

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

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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 visi-

bility, 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 (Margari-toulis 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 south-eastern 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 (Margari-toulis 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

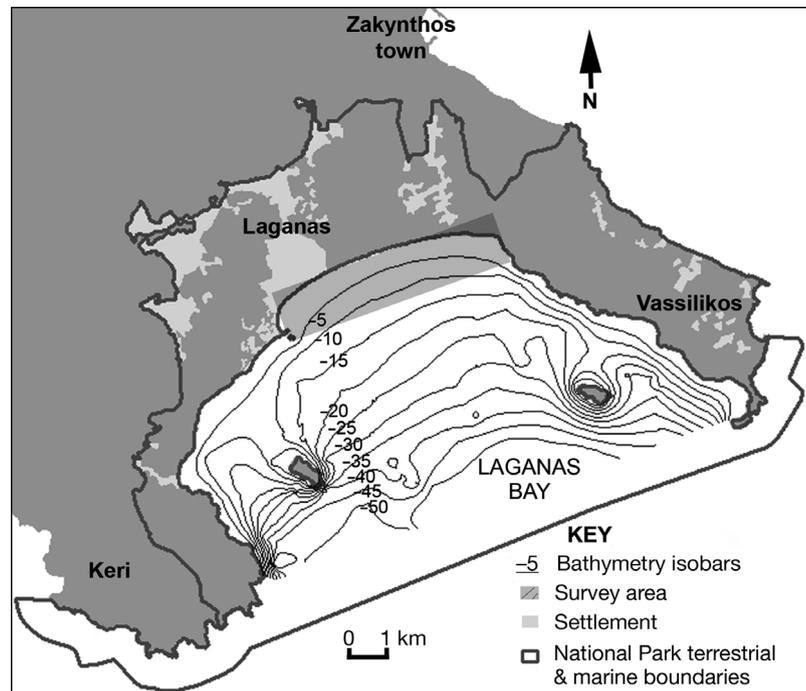


Fig. 1. Laganas Bay situated on the southern part of Zakynthos Island, showing the survey area

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 seabed 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

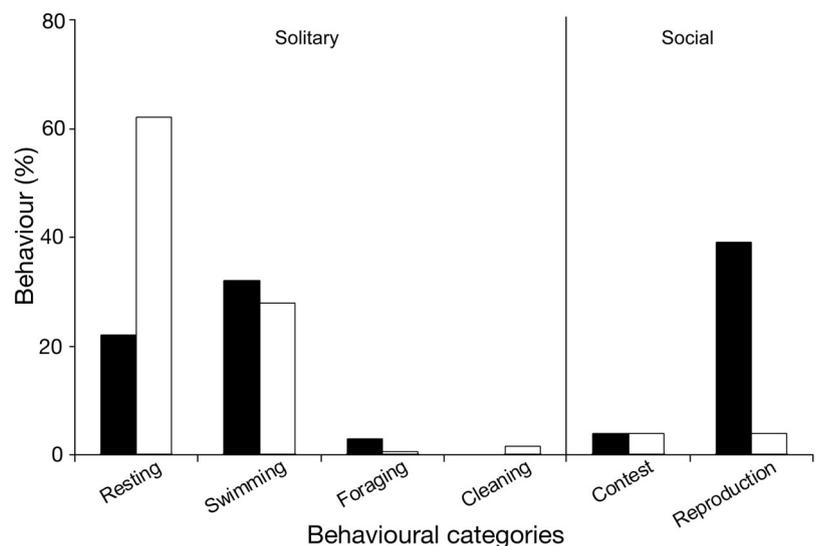


Fig. 2. *Caretta caretta*. Relative proportions of behaviour exhibited by male (black, $n = 139$) and female (white, $n = 1449$) loggerhead sea turtles at initial sighting

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
	Swimming	Surface-basking	M	4
			F	226
		Along seabed	M	8
			F	89
			M	12
		In water column	F	197
			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.

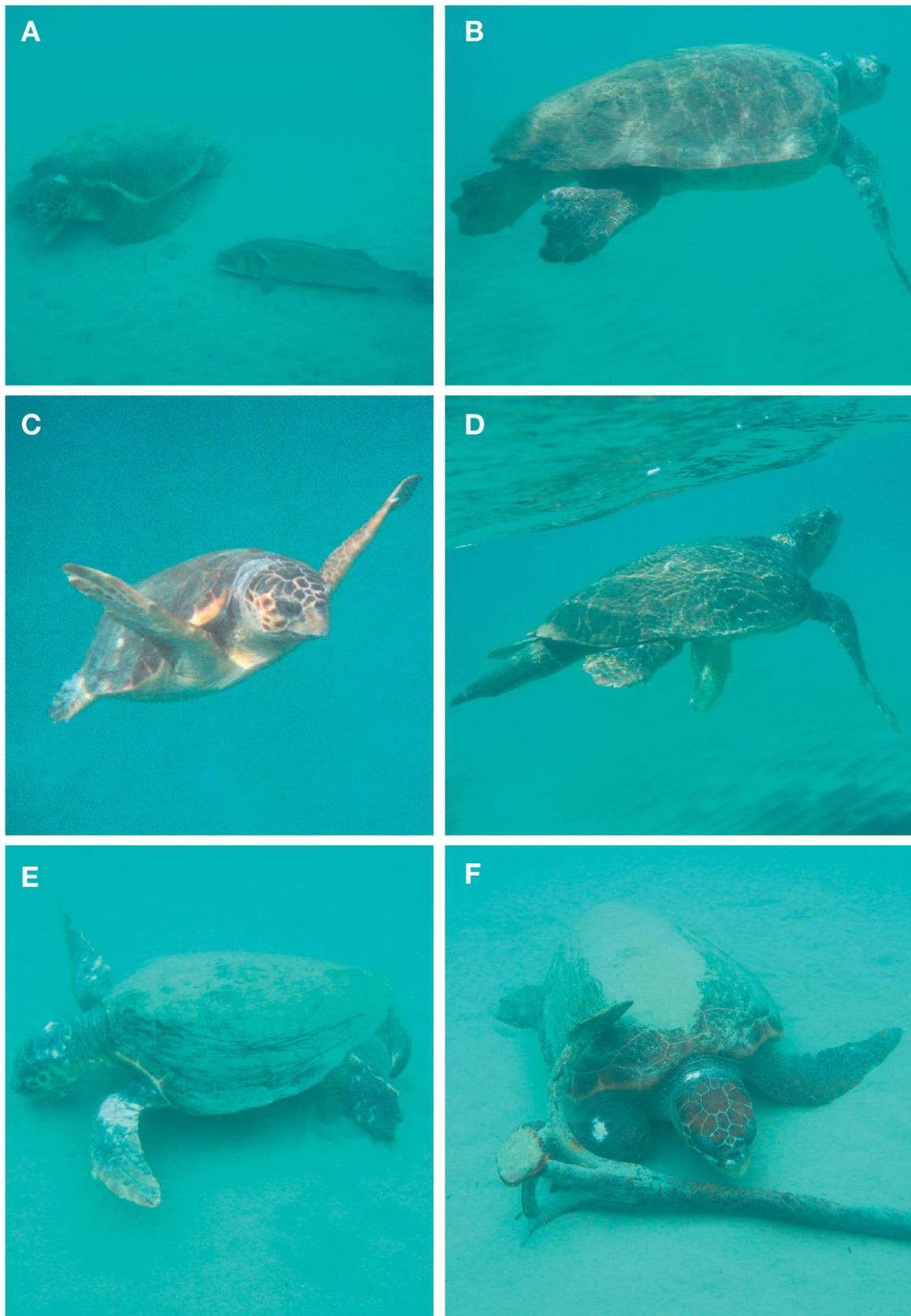


Fig. 3. *Caretta caretta*. (A) Female loggerhead resting on the seabed; (B) female surface-basking; (C) female swimming; (D) male patrolling for females; (E) male foraging for molluscs; (F) female rubbing against an anchor; (G) female posing at a fish cleaning station manned by sheephead bream *Diplodus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

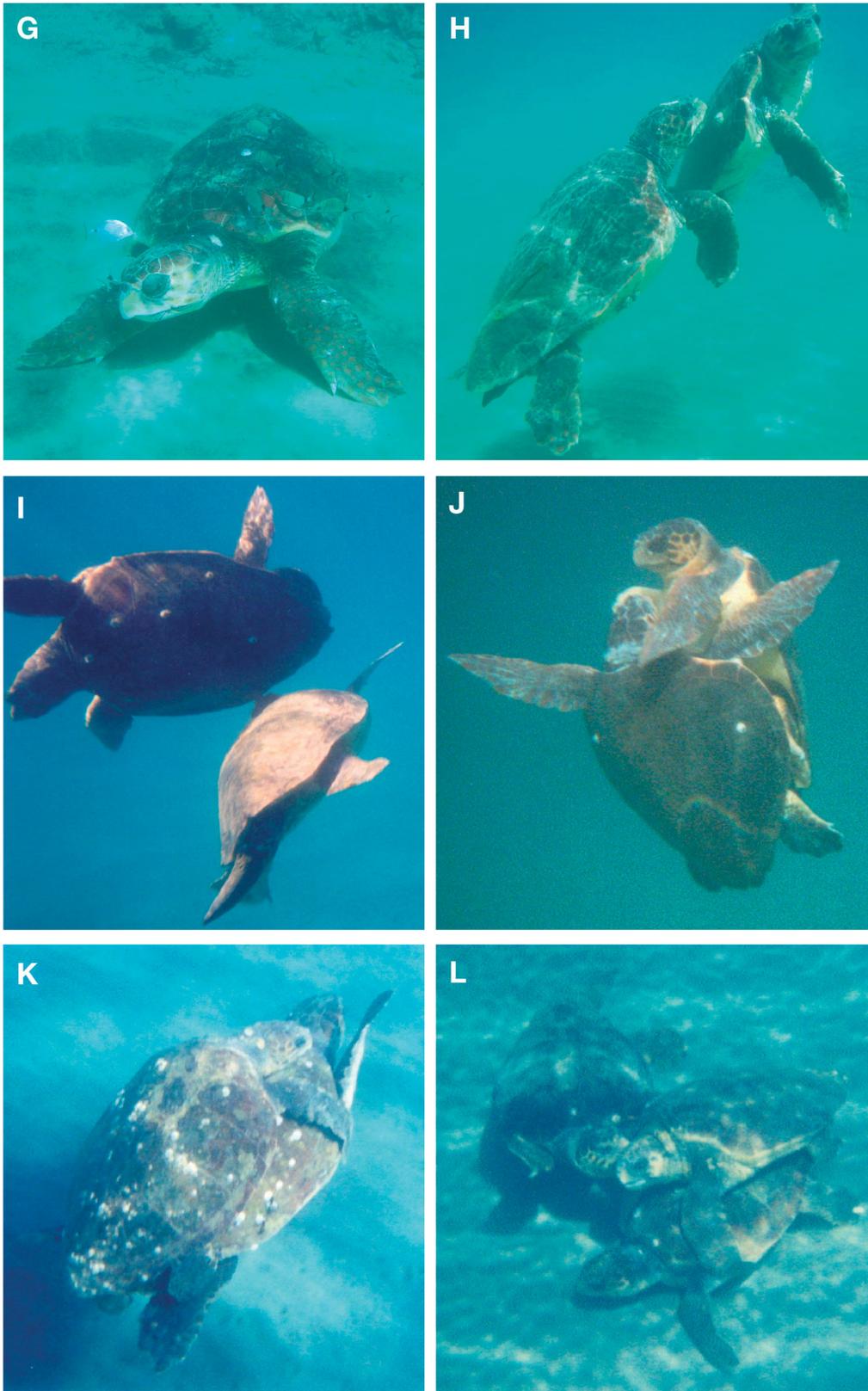


Fig. 3 (continued)

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 (Bjornedal 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.

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