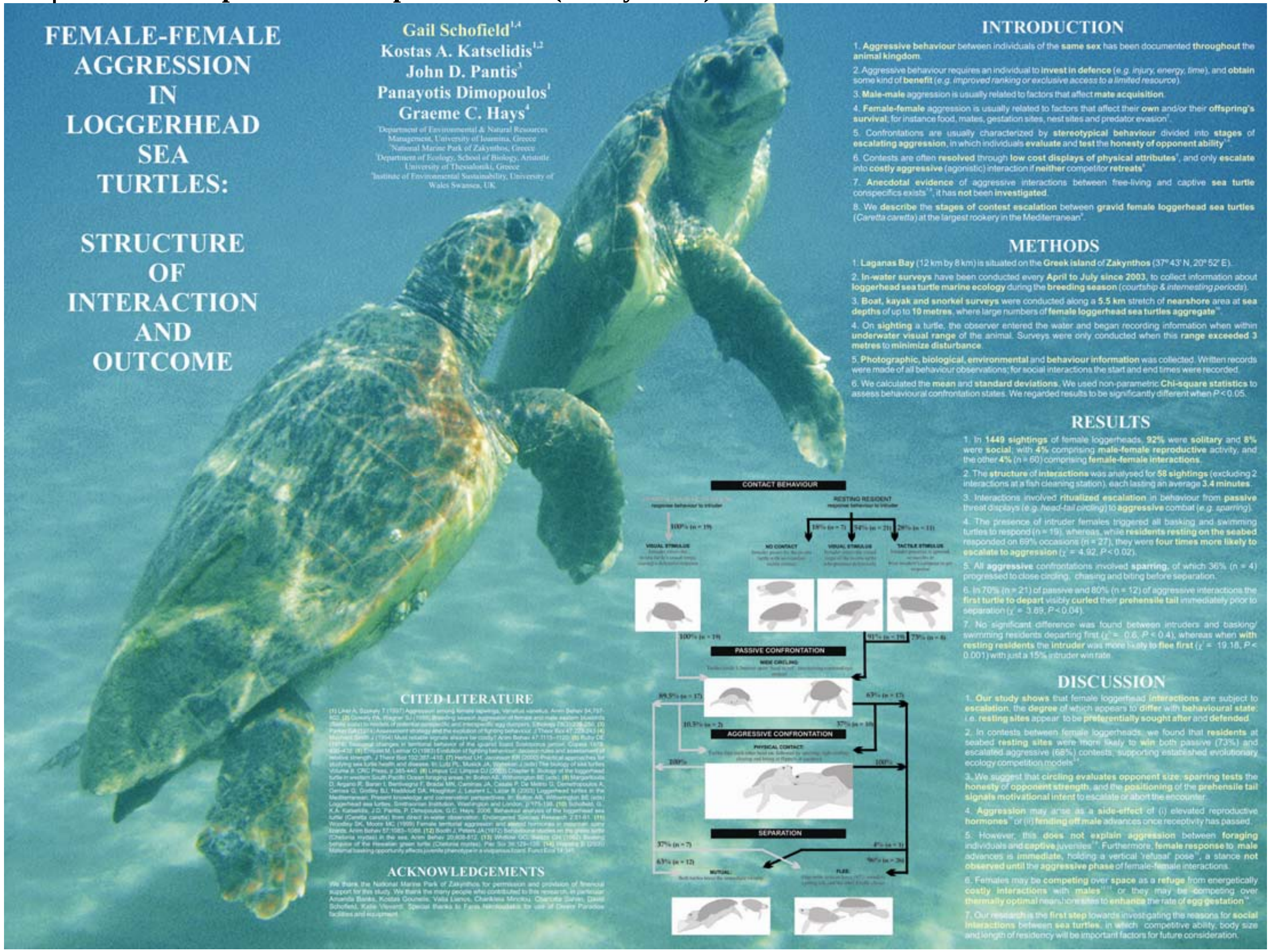
COMPETITION: male-male

REPRODUCTIVE: courtship

REPRODUCTIVE: copulation

REPRODUCTIVE: copulation with attendants

Κεφάλαιο / Chapter 3. Poster presentation (1m by 1.2m)



FEMALE-FEMALE AGGRESSION IN LOGGERHEAD SEA TURTLES:

STRUCTURE OF INTERACTION AND OUTCOME

Gail Schofield[1,4]
Kostas A. Katselidis[1,2]
John D. Pantis[3]
Panayotis Dimopoulos[1]
Graeme C. Hays[4]
[1]Department of Environmental & Natural Resources Management, University of Ioannina, Greece
[2]National Marine Park of Zakynthos, Greece
[3]Department of Ecology, School of Biology, Aristotle University of Thessaloniki, Greece
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INTRODUCTION

1. **Aggressive behaviour** between individuals of the **same sex** has been documented **throughout** the **animal kingdom**.

2. Aggressive behaviour requires an individual to **invest in defence** (*e.g. injury, energy, time*), and **obtain** some kind of **benefit** (*e.g. improved ranking or exclusive access to a limited resource*).

3. **Male-male** aggression is usually related to factors that affect **mate acquisition**.

4. **Female-female** aggression is usually related to factors that affect their **own** and/or their **offspring's survival**; for instance food, mates, gestation sites, nest sites and predator evasion[1].

5. Confrontations are usually characterized by **stereotypical behaviour** divided into **stages** of **escalating aggression**, in which individuals **evaluate** and **test the honesty of opponent ability**[3,4].

6. Contests are often **resolved** through **low cost displays of physical attributes**[5], and only **escalate** into **costly aggressive** (agonistic) interaction if **neither** competitor **retreats**[6].

7. **Anecdotal evidence** of aggressive interactions between free-living and captive **sea turtle** conspecifics exists[7,8], it has **not** been **investigated**.

8. We **describe** the **stages of contest escalation** between **gravid female loggerhead sea turtles** (*Caretta caretta*) at the largest rookery in the Mediterranean[9].

METHODS

1. **Laganas Bay** (12 km by 8 km) is situated on the **Greek island** of **Zakynthos** (37° 43' N, 20° 52' E).

2. **In-water surveys** have been conducted every **April to July since 2003**, to collect information about **loggerhead sea turtle marine ecology** during the **breeding season** (*courtship & internesting periods*).

3. **Boat, kayak and snorkel surveys** were conducted along a **5.5 km** stretch of **nearshore** area at **sea depths** of up to **10 metres**, where large numbers of **female loggerhead sea turtles aggregate**[10].

4. On **sighting** a turtle, the observer entered the water and began recording information when within **underwater visual range** of the animal. Surveys were only conducted when this **range exceeded 3 metres** to **minimize disturbance**.

5. **Photographic, biological, environmental** and **behaviour information** was collected. Written records were made of all behaviour observations; for social interactions the start and end times were recorded.

6. We calculated the **mean** and **standard deviations**. We used non-parametric **Chi-square statistics** to assess behavioural confrontation states. We regarded results to be significantly different when $P < 0.05$.

RESULTS

1. In **1449 sightings** of female loggerheads, **92%** were **solitary** and **8%** were **social**; with **4%** comprising **male-female reproductive** activity, and the other **4%** (n = 60) comprising **female-female interactions**.

2. The **structure of interactions** was analysed for **58 sightings** (excluding 2 interactions at a fish cleaning station), each lasting an average **3.4 minutes**.

3. Interactions involved **ritualized escalation** in behaviour from **passive** threat displays (*e.g. head-tail circling*) to **aggressive** combat (*e.g. sparring*).

4. The presence of intruder females triggered all basking and swimming turtles to respond (n = 19), whereas, while **residents resting on the seabed** responded on 69% occasions (n = 27), they were **four times more likely to escalate to aggression** ($\chi^2 = 4.92$, $P < 0.02$).

5. All **aggressive** confrontations involved **sparring**, of which 36% (n = 4) progressed to close circling, chasing and biting before separation.

6. In 70% (n = 21) of passive and 80% (n = 12) of aggressive interactions the **first turtle to depart** visibly **curled** their **prehensile tail** immediately prior to separation ($\chi^2 = 3.89$, $P < 0.04$).

7. No significant difference was found between intruders and basking/swimming residents departing first ($\chi^2 = 0.6$, $P < 0.4$), whereas when **with resting residents** the **intruder** was **more likely to flee first** ($\chi^2 = 19.18$, $P < 0.001$) with just a 15% intruder win rate.

DISCUSSION

1. **Our study shows** that female loggerhead **interactions** are subject to **escalation**, the **degree** of which appears to **differ with behavioural state**; i.e. **resting sites** appear to be **preferentially sought after** and **defended**.

2. In contests between female loggerheads, we found that **residents** at seabed **resting sites** were more likely to **win** both passive (73%) and escalated aggressive (68%) contests, supporting established evolutionary ecology competition models[3,4].

3. We suggest that **circling evaluates opponent size**, **sparring tests** the **honesty** of **opponent strength**, and the **positioning** of the **prehensile tail signals motivational intent** to escalate or abort the encounter.

4. **Aggression** may arise as a **side-effect** of (i) elevated reproductive **hormones**[11] or (ii) **fending off male** advances once receptivity has passed.

5. However, this **does not explain aggression** between **foraging** individuals and **captive** juveniles[12]. Furthermore, **female response to male** advances is **immediate**, holding a vertical 'refusal' pose[13], a stance **not observed until** the **aggressive phase** of female-female interactions.

6. Females may be **competing** over **space** as a **refuge** from energetically **costly interactions** with **males**[10] or they may be **competing** over **thermally optimal** nearshore **sites** to **enhance** the rate of **egg gestation**[14].

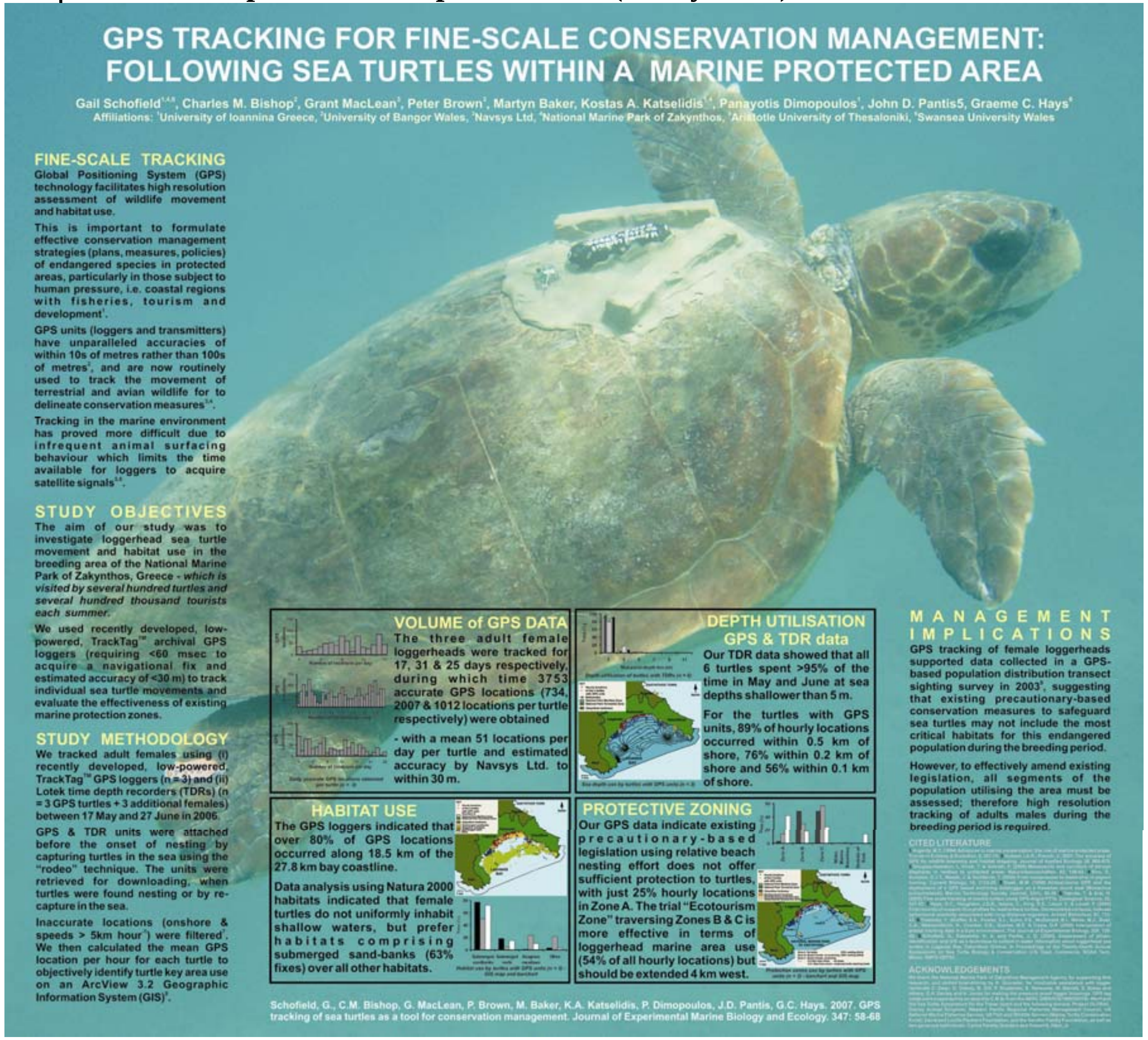
7. Our **research** is the **first step** towards investigating the reasons for **social interactions** between **sea turtles**, in which competitive ability, body size and length of residency will be important factors for future consideration.

CITED LITERATURE

ACKNOWLEDGEMENTS

We thank the National Marine Park of Zakynthos for permission and provision of financial support for this study. We thank the many people who contributed to this research, in particular Amanda Banks, Kostas Gounelis, [illegible], [illegible], [illegible], David Schofield, [illegible]. Special thanks to [illegible] for use of [illegible] facilities and equipment.

Κεφάλαιο / Chapter 4. Poster presentation (1m by 1.2m)



GPS TRACKING FOR FINE-SCALE CONSERVATION MANAGEMENT: FOLLOWING SEA TURTLES WITHIN A MARINE PROTECTED AREA

Gail Schofield[1,4,6], Charles M. Bishop[2], Grant MacLean[3], Peter Brown[3], Martyn Baker, Kostas A. Katselidis[1,4], Panayotis Dimopoulos[1], John D. Pantis5, Graeme C. Hays[6]
Affiliations: [1]University of Ioannina Greece, [2]University of Bangor Wales, [3]Navsys Ltd, [4]National Marine Park of Zakynthos, [5]Aristotle University of Thesaloniki, [6]Swansea University Wales

FINE-SCALE TRACKING

Global Positioning System (GPS) technology facilitates high resolution assessment of wildlife movement and habitat use.

This is important to formulate effective conservation management strategies (plans, measures, policies) of endangered species in protected areas, particularly in those subject to human pressure, i.e. coastal regions with fisheries, tourism and development[1].

GPS units (loggers and transmitters) have unparalleled accuracies of within 10s of metres rather than 100s of metres[2], and are now routinely used to track the movement of terrestrial and avian wildlife for to delineate conservation measures[3,4].

Tracking in the marine environment has proved more difficult due to infrequent animal surfacing behaviour which limits the time available for loggers to acquire satellite signals[5,6].

STUDY OBJECTIVES

The aim of our study was to investigate loggerhead sea turtle movement and habitat use in the breeding area of the National Marine Park of Zakynthos, Greece - *which is visited by several hundred turtles and several hundred thousand tourists each summer.*

We used recently developed, low-powered, TrackTag™ archival GPS loggers (requiring <60 msec to acquire a navigational fix and estimated accuracy of <30 m) to track individual sea turtle movements and evaluate the effectiveness of existing marine protection zones.

STUDY METHODOLOGY

We tracked adult females using (i) recently developed, low-powered, TrackTag™ GPS loggers (n = 3) and (ii) Lotek time depth recorders (TDRs) (n = 3 GPS turtles + 3 additional females) between 17 May and 27 June in 2006.

GPS & TDR units were attached before the onset of nesting by capturing turtles in the sea using the "rodeo" technique. The units were retrieved for downloading, when turtles were found nesting or by re-capture in the sea.

Inaccurate locations (onshore & speeds > 5km hour^{-1}) were filtered[7]. We then calculated the mean GPS location per hour for each turtle to objectively identify turtle key area use on an ArcView 3.2 Geographic Information System (GIS)[8].

VOLUME of GPS DATA

The three adult female loggerheads were tracked for 17, 31 & 25 days respectively, during which time 3753 accurate GPS locations (734, 2007 & 1012 locations per turtle respectively) were obtained

- with a mean 51 locations per day per turtle and estimated accuracy by Navsys Ltd. to within 30 m.

DEPTH UTILISATION GPS & TDR data

Our TDR data showed that all 6 turtles spent >95% of the time in May and June at sea depths shallower than 5 m.

For the turtles with GPS units, 89% of hourly locations occurred within 0.5 km of shore, 76% within 0.2 km of shore and 56% within 0.1 km of shore.

HABITAT USE

The GPS loggers indicated that over 80% of GPS locations occurred along 18.5 km of the 27.8 km bay coastline.

Data analysis using Natura 2000 habitats indicated that female turtles do not uniformly inhabit shallow waters, but prefer habitats comprising submerged sand-banks (63% fixes) over all other habitats.

PROTECTIVE ZONING

Our GPS data indicate existing precautionary-based legislation using relative beach nesting effort does not offer sufficient protection to turtles, with just 25% hourly locations in Zone A. The trial "Ecotourism Zone" traversing Zones B & C is more effective in terms of loggerhead marine area use (54% of all hourly locations) but should be extended 4 km west.

MANAGEMENT IMPLICATIONS

GPS tracking of female loggerheads supported data collected in a GPS-based population distribution transect sighting survey in 2003[9], suggesting that existing precautionary-based conservation measures to safeguard sea turtles may not include the most critical habitats for this endangered population during the breeding period.

However, to effectively amend existing legislation, all segments of the population utilising the area must be assessed; therefore high resolution tracking of adults males during the breeding period is required.

CITED LITERATURE

ACKNOWLEDGEMENTS

Schofield, G., C.M. Bishop, G. MacLean, P. Brown, M. Baker, K.A. Katselidis, P. Dimopoulos, J.D. Pantis, G.C. Hays. 2007. GPS tracking of sea turtles as a tool for conservation management. Journal of Experimental Marine Biology and Ecology. 347: 58-68

ΠΑΡΑΤΗΜΑ / APPENDIX 5: MULTIMEDIA FILES

Κεφάλαιο / Chapter 2

Video clips of behaviour observed

Video Clip	Behaviour Category	Behaviour sub-category	Clip Length	Description of footage
1	Resting	Resting on seabed	10	Female resting on seabed near to a seabass
2		Surface-basking - in water column	15	Female basking in water column
3		Surface-basking - at surface	15	Female basking at surface
4	Swimming	Female swimming	15	Female swimming in water column, with a fish swimming around her
5		Male swimming	15	Male, non-patrolling swim
6		Male patrolling	14	Male patrolling swim for females
7	Foraging	Male foraging	60	Male foraging (part of a 40 min video of constant foraging activity)
8		Female foraging	20	Female swimming into brief foraging attempt before resting
9	Cleaning	Self-cleaning by female	17	Female rubbing against anchor (part of a 10 min observation)
10		Female at fish cleaning station	20	Female being cleaned at a fish cleaning station manned by Sheepshead bream (part of a 15 min observation)
11	Contests	Female interaction - passive	17	Passive female interation after entering visual range of one another; brief circling and separation in opposite directions
12		Female interaction - aggressive	33	Aggressive female interaction: the intruder female attacks resident resting female, chases her off and then rests on the seabed
13		Male interaction	40	Part of a 2 minute interaction is shown in which an intruder male (tail straight) swims into visual range of a resident resting male (tail curled), they circle, spar and chase one another with the intruder eventually chasing off the resident
14	Reproductive	Male advancing on female	41	Male swimming up to female and biting at the carapace
15		Evasive manoeuvres by courted females (1)	11	Female deterring male by exposing her plastron
16		Evasive manoeuvres by courted females (2)	13	Male locking plastrons with a female attempting to deter him by exposing her plastron
17		Evasive manoeuvres by courted females (3)	14	Female facing the male head to head, shifting sideways and remaining higher
18		Evasive manoeuvres by courted females (4)	21	Female spinning out from under the male
19		Evasive manoeuvres by courted females (5)	21	Female getting behind the male and biting at the tail (note curling of tail)
n/a		Copulation	0	Photographs only
n/a		Copulation with attendant male	0	Photographs only

Schofield, G., K.A. Katselidis, J.D. Pantis, P. Dimopoulos & G.C. Hays. 2006. Preliminary documentation of loggerhead solitary and social behaviour in the maritime breeding area of Laganas Bay, Zakynthos, Greece (DVD & poster presentation). Twenty-Sixth International Symposium on Sea Turtle Biology and Conservation. Pp110-112

Κεφάλαιο / Chapter 4

A video animation showing the day by day movements of the three turtles with GPS loggers from attachment to retrieval (applying the Maptool program, www.seaturtle.org) (Animated gif).

Κεφάλαιο / Chapter 5

An animation showing the day by day movements of the eleven turtles across a 55 day period with GPS loggers from attachment to retrieval; blue range squares = 2007 males (n = 4), green range triangles = 2006 females (n = 3), red range circles = 2007 females (n = 4) (Animated gif).