Predation by white sharks Carcharodon carcharias (Chondrichthyes: Lamnidae) upon chelonians, with new records from the Mediterranean Sea and a first record of the ocean sunfish Mola mola (Osteichthyes: Molidae) as stomach contents

Ian K. Fergusson*.4, Leonard J.V. Compagno* & Mark A. Marks*

*The Shark Trust, National Marine Aquarium, Rope Walk, Coxside, Plymouth, Devon PL4OLF, England

Shark Research Center, Division of Life Sciences, South African Museum, PO Box 61,

Cape Town 8000, South Africa

SPPA, P.O. Box 712367, Santee, CA 92072, U.S.A.

Correspondence address: 46 Lincoln Close, Welwyn Garden City, Herts. AL7 2NN,

England (e-mail: shark.bureau@zoo.co.uk)

Received 29 April 1999

Accepted 22 December 1999

Key words: marine turtles, prey, feeding, grab-release

Synopsis

The occurrence of marine turtles in the diet of white sharks, Carcharodon carcharias, is reviewed worldwide. Four records of chelonians eaten by white sharks in the Mediterranean Sea are described, which on the basis of carapace remnants confirmed both the loggerhead Caretta caretta and green turtle Chelonia mydas to be preyed upon in those waters. The condition of these remains indicates that large white sharks can ingest turtles essentially intact. As well as falling prey to white sharks, we suspect that some interactions involve turtles being 'grab-released' in a non-predatory mannner and their survivability from such low-intensity bites or other mouthings may be quite high. The white shark may be the chief marine predator of adult chelonians in the Mediterranean Sea, albeit the impact of this predation upon turtle populations is nominal compared to other sources of mortality. Further, we give an account describing an adult ocean sunfish, Mola mola, in the stomach of a white shark taken in Italian waters.

Introduction

The white shark Carcharodon carcharias is a versatile, cosmopolitan predator and scavenger upon a wide spectrum of vertebrate and invertebrate taxa, including marine mammals, teleosts, chondrichthyans, cephalopods, crustaceans, molluscs, reptiles and occasionally sea birds (Compagno 1984). Much contemporary study has been directed towards the white shark's predatory association with pinnipeds, principally through interactions witnessed at the surface in Californian and South African waters (e.g., Ainley et al. 1981, 1985, Klimley et al. 1992, authors' collective observations at Dyer Island, South Africa). Stomach content data from these regions and elsewhere demonstrates that the white shark is primarily piscivorous at all size classes despite a shift with maturity towards favouring proportionately larger prey, including marine mammals. Elasmobranchs and teleosts tend to provide the greater numerical proportion of dietary intake when compared to marine mammals or other prey (Tricas & McCosker 1984, Cliff et al. 1989, Compagno's unpublished data from southern African specimens) and in those areas where pinnipeds are scarce or essentially absent, such as the Mediterranean Sea, large juvenile and adult white sharks will feed upon odontocetes or large pelagic fish (Fergusson 1996). These sharks also feed sporadically upon chelonians in various parts of

their range worldwide (e.g., Long 1996). In this paper, we review records describing predation upon marine turtles, emphasising the Mediterranean Sea.

Summary of recorded data describing white shark predation upon chelonians

In a global overview of marine turtle biology, Marquez (1990) notes that sharks are predators of all marine turtles and are the most important predators of adults and large juveniles. However, although citing the tiger shark Galeocerdo cuvier in this capacity, he does not specifically identify C. carcharias as such. While the white shark has been previously recognised as a (sporadic) predator of turtles (Bigelow & Schroeder 1948, Tortonese 1956, Davies 1964, D'Aubrey 1964, Tricas & McCosker 1984, Compagno 1984, 1991), dedicated commentary on such predation is scarce. Coles (1919) wrote of an attack by a large white shark upon a loggerhead turtle Caretta caretta off North Carolina and Postel (1958) described remains of a green turtle Chelonia mydas from a white shark taken in Tunisian waters. Long (1996) described records from Californian waters of two stranded leatherback turtles Dermochelys coriacea which exhibited wounds attributable to white shark predation or scavenging.

Bigelow & Schroeder (1948, p. 139) give brief mention of chelonians in the diet of white sharks, stating: 'Sea turtles are also described as a regular item in [the white shark's] diet in southern waters', but give no originating sources or precise geographical remits for their remark. Tricas & McCosker (1984, their figure 11) list marine turtles as present in a small (unquantified, but under 10%) percentage of 33 white sharks considered in their study. Klimley (1985) reports stomach contents in his study of 109 specimens taken in Pacific North American waters, none of which contained turtles. Casey & Pratt (1985) do not report chelonians from the 54 stomachs of juveniles pooled in their discussion of western North Atlantic white sharks, nor do they cite them as being a component of adult white shark diets considered in their study. Bruce (1992) discusses stomach contents from 17 South Australian specimens; Bass et al. (1975) those of 43 South African examples and Cliff et al. (1989) those from 299 juvenile white sharks taken off KwaZulu-Natal; similarly, LJVC has compiled stomach content data from a further 75 southern African specimens. Collectively, none of the sharks in these four datasets from the southern hemisphere

had ingested turtles. Therefore, based upon available information the significance of turtles in the global dietary repertoire of *C. carcharias* would appear very small when compared to certain other sharks. Specifically, the pan-tropical *G. cuvier* is a frequent predator of chelonians and other marine reptiles (Balazs 1979, Witzell 1987, Randall 1992), and the bull or Zambesi shark *Carcharhinus leucas* is also known to take turtles among its prey (Compagno 1984, Cliff & Dudley 1991). Closer interspecific comparisons are difficult, however, due to the nature of the white shark data (predominantly cold-temperate to subtropical records from specimens mostly < 4 m total length) and that for tiger and bull sharks.

Mediterranean records

The feeding ecology of white sharks is scantily known within many parts of its almost circumglobal range, One of us (IKF) has collected data describing a total of 234 captures and sightings of white sharks in Mediterranean waters since 1870, a preliminary summary of which is presented by Fergusson (1996). Since 1992, special effort has been given to amass stomach content data both from published accounts and reliable communications from fishermen or fisheries workers. The stomach contents from 24 Mediterranean white sharks ranging 250 cm to 550 cm TL indicates a cosmopolitan diet that includes pelagic bony fishes such as bluefin tuna Thunnus thynnus, Atlantic bonito Sarda sarda, broadbill swordfish Xiphias gladius and bullet tuna Auxis rochei; elasmobranchs including blue sharks Prionace glauca, shortfin mako Isurus oxyrinchus and stingrays Dasyatis spp.; cetaceans including Tursiops truncatus, Delphinus delphis and Stenella coeruleoalba (Postel 1956, Fergusson 1994, 1996 and unpublished data), and other items including molluses, terrestrial mammalian carcasses, inanimate garbage, human cadavers and the occasional ingestion of marine turtles. The remains of marine turtles were found from 4 (17%) of the sharks examined, all large juvenile or adult specimens ≥ 350 cm total length. Despite the rather small sample size, this Mediterranean data represents the highest proportion of chelonians as a dietary component of C. carcharias when compared to analyses worldwide.

A definitive published account of turtle remains found in a white shark stomach is that of Postel (1956), who described the capture of white sharks during the 1950s within the coastal bluefin tuna trap fishery off

Table 1. Records of white shark predation upon chelonians, Mediterranean Sea, in chronological order, as mapped in Figure 1.

No.	Date	Location	Species	Remarks/Source
1	16.5.1956	N.W. Cape Bon, Tunisia	Chelonia mydas	Carapace fragments found in the stomach of a 520 cm female (Postel 1958).
2	6.1963	Ganzirri, Messina, Sicily (Italy)	Caretta caretta	Entire carapace of a large specimen found in stomach of a 350 cm white shark. Donato Nicola personal communication.
3	14.8.1974	S. Caterina Pittinurri, Western Sardinia (Italy)	unknown	Remnants in stomach of a ca. 450 cm male white shark. Franco Moroni personal communication to Marco Zuffa.
4	17.4.1987	Filfla Islet, S.W. Malta	Caretta caretta	Carapace of 60 cm length in stomach of a ca. 530 cm female white shark; J. Abela & A. Cutajar personal communication

Sidi Daoud, on the western tip of Tunisia's Cape Bon. One such example (adult female, 520 cm TL, taken 22 May 1956) contained two dolphins Delphinus delphis, an elasmobranch (almost certainly a juvenile short-fin make Isurus exyrinchus) and turtle remains. Carapace fragments of the latter were identified by Postel as C. mydas. Our records also identified the logger-head turtle as present in two (and possibly three; identity uncertain for one set of remains from Sardinia) of the four white shark stomachs containing chelonian remains (Table 1, Figure 1).

In the Straits of Messina, loggerhead turtles can often be seen at the surface, close inshore during the spring and summer months (IKF and MAM, personal observations; Antonio Potoschi, Universita di Messina, personal communication) in the same areas near Ganzirri (north of Messina) where adult white sharks have previously been captured or sighted by fishermen harpooning swordfish. One of these operators, Donato Nicola (personal communication to IKF and MAM, June 1995), recalled very clearly the condition of the turtle remains he removed from a 350 cm TL white shark harpooned ca. 3 km offshore from Ganzirri in June 1963. The stomach also contained a large volume of small teleost fish remains; none, however, were readily identifiable even at a familial level. The accompanying illustration (Figure 2) is redrawn from an original field-note sketch compiled under Nicola's direction. The turtle was apparently subjected to one powerful bite that left a semicircular impression, manifested by a fractured and crushed area of the carapace. The prey was then ingested essentially intact with little further manipulation. According to Nicola, a substantial amount of soft body tissue had remained attached to the inside of the plastron.

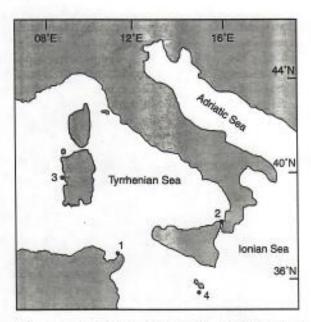


Figure 1. Locations of white shark captures containing sea turtle remains in their stomachs. Numbers refer to the specimens listed in Table 1.

Intact ingestion is also inferred by the remains of a (probably large juvenile) loggerhead turtle, carapace length ca. 60 cm, found in the stomach of a very large female white shark (allegedly 713 cm TL but no larger than ca. 550 cm TL based upon forensic analysis of previously unexamined photographs; Fergusson's unpublished data), caught near the islet of Filfla, Malta, on 17 April 1987 (see Fergusson 1996 and Mollet et al. 1996 for details). The shark's stomach contents were reported accurately, having been seen by various

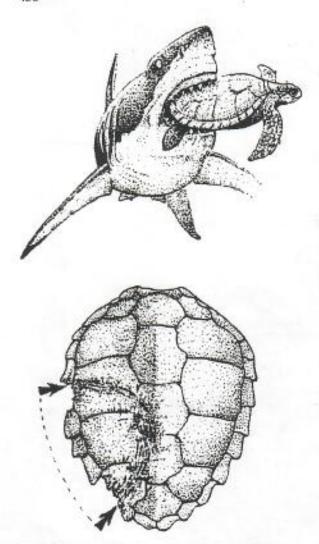


Figure 2. Representation of reported carapace damage inflicted by a white shark upon a loggerhead turtle off Ganzirri, Sicily. The accompanying illustration depicts the likely mode by which the prey was seized and manipulated (illustration by IKF).

bystanders as the animal was eviscerated and supported, in part, by photographs. The ingested turtle's carapace and plastron were intact and marked by only a few superficial teeth marks on both dorsal and ventral surfaces. The fleshy parts were totally unmarked, including limbs and head, suggesting that its ingestion had been accomplished with very little manipulation. Indeed, the turtle appeared so fresh that it was reputedly sold shortly afterwards by the shark's captor to a local buyer (John Abela & Alfredo Cutajar personal communication).

First record of Mola mola from a white shark stomach

Our discussions with Donato Nicola revealed his capture of a second specimen of C. carcharias near Messina. In this case it was a shark measuring over 500 cm TL (sex unknown), harpooned on 9 March 1965. The shark was first observed near the breakwater at Ganzirri, where Nicola approached it with his boat as it cruised conspicuously at the surface some 100 m parallel to the shore, in zig-zagging northerly vectors. It was killed by a single hand-thrown swordfish harpoon and taken to shore. Two of us (IKF and MAM) were able to examine the preserved jaws of this shark at the nearby Universita di Messina's Istituto di Idrobiologia e Pescicoltura, and verify a total length > 500 cm based on the jaw dimensions.

The shark was eviscerated by Nicola and colleagues, who found in the stomach a freshly-ingested adult ocean sunfish *Mola mola*, bitten into three sections (head, mid-trunk and posterior with dorsal fin, anal fin and clavus). When combined, the sunfish measured about 2 m total length. To our knowledge, this represents the first described account of white shark predation (or possible scavenging) upon this cosmopolitan epipelagic species and further illustrates the impressive capabilities of large *C. carcharias* in dismembering substantially-apportioned prey items.

Discussion

The white shark is best described as an occasional and opportunistic predator of marine turtles, particularly so in the Mediterranean Sea. While it is possible that some tiger sharks selectively hunt for turtles (Witzell 1987), the white shark, on the other hand, apparently eats them fortuitously and erratically while seeking more desirable prey.

There are presently insufficient stomach content data from Mediterranean white sharks to infer the overall importance of marine turtles in their diet, nor to assess any seasonal, gender or age-class related trends in their vulnerability to predation. The only other confirmed predator of adult loggerhead turtles in the region is the (endangered) Mediterranean monk seal Monachus monachus (Margaritoulis et al. 1996), and potential elasmobranch predators of both juvenile and adult chelonians in the Mediterranean are few. Included with C. carcharias in this category may be adult dusky

sharks Carcharhinus obscurus and bronze whalers Carcharhinus brachyurus, blue sharks Prionace glauca, adult shortfin makos Isurus oxyrinchus and bluntnose sixgills Hexanchus griseus. However, we have no reliable data to confirm this suspicion. Basso (1992) also proposed the smalltooth sandtiger Odontaspis ferox as a likely chelonian predator in Italian waters, but we believe this improbable given the essentially piscivorous diet of this species and its unrobust dentition which appears incapable of dismembering the carapaces or other hard parts of marine turtles.

The Mediterranean is suspected to support the third largest loggerhead population in the world, after those of Oman and the U.S.A. (Laurent et al. 1997). The species nests in various parts of the region, particulary at beaches on the Greek Ionian islands, along the southern Turkish coast, around Cyprus and along Libya's largely undeveloped coastline (Margaritoulis 1988, Hays et al. 1991, Laurent et al. 1997), with the latter area suspected to host one of the largest nesting populations in the Mediterranean (Laurent et al. 1997, Laurent personal communcation). The two white sharks containing C. caretta remains were taken in the western-central Mediterranean (Malta and Messina), some distance from known nesting sites and earlier than the late Spring-Summer nesting season. Conceivably, a proportion of turtles found in warm waters largely outside of the white shark's Mediterranean range in summer are more vulnerable to predation during the cooler months, when some migrate to overwinter and feed in Tunisia's Gulf of Gabés (Laurent & Lescure 1994) and perhaps likewise in the north and eastern Adriatic Sea (Lazar & Tvrtkovic 1995) regions where C. carcharias can be encountered with some regularity. Conversely, the white shark is considerably scarcer in waters to the east of the Ionian Sea and Peloponnese (Fergusson 1996) and whilst inhabiting eastern regions such as the Aegean Sea, or off southern Turkey and around Cyprus, turtles may be rarely exposed to white shark predation.

The impact of white shark predation upon turtle populations is unknown but probably extremely small compared to other sources of mortality, especially those caused by anthropogenic factors and commercial fisheries in particular. Annually, over 20 000 loggerhead turtles are suspected to be accidentally ensnared (and many killed) just by the Spanish swordfish longline fishery alone in the Western Mediterranean (Aguilar et al. 1). Equally, human degradation of traditional nesting sites and other interference with these animals in the region has a tangible impact on their mortality, both in juveniles and adults (e.g., Peters & Verhoeven 1994, Venizelos 1993). By way of numerical example, 20% of 99 loggerhead turtles examined from the central Mediterranean during 1986 were contaminated with plastic, metal or hydrocarbons (Gramentz 1988).

A problem in assessing the wider impact of white shark predation upon marine turtles comes in distinguishing wounds inflicted by C. carcharias versus those caused by other sources or indeed other species of shark. Marine turtles are occasionally observed with injuries such as limb amputations that could be equally attributable to boat collisions, fishing gear entanglement, deliberate mutilation by fishermen or shark attack. In an instructive paper, Gramentz (1989) examined 82 loggerhead turtles taken from Maltese waters for injuries attributable to predators, and found that 19.5% exhibited damage ranging from small notches on the flippers and posterior marginal plates to entire loss of one of the extremities in 4.9% of the cases. Interestingly, these more seriously injured animals seemed in good condition and Gramentz attributes the ability of turtles to survive such trauma by virtue of the rapidity with which their blood coagulates. Similarly, turtles observed in the Red Sea and central-western Persian Gulf with evidence of shark-inflicted injuries (likely made by either tiger sharks or bull sharks), including flippers amputated and carapaces damaged, appear remarkably resilient to such trauma and have a high recovery rate (Elizabeth Salter personal communication). However, the powerful impact forces generated by white sharks during motivated biting (with palatoquadrate protrusion) can apparently readily puncture and crush the dorsal carapace of even well-protected chelonids, thereby causing serious internal injuries. Even if forcefully bitten and then released, such injuries are perhaps invariably fatal to turtles.

On the other hand, marine turtles may recover from less intensive white shark 'mouthings', such as might conceivably account for a proportion of the limb amputations and other injuries in the sample

¹ Aguilar R., J. Mas & X. Pastor. 1995. Impact of Spanish

swordfish longline fisheries on the loggerhead sea turtle Caretta caretta population in the western Mediterranean. pp. 1–6. In: J.I. Richardson & T.H. Richardson (ed.) Proceedings of the Twelfth Annual Workshop on Sea Turtle Biology and Conservation, NOAA Technical Memorandum NMFS-SEFSC-361, U.S. Department of Commerce, National Oceanographic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Miami.

of C. caretta described and illustrated by Gramentz (1989, his figure 5). Similarly, loggerhead turtles with missing flippers have been observed at various other Mediterranean localities (Luc Laurent personal communication). According to Dimitris Margaritoulis (personal communication), some 20% of nesting females observed by researchers at Greek nesting beaches have missing posterior parts, either on the carapace or flippers, similar to those described by Gramentz (1989).

Thus although our data and that of others clearly demonstrates that turtles are ingested as prey items, we also suspect that conversely, a proportion of white shark attacks on turtles are non-predatory in motivation. The white shark is a habitual 'grab-releaser' of various marine animals, most notably sea otters Enhydra lutris (Ames & Morejohn 1980, Ames et al. 1996), jackass penguins Spheniscus demersus (Randall et al. 1988, MAM unpublished data), other seabirds, marine mammals and indeed conspecifics (author's collective observations at Dyer Island). Such interactions, with either fatal or non-fatal consequences, are manifested by injuries including 'bashing' puncture marks generated by the lower and upper jaw teeth of white sharks, cursory slash marks made by the lower teeth and possibly the upper teeth, and more symmetric sets of wounds without substantial flesh removal, made as sharks undertake more complete bites but using surpressed force. Marine turtles might represent another target for non-predatory 'grab-release' bouts, leaving injuries comparable to those observed in other animals subjected to this mode of white shark attention. In seeking to confirm this possibility, we urge detailed future examination of injured Mediterranean turtles which may have been inflicted by C. carcharias in 'grabrelease' scenarios.

Acknowledgements

We sincerely thank those individuals whose kind provision of data and their time gave rise to this report: Marco Zuffa (Italy); Donato Nicola (Ganzirri, Sicily); Antonio Potoschi (Universita di Messina, Sicily); John Abela and Alfredo Cutajar (Malta); Grant Sonnex and Mark Carwardine (BBC Natural History Unit) and Elizabeth Salter, Patrick J. Schembri made useful early comments on the manuscript and directed the authors to the important local paper by Gramentz (1989). Luc Laurent and Dimitris Margaritoulis generously shared their extensive specialist knowledge and observations of Mediterranean marine turtles, and offered invaluable opinions and guidance concerning various elements of this paper. Finally, we thank the two anonymous reviewers who offered useful and constructive suggestions for preparing our final manuscript.

References cited

Ainley, D.G., C.S. Strong, H.R. Huber, T.J. Lewis & S.H. Morrell. 1981. Predation by sharks on pinnipeds at the Farallon Islands. U.S. Fish. Bull. 78: 941-945.

Ainley, D.G., R.P. Henderson, H.R. Huber, R.J. Boekelheide, S.G. Allen & T.L. McElroy. 1985. Dynamics of white shark/pinniped interactions in the Gulf of the Farallones. Memoirs South. Calif. Acad. Sci. 9: 109-122.

Ames, J.A. & G.V. Morejohn. 1980. Evidence of white shark, Carcharodon carcharias, attacks on sea otters, Enhydra lutris.

Calif. Fish Game 66: 196-209.

Ames, J.A., J.J. Geibel, F.E. Wendell & C.A. Pattison. 1996. White shark-inflicted wounds of sea otters in California, 1968-1992. pp. 309-316. In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: The Biology of Carcharodon carcharias, Academic Press, San Diego.

Balazs, G.H. 1979. Loggerhead turtle remains recovered from a tiger shark at Kure Atoll. Elepsio 39 (12): 145-147.

Bass, A.J., J.D. D'Aubrey & N. Kistnasamy, 1975. Sharks of the east coast of Southern Africa. IV. The families Odontasipididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. So. Afr. Ass. Mar. Biol, Res. Oceanogr. Res. Inst., Invest. Rept. 39. 102 pp.

Basso, R. 1992. Osservazioni e ricerche sulle tarturughe marine presenti nei mari italiani (Observations and research of marine turtles in Italian seas). Edizioni del Grifo, Lecce. 71 pp.

Bigelow, H.B. & W.C. Schroeder. 1948. Sharks. pp. 59-546. In: A.E. Parr & Y.H. Olsen (ed.) Fishes of the Western North Atlantic, Part 1, Lancets, Cyclostomes and Sharks, Memoirs Sears Found. Mar. Res., New Haven.

Bruce, B.D. 1992. Preliminary observations on the biology of the white shark, Carcharodon carcharias, in South Australian waters. Aust. J. Mar. Freshwater Res. 43: 1-11.

Casey, J.G. & H.L. Prutt, Jr. 1985. Distribution of the white shark Carcharodon carcharias in the western North Atlantic, Memoirs South, Calif. Acad. Sci. 9: 2-14.

Cliff, G., S.F.J. Dudley & B. Davis. 1989. Sharks caught in the protective gill-nets off Natal, South Africa. II. The great white shark Carcharodon carcharias (Linnneus), South Afr. J. Mar. Sci. 8: 131-144.

Cliff, G. & S.F.J. Dudley. 1991. Sharks caught in the protective gill-nets off Natal, South Africa. The bull or Zambezi shark Carcharhinus leucas (Valenciennes). South Afr. J. Mar. Sci. 10: 253-270.

Coles, R.J. 1919. The large sharks of Cape Lookout, North Carolina. The white shark or maneater, tiger shark and ham-

merhead. Copeia 1919: 34-43.

Compagno, L.J.V. 1984. Sharks of the world. Part 1, Hexanchiformes to Lamniformes. FAO Species Catalogue 4, FAO Fish. Synop. 125, Food and Agriculture Organisation of the United Nations, Rome. 249 pp.

- Compagno, L.J.V. 1991. Feeding ecology. pp. 48–50. In: Great White Sharks, Underwater Journal Special Edition, T. & V. Condon Publications, Cape Town.
- Davies, D.H. 1964. About sharks and shark attack. Shuter and Shooter, Pietermaritzburg. 257 pp.
- D'Aubrey, J.D. 1964. Preliminary guide to the sharks found off the east coast of South Africa. So. Afr. Ass. Mar. Biol. Res. Oceanogr. Res. Inst., Invest. Rept. 8, 95 pp.
- Fergusson, I.K. 1994. Preliminary notes on white shark (Carcharodon carcharias) predation and scavenging upon odontocetes in the Mediterranean Sea. pp. 52–55. In: S.L. Fowler & R.C. Earll (ed.) Proceedings 2nd European Shark and Ray Workshop, February 1994, Joint Nature Conservancy Council (JNCC), Peterborough.
- Fergusson, I.K. 1996. Distribution and autecology of the white shark in the eastern North Atlantic Ocean and the Mediterranean Sea. pp. 321–345. In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: The Biology of Carcharodon carcharias, Academic Press, San Diego.
- Gramentz, D. 1988. Involvement of loggerhead turtle with plastic, metal and hydrocarbon pollution in the central Mediterranean. Mar. Pollution Bull. 19: 11–13.
- Gramentz, D. 1989. Marine turtles in the central Mediterranean Sea. CENTRO 1 (4): 41–56.
- Hays, G.C., P.I. Webb, J.P. Hayes, L.G. Priede & J. French. 1991.
 Satellite tracking of a loggerhead turtle (Caretta caretta) in the Mediterranean. J. Mar. Biol. Ass. U.K. 71 (3): 743–746.
- Klimley, A.P. 1985. Areal distribution and autecology of the white shark off the western coast of North America. Memoirs South. Calif. Acad. Sci., 9: 109–122.
- Klimley, A.P., S.D. Anderson, P. Pyle & R.P. Henderson. 1992.
 Spatiotemporal patterns of white shark (Carcharodon carcharias) predation at the South Farallon Islands, California.
 Copeia 1992: 680–690.
- Laurent, L., M.N. Bradai, D.A. Hadoud & H.M. El Gomati. 1997. Assessment of sea turtle nesting activity in Libya. Marine Turtle Newsletter 76: 2–6.
- Laurent, L. & J. Lescure. 1994. L'hivernage des tortues marines Caouanne Caretta caretta (L.) dans le Sud Tunisien. Revue d'Ecologie (Terre et Vie) 49: 63–86.
- Lazar, B. & N. Tvrtkovic. 1995. Marine turtles in the eastern part of the Adriatic Sea: Preliminary research. Nat. Croatica 4: 59-74.
- Long, D.J. 1996. Records of white shark-bitten leatherback sea turtles along the Central California Coast. pp. 317–319. In:

- A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: The Biology of Carcharodon carcharias, Academic Press, San Diego.
- Margaritoulis, D. 1988. Post-nesting movements of loggerhead sea turtles tagged in Greece. Rapports et Procès-verbaux des Réunions, Comm. Int. Expl. Sci. Mar Médit. Paris 31: 284
- Margaritoulis, D., D. Karavellas & C. Irvine. 1996. Predation of adult loggerheads by Mediterranean monk seals. pp. 193–196. In: J.A. Keinath, D.E. Barnard, J.A. Musick & B.A. Bell (compilers). Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation, NOAA Technical Memorandum NMFS-SEFSC-387.
- Marquez, M.R. 1990. Sea turtles of the world. An annotated and illustrated catalogue of sea turtle species known to date. FAO Species Catalogue 11, FAO Fish. Synop. 125, Food and Agriculture Organisation of the United Nations, Rome. 81 pp.
- Mollet, H.F., G.M. Cailliet, A.P. Klimley, D.A. Ebert, A.D. Testi & L.J.V. Compagno. 1996. A review of length validation methods for large white sharks. pp. 91–108. In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: The Biology of Carcharodon carcharias, Academic Press, San Diego.
- Peters, A. & J.F. Verhoeven. 1994. Impact of artificial lighting on the seaward orientation of hatchling loggerhead turtles. J. Herpetology 28: 112–114.
- Postel, E. 1958. Sur le presence de Carcharodon carcharias (L. 1758) dans les eaux tunisiennes. Mus. Natl. Hist. Nat. Paris, Bull. (Ser. 2) 30: 342–244.
- Randall, B.M., R.M. Randall & L.J.V. Compagno. 1988. Injuries to jackass penguins (Spheniscus demersus): evidence for shark involvement. J. Zool. 213: 589–599.
- Randall, J.E. 1992. Review of the biology of the tiger shark (Galeocerdo cuvier). Aus. J. Mar. Fresh. Res. 43: 21–31.
- Taylor, L.R. 1993, Sharks of Hawai'i: their biology and cultural significance. University of Hawaii Press, Honolulu. 126 pp.
- Tortonese, E. 1956. Leptocardia, Celostomata, Selachii. Fauna d'Italia 2, Calderini, Bologna, 334 pp.
- Tricas, T.C. & J.E. McCosker. 1984. Predatory behaviour of the white shark, Carcharodon carcharias, with notes on its biology. Proc. Calif. Acad. Sci. 43 (14): 221–238.
- Venizelos, L. 1993. Speed boats kill turtles in Laganas Bay. Zakynthos. Marine Turtle Newsletter 63: 15.
- Witzell, W.N. 1987. Selective predation on large cheloniid sea turtles by tiger sharks (Galeocerdo cuvieri). Japan. J. Herpetol. 12: 22–29