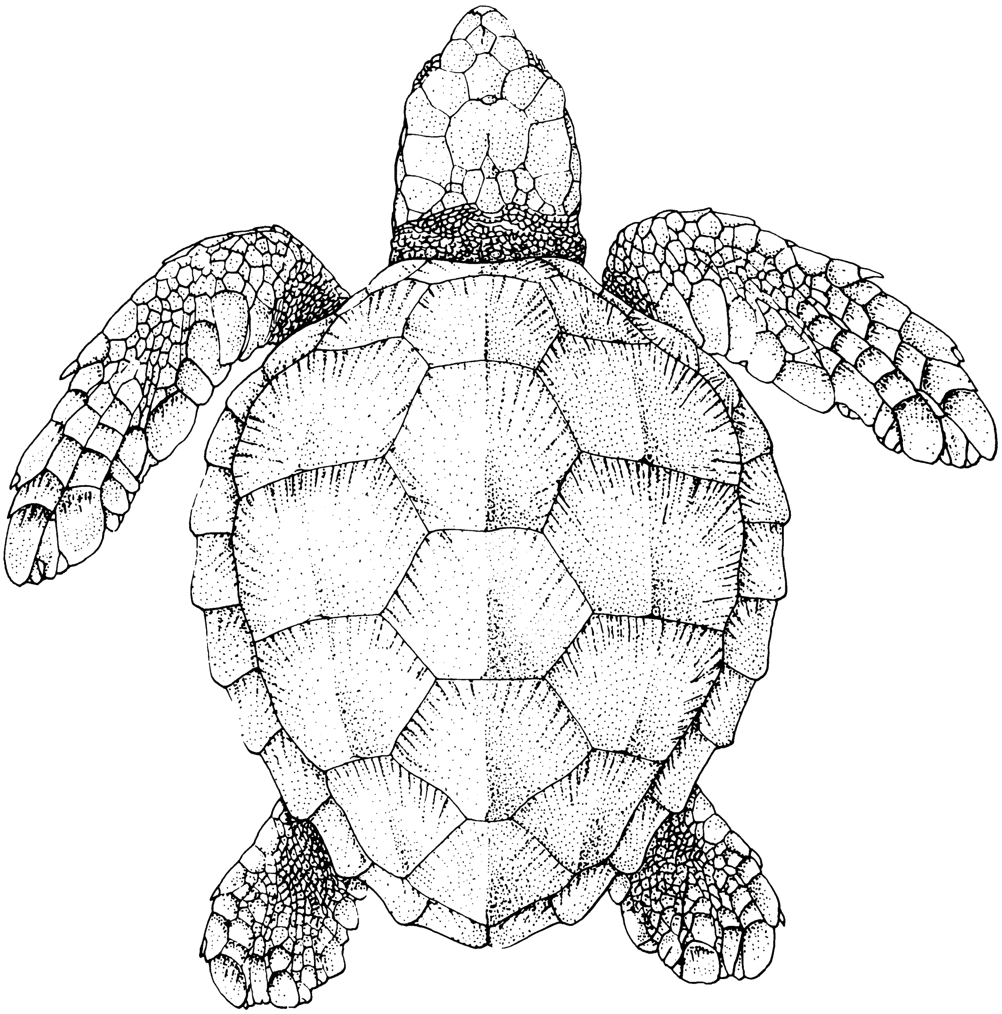
BIOLOGICAL REPORT 88(14)
MAY 1988

SYNOPSIS OF THE BIOLOGICAL DATA ON THE LOGGERHEAD SEA TURTLE *CARETTA CARETTA* (LINNAEUS 1758)



Fish and Wildlife Service
U.S. Department of the Interior

Biological Report

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Copies of this publication may be obtained from the Publications Unit, U.S. Fish and Wildlife Service, Washington, DC 20240, or may be purchased from the National Technical Information Service (NTIS), 5285 Port Royal Road, Springfield, VA 22161.

Library of Congress Cataloging-in-Publication Data

Dodd, C. Kenneth.
Synopsis of the biological data on the loggerhead sea turtle.

(Biological report ; 88(14) (May 1988))
Supt. of Docs. no. : I 49.89/2:88(14)
Bibliography: p.
1. Loggerhead turtle. I. U.S. Fish and Wildlife Service.
II. Title. III. Series: *Biological Report*
(Washington, D.C.) ; 88-14.
QL666.C536D63 1988 597.92 88-600121

This report may be cited as follows:

Dodd, C. Kenneth, Jr. 1988. Synopsis of the biological data on the Loggerhead Sea Turtle *Caretta caretta* (Linnaeus 1758). U.S. Fish Wildl. Serv., *Biol. Rep.* 88(14). 110 pp.

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May 1988

Synopsis of the Biological Data on the Loggerhead Sea Turtle *Caretta caretta* (Linnaeus 1758)

by

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FAO Synopsis NMFS-149

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Preparation of this Synopsis

This review is the first to collate and synthesize the published data on the biology and management requirements of the loggerhead sea turtle. It is likely that much additional information may be found in little known or difficult to obtain unpublished reports or governmental documents. With the publication of this synopsis, it is hoped that those working on loggerhead projects will be stimulated to publish their information and thus make it available to biologists and resource managers who need it to plan for the conservation of this threatened species. General reviews of loggerhead biology have been provided by Carr (1952), Ernst and Barbour (1972), Hendry et al. (1982), and Nelson (1986). This review follows the FAO synopsis format prepared by Rosa (1965). The purpose of the FAO synopses is to make available existing data to biologists and, by doing so, to draw attention to gaps in our knowledge and thus stimulate research in areas needing study.

Governments and conservation organizations throughout the world have designated the loggerhead and other species of sea turtles as vulnerable or threatened species in need of management in order to ensure continued survival and evolutionary potential. The widespread distribution of the species, its elusive life history, the many unknowns concerning its biology and habitat requirements, and the global threats to the oceanic ecosystem illustrate the complexity in formulating effective management strategies.

I thank the many individuals who assisted me in bringing together these literature sources, particularly Kay Lindgren and Bert Charest of the National Ecology Research Center. I especially thank the following who generously donated reprints, translated articles, or reviewed the manuscript: Mehmet K. Atatür, George Balazs, Karen Bjorndal, Richard Byles, Heike Charest, Nat Frazer, Carol Hahn, Terry Henwood, Kazuo Horikoshi, George Hughes, Anne Meylan, Jeffrey Miller, Larry Ogren, David Owens, Peter Pritchard, J. Perran Ross, Hobart S. Smith, Rosalie Vaught, Myrna Watanabe, Jeanette Wyneken, and George Zug. Susan Strawn and Bert Charest prepared the figures. Preparation of this synopsis was supported by a grant from the Endangered Species Office, U.S. Fish and Wildlife Service, Albuquerque, New Mexico. I thank Jack Woody for arranging this support. This synopsis is dedicated to the memory of the late Archie F. Carr, Jr., who inspired me, as he inspired others, with his love of and concern for these giant reptiles.

Abstract

This synopsis compiles and reviews the available information on the identity, distribution, life history, populations, exploitation, protection, and management of the loggerhead sea turtle, *Caretta caretta* (Linnaeus 1758), a species threatened by exploitation and the alteration and destruction of its habitat.

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Testudo Caretta: Linnaeus, Syst. Nat., ed. 10, 1758, p. 197: "insulas Americanas," (restricted to Bermuda by Smith and Taylor, Bull. USNM 1950, 199, p. 16; to Bimini, Bahamas by Schmidt, University of Chicago Press 1953).

Testudo Cephalo: Schneider, Allgem. Naturgesch. Schildkr. 1783, p. 303: unknown (restricted to Charleston, SC by Smith and Taylor, Bull. USNM 1950, 199, p. 16).

Testudo nasicornis: Lacépède, Hist. Nat. Quadrup. Ovip. 1788, 1, table *Synopsis:* "mers du nouveau Continent, voisines de l'equateur," (restricted to Ascension Island by Smith and Smith, Syn. Herp. Mex. 1980, 6, p. 302).

Testudo Caouana: Lacépède, Hist. Nat. Quadrup. Ovip. 1788, 1, table *Synopsis* (substitute name for *Testudo caretta* Linnaeus 1758).

Chelone caretta: Brongniart, Essai Classif. Hist. Rep. 1805:27.

Chelonia Caouanna: Schweigger, Konigsberg. Arch. Naturwiss. Math. 1812, 1, p. 279 (typographical error according to Pritchard and Trebbau, Turt. of Venezuela 1984, p. 303).

Caretta nasuta: Rafinesque, Spec. Sci. Palermo 1814, 2, p. 66: Sicily.

Chelonia cavanna: Oken, Lehrb. Naturgesch. 1816, 3, p. 350.

Caretta atra: Merrem, Tent. Syst. Amphib. 1820, p. 17: "Isularum Adscensionis."

Caretta Cephalo: Merrem, Tent. Syst. Amphib. 1820, p. 18.

Caretta nasicornis: Merrem, Tent. Syst. Amphib. 1820, p. 18.

Chelonia caretta: Bory de Saint-Vincent, Resume d'Erpét. Hist. Nat. Rep. 1828, p. 79.

Testudo Corianna: Gray, Synops. Rep. pt. 1 Tortoises 1831, p. 53.

Chelonia pelasgorum: Valenciennes, *in* Bory de Saint-Vincent, Exped. Morée Zool. 1833, plate 6: beach between Arcadia and mouth of the Neda River, Greece.

Chelonia cephalo: Gray, Isis v. Oken 1829, 22, p. 201.

Chelonia (Caretta) cephalo: Lesson, *in* Bélanger, Voy. Ind.-Orient. Zool. 1834, p. 300.

Chelonia caouana: Duméril and Bibron, Erpét. Gen. 1835, 2, p. 553.

Chelonia (Thalassochelys) Caouana: Fitzinger, Ann. Wien. Mus. 1836 (1835), 1, p. 128.

Chelonia (Thalassochelys) atra: Fitzinger, Ann. Wien. Mus. 1836 (1835), 1, p. 128.

Thalassochelys caretta: Bonaparte, Arch. Naturgesch. 1838, 4, p. 64.

Chelonia (Caouana) cephalo: Cocteau, *in* Cocteau and Bibron *in* Ramon de la Sagra, Hist. Fis. Pol. Nat. Cuba, IX, 1838, 1, p. 31.

Halichelys atra: Fitzinger, Syst. Rep. 1843, p. 30.

Caounana Caretta: Gray, Cat. Tort. Croc. Amphisb. Brit. Mus. 1844, p. 52.

Caouana elongata: Gray, Cat. Tort. Croc. Amphisb. Brit. Mus. 1844, p. 53: unknown (restricted to Ascension Island by Smith and Smith, Syn. Herp. Mex. 1980, 6, p. 303).

Thalassochelys Caouana: Agassiz, Contrib. Nat. Hist. U.S. 1857, 1, p. 384.

Thalassochelys corticata: Girard, U.S. Explor. Exped. 1858, 20 Herpetol., p. 431: Funchal, Madeira.

Chelonia corticata: Strauch, Mém. Akad. Imper. Sci. St. Pétersb. ser. 7, 1862, 5(7), p. 19.

Thalassochelys elongata: Strauch, Mém. Akad. Imper. Sci. St. Pétersb. ser. 7, 1862, 5(7), p. 63.

Thalassiochelis caouana: Nardo, Atti Inst. Ven. Sci. Lett. Arti. 1864, (3)9, p. 1421.

Eremonia elongata: Gray, Proc. Zool. Soc. Lond. 1873, p. 408.

Caretta caretta: Stejneger, Ann. Rep. U.S. Natl. Mus. 1904, 1902, p. 715.

Thallasochelys cephalo: Barbour and Cole, Bull. Mus. Comp. Zool. Harvard 1906, 50, p. 148.

Caretta caretta caretta: Mertens and Muller, Abh. Senckenberg. Naturf. Ges. 1928, 41, p. 23.

Caretta gigas: Deraniyagala, Ceylon J. Sci. sect. B 1933, 18, p. 66: Gulf of Manaar, Ceylon.

Caretta caretta gigas: Deraniyagala, Tetrap. Rep. Ceylon 1939, 1, p. 164.

Caretta caretta tarapacana: Caldwell, Los Angeles Co. Mus. Contrib. Sci. 1962, 61, p. 24.

Chelonia cahuano: Tamayo, Inst. Mex. Inv. Econ. 1962, p. 373.

Caretta careta: Tamayo, Inst. Mex. Inv. Econ. 1962, p. 373.

The synonymy is based on information from Brongersma (1961), Wermuth and Mertens (1977), Smith and Smith (1980), Cogger (1983*b*), Pritchard and Trebbau (1984), Frazier (1985), and Wallin (1985). There is considerable variation between synonymies.

Wallin (1985) argued that inasmuch as Linnaeus' (1758) concept of *Chelonia mydas* included both *Eretmochelys imbricata* and *Caretta caretta* and that surviving type material included both *C. mydas* and *C. caretta*, the Linnaean species name *caretta* was not available for *C. caretta* as currently recognized. He stated that the name *caretta* was available in Walbaum (1782) and that the correct citation should be *Caretta caretta* Walbaum, 1782. This interpretation was disputed by Pritchard (personal communication) who contended Walbaum was not describing *Caretta* but merely restating Linnaeus' description.

The synonymy follows Yañez (1951) and Frazier (1985) in relegating material described as *Thalassiochelys tarapacona* by Philippi (1887) to *Lepidochelys olivacea*. Frazier (1985) provided a synonymy of specimens previously considered *Caretta* from South America which should henceforth be considered synonymous with *Lepidochelys*.

1.2 Taxonomy

1.2.1 Affinities

- Suprageneric
  - Phylum Chordata
    - Subphylum Vertebrata
      - Superclass Tetrapoda
        - Class Reptilia
          - Subclass Anapsida
            - Order Testudines
              - Suborder Cryptodira
                - Superfamily Chelonioidae
                  - Family Cheloniidae
- Generic

Genus *Caretta* (from Wermuth and Mertens 1977; Smith and Smith 1980; Cogger 1983*b*)

Caretta Rafinesque, Spec. Sci. Palermo 1814, 2, p. 66. Type: *Caretta nasuta* Rafinesque, 1814 (by monotypy).

Chelonia (Thalassochelys) Fitzinger, Ann. Mus. Wien 1835, 1, p. 121, 128. Type: *Testudo caouana* Lacépède, 1788 = *Testudo caretta* Linnaeus, 1758 (by subsequent designation by Fitzinger 1843, p. 30; explicitly proposed as a subgenus).

Thalassochelys Bonaparte, Arch. Naturgesch. 1838, 4, p. 142 (first use as a full genus).

Caouana Cocteau, *in* Ramon de la Sagra, Hist. Fis. Pol. Nat. Cuba, IX, 1838, 1, p. 31. Type: *Testudo caouana* Lacépède, 1788 (by tautonymy).

Halichelys Fitzinger, Syst. Rep. 1843, p. 30. Type: *Caretta atra* Merrem, 1820 (by original designation).

Eremonia Gray, Proc. Zool. Soc. Lond. 1873, p. 408. Type: *Caouana elongata* Gray, 1844 (by monotypy).

?*Pliochelys* Portis, privately printed 1890, p. 17, 18, 30. Type: *Pliochelys derelicta* Portis, 1890 (by monotypy).

?*Proganosaurus* Portis, privately printed 1890, p. 25, 30. Type: *Proganosaurus pertinax* Portis, 1890 (by monotypy).

Both *Pliochelys* and *Proganosaurus* were described by A. Portis, in a privately printed booklet, based on Pliocene fossils in Italy. *Pliochelys* was described on the basis of a small fragment of shell and *Proganosaurus* on the basis of a single vertebra. Romer (1956), citing the date of publication as 1891, questionably placed both in synonymy with *Caretta* without discussion, while neither was placed by Mlynarski (1976). Other authors have aligned *Proganosaurus* with the pleurodires (see discussion in Smith and Smith 1980).

- Generic

Genus *Caretta* monotypic, see specific diagnosis.

- Specific

Diagnosis. Two pairs of prefrontal scales; carapace elongated, somewhat tapered posteriorly, and thickened above caudal region; dorsal scutes not imbricate, except in some young specimens; adult vertebral scutes smooth, although small turtles have projections toward the rear of lateral and vertebral scutes (best defined on vertebrals); five pairs of pleurals, first contacting the precentral; usually three or four inframarginal laminae enlarged and poreless; two claws on each flipper as hatchlings; head very broad and triangular with powerful jaws; carapace reddish-brown; plastron yellowish-white to yellowish-brown. Detailed descriptions are in Deraniyagala (1930, 1939, 1953), Carr (1952), Loveridge and Williams (1957), Brongersma (1961, 1972), Ernst and Barbour (1972), Hughes (1974*b*), Smith and Smith (1980), Pritchard et al. (1983), and Pritchard and Trebbau (1984).

1.2.2 Taxonomic status

The loggerhead turtle is a morpho-species.

1.2.3 Subspecies

Deraniyagala (1933) described the Indo-Pacific red-brown loggerheads as *C. gigas* to distinguish them from the Atlantic red-brown loggerheads (*C. caretta*) and the olive-brown loggerheads (i.e., ridleys), which he also placed within the genus *Caretta*. The diagnostic characteristics of the Indo-Pacific red-brown species were said to be the higher number of marginal scutes in *C. gigas* (13 as opposed to 12 in *C. caretta*) and the greater variation in the number of neural bones in *C. gigas* (7-12 as opposed to 7-8 in *C. caretta*). Deraniyagala (1939) later declared *gigas* to be a subspecies of *C. caretta* after examining a series of museum specimens from a wide geographic area, and at the same time resurrected *Lepidochelys* Fitzinger (1843) for the olive-brown loggerheads.

In 1943, Deraniyagala further subdivided *Lepidochelys* into two subspecies, *L. olivacea olivacea* and *L. olivacea kempi*, and reaffirmed the validity of *C. c. gigas*. All four taxonomic entities were placed within Gray's (1825) family Carettidae to distinguish them from the family Cheloniidae (*Chelonia* and *Eretmochelys*). [Note, however, that Deraniyagala (1934) had previously used the family Carettidae to include the genera *Eretmochelys*, *Colpochelys*, and *Caretta.*] He later placed these four subspecies in the subfamily Carettinae (Deraniyagala 1953), although the first mention of the subfamily Carettinae actually appeared in Deraniyagala (1952) without explanation or subfamilial definition. Subsequent papers continued to maintain that *C. c. gigas* was distinct from *C. c. caretta*, although no new diagnostic characters were added (Deraniyagala 1945, 1946).

The range of *C. c. gigas* initially was thought to include only the Indo-Pacific Ocean to Western Australia (Deraniyagala 1933), but was later expanded to include China and the East Indies (possibly based on misidentified *Lepidochelys*; Nishimura 1967) and South Africa (Deraniyagala 1939), west Africa (Deraniyagala 1943; Villiers 1958 [who nevertheless expressed doubt as to the validity of *gigas*]), the Pacific coast of Mexico (Shaw 1947), and Europe (Deraniyagala 1952). *C. c. caretta* was considered to be the subspecies in the western Atlantic region (Carr 1952), although Carr (1952) believed that southern Africa marked the boundary between the subspecies *gigas* and *caretta*. Deraniyagala (1952) considered redbrown loggerheads in Europe possibly to have been derived from a breeding colony in the Azores rather than rafting on currents from the United States.

The diagnostic characters used to distinguish *C. c. gigas* from *C. c. caretta* are not valid. Brongersma (1961), using data on marginals from Caldwell et al. (1959*a*), Willgohs (1952), Cadenat (1949), Carr (1942, 1952), Deraniyagala (1946), and Scott and Mollison (1956), in addition to counts made on museum specimens, showed that the average number of marginals varied as follows: western Atlantic—12.62; western Europe—12.71; Senegal—12.83; Mediterranean—12.57; Indo-Pacific—12.78. Pritchard (1979) added counts of 11.07 for Mexican Pacific loggerheads and 11.44 for Japanese specimens, although he did not count supracaudals. Brongersma (1961), Hughes (1974*b*), Pritchard (1979), and Pritchard and Trebbau (1984) concluded that such slight variation could not justify recognition of the two subspecies, and the name *gigas* was rejected in the checklist of Wermuth and Mertens (1977).

This conclusion is bolstered by the observations of Coker (1910) who, after studying scute variation in hatchling loggerheads in North Carolina, found ranges between 12 and 15 and concluded that no definite number of marginals could be considered normal. Brongersma (1961) believed Deraniyagala failed to include counts of the supracaudals, which other authors may have included, thus leading to the differences reported in the literature. Some authors (e.g., Ernst and Barbour 1972) continue to recognize *C. c. gigas*.

The number of neurals is also polymorphic, but a sufficient sample size has yet to demonstrate that Atlantic *Caretta* have consistently fewer neurals. Pritchard and Trebbau (1984) reported an average of 9.1 neurals in a sample of 11 Atlantic *Caretta*, the same value reported by Deraniyagala (1939) for a sample of 12 *Caretta* from Sri Lanka. Brongersma (1961) also concluded that the number of neurals was probably a poor diagnostic character since so few data were available over the range of the species.

Smith and Smith (1980) proposed that the name *Thalassiochelys tarapacona*, used to describe a new species of loggerhead on the Pacific coast of South America by Philippi (1887), had priority over the name *C. c. gigas*. They relegated *gigas* to a junior synonym, and used a misspelling of Philippi's name for the new subspecies, *C. c. tarapacana* (see also Frazier 1985). While acknowledging Brongersma's (1961) observations, they stated that the literature was "now sufficiently massive to justify that the Indo-Pacific and Atlantic populations are indeed differentiated at the subspecific level." They distinguished the Indo-Pacific subspecies by a suite of characters, including the following: vertebrals II and III relatively broad, supracaudals never longer than wide, plastron much lighter than carapace in young, carapace indented dorsal to hindlimbs, lateral keel over all the costals, neck light with a dark vertebral streak, usually three or more pleurals in contact mesially, usually nine or more neurals, peripherals III not contacted by a rib, and larger adults than *C. c. caretta*. Hughes (1974*b*) and Pritchard and Trebbau (1984) noted that none of these characters has been confirmed and that there is no basis for considering the Indo-Pacific loggerheads to be larger than Atlantic loggerheads.

In addition, Yañez (1951) and Frazier (1985) have clearly demonstrated that Philippi's (1887) description was based on misidentified specimens of *Lepidochelys olivacea*. Hence, the name *Thalassiochelys tarapacana* is a synonym of *L. olivacea* and thus is unavailable for the Indo-Pacific red-brown loggerhead even should subspecific status eventually be found warranted. Until the characters identified by Smith and Smith (1980) can be verified or until other significant differences can be found in populations of *Caretta*, the species *Caretta caretta* should be considered monotypic.

1.2.4 Standard common names

From Pritchard et al. (1983): loggerhead (English); logrit (Caribbean English); caguama, cabezona, jabalina (Spanish); caouane, caouanne (French); avo de tartaruga (Portugese-Brazil); onechte karet (Dutch-Surinam).

Other common names: aka-umigame (Japanese—Nishimura 1967); cardon (Spanish—Roze 1956); tortuga franca (Spanish, Argentina—Freiberg 1981); tartaruga del mar, uruana, surana (Portugese, Brazil—Freiberg 1981); falso carey (Spanish—Cornelius 1982); Karettschildkrote (German); remani (Arabic—Ross 1979); tao-ya, tao-charmed (Thai—Phasuk and Rongmuangsart 1973; Nutaphand 1979); and tartaruga caretta (Italian).

Vernacular names used within certain localized geographic regions or by indigenous peoples are provided in the following references: Brazil (Ferreira de Menezes 1972); French Guiana (Fretey and Renault-Lescure 1978); Lesser Antilles (Meylan 1983); Madagascar (Vaillant and Grandidier 1910); Mozambique (Hughes 1971*a*); New Guinea (Rhodin et al. 1980); Seychelles (Frazier 1971, 1984*b*); South Africa (Hughes 1974*b*); South America (Mittermeier et al. 1980); Sinhalese-speaking peoples (Deraniyagala 1939); Tamil-speaking peoples (Deraniyagala 1939; Jones and Fernando 1973; Valliappan 1973); Tanzania (Frazier 1976); and Venezuela (Brownell 1974).

The name *Caretta* is a latinized version of the French word "caret," meaning turtle, tortoise, or sea turtle (Smith and Smith 1980). The name caret or carey (Spanish) is usually associated in the vernacular with the hawksbill (*Eretmochelys imbricata*) rather than the loggerhead, and the name transfer probably resulted from Linnaeus' confusion over the identity of these species (Brongersma 1961; Wallin 1985).

1.2.5 Definition of size categories

Size categories for loggerhead turtles are defined as follows:

hatchling—from hatching to the first few weeks of life as it begins rafting on currents for the life stage known as the "lost year;" attains about 10 cm straight-line carapace length (SLCL); characterized by the presence of the umbilical scar.

juvenile—the pelagic rafting life stage. The center of dorsal scutes is elevated forming a sharp keel or spine, to approximately 40 cm SLCL.

subadult—from the end of the pelagic rafting stage to the onset of sexual maturity, to 70-90 cm SLCL in females, depending on the population.

adult—attainment of reproductive maturity at >70-90 cm SLCL, depending on population (Table 7); the size at sexual maturity for males is assumed to be similar to that of females.

1.3 Morphology

1.3.1 External/internal morphology and coloration

General external loggerhead morphology is described in Deraniyagala (1930, 1939, 1953), Carr (1952), Loveridge and Williams (1957), Brongersma (1961, 1972), Ernst and Barbour (1972), Hughes (1974*b*), Smith and Smith (1980), Pritchard et al. (1983), and Pritchard and Trebbau (1984). Good illustrations are found in Deraniyagala (1939), Brongersma (1972), Marquez (1978*a*), and Pritchard and Trebbau (1984). See section 1.2.1.

The identification of loggerhead subspecies was based on alleged morphological differences in the number of neurals and marginal scutes between western Atlantic and other populations (section 1.2.3). The following section will cover references on morphometric data, coloration, photographs, geographic locations, and size classes.

Morphometric measurements of loggerheads are presented in the following sources: Deraniyagala (1930, 1939, 1953), Sri Lanka, hatchlings, subadults, adults; Carr (1952), Solomon Island, hatchlings; Fahy (1954), North Carolina, adults; Caldwell et al. (1955), Florida, hatchlings; Caldwell (1959), South Carolina, hatchlings, adults; Caldwell et al. (1959*a*), Georgia, adult females; Caldwell (1962*b*), Georgia, hatchlings; Nishimura (1967), Japan, hatchlings; Hughes et al. (1967), South Africa, hatchlings, adult females; Hughes and Mentis (1967), South Africa, hatchlings, adult females; Kaufmann (1968, 1973, 1975*b*), Colombia, hatchlings, adult females; Hughes (1970*a*, 1971*d*, 1972, 1974*b*, 1975*a*), South Africa, hatchlings, adults; Gallagher et al. (1972), Florida, adult females; Brongersma (1972), Europe (strandings), juveniles, subadults, adults; Hughes and Brent (1972), South Africa, adult females; Graham (1973), Maryland, hatchlings; Worth and Smith (1976), Florida, adult females; Davis and Whiting (1977), Florida, adult females; Ehrhart and Yoder (1978), Florida, adult females; Kraemer (1979), Georgia, hatchlings; Ehrhart (1979*c*, 1983), Florida, hatchlings, subadults, adults; Hirth (1980), Oman, adult females; Stoneburner (1980), North Carolina, Georgia, and Florida, adult females; Margaritoulis (1982), Greece, hatchlings; Mendonça and Ehrhart (1982), Florida, subadults, adults; Hirth (1982), Florida, adults, regression of log [length] versus log [carapace length]; Bjorndal et al. (1983), Florida, adult females; Frazier (1984*a*), Uruguay and Argentina, subadults, adults; Limpus et al. (1984), Queensland, hatchlings, adult females; Sutherland (1985), Greece, hatchlings, adult females; Limpus (1985), Queensland and Papua New Guinea, hatchlings, adults; Mapes (1985), Florida, adult females; Carr (1986*b*), Oceanic (in *Sargassum* lines), Azores, and Baleares Islands, juveniles; Meylan and Sadove (1986), New York, subadults; and Witherington (1986), Florida, adult females.

The loggerhead's carapace and plastron undergo substantial changes after hatching. Growth is allometric. Hatchlings have three dorsal keels on a roughly heart-shaped carapace and there are two longitudinal ridges on the plastron which disappear with age. In both hatchlings and juveniles, the vertebral scutes are wider than long, but as the turtle grows, the length increases relatively greater than the width. Eventually, vertebrals II through IV become longer than their width, although the increase in length does not occur simultaneously in all scutes or at the same rate (Brongersma 1972). A reversal of the length-to-width ratio is rare in vertebrals I and V, although it has been observed. Juvenile vertebrals are keeled with a knob-like process on the posterior portion of each keel (it is most distinct on the anterior vertebrals). By 35.0 cm SLCL, the knobs generally disappear although the keels are still present, and by 58.0 cm SLCL the keels also disappear (Brongersma 1972).

An account of hatchling and adult coloration of Indian Ocean loggerheads follows (Deraniyagala 1953):

hatchling—head reddish-brown dorsally; beaks and cheeks dark brown; neck yellow-ochre with dark neural band; carapace reddish-brown and darker between ridges; plastron lighter than carapace with diffuse dark margin.

adult—reddish-brown dorsally with diffuse yellow lateral band extending along head and merging into yellow of neck; orbits dark; plastron pale orange.

Deraniyagala (1939) provided additional notes on coloration of hatchlings and an adult female.

According to Caldwell (1959), there is a considerable range of variation in coloration in loggerhead hatchlings from South Carolina, even within the same clutch. The carapace is described as a yellowish buff through all shades of brown to gray-black. The coloration is not uniform, and is usually lighter on the margins of the carapace. The plastron varies from creamy white through gray-black mottled with white. Prominent points on the plastron are lighter than the grooved or flat areas. In South Africa, Hughes (1974*b*) described hatchling coloration as plain gray-brown when dry, and pale red-brown when wet. The underparts are dark brown, but the plastral shields are lighter in tone. By the time the turtle reaches 10 cm SLCL, the color is predominantly red-brown with streaking in either light or dark brown. Pritchard et al. (1983) showed three hatchlings that range from light brown to nearly black.

The carapace of loggerhead adults in the western Atlantic is also reddish-brown, but it may be tinged with olive, and the scutes are sometimes bordered in yellow. The bridge and plastron are yellow to cream-colored. The head is reddish to yellow-brown and the scales often are bordered in yellow. The jaws are yellow-brown, and the limbs and tail are dark centrally with yellow borders. The underside of the throat, limbs, and tail are also yellowish (Ernst and Barbour 1972). In Tongaland, South Africa, a streaked carapace is more common than a plain red-brown carapace (Hughes 1974*b*). Streaking has also been recorded in the Sri Lankan *Caretta* (Deraniyagala 1939).

Albinism has been reported in embryos and hatchlings from Florida (Lee 1969; Pond 1972; McGehee 1979; Witherington 1986; Ehrhart and Witherington 1987), North Carolina (Ferris 1986), South Carolina (Caldwell 1959), South Africa (Hughes et al. 1967; Hughes and Mentis 1967), and Australia (Miller 1982; Limpus 1985). Cranial abnormalities are often associated with albinism (Caldwell 1959; Hughes et al. 1967; Hughes and Mentis 1967; Pond 1972; McGehee 1979; Miller 1982) although albinism per se is not necessarily lethal. One albinistic or amelanic adult female has been reported to nest in Australia (Limpus et al. 1979*b*).

Color descriptions of the loggerhead are presented in the following sources: Deraniyagala (1930, 1939, 1953), Sri Lanka, hatchlings, subadults, adults; Carr (1952), western Atlantic, adults; Stebbins (1954), western North America, hatchlings, adults; Villiers (1958), west Africa, adults; Caldwell (1959), South Carolina, hatchlings; Ernst and Barbour (1972), United States, adults; Hughes (1974*b*), South Africa, hatchlings, adults; Cogger (1983*a*), Australia, hatchlings, adults; Pritchard and Trebbau (1984), western Atlantic, hatchlings, subadults, adults; and Fretey (1986), Mediterranean, hatchlings, adults. Note, however, that the color description given by Deraniyagala (1930) is a combination of color characters for *Caretta* and *Lepidochelys* which he considered synonymous at the time.

Photographs illustrating general external morphology and color of loggerheads are presented in the following sources: Coker (1906), North Carolina, nesting female, hatchlings; McAtee (1934), Georgia, frontal view of nesting female; Pope (1939), western Atlantic, dorsolateral and plastral views of subadult; Carr (1952), western Atlantic, dorsolateral view of adult female, plastron and head of adult, carapace of juvenile and subadult; Willgohs (1952), Norway, adult carapace and plastron; Wood (1953), captive adults, copulating; Roze (1956), Islas Los Roques, subadult carapace; Villiers (1958), west Africa, head, carapace, plastron, frontal view, hatchling; Caldwell (1960), United States, head of hatchling, carapace and plastron of hatchlings and subadults; McAllister et al. (1965), South Africa, hatchlings; McCann (1966), New Zealand, juvenile, subadult [Note: Plate IV, No. 3, purporting to be a loggerhead is actually an olive ridley]; Bustard (1968*a*, 1968*b*, 1969*a*, 1976), Australia, nesting female, head of nesting female; LeBuff (1969), Florida, hatchlings, nesting adult, head of nesting female; Flores (1969), Venezuela, subadult (?) carapace and plastron; Hughes (1971*a*), Mozambique, female on beach; Frazier (1971), Seychelles, adult head and carapace; Cardona and de la Rúa (1971), Cuba, frontal view of adult, subadult, hatchlings; Abascal (1971), Cuba, adult in water (cover), nesting; Bustard et al. (1975), Australia, nesting female; Ernst and Barbour (1972), United States, dorsolateral view of subadult and nesting female, adult plastron, adult head, hatchling; Brongersma (1972), Europe, dorsal and lateral views of subadults, vertebral keels; Bustard (1972), Australia, nesting female, adult head; Uchida (1973), Japan, frontal and lateral view of head, nesting female; Hughes (1974*a*), South Africa, dorsal view of hatchling, barnacles on hatchlings and subadults; Hughes (1974*b*), South Africa, female in surf; Rebel (1974), western Atlantic, hatchlings, juveniles, subadults, adults; Massa (1974), Mediterranean, subadult (?); Fretey (1976), French Guiana (?), female on beach; Hughes (1977), South Africa, head and carapace of nesting female; Anonymous (1977), Japan, nesting female; Limpus (1978), Australia, adults underwater; Seyfert (1978), Florida, dead adult; Di Palma (1978), Lampedusa Island, hatchlings; Pritchard (1979), western Atlantic, adults nesting, swimming and copulating, hatchling swimming; Rudloe (1979), Florida (?), adults swimming and on beach, copulating pair; Carr (1979), western Atlantic, frontal view of subadult; Nutaphand (1979), Thailand, hatchling, head of hatchling; Sengoku (1979), Japan, adult female nesting; Lipske (1979), Georgia, frontal view of adult, hatchlings; Stone (1979), Florida, close-up of head, female nesting; Behler and King (1979), adult on beach; Martof et al. (1980), Virginia, dorsolateral view of subadult; Patnaude (1980), Florida, juvenile swimming; Rudloe (1981), Florida, plastron, mutilated adults and subadults; Freiberg (1981), western Atlantic, swimming adult; Garmon (1981), Georgia, adult nesting; Miller (1982, 1985), Australia, developmental stages, malformed embryos; Sella (1982*b*), Israel, carapace of subadults; Timko and Kolz (1982), Mississippi, adult swimming; Demetropoulos and Hadjichristophorou (1982), Cyprus, hatchlings; Stone (1983), Florida, head, carapace of nesting females, hatchlings; Cogger (1983*a*), Australia, nesting female, hatchling; Pritchard et al. (1983), western Atlantic, adult carapace and plastron, juvenile swimming, hatchling carapace and plastron; Meylan (1983), Lesser Antilles, subadult carapace and plastron; Pritchard and Trebbau (1984), western Atlantic, adult swimming, nesting female, adult head, hatchling head, adults in courtship and copulating; Carr (1984), western Atlantic, juvenile plastron; Anonymous (1984*a*), Japan, adults, hatchlings; Rouse (1984), Florida, adult in mud; Downey (1984), Florida, adult head, posterior carapace, hatchlings; Ashton and Ashton (1985), Florida, adult female in surf, hatchlings; Bearse (1985); Gulf Stream in North Carolina, adults copulating; Salvador (1985), Mediterranean, adult, hatchlings; Fretey (1986), Mediterranean, nesting female; Carr (1986*a*), pelagic, hatchlings, juveniles; Carr (1986*b*), pelagic, juvenile carapace and plastron.

There have been few studies of the internal anatomy of the loggerhead sea turtle. Much of the early literature is obscure and published in German, such as Schimkewitsch's (1910) general anatomical account, which perhaps accounts for this oversight. A reference to the literature on the descriptive morphology of *C. caretta* is provided in Table 1.

There are two comprehensive guides to *Caretta* anatomy presently available. Rainey (1981) used black and white photographs to illustrate the locations of organ systems in a juvenile male *Caretta* and three other species of sea turtles. Numbers on the photographs correspond to a description of each organ system. Additional information is provided on data that should be recorded from a carcass, tissue sampling methods, and recommendations for dissection. Wolke and George (1981) presented a guide for conducting necropsies under field conditions. Line drawings supplement a description of dissection methods, and information on fixatives, equipment, and data forms is provided.

The bones of the shell of the loggerhead are described in detail by Pritchard and Trebbau (1984). The carapace is illustrated in Deraniyagala (1939), Zangerl and Turnbull (1955), Zangerl (1958), and Pritchard and Trebbau (1984); and the plastral bones in Deraniyagala (1939), Zangerl (1958, 1980), and Pritchard and Trebbau (1984). The bones in the shell are thick, and the pleurals contact the peripherals by way of free tips at the end of the ribs. The nuchal is large and notched laterally. The neural bones (usually 7–11) are narrow, forming a continuous series anteriorly; posteriorly they are highly variable. Each neural bone usually has a vertebral centrum attached to the ventral surface. Secondary fragmentation of the neural series has occurred independently several times in the Cheloniidae, including *Caretta* (Deraniyagala 1939; Zangerl 1969).

The carapace of *Caretta* normally has two suprapygal bones and a single pygal that is notched posteriorly, although Deraniyagala (1939) noted up to four suprapygals in some individuals. The shell is very thick at the suprapygal–pygal suture. There are 8 pairs of pleural bones, each with a rib, and usually 12 pairs of peripheral bones (Fig. 1). Rhodin et al. (1984) pointed out that previous authors had confused kyphosis with scoliosis in interpreting the spinal deformity section of Coker's (1910) paper on *Caretta*. Hughes (personal communication) also found a loggerhead with a deformed spine, but misidentified it as an olive ridley. These are the only reported incidences of spinal deformities in the species.

The plastron contains nine bones. The hyoplastra and hypoplastra are similar in shape, with interdigitating projections on the anterolateral faces of the hyoplastra and posterolateral faces of the hypoplastra. The epiplastra are reduced, and the entoplastron is elongate. The xiphiplastra are also elongate and nearly straight (Fig. 2).

Both the carapace and plastron of the loggerhead are heavily keratinized as a protective barrier against attack and the environment. The epidermis contains the pigment cells, and is much thicker on the plastron of the loggerhead compared with that of the green turtle (*Chelonia mydas*). The keratin is of the hard variety and assists in reducing frictional drag in water (Solomon et al. 1986). These authors provide photographs of

Table 1. *Literature summary of papers on the descriptive morphology of* Caretta caretta.

Subject	Reference	Subject	Reference
Adrenal	Holmberg and Soler (1942); Gabe (1970)	Hatchling morphology	Deraniyagala (1939); Caldwell (1959)
Adult morphology	Deraniyagala (1930, 1939); Carr (1952); Loveridge and Williams (1957); Brongersma (1961, 1972); Ernst and Barbour (1972); Hughes (1974*b*); Smith and Smith (1980); Pritchard et al. (1983); Pritchard and Trebbau (1984)	Heart/pulmonary artery	Sapsford (1978)
		Innervation: limbs	Poglayen-Neuwall (1953)
		Lacrimal glands	Schmidt-Nielsen and Fange (1958); Abel and Ellis (1966)
		Lung	Rothley (1930); Ludicke (1940)
		Lung: musculature	Shah (1962)
		Lymphatic system	Panizza (1833); Azzali (1958); Ottaviani and Tazzi (1977)
Alimentary canal	Thompson (1980)		
Anatomy: general	Schimkewitsch (1910); Rainey (1981); Wolke and George (1981)	Musculature: head	Poglayen-Neuwall (1953); Schumacher (1973)
		Musculature: hyolaryngeal	Schumacher (1973)
Arteries: cranial	Albrecht (1976)	Musculature: limbs	Sieglbauer (1909); Poglayen-Neuwall (1953); Walker (1973)
Bone: deformities	Coker (1910); Rhodin et al. (1984)		
Bone: growth rings	Zug et al. (1983, 1986)	Nose	Walker (1959); Parsons (1970)
Bone: histology	Rhodin (1985); Zug et al. (1986)	Oral cavity	Thompson (1980)
		Osteology: general	Deraniyagala (1939); Romer (1956); Pritchard and Trebbau (1984)
Brain: weight	Crisp (1855 *in* Plate l, 1979)		
Choanae	Parsons (1958, 1968)		
Cloacal bursae: absence	Smith and James (1958)	Osteology: limbs	Sieglbauer (1909); Walker (1973)
Digestive system	Jacobshagen (1920, 1937); Pernkopf and Lehner (1937); Parsons and Cameron (1977); Thompson (1980)	Osteology: shell	Zangerl (1969, 1980); Pritchard and Trebbau (1984)
		Osteology: skull	Gray (1869); Deraniyagala (1939); Gaffney (1979); Pritchard and Trebbau (1984)
Digestive tract: histology	Luppa (1977); Thompson (1980)		
Embryonic morphology	Ewert (1985); Miller (1982, 1985)	Paraphyseal	Owens and Ralph (1978)
		Penis	Zug (1966)
Epidermis/scutes	Solomon et al. (1986)	Pineal	Owens and Ralph (1978)
Eye	Underwood (1970)	Red blood cells	Frair (1977*a*, 1977*b*)

histological preparations of the carapace and epidermis, and a scanning electron microscope photograph of the carapace.

The skull of *C. caretta* is broad and massive (Fig. 3), and anchors the jaw musculature needed to crush mollusk shells. Gray (1869) compared the skull of the leatherback with other sea turtles and concluded that the differences were such as to place them in different families, the Sphargididae and the Cheloniadae, which included *Caretta*. A comprehensive description of the skull is provided by Deraniyagala (1939), Gaffney (1979), and Pritchard and Trebbau (1984). The skull is illustrated in the following references: Gadow (1901), line drawing of dorsal and ventral view; Deraniyagala (1939, 1953), line drawings of dorsolateral and ventral views of skull and lower jaw; Carr (1942), line drawing of palate; Cadenat (1949), dorsal, frontal, and lateral photograph of skull; Carr (1952), line drawings of upper palate, lower jaw, and plastral bones; Romer (1956), lateral view of skull; Villiers (1958), dorsal and ventral photograph of skull and lower jaw; Wermuth and Mertens (1961), line drawings of dorsolateral and ventral views; Ernst and Barbour (1972), dorsal, ventral, and lateral photographs of skull and lower jaw; Gaffney (1979), line drawings of palatal sutures, comparison of symphysis depths, palatal, lateral, and occipital views of skull; and Pritchard and Trebbau (1984), line drawings of dorsal, lateral, ventral views, and photograph of skull. Feuer (1970) provided a key to the skulls of

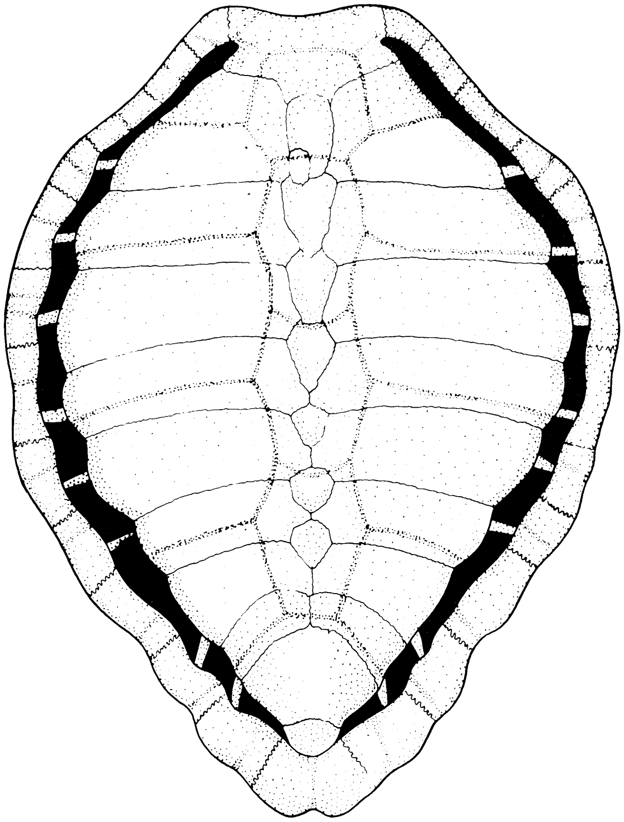

Fig. 1. Dorsal view of carapace of adult loggerhead (Deraniyagala 1939).

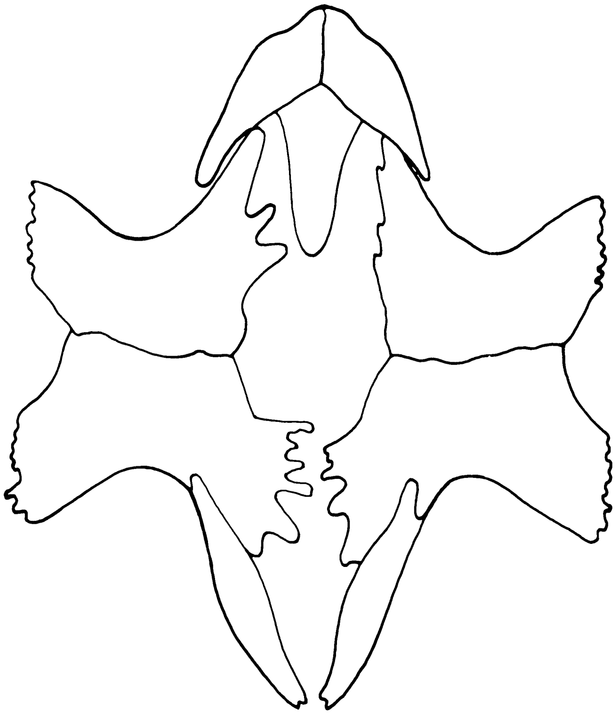

Fig. 2. Ventral view of plastron of adult loggerhead (Pritchard and Trebbau 1984).

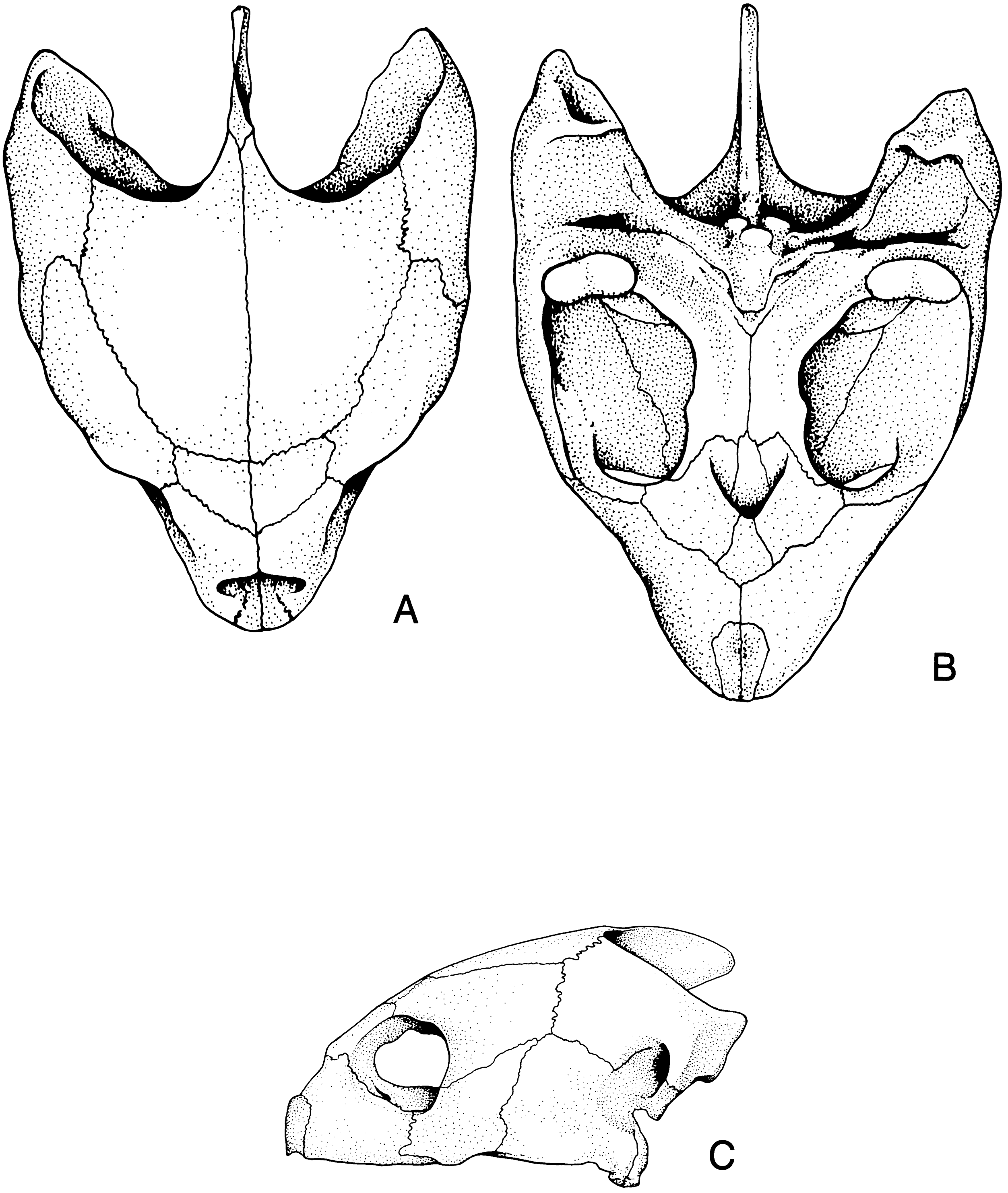

Fig. 3. *A–C* Dorsal, ventral, and lateral views of skull of adult male loggerhead (100 cm CL) from Sanibel Island, FL (Pritchard and Trebbau 1984).

North and Central American turtles, including sea turtles.

Gaffney (1979) mentioned the following features of the skull of *Caretta* which, although not necessarily unique to the genus, are different from other groups of turtles: (1) The depressor mandibulae may attach in a trough on the ventrolateral surface of the squamosal, (2) a ridge may develop within the origin area of the depressor mandibulae which reflects the division of the muscle into two heads, (3) the maxillae meet medially between the premaxillae and vomer, (4) serrations or small tubercles may form on the rhamphotheca but not on the maxilla bone, (5) the choana lies some distance behind the posterior termination of the vomer pillar, (6) the vomer contacts the premaxillae on its dorsal surface, but not ventrally, (7) the anterior two foramina on the exoccipital combine so that only two rather than three canals exit the skull for the hypoglossal nerve, and (8) the foramen aquaducti vestibuli is present. Poglayen-Neuwall (1953) reported the presence of the chorda tympani, but Gaffney (1979) was unable to locate the canalis chorda tympani mandibularis or its foramina in any living turtle.

The head muscles of *C. caretta* are reviewed by Poglayen-Neuwall (1953) and Schumacher (1973). The following muscles are illustrated by Poglayen-Neuwall (1953): pars media, pars profunda, pars superficialis, M. adductor mandibulae internus pterygoideus, M. depressor mandibulae, M. pseudotemporalis and associated tendons, and M. intramandibularis. Poglayen-Neuwall (1953) also provided an illustration of the trigeminal nerve structure in *Caretta*.

Schumacher (1973) included specific references to the following muscles and cartilages and how they attach in the loggerhead: tendons of the M. adductor mandibulae; pars superficialis of the M. adductor mandibulae externus; M. adductor mandibulae posterior; M. pseudotemporalis; M. intramandibularis (first described by Poglayen-Neuwall 1953); pars ventralis of the M. pterygoideus; and cartilago transiliens. The innervation of the trigeminal muscles in the loggerhead are also discussed, and an illustration of the mandibular branch of the trigeminal nerve is included. Further, the following illustrations of *Caretta* head musculature are provided: dorsal view of head with temporal roof partly resected and muscle fibers removed, basal view of external tendon, lateral view of M. adductor mandibulae externus, and lateral view of left temporal fossa after resection of temporal roof and removal of M. adductor mandibulae externus. Loggerheads lack pterygoid muscles (Poglayen-Neuwall 1953).

Schumacher (1973) also discussed the musculature of the hyoid arch, skin, and trunk in chelonians. Included are specific references to the M. depressor mandibulae, M. coracohyoideus, and the cricoid cartilage, Cartilago cricoidea, of the loggerhead. *Caretta* has seven tracheal rings composing the Cartilago thyreoidea.

The bones of the forearm and hand (Fig. 4) of *Caretta* are illustrated by Walker (1973), and the humerus by Zangerl (1958) and Zug et al. (1986: line drawings and photographs). Rhodin (1985) noted similarities in patterns of skeletal growth between *Caretta* and freshwater turtles. In both groups, noncalcified cartilage remains unvascularized, and a subphyseal plate is formed causing transient isolation of a metaphyseal cartilage cone. However, in the loggerhead, the central cartilaginous zone does not hypertrophy and remains uncalcified even as the peripheral zone of the subphyseal plate becomes ossified. Also, the basophilic network of Suzuki's tissue is localized in the zone of cartilaginous expansion in the center of the subphyseal plate rather than in the epiphysis (Rhodin 1985). These modifications may be related to the rapid growth in the uncalcified portion of the subphyseal plate.

Walker (1973) provided a general discussion of the pectoral and pelvic girdles of the Cheloniidae without mentioning *Caretta* specifically. The pelvis of the loggerhead is described by Deraniyagala (1939) as expanded and depressed, a common feature of aquatic turtles. The ilia is shortened and the upper ends curve posteriorly. The pubic bone supports a prepubic cartilaginous process anteriorly and each bone supports an outer lateral process. The ischia are much smaller than the pubic bones, and are separated by a cartilaginous septum. A line drawing of the pelvis is provided by Deraniyagala (1939). In *Caretta*, like other marine turtles, ossification of the tarsals is reduced. Bones of the pes are illustrated in Romer (1956).

The musculature of the appendages of the loggerhead has been described by Rudinger (1868), Sieglbauer (1909), Poglayen-Neuwall (1953), and Walker (1973). Walker (1973) summarized existing literature and added additional information on *Caretta* musculature, including descriptions of the M. supinator manus (reduced; see also Sieglbauer 1909), M. flexor carpi ulnaris (particularly powerful), M. palmaris longus, M. flexor carpi radialis, pronator teres (reduced; see also Sieglbauer 1909), Mm. lumbricales (reduced), M. adductor digiti minimi (absent), Mm. interossei volares, M. iliofemoralis (closely associated with the M. puboischiofemoralis), M. triceps femoris, M. adductor femoris, peroneus complex (M. peroneus anterior is normal;

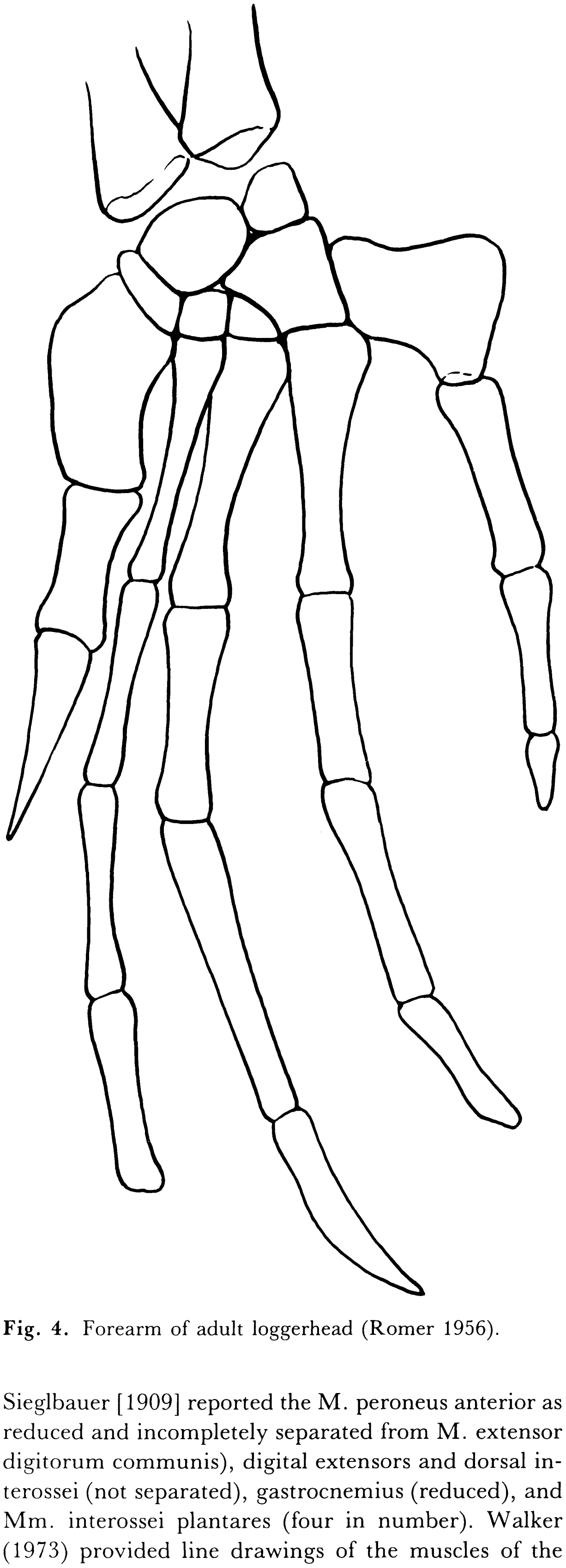

Fig. 4. Forearm of adult loggerhead (Romer 1956).

Sieglbauer [1909] reported the M. peroneus anterior as reduced and incompletely separated from M. extensor digitorum communis), digital extensors and dorsal interossei (not separated), gastrocnemius (reduced), and Mm. interossei plantares (four in number). Walker (1973) provided line drawings of the muscles of the forearm and hand, and the pelvis and thigh. Innervation to the limbs has been discussed by Poglayen-Neuwall (1953).

The alimentary canal, oral cavity, and intestinal morphology have been described by Thompson (1980). *Caretta* normally has a small papilla that varies in shape near the anterior end of the lateral choanal margin (Deraniyagala 1939; Carr 1942; Parsons 1958, 1968). Parsons (1958) was unable to ascribe a function for it in *Caretta*. It apparently is not present in all individuals since he was unable to locate it in three turtles (Parsons 1968). Black and white photographs are provided by Parsons (1958, 1968).

Although a substantial amount of recent work has centered on buoyancy and respiration (e.g., Davenport and Clough 1986), few studies have described the lung of *Caretta*. Rothley (1930) gave a general anatomical account of adaptations of reptiles to breathing, including *Caretta*, and Ludicke (1940) briefly mentioned *Caretta* in his comparative study of blood volume in the lungs and kidneys of snakes. Shah (1962) noted the absence of the M. striatum pulmonale in marine turtles, including *Caretta*, and provided a line drawing of the respiratory muscles.

Parsons and Cameron (1977) provided a general review of the digestive tract in chelonians. They cited Jacobshagen's (1920) description of the small intestine as plain, tall, and having a net-like pattern. The height of the folds vary, giving a false impression of a double pattern. Luppa (1977) noted that tubular glands in the stomach are combined into groups by connective tissue in the transition between gastric and intestinal epithelium. *C. caretta* lacks the normal ring-fold or funnel-shaped pyloric valve. Further, the longitudinal layer of the tunica muscularis decreases in thickness as one proceeds in the direction of the pylorus (Luppa 1977). Further descriptions of intestinal morphology were provided by Jacobshagen (1937), and the morphology of the esophagus and stomach were described by Pernkopf and Lehner (1937). *C. caretta* lacks cloacal bursae (Smith and James 1958).

There are no detailed descriptions of the heart or circulatory system of *Caretta* within the body. Sapsford (1978) described the pulmonary arteries and noted the presence of a muscular sphincter distal to the origin of the ductus Botalli. He speculated that this structure allows shunting blood from the right to the left through the heart during diving, and that such action may assist in the regulation of heat flux with the environment. Albrecht (1976) described the cranial arteries from 2 hatchlings and the cranial arterial foramina from

38 skulls. The cheloniids have generally the same patterns of arteries (illustrated in a diagram of *Chelonia mydas*) and foramina although some differences were noted. For instance, the canalis cavernosus opens lateral to the foramen nervi trigemini by way of the foramen arteriomandibulare in *Chelonia*, *Caretta*, and *Lepidochelys*, but differently in *Eretmochelys*.

The morphology of the lymphatic system has been described in detail by Panizza (1833) and Azzali (1958), and reviewed by Ottaviani and Tazzi (1977). Ottaviani and Tazzi (1977) provided information on the formation and descriptive morphology of the pericardial sinus, and described the loggerhead's lymphatic system in the following organs and tissues: lumbar trunk, cistern chyli, anterior limbs, esophagus, stomach, small intestine (including a photograph of the mesenteric collectors), large intestine, liver, gall bladder, adipose tissue, pulmonary and serosal nets (photograph), kidney, bladder, ovaries and oviducts, testes, and heart and spleen. They further discussed the lymphatic hearts (including photographs of gross morphology and histological sections), and provided a photograph of a lymphoid body in the cavity of a lymph heart. Azzali (1958) included black and white photographs of many parts of the lymphatic system of three species of turtles, including the loggerhead.

Other than for bone structure and musculature, there have been few studies of the cranial structures in *Caretta*. Crisp (1855 *in* Platel 1979) gave the weight of the brain of a 5,443 g animal as 2.7 g. Walker (1959) observed that loggerheads lacked specialized nasal flaps or valves, yet were able to close the nostril while submerged. Histological examination of nasal tissue showed large amounts of vascular tissue, and Walker (1959) speculated that closure of the nostril was effected by blood filling nasal sinuses, causing the tissues to swell and thus block seawater from entering. He provided photographs of the closed and open nostrils and of a slide showing the highly vascularized tissue.

The pineal-paraphyseal complex was described by Owens and Ralph (1978) in juvenile loggerheads. They considered it an ''impressively'' large structure, and described the presence of two pineal cell types corresponding to the neuroglial supportive cells and the secretory rudimentary photoreceptor cells of other amniotic vertebrates. A drawing and photographs of the saggital section of the pineal complex are provided.

Holmberg and Soler (1942) described the structure of the adrenal gland in the loggerhead. They noted that ''the connective tissue capsule forms an uninterrupted plate bridging the median line and resulting in a median coalescence of the two adrenal glands.'' Gabe (1970) gave the relative weight as 33 mg/100 g.

The eye of *Caretta* has 11-13 scleral ossicles, a markedly convex cornea, and 60 disposed ciliary processes (Underwood 1970). The cornea's curvature is slight and the lens is strongly curved. Some blood vessels are in the sclera at the level of Schlemm's canal. Bass and Northcutt (1975) described the pattern of retinal projections in six juvenile loggerheads, and note that the dorsal geniculate nucleus is far larger than that of other reptiles with the possible exception of snakes. There are 12 primary retinal targets in the diencephalon and mesencephalon, and their pattern is similar with freshwater turtles, although the differentiation varies between genera (Bass and Northcutt 1981). Loggerheads have a large, reddish-brown, globular, compound, branched, and tubular lacrymal gland in the corner of the eye, which is involved in salt excretion. The gland's gross morphology and histology have been described by Schmidt-Nielsen and Fange (1958) and by Abel and Ellis (1966). Abel and Ellis (1966) also provided extensive data on the histochemistry and fine structure of the gland.

The penis of the loggerhead is described by Zug (1966). The glans is formed by a U-shaped fold which is an enlarged continuation of the seminal ridges. The seminal groove is singular, and no sinuses are present. The penis of an *Eretmochelys* is illustrated, but Zug (1966) noted that the penes of all sea turtles are similar in structure.

1.3.2 Cytomorphology

Abel and Ellis (1966) described in detail the morphology of cells in the lacrymal glands of *Caretta* and *Chelonia*, and noted that it is similar between the two species. Two types of epithelial cells line the duct system: basal cells and goblet cells. The principal cells close to the arterial blood supply contain the highest concentration of oxidative enzymes and have modifications on their surface related to activity involving salt concentration and secretion.

Frair (1977*b*) reported that Atlantic loggerheads with longer carapace lengths have higher packed-cell volumes of red blood cells, larger red blood cells by length-width product and volume, lower red-cell counts, and probably more rounded red cells than turtles with smaller carapace lengths. Frair (1977*a*) provided data on erythrocytes of loggerheads for packed volume, size, and number (Table 2).

Owens and Ruiz (1980) described a method for obtaining blood samples from sea turtles through the dorsal cervical sinus, and cerebrospinal fluid through the foramen magnum without causing stress to the animals. Although Owens and Ruiz (1980) found difficulty using this method on hatchlings, Bennett (1986) found sampling blood through the dorsal cervical sinuses of hatchlings simple and atraumatic.

Gyuris and Limpus (1986) described a restraining device to immobilize sea turtles while obtaining muscle biopsies. Muscle masses, especially the triceps brachii and the brachialis inferior, were located by palpation and biopsies taken via a biopsy needle with a minimum of stress to the turtle.

The karyotype of *Caretta caretta* consists of 56 nearly identical chromosomes; sex chromosomes are unknown from this species (Bickham 1979).

1.3.3 Protein composition and specificity

The serum protein level of 14 *Caretta caretta* was found to be 4.7 g% (Frair 1964) while Musquera et al. (1976) gave a figure of 3.8 g% for a single individual. Immunoprecipitation tests indicated a close affinity among all sea turtles with *Caretta* aligning with *Lepidochelys* and *Eretmochelys*. Frair (1982) later noted the similarity between blood serum proteins of *Caretta*, *Eretmochelys*, and *Lepidochelys*, although proteins were more similar between *Chelonia*, *Caretta*, and *Lepidochelys* than between *Chelonia* and *Eretmochelys*. Sea turtles with longer carapace lengths have higher concentrations of total serum protein over a wide range of carapace lengths although in the largest turtles the concentration of total serum protein appears to drop (Frair and Shah 1982).

Friedman et al. (1985) compared the internal structures of deoxygenated and oxygenated hemoglobins of *Caretta* and *Chelonia* and found that sea turtle hemoglobins are structurally designed for efficient oxygen transport and release rather than storage. The structural feature involves an oxygen binding site that remains strained under all physiological conditions.

The kinetic properties of lactate dehydrogenases resemble those reported from homopolymers of most other vertebrates. However, *Caretta* M4 and H4 isoenzymes do not display similar sensitivities to substrate inhibition by pyruvate as the freshwater turtle *Pseudemys* sp. (Baldwin and Gyuris 1983).

Table 2. *Red blood cell data of Atlantic loggerhead sea turtles (Frair 1977*a*).*

Statistic	Packed cell volume ($cm^3/100\ cm^2$)	Length/width (μm)	Red cell count ($mm^3 \times 10^3$)
Mean	26.4 ± 0.8	$\frac{22.1 \pm 0.2}{13.4 \pm 0.2}$	429 ± 22
Range	19–40	$\frac{15.0–28.4}{8.0–18.8}$	292–650
Sample	54	26	21

Isoelectric focusing techniques as a tool for the identification of unknown samples of sea turtle meat is discussed by Braddon et al. (1982). These authors showed that muscle extract samples can be identified by protein banding patterns, and provided several figures of gel patterns of loggerhead and other species obtained at various pH and power ranges. Seven loggerhead samples showed excellent replication patterns while the eighth, a juvenile, showed extra bands indicative of embryonic blood proteins, such as fetal hemoglobin.

Electrophoretic techniques have been used to examine 13 proteins from loggerheads ($N = 106$) in the southeastern United States; heterozygosity averaged 3.4%, with 7.7% of the loci being polymorphic (Smith et al. 1978). The intergeneric similarity value was 0.21 between *Caretta* and *Chelonia mydas*. Smith et al. (1978) argued that the low level of variability in the loggerhead indicated that it is a "fine-grained" species, that is, a large, marine, temperate, migratory carnivore likely to encounter a variety of habitat conditions. Gyuris (1984 *in* Limpus 1985) was unable to distinguish mainland from island nesting populations of loggerheads in Australia using electrophoretic techniques.

Analysis of oil from *Caretta caretta* in Mexico showed that its fatty acids closely resembled fats of amphibians and other reptiles in its palmitic (21.8%) and myristic (6.6%) content, but contained a high content of stearic (15.5%) and palmitoleic acid (Giral and Marquez 1948). These authors also reported a low content of certain unsaturated acids (C18 and C20). Total acids make up 90% of turtle oil (Giral and Cascajares 1948; Giral 1955).

A summary of the literature on the biochemistry, genetics, and physiology of *Caretta caretta* is provided in Table 3.

Table 3. *Literature summary of papers dealing with the physiology, biochemistry, and genetics of* Caretta caretta.

Subject	Reference
Biochemistry: corticosterone	Schwantes (1986)
Biochemistry: LDH	Baldwin and Gyuris (1983)
Biochemistry: oils	Giral (1955); Giral and Cascajares (1948); Giral and Marquez (1948)
Biochemistry: steroids	Morris (1982)
Biocides: DDE, organochlorines	Clark and Krynitsky (1980, 1985); Fletemeyer (1980); McKim and Johnson (1983)
Biocides: other categories	Hillestad et al. (1974); Stoneburner et al. (1980)
Blood: chemistry (review)	Dessauer (1970)
Blood: chemistry, general	Lutz and Dunbar-Cooper (1987)
Blood: hemoglobin structure	Friedman et al. (1985)
Blood: O_2 affinity	McCutcheon (1947); Palomeque et al. (1977); Isaacks et al. (1978); Isaacks et al. (1982); Lapennas and Lutz (1979, 1982); Lutz and Lapennas (1982)
Blood: plasma concentration	Figler et al. (1986)
Blood: proteins	Frair (1964); Musquera et al. (1976); Frair and Shah (1982)
Blood: serology	Frair (1964, 1979, 1982)
Blood: serum corticosterone	Schwantes and Owens (1986)
Blood: serum testosterone	Wibbels et al. (1986*a*); Wibbels et al. (1987*a*)
Body fluids: general	Thorson (1968)
Chemoreception	Grassman and Owens (1981*a*, 1981*b*); Grassman (1984); Owens et al. (1986)
Colloid osmotic pressure	Scholander et al. (1968)
Dehydration	Bennett (1983); Bennett et al. (1986)
Drowning: time until	Parker (1925)
Eggs: chemistry	Yamauchi et al. (1984)
Eggs: water absorption	Cunningham and Hurwitz (1936)
Electrical activity	Šušic (1972)
Endocrinology	Owens and Morris (1985)
Gas exchange: adults	Lutcavage et al. (1987)
Gas exchange: eggs	Ackerman (1980)
Gas exchange: embryos	Ackerman (1981*a*, 1981*b*)
Gas exchange: nests	Ackerman (1977)
Genetic variation	Smith et al. (1978); Harry (1983); Gyuris (1984)
Gut: function	Birse and Davenport (1987)
Heart beat: diving	Lanteri et al. (1981)
Histochemistry: kidney	More (1977)
Histochemistry: lacrimal glands	Schmidt-Nielsen and Fange (1958); Abel and Ellis (1966)
H-Y antigen: cytotoxicity assay	Wellins (1987)
Hybridization	Kamezaki (1983)
Immune reaction	Wangersky and Lane (1960)
Immunocytochemistry	Pearson et al. (1983)
Karyotypes	Bickham (1979)
Nutrition	Bjorndal (1985)
Pineal: melatonin activity	Owens and Gern (1985)
Proteins: electrophoresis	Smith et al. (1978); Braddon et al. (1982)
Renal function: adaptation	Tercafs et al. (1963); Schoffeniels and Tercafs (1966)
Renal function: salts and water	Prange (1985)
Respiration: anoxia	Bentley and Lutz (1979); Lutz et al. (1980)
Respiration: diving	Lutz and Bentley (1985); Lutcavage (1987)
Respiration: lung volume	Milsom and Johansen (1975)
Retina: function	Bass and Northcutt (1975, 1981)
Sound reception	Lenhardt et al. (1983)
Thermal biology	Mrosovsky (1980); Spotila and Standora (1985)
Thyroid physiology	Wibbels et al. (1986*b*)
Techniques	
Blood sampling	Owens and Ruiz (1980); Bennett (1986)
Electrode implants	Kovacevic and Šušic (1971)
Electrophoresis	Braddon et al. (1982)
Muscle biopsies	Gyuris and Limpus (1986)
Sexing	Wibbels et al. (1987*a*)

2. DISTRIBUTION

2.1 Total Area

Loggerhead turtles are circumglobal, inhabiting continental shelfs, bays, lagoons, and estuaries in the temperate, subtropical and tropical waters of the Atlantic, Pacific, and Indian Oceans. The major nesting grounds are generally located in warm temperate and subtropical regions, with the exception of Masirah Island, Oman. Nesting does occur in tropical regions, but such nesting is scattered and represents a small fraction of the species' nesting efforts. Foraging areas are largely unknown, although warm temperate zone nesters are known to migrate to tropical waters in Australia and Africa after the nesting season.

Individual loggerheads have been reported in waters as far north as Newfoundland (Squires 1954) and northern Europe to the U.S.S.R. (Konstantinov 1965; Brongersma 1972) in the Atlantic, and the State of Washington, U.S.A. (Hodge 1982) and Peter-the-Great Bay in the Maritime Province of the U.S.S.R. (Terentjev and Chernov 1949). In the Southern Hemisphere, the loggerhead is found as far south as Tasmanian waters (Scott and Mollison 1956; Green 1971), to 42°S in New Zealand (McCann 1966; Robb 1980; Pritchard 1982*a*), and even to Stewart Island off southern New Zealand (Ballance et al. 1985-1986). In South America, loggerheads are known from as far south as Mar del Plata in Argentina (Frazier 1984*a*) on the east coast and to Coquimbo on the coast of Chile (Frazier and Salas 1982). Specific nesting locations are discussed in this section, listed in Tables 4 and 5, and delineated in Figures 5 and 6. The worldwide distribution of the loggerhead has been summarized by National Marine Fisheries Service (1978), Pritchard (1967, 1979), Sternberg (1981), Groombridge (1982), Ross (1982), and Mager (1985). Both nesting and nonnesting range extensions are many, and a brief summary by ocean follows.

In the northeastern Atlantic, there are widespread records of loggerheads from Europe, especially from the British Isles; strandings have been summarized by Brongersma (1972) and are primarily of juvenile and subadult turtles (Fig. 7). Additional observations have been recorded for Ireland (O'Riordan and Holmes 1978), Spain (Pascual 1985), and France (Fretey 1986). Loggerheads do not nest anywhere on the Atlantic coast of Europe.

In the Mediterranean, *Caretta* has been recorded from Spain, including the Baleares Islands (Salvador 1978, 1985; Pascual 1985; Carr 1986*b*), France (Euzet and Combes 1962; Euzet et al. 1972; Dumont 1974; Fretey 1975, 1986), Corsica (Bruno 1973; Dumont 1974: mostly 60-70 cm animals; Fretey 1975, 1986), Italy, including Sicily and Lampedusa Island (Doderlein 1881; Despott 1924; Bruno 1969, 1970, 1973, 1978; Brongersma 1972; Massa 1974; Bruno and Maugeri 1976-1977; Di Palma 1978; Honegger 1978; Argano and Baldari 1983; Gramentz 1986), Sardinia (Bruno 1969; Argano and Baldari 1983), Greece (Werner 1984 *in* Mertens 1961; Basoglu 1973; Honegger 1978; Marinos 1977, 1981; Margaritoulis 1982, 1983, 1985; Argano and Baldari 1983; Sutherland 1985; Langton 1987), Bulgaria (Beskov and Beron 1964; Basoglu 1973), the Adriatic (Steuer 1905), Turkey (Hathaway 1972; Basoglu 1973; Basoglu and Baran 1982; Geldiay et al. 1982; Sella 1982*a*; Argano and Baldari 1983), Israel (Basoglu 1973; Sella 1982*a*), Cyprus (Demetropoulos and Hajichristophorou 1982; Ross 1982; Argano and Baldari 1983; Demetropoulos and Lambert 1986), Egypt (Looss 1899, 1901, 1902; Baylis 1923; Sey 1977; Sella 1982*a*, Brongersma 1982), Libya (Bruno 1969; Pritchard 1979; Schleich 1987), and Tunisia (Argano and Baldari 1983).

According to Pritchard (1979), nesting probably occurs at scattered localities all along the north African coast, but has been recorded only for Tunisia and Libya. Nesting still occurs on Lampedusa Island, Cyprus, Greece (particularly on Zakynthos Island and perhaps at Korfu), Israel, and Turkey (see references in Tables 4 and 5). Bruno (1970) was told of dead hatchlings found on Isole Eolie, and Di Palma (1978) speculated that nesting might still occur on Isole Egadi. Fretey (personal communication) believes reports of nesting in Sicily to be in error. Fretey (1986) stated that loggerheads nested, or might still nest, at Aleria on the east side of Corsica although the last confirmed nesting in Corsica was in 1932 (Bruno 1973). Bruno (1969) and Honegger (1978) mentioned a number of nesting locations on the Italian coasts. Bruno (1978) showed a map with historic and present locations of records of sea turtles along the Italian coasts, but the map is a composite record for several species, and nesting is not necessarily indicated at each location.

On the west coast of Africa, there is little precise distributional information. Loveridge and Williams (1957) recorded loggerheads from Morocco, Senegal, Ivory Coast, Gabon, Zaire, Southwest Africa (Namibia), and questionably from Cameroon. Brongersma (1982) believed the records for Ivory Coast, Cameroon, Gabon, and Zaire were based on *Lepidochelys olivacea* rather than *C. caretta*. Additional records for Morocco were provided by Doumergue (1899) and Pasteur and Bons (1960), and *Caretta* is included in Pellegrin's

Table 4. *Nesting locations and nesting seasons for loggerhead sea turtles,* Caretta caretta. *(Not every reference contains specific mention of the nesting season although at least one of the references listed does so.*

Location	Month												Reference
	J	F	M	A	M	J	J	A	S	O	N	D	
Western Atlantic Ocean													
United States													
New Jersey							J						Brandner (1983)
Delaware							J						Mohr (1973)
Maryland							J						Graham (1973)
Virginia						J	J	A					Coker (1906); Carr (1952); Dodd (1978); Musick (1979*a*, 1979*b*)
North Carolina					M	J	J	A					Coker (1906); Coles (1914); Rebel (1974); Dodd (1978); Musick (1979*a*); Stoneburner (1981); Crouse (1984*a*, 1985); Ferris (1986)
South Carolina					M	J	J	A					Caldwell (1959); Caldwell et al. (1959*a*, 1959*b*); Dodd (1978); Hopkins et al. (1978); Stancyk et al. (1980); Talbert et al. (1980); Andre and West (1981)
Georgia					M	J	J	A					DeSola and Abrams (1933); Caldwell et al. (1959*a*, 1959*b*); Ragotzkie (1959); Caldwell (1962*b*); Johnson et al. (1974); Dodd (1978); Richardson (1978, 1982); Richardson et al. (1978*a*, 1978*b*); Kraemer (1979); Kraemer and Bennett (1981); Stoneburner (1981); Richardson and Richardson (1982); Frazer and Richardson (1985*a*, 1985*b*; 1986)
Florida (mainland)				A	M	J	J	A	S				Catesby (1731-1743); Loennberg (1894); Carr (1940); Caldwell et al. (1955, 1959*a*, 1959*b*); Routa (1968); LeBuff (1969, 1970, 1974); Gallagher et al. (1972); Worth and Smith (1976); Dodd (1978); Ehrhart and Yoder (1978); LeBuff and Hagan (1978); Ehrhart (1979*c*, 1982); McGehee (1979); Ehrhart (1980); Demmer (1981); Stoneburner (1981); Carr et al. (1982); Fritts and Hoffman (1982); Bjorndal et al. (1983); Meylan et al. (1983); Williams-Walls et al. (1983); Ehrhart and Raymond (1983); Raymond (1984*b*); Frazer and Ehrhart (1985); Kushlan (1986); Witherington (1986); Lund (1978, 1986); Ehrhart and Witherington (1987); Ehrhart and Raymond (1987); Provancha and Ehrhart

Table 4. *Continued.*

Location	Month J	F	M	A	M	J	J	A	S	O	N	D	Reference
													(1987); Conley and Hoffman (1987)
Florida (keys)				A	M	J							Fowler (1906); Audubon (1926); Pritchard (1982*b*)
Mississippi						J							Allen (1932); Carr et al. (1982)
Bahamas				A	M	J	J						Carr et al. (1982); Bacon et al. (1984)
Cuba[a]						J	J	A					Caldwell et al. (1955); Cardona and de la Rua (1971); Kermarrec (1976); Gavilan and Andreu (1983)
Mexico													
Quintana Roo					M	J	J	A					Ramos (1974); Rebel (1974); Marquez (1976, 1978*b*); Hildebrand (1982); Carr et al. (1982); Bacon et al. (1984).
Tamaulipas							J	A	S				Marquez (1978*b*); Carr et al. (1982); Hildebrand (1982, 1983)
Panama							J						Carr et al. (1982)
Colombia				A	M	J	J	A	S				Kaufmann (1966, 1968, 1971*b*, 1973, 1975*b*); Bacon et al. (1984)
Trinidad[a]				A	M	J	J	A	S				Rebel (1974); Pritchard and Trebbau (1984)
Grenada						J	J	A	S				Rebel (1974); Carr et al. (1982)
French Guiana	J	F	M	A	M	J	J	A	S				Pritchard (1971); Fretey (1976); Fretey and Renault-Lescure (1978); Pritchard and Trebbau (1984)
Brazil	J										N	D	Maximilian (1820); Hartt (1870); Bacon (1981); Pritchard and Trebbau (1984)
Eastern Atlantic Ocean													
Senegal							J	A	S	O			Cadenat (1957); Villiers (1958); Ross (1982); Maigret (1977, 1983); Dupuy (1986)
Mediterranean Sea													
Greece (including Crete)						J	J	A	S				Mertens (1961, after Werner 1894); Honegger (1978); Marinos (1977, 1981); Margaritoulis (1982, 1983, 1985); Argano and Baldari (1983);Sutherland (1985)
Turkey					M	J	J	A					Geldiay et al. (1982); Argano and Baldari (1983); Basoglu and Baran (1982)
Cyprus						J	J	A					Demetropoulos and Hadjichristophorou (1982); Ross (1982); Argano and Baldari (1983); Demetropoulos and Lambert (1986)

Table 4. *Continued.*

Location	Month J	 F	 M	 A	 M	 J	 J	 A	 S	 O	 N	 D	Reference
Lampedusa Island						J	J						Di Palma (1978); Argano and Baldari (1983); Gramentz (1986)
Libya						J	J						Schleich (1987)
Western Indian Ocean													
Oman (Masirah Island)				A	M	J	J	A	S				Ross (1979, 1982); Frazier (1980); Hirth (1980); Ross and Barwani (1982)
Madagascar	J	F							S	O	N	D	Vaillant and Grandidier (1910); Hughes (1971*c*, 1971*e*, 1974*a*, 1974*b*, 1976*a*, 1982*b*); Pritchard (1979); Frazier (1980)
Mozambique	J										N	D	Hughes (1971*a*, 1971*c*, 1971*e*, 1974*b*, 1976*a*); Frazier (1980)
South Africa (Tongaland, Natal)	J	F							S	O	N	D	Bass and McAllister (1964); McAllister et al. (1965); Hughes et al. (1967); Hughes and Mentis (1967); Hughes (1970*a*, 1970*b*, 1971*c*, 1971*d*, 1971*e*, 1972, 1974*a*, 1974*b*, 1975*a*, 1976*a*, 1976*b*, 1982*a*, 1982*b*, 1984); Hughes and Brent (1972)
Northern Indian Ocean													
India[b] (Gulf of Mannar)									S	O	N	D	Jones and Fernando (1973); Murthy and Menon (1976)
Sri Lanka[b]							J	A	S				Deraniyagala (1930, 1939)
Western Pacific Ocean													
Japan				A	M	J	J	A					Nishimura (1967); Miyawaki (1981); Uchida and Nishiwaki (1982); Anonymous (1984*a*, 1984*b*); Iwamoto et al. (1985); Kamezaki (1986)
China[b] (including Taiwan)				A	M	J	J	A					Huang (1982)
Australia	J	F	M							O	N	D	Bustard and Limpus (1970, 1971); Bustard (1972, 1974, 1976); Limpus (1973*a*, 1973*b*, 1978, 1982*a*, 1982*b*, 1985); Bustard et al. (1975); Cribb (1978); Limpus et al. (1979*a*, 1983, 1985); Limpus and Reed (1985)
Southern Pacific Ocean													
Tokelau[a]						J	J	A	S	O	N	D	Balazs (1983)
Eastern Pacific Ocean													
Panama[a][b]					M	J	J	A	S	O	N	D	Sternberg (1981); Cornelius (1982)

[a] Nesting season includes other species as well as *Caretta*.

[b] There is some question about the accuracy of reports of loggerhead nesting at these localities.

Table 5. *Literature records of nesting by loggerhead sea turtles for which the nesting season was not recorded.*

Location	Reference
Western Atlantic Ocean	
United States	
Alabama	Jackson and Jackson (1970); Mount (1975); Carr et al. (1982); Shoop et al. (1985)
Louisiana	Hildebrand (1982); Carr et al. (1982)
Texas	Hildebrand (1982, 1983); Carr et al. (1982)
Mexico	
Veracruz	Carr et al. (1982); Hildebrand (1982, 1983)
Tabasco	Carr et al. (1982)
Tabasco-Campeche	Bacon et al. (1984)
Campeche	Carr et al. (1982); Hildebrand (1982); Bacon et al. (1984)
Yucatan	Hildebrand (1982); Carr et al. (1982); Bacon et al. (1984)
Belize	Rebel (1974); Carr et al. (1982); Moll (1985)
Guatemala	Carr et al. (1982)
Honduras	Carr et al. (1982)
Nicaragua	Rebel (1974); Carr et al. (1982).
Costa Rica	Caldwell et al. (1955); Caldwell et al. (1959*a*)
Venezuela	Donoso-Barros (1964); Flores (1969); Pritchard and Trebbau (1984)
Surinam	Schulz (1971, 1975, 1982); Pritchard and Trebbau (1984)
Brazil	
Maranhao to Espirito Santo	Sternberg (1981); Marcovaldi (1987)
Ceara	Pritchard and Trebbau (1984)
Sergipe southward	Reichart (1981); Pritchard and Trebbau (1984)
Bahia	Pritchard and Trebbau (1984)
Rio de Janeiro	Pritchard and Trebbau (1984)
Bermuda	Carr (1984)
Cayman Islands	Lewis (1940); Pritchard and Trebbau (1984)
Dominican Republic	Carr et al. (1982)
Guadeloupe	Carr et al. (1982)
Jamaica	Carr et al. (1982)
Netherlands Antilles	Rebel (1974)
Providencia, San Andres, Albuquerque Cays	Pritchard (1979)
Puerto Rico	Carr et al. (1982)
St. Lucia/Grenadines	Carr et al. (1982)
Turks and Caicos	Rebel (1974); Carr et al. (1982)
Eastern Atlantic Ocean	
Cape Verde Islands	Schleich (1979); Brongersma (1982)
Morocco	Doumergue (1899); Pasteur and Bons (1960); Brongersma (1972, 1982)
Namibia	Hughes (1982*b*)
Mediterranean Sea	
Corsica	Bruno (1973); Dumont (1974); Fretey (1975, 1986); Groombridge (1982)
Sardinia	Bruno (1969); Argano and Baldari (1983)
Italy (including Sicily)	Bruno (1969, 1970, 1973, 1978); Brongersma (1972); Di Palma (1978); Honegger (1978); Argano and Baldari (1983)
Israel and North Sinai	Sella (1982*a*); Argano and Baldari (1983)
Libya	Bruno (1969); Pritchard (1979)
Tunisia	Argano and Baldari (1983)
Northern Indian Ocean	
Maldives	Deraniyagala (1933)
Eastern Indian Ocean	
Thailand	Petpaidit (1953); Suvatti (1950 *in* Phasuk and Rongmuangsart 1973)
Western Sumatra	Polunin and Nuitja (1982)
Java	Polunin and Nuitja (1982)
Western Australia	Limpus (1982*a*)
Western Pacific Ocean	
Taiwan[a]	Huang (1982)
Sarawak[a]	Harrisson (1965)
Papua-New Guinea	Spring (1982)
South Pacific Ocean	
Solomon Islands	Carr (1952); Pritchard (1979)
New Caledonia	Sternberg (1981)
Fiji	Pritchard (1979)
Cook Islands	Gill (1876 *in* Wiens 1962)
Eastern Pacific Ocean	
Nicaragua[a]	Cornelius (1982)

[a] The validity of these reports is questionable. See text.

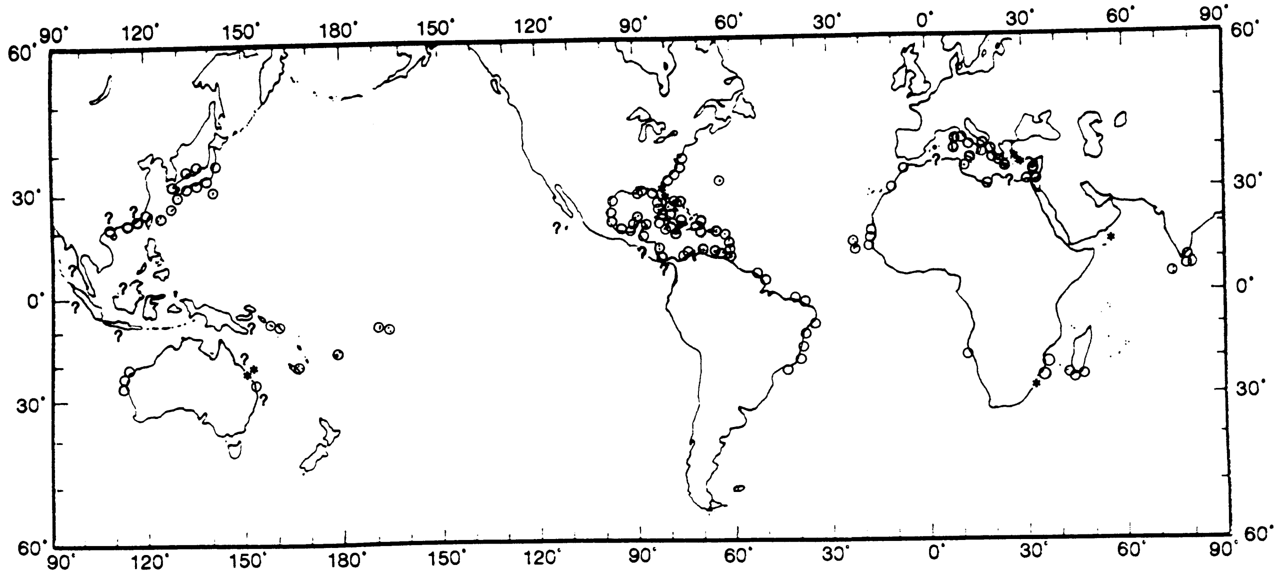

Fig. 5. Worldwide nesting locations of the loggerhead. *Stars* represent major nesting locations and *circles* indicate minor nesting areas.

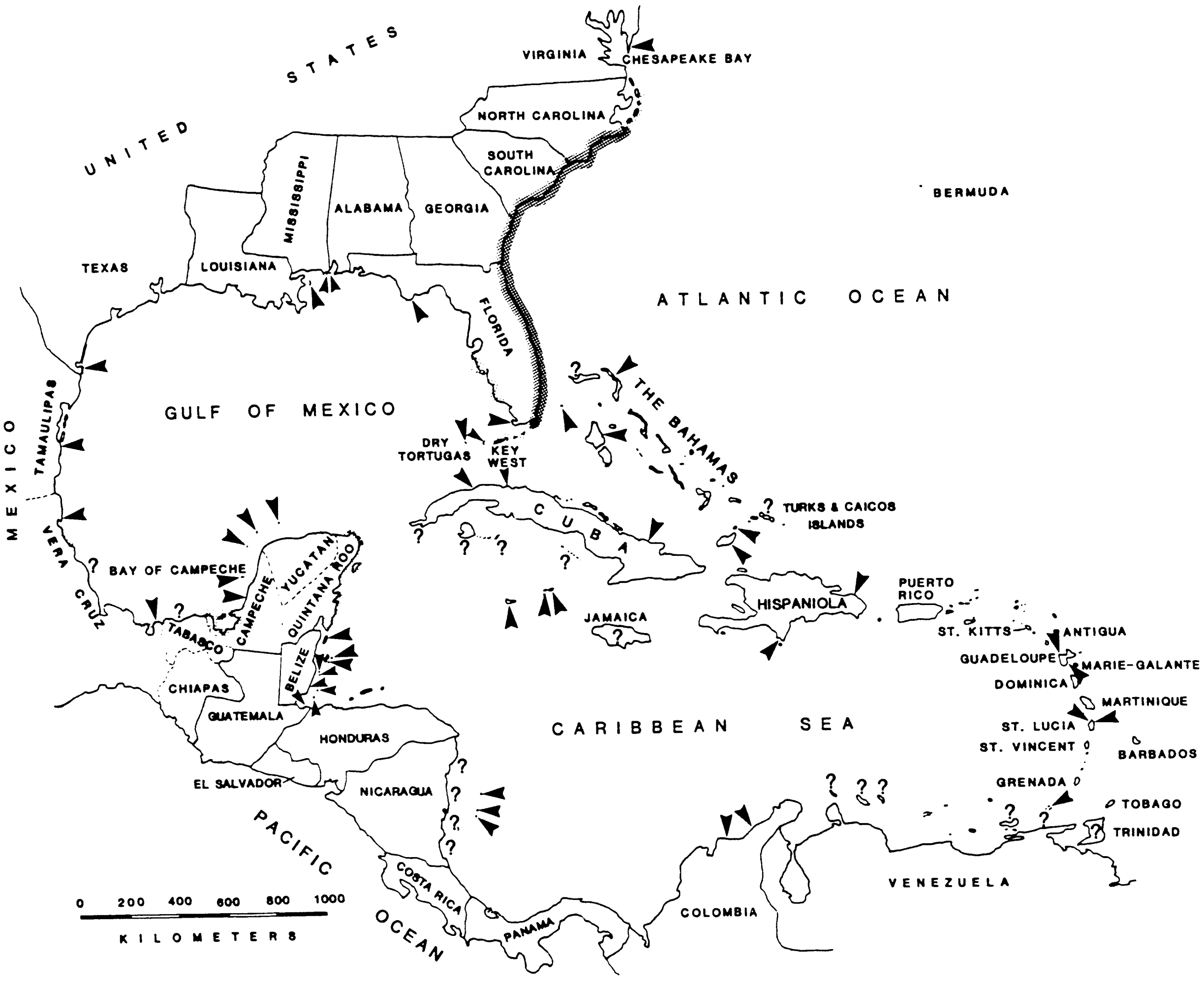

Fig. 6. Nesting locations of the loggerhead in the west-central Atlantic Ocean and Caribbean Sea. *Heavy stippling* represents major areas of nesting; *light stippling* represents areas of lesser but still important nesting concentrations; *arrows* represent areas with sporadic but consistent nesting, or areas where loggerheads have nested only rarely.

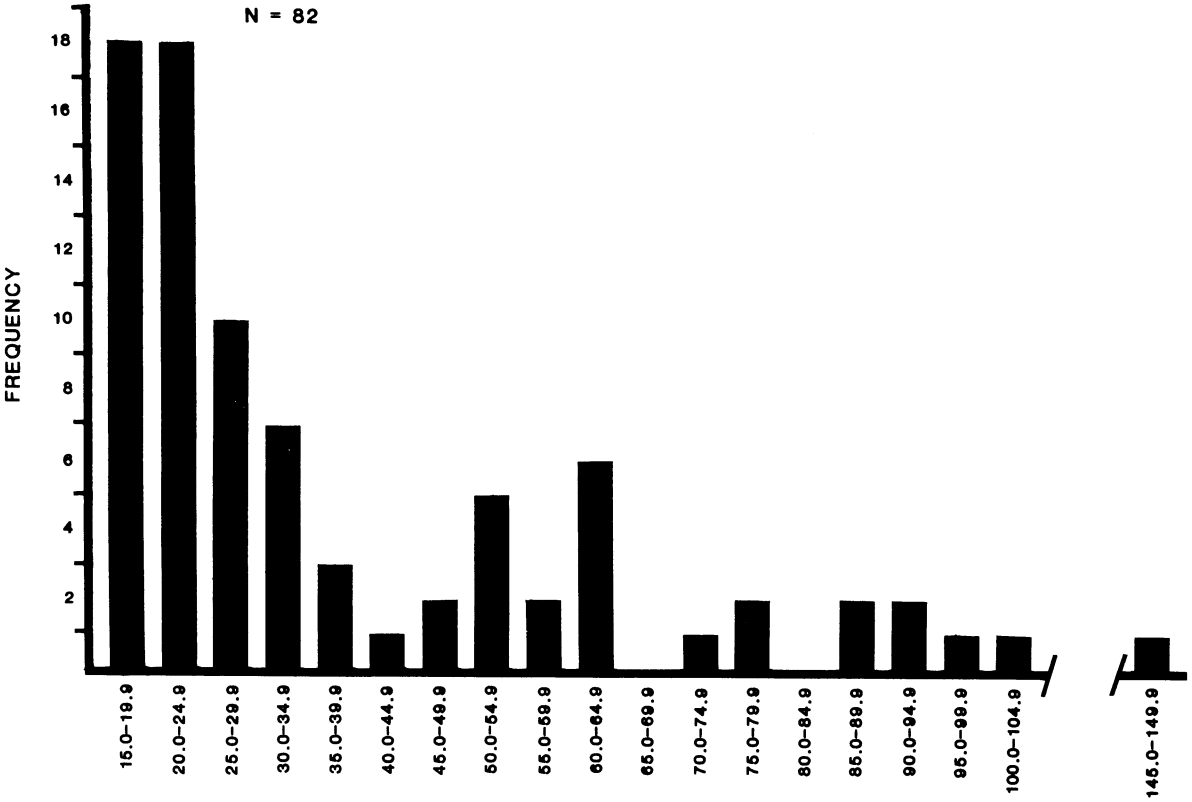

Fig. 7. Histogram showing size frequency distribution of loggerheads stranded along European coasts of the Atlantic Ocean (Brongersma 1972).

(1912) and Bons' (1972) checklists of Moroccan herpetofauna.

Loggerheads have also been reported from Mauritania (Maigret 1983), Senegal (Cadenat 1949, 1957; Villiers 1958; Maigret 1977, 1983; Dupuy 1986), Cape Verde Islands (*in* Brongersma 1982; Schleich 1979), Nigeria (*in* Brongersma 1982), Angola (Hughes et al. 1973), and Namibia (Sternberg 1981; Hughes 1982*b*). In Macronesian waters, *Caretta* is found in the Azores (Barth 1964; Brongersma 1971, 1982; Carr 1986*b*), the Canary Islands (Steindachner 1891; Brongersma 1968*b*), and the Madeira and Selvagens islands (Brongersma 1982). Of the areas listed, nesting has only been documented for Senegal and the Cape Verde Islands although it may occur at scattered locations elsewhere. Hughes (1982*b*) speculated on the possibility of nesting at Skeleton Coast Park in northwest Namibia.

In the Indian Ocean, loggerheads are reported from the eastern coast of Africa from the following locations: South Africa (Bass and McAllister 1964; McAllister et al. 1965; Hughes et al. 1967; Hughes and Mentis 1967; Hughes 1969*a*, 1969*b*, 1970*a*, 1970*b*, 1971*b*, 1971*c*, 1971*d*, 1971*e*, 1972, 1974*a*, 1974*b*, 1975*a*, 1976*a*, 1976*b*, 1977, 1978 [*in* Heydorn et al. 1978], 1982*a*, 1982*b*, 1984; Hughes and Brent 1972), Mozambique (Hughes 1971*a*, 1971*c*, 1971*e*, 1974*b*, 1976*a*, 1982*b*; Frazier 1980), Madagascar (Vaillant and Grandidier 1910; Hughes 1971*c*, 1971*e*, 1974*a*, 1974*b*, 1976*a*, 1982*b*; Pritchard 1979; Frazier 1980), Tanzania (Frazier 1976, 1982; Hughes 1982*b*), and Kenya (Frazier 1975). Loggerheads also have been reported in the St. Brandon Islands (Hughes 1975*b*) and in the vicinity of Aldabra (Frazier 1971, 1984*b*). Nesting occurs in Tongaland (Natal, South Africa), on adjacent beaches in Mozambique, and on the southern and southwestern portions of Madagascar. The loggerhead is considered rare in Tanzania, Kenya, and the oceanic islands, although they may be more common in waters of the Seychelles than literature records indicate (J. Mortimer, personal communication).

Hughes (*in* Heydorn et al. 1978) noted that loggerhead hatchlings enter the warm Agulhas Current and may spend up to three years in a pelagic life stage riding the current around the Indian Ocean. He further suggested that small turtles found in Western Australia might have originated in Tongaland. He mentioned that large numbers of loggerheads have been seen passing Reunion Island in the Mascarenes.

In the northwestern Indian Ocean, loggerheads are rare except for the large nesting colony at Masirah Island, Oman (Ross 1979; Hirth 1980; Frazier 1980; Ross and Barwani 1982). A small number of tag returns ($N = 8$) indicate that the distribution extends from the Masirah nesting grounds west toward the Horn of Africa, and east toward Pakistan and into the Arabian Gulf (Ross, personal communication). Ross and Barwani (1982) also report that loggerheads are found in the Red Sea in the Sinai area and that nesting might occur there, but these reports remain unconfirmed. Until recently, loggerheads from the Persian Gulf were unknown, but T. Preen (personal communication) reported that surveys conducted by J.D. Miller have turned up four observations of nonnesting loggerheads in this area. There are a few records of loggerheads in the vicinity of the United Arab Emirates in the Arabian Gulf and the Gulf of Oman (Brown 1979, 1983, 1984, 1985) and one tag return from the Masirah colony in Saudi Arabia (Ross, personal communication).

Except for the observations of Deraniyagala (1930, 1939), Jones and Fernando (1973), Murthy and Menon (1976), and Kar and Bhaskar (1982) of loggerheads in the Gulf of Mannar between India and Sri Lanka, *Caretta* seems conspicuously absent from the northern Indian Ocean. Minton (1966) thought that they might occur in the coastal waters of Pakistan, but was unable to confirm this. However, Ghalib and Zaidi (1976) reported *Caretta* occurs in Pakistani waters, but that nesting does not. The loggerhead is reported to be common off the coast of Tuticorin in the months of March and April (Valliappan 1973). Nesting apparently occurs in Sri Lanka, but Das (1985) stated that *Caretta* does not nest along Indian shores despite claims to the contrary as previously noted. Also, there is a curious discrepancy between the nesting seasons reported for these nearby areas (Table 4) and it is possible that confusion exists in the identification of species (Das 1985). Loggerheads also have been reported to nest in the Maldives (Deraniyagala 1933), but this claim is disputed by Hughes (1974*b*).

There has been considerable confusion concerning the identification of *Caretta* and *Lepidochelys* in the herpetological literature of the western Pacific (Nishimura 1967). Smith (1931) reported that although the loggerhead is rare in the Gulf of Siam, 1.5 million eggs were taken annually in Burma prior to 1911. However, it appears that he was referring to *Lepidochelys* rather than *C. caretta* since he calls them *Caretta caretta olivacea*. Taylor (1970) mentioned loggerheads in Thai waters, but gave no information on them. Both Smith (1916) and Nutaphand (1979) considered the species rare. However, Suvatti (1950) and Petpaidit (1953)—both cited by Phasuk and Rongmuangsart (1973), but with an incorrect date for Petpaidit—recorded nesting by loggerheads in Thailand, although those illustrated in Petpaidit (1953) appear to be olive ridleys. These records need confirmation.

Suwelo (1971) and Polunin and Nuitja (1982) reported that loggerheads occur in the seas around Indonesia, but that nothing is known of the species' status. They stated that loggerheads reputedly nest in west Sumatra and occasionally in Java, although Limpus (1985) stated that there are no positive records for nesting in Indonesia. Although De Rooj (1915) reported a number of localities for *Caretta caretta* in Southeast Asia, including Java, Borneo, the Aru Islands, the Malay Peninsula, and the Philippines, it is possible that she was not distinguishing the olive ridley from the loggerhead (Nishimura 1967). Taylor (1920) clearly referred to *Lepidochelys* rather than *C. caretta* in his discussion of the loggerhead in the Philippines. If they occur in the Philippines, they are rare; Gomez (1980) reported no recent observations of either loggerheads or olive ridleys.

The behavior of loggerhead hatchlings, presumably collected locally, was compared with green and hawksbill hatchling behavior in Sarawak by Harrisson (1965). Although the hatchlings were not described, these three species were mentioned as being the "less scarce Indo-Pacific marine turtles," and that they bred in the Sarawak Turtle Islands. As such, this is probably a reference to *Lepidochelys* rather than *Caretta*. Harrisson previously misidentified *Caretta* hatchlings when he reported loggerhead nesting at Pulau Gulisaan in Sabah (de Silva 1982). Likewise, Gadow's (1899) discussion of orthogenetic variation in *Caretta* hatchlings from New Britain likely was based on misidentified *Lepidochelys* (Nishimura 1967).

Loggerheads have been reported in Chinese and Taiwanese waters (Fang 1934 *in* Nishimura 1967; Huang 1979, 1982) either as *Caretta caretta*, *C. c. olivacea*, or *C. olivacea*. For instance, Fang's (1934) synonymy and list of distinguishing characters clearly confused the red-brown with the olive "loggerhead," so much so that he recommended *olivacea* be placed in synonymy with *caretta*. Huang (1982) recorded nesting, and stated that loggerheads were found in coastal waters of Taiwan, Gungdong, Guangxi, Fujian, Zhejiang, Jiangsu, Shandong, and Hebei. However, he previously referred to loggerheads as *C. c. olivacea* (Huang 1979) so it remains unclear whether these records are for *Caretta* rather than *Lepidochelys*. Huang (1976) did not record *Caretta* from the Xisha Islands. There appears to be no nesting records for the coast of Indochina although both Bourret (1941) and Huong (1978) listed *Caretta olivacea* from Vietnam, thus suggesting loggerheads or olive ridleys might occur in coastal waters. It is probable these records are for the olive ridley.

Nishimura (1967) reviewed the status of *Caretta* in Japan and noted that references to *Lepidochelys* in Japanese waters probably were based on *Caretta*. *Lepidochelys* is actually quite rare in Japan (Nishimura and Hara 1967). Additional records of *Caretta* in Japan are in the following sources: Takeshima (1958), Nishimura (1967), Uchida (1973, 1975, 1981, 1982), Miyawaki (1981), Uchida and Nishiwaki (1982), Anonymous (1977, 1984*a*, 1984*b*), Iwamoto et al. (1985), and Kamezaki (1986). Nesting occurs on islands in the south and along the east and west coasts of Kyushu, the southeast coast of Shikoku, and the southeast and northeast coasts of Honshu (see references in Table 4).

Loggerheads have been reported in Korea, the Ryukyu Islands, and Formosa by Takeshima (1958), although Nishimura (1967) suggested these observations may have been of olive ridleys as well as loggerheads. The furthest north that loggerheads have been documented is Peter-the-Great Bay in the Soviet Union (Terentjev and Chernov 1949).

Loggerheads occur in waters all around Australia (Cogger 1983*a*), with specific nesting records for Western Australia at Shark's Bay (Babcock 1930; Brongersma 1961; Lester et al. 1980: turtles caught in sea; Limpus 1982*a*) and Barrow Island (Limpus 1982*a*). Nesting also may occur at Exmouth Gulf (R. Johannes, personal communication to J.P. Ross). The largest concentration of loggerheads in Australia occurs along the coast of Queensland, with extensive nesting on offshore islands and the mainland of south Queensland (Bustard 1968*a*, 1968*b*, 1969*a*, 1969*b*, 1971, 1972, 1974, 1976; Bustard and Limpus 1970, 1971; Limpus 1973*a*, 1973*b*, 1975, 1978, 1979, 1982*a*, 1985; Bustard et al. 1975; Cribb 1978; Limpus et al. 1983; Limpus et al. 1984; Limpus and Reed 1985; Limpus et al. 1985). One incidence of nesting has been reported for Lizard Island in the midpart of the Great Barrier Reef (Limpus 1982*b*). Sporadic nesting occurs as far south as Newcastle, New South Wales (Limpus 1982*a*).

Nonnesting loggerheads are reported to be plentiful in the waters off the Northern Territory (Cogger and Lindner 1969), and are occasionally sighted in south Australia (Cotton 1943; Houston 1979) and Tasmania (Scott and Mollison 1956; Green 1971). Australian loggerheads are known to migrate to tropical portions of the Great Barrier Reef, New Guinea, the Gulf of Carpentaria, and the Trobriand Islands (Bustard and Limpus 1970; Limpus 1982*a*; Limpus and Parmenter 1986). Although the species is generally uncommon in New Guinea, Spring (1982) reported nesting in the Trobriand Islands.

Loggerheads are also occasional visitors to New Zealand waters (McCann 1966; Robb 1980; Pritchard 1982*a*; Ballance et al. 1985–1986) and other areas of the South Pacific. Pritchard (1982*a*) suggested that the presence of small animals in New Zealand waters, and the reports of turtle tracks, indicated that the loggerhead might rarely nest on northern beaches in New Zealand. In other regions of the South Pacific, valid records of loggerheads are scarce although Hirth (1971) considered the loggerhead the third most abundant sea turtle in the South Pacific. He mentioned records for both Fiji and Tonga. In the Solomon Islands, Pritchard (1982*a*) reported that nesting was unknown, although Carr (1952) provided data on hatchlings from the Solomons (see also Pritchard 1979). Pritchard (1979) mentioned nesting in Fiji, and some nesting is known to occur in New Caledonia (Pritchard, personal communication). Gill (1876 *in* Wiens 1962) stated that loggerheads were plentiful during the breeding season at Rakahanga in the Cook Islands, but this needs to be confirmed.

In the central Pacific, records of loggerheads are very scarce. Balazs (1979) provided data on three historic records of *Caretta* in Hawaiian waters. Nesting occurs only in Tokelau, although the turtle is considered rare (Balazs 1983).

In the eastern Pacific, the loggerhead also appears to be uncommon. It has been reported from the States of Washington (Hodge 1982) and California (Shaw 1947; Stebbins 1954; Guess 1981, 1982) in the United States. Van Denburgh (1922) recorded *C. olivacea* from Baja California, Mexico, although it seems he was referring to *Lepidochelys*. The first valid reference to *C. caretta* in Baja California, and indeed the entire eastern Pacific, appears to be that of Shaw (1946) who misidentified *Caretta* as *Lepidochelys* (Caldwell 1962*a*; Frazier 1985). Brattstrom (1955) reported hatchling *Caretta* from the Revillagigedo Islands, but Frazier (1985) believed that these were misidentified *Chelonia* or *Lepidochelys*.

Additional loggerhead specimens from Baja and the Gulf of California were recorded by Caldwell (1962*a*, 1963), Marquez (1969), and Clifton et al. (1982). Elsewhere in Mexico, Hardy and McDiarmid (1969) reported *Caretta* from Mazatlan in Sinaloa, but Frazier (1985) pointed out that these were olive ridleys rather than loggerheads. Jack Woody (personal communication) reported large numbers of subadult loggerheads about 42 km off the Baja coast in deep water, but more information regarding these turtles is needed. The loggerhead is not known to occur in southern Mexico (Clifton et al. 1982).

The loggerhead is rare in Pacific Central America if it occurs there at all. Unconfirmed reports include observations in El Salvador and Nicaragua (J. Woody, personal communication). Cornelius (1982) reported the possibility of nesting in Nicaragua and on the Osa Peninsula in Costa Rica, but these observations have never been verified (Cornelius, personal communication). Cornelius (1982) stated that the loggerhead was the most abundant turtle on the nesting beaches in Panama, but A. Ruiz (personal communication to C. Limpus; see Limpus 1985) could not substantiate nesting in Panama. Cornelius (personal communication) now believes these records to be based on misidentified olive ridleys.

Loggerheads have been reported for the northern coast of South America from Colombia (Green and Ortiz-Crespo 1982). There are no other records for South America except for northern Chile (Frazier and Salas 1982), and nesting is unknown. Frazier (1985) has discussed the records of the loggerhead in the southeastern Pacific Ocean and noted that there has been much confusion in the identification of *Caretta* and *Lepidochelys*. Many of the observations of loggerheads in this region probably refer to olive ridleys rather than to *Caretta*. Loggerheads are very rare in South American waters, although better surveys may reveal more confirmed observations.

In the northeastern Atlantic, loggerheads have been reported in Newfoundland (Squires 1954) and Nova Scotia (Bleakney 1967), and Bleakney (1965) mentioned that the loggerhead is commonly reported by fisheries officers elsewhere in Canadian waters. In the United States, it occurs occasionally in Maine (Scattergood and Packard 1960; Lazell 1980) and commonly off Cape Cod and Martha's Vineyard (Babcock 1919, 1938; Lazell 1976; Shoop 1980). In New York, loggerheads are found frequently in summer and may be cold-stunned with the onset of cold weather (Murphy 1916; Meylan and Sadove 1986).

In the United States, loggerhead nesting was first reported by Catesby (1731–43). Nesting occurs from New Jersey southward and throughout the southeastern United States into the Caribbean (Carr et al. 1979; Shoop et al. 1985; Tables 4 and 5; Fig. 6). A large subadult population feeds in the rich waters of Chesapeake Bay (Musick 1979*a*, 1979*b*, 1983; Lutcavage 1981; Lutcavage and Musick 1985) and loggerheads are known to overwinter in the Canaveral Ship Channel off the coast of Florida (Ogren and McVea 1982; Carr et al. 1981; Rudloe 1981; Moulding 1981; Joyce 1982). For surveys conducted in 1982, Butler et al. (1987) estimated 410–992 loggerheads were found in February in the Canaveral Ship Channel, but only 12–64 turtles used the channel in August; only 18 loggerheads were found in trawl surveys at other Florida and south Georgia inlets. A subadult population occurs in the Indian River lagoon system of east-central Florida (Brice 1896; Mendonça 1981; Mendonça and Ehrhart 1982; Ehrhart 1983).

Other nonnesting records exist for Delaware (Spence 1981), Maryland (Cooper 1947), Virginia (Brady 1925; Reed 1957; Tobey 1985), North Carolina (True 1887; Schwartz 1977; Lee and Palmer 1981), Mississippi (Gunter 1981), and Texas (Brown 1950; Neck 1978; Rabalais and Rabalais 1980; Hildebrand 1982, 1983; Reeves and Leatherwood 1983). Fritts and Reynolds (1981), Lee and Palmer (1981), Irvine et al. (1981), Hoffman and Fritts (1982), Fritts et al. (1983*a*), Fritts et al. (1983*b*), and Schroeder and Thompson (1987) noted the distribution of loggerheads off the coast of the southeastern United States from the shore into the Gulf Stream.

Maigret (1983) reported that a lobster trawler encountered thousands of sea turtles swimming in the Atlantic at 33°N, 74°W in water 21°C. This location would be roughly 800 km east of Cape Hatteras, NC. He identified these 30 cm SLCL turtles as *Lepidochelys kempi*, but Peter Pritchard (personal communication) later examined photographs supplied by Maigret and confirmed that they were *C. caretta*. The location also was misprinted. It should have read 33°N, 14°W, which places the location in waters west of Gibraltar rather than in the western Atlantic. Elsewhere in the central Atlantic, loggerheads are reported from Bermuda (Garman 1884; Babcock 1937). Carr (1986*b*) recorded loggerhead hatchlings and juveniles associated with pelagic *Sargassum* lines off the coasts of the Bahamas, Bermuda, 500 km east of Nantucket, and Florida and Georgia in the Atlantic; and Florida, Texas, and Mexico in the Gulf of Mexico. Hatchling loggerheads probably remain in these currents several years through the juvenile life stage until they leave for developmental habitats as subadults.

Loggerheads occur throughout the western Atlantic region. Summaries of their distribution, both nesting and nonnesting, are provided by Bacon (1975, 1981), Carr et al. (1982), Bacon et al. (1984), and Pritchard and Trebbau (1984). In the Greater Antilles, the loggerhead is common in Cuba on the islands off the southern coast (Abascal 1971; Cardona and de la Rúa 1971; Gavilan and Andreu 1983) but uncommon elsewhere (Carr et al. 1982). About 60 nests per year are oviposited along the northeastern and southwestern coasts of the Dominican Republic (J. Ottenwalder, personal communication). In the Lesser Antilles, Reinhardt and Lutken (1862) noted its absence from the Virgin Islands. Elsewhere in the Lesser Antilles, it is uncommon (Meylan 1983); Meylan (personal communication) was told of low-level nesting but never saw any conclusive evidence of such. Nesting formerly occurred in Jamaica, Grenada, and in the San Andres Islands, and rare nestings may still occur on these islands although there are no recent reliable records.

From Mexico through Central America, the loggerhead varies from uncommon (one subadult reported from Tortuguero, Costa Rica, K. Bjorndal, personal communication) with sporadic nesting, to common with areas of concentrated nesting (Tables 4 and 5; Fig. 6). One nesting concentration appears centered around the northern and eastern portion of the Yucatan Peninsula (J. Woody and R. Marquez, personal communication) where loggerhead nests outnumber green turtle nests. Meylan (personal communication) has been unable to confirm reports of occasional nesting at Bocas del Toro, Panama. It nests in South America in Colombia (Kaufmann 1966, 1967, 1968, 1971*a*, 1971*b*, 1972, 1973, 1975*a*, 1975*b*), although the population has declined markedly since 1975, and occurs into Venezuelan waters (Roze 1955; Donoso-Barros 1964; Flores 1969; Brownell 1974; Pritchard and Trebbau 1984). Only 24–32 nests per year now occur in Colombia. Loggerheads are reported in the waters off Los Roques, but nesting does not occur there (Roze 1956).

Brongersma (1968*c*) reported museum specimens of *Caretta* from Surinam, and Schulz (1975) mentioned a single loggerhead nesting in May 1969. The loggerhead is an accidental visitor to Surinam and French Guiana (Fretey 1981, 1987). The loggerhead had been seen only once in French Guiana, at least through the late 1960's (Pritchard 1969, 1971), although Fretey (1987) has recorded a few more observations since then. Loggerheads occur in Brazilian waters (Luederwaldt 1926; Ferreira de Menezes 1972), including an unknown amount of nesting (Tables 4 and 5). Nesting was first reported by Maximilian (1820) as green turtle nesting, but subsequently shown to be loggerheads. Luederwaldt (1926) mentioned specimens from Empalhado and the State of Sao Paulo. Marcovaldi (1987) noted that 114 *Caretta* have been tagged and 62,354 hatchlings have been released between 1982 and 1986 as part of a conservation project in Brazil. After *C. mydas*, the loggerhead was the most abundant turtle encountered; about 400 loggerheads nest per year in Brazil (Marcovaldi, personal communication). Loggerheads have been recorded as far south as Rio Grande in Brazil (Frazier 1984*a*), Uruguay (Gudynas 1980; Frazier 1984*a*), and Argentina (Frazier 1984*a*). Murphy (1914) reported "numbers" of adult loggerheads between 670 km and 830 km east off the coast of Uruguay in November 1912, but there was no indication where these turtles originated or where they were going.

Although Smith and Smith (1980) restricted the type localities of *Testudo nasicornis* Lacépède and *Caounana Caretta* Gray (synonyms of *C. caretta*; see section 1.1.2) to Ascension Island in the south Atlantic, there are no records of this species from Ascension.

2.2 Differential Distribution

2.2.1 Hatchlings

After leaving the nesting beach, loggerhead hatchlings swim perpendicular to the shore until they reach drift lines created by upwellings, downwellings, currents, and other types of convergences of different bodies of water (Carr 1986*a*, 1986*b*, 1987). These convergences produce concentrations of resources that are rich in potential prey items for young turtles, particularly insects (A. Carr, personal communication). Accumulated material, such as *Sargassum* and debris from land sources, provide refuges both for turtles and prey. Hatchling loggerheads have been reported in *Sargassum* associated with such convergences in the western Atlantic (Smith 1968; Caldwell 1968; Carr 1984) and in mats of *Physalia* off South Africa (Hughes *in* Heydorn et al. 1978). Witham (1974) reported loggerhead hatchlings in the stomachs of predatory fish feeding along drift lines. Fletemeyer (1978) followed hatchlings off a south Florida nesting beach for several hours. Except for one individual, the hatchlings invariably swam to and remained in patches of *Sargassum*. Carr (1986*b*) summarized occurrences of loggerheads associated with pelagic drift lines.

Carr (1986*a*, 1986*b*) speculated that hatchlings and juveniles may ride currents and gyres in a great circular path from North America through Europe and the Azores back to subadult developmental habitats in the western Atlantic. Hughes (*in* Heydorn et al. 1978) speculated that Tongaland hatchlings ride the Agulthas Current around the southern Indian Ocean. The possible locations of hatchling habitats for other populations have not been delineated, although Limpus (1985) speculated that Australian hatchlings might move downstream along the east Australian Current and along the convergence of the east Australian Current with the Tasman Front east of northern New South Wales.

Stoneburner et al. (1982) reported that 15 hatchlings fitted with transmitters dispersed to marshes in the St. Andrews Sound of southern Georgia rather than swim offshore to the sea (see also Garmon 1981). However, it is likely that these turtles drifted with tidal currents to these locations instead of deliberately selecting marshes as hatchling habitat (Richardson, personal communication).

2.2.2 Juveniles, subadults, and adults

After hatchling loggerheads enter the ocean, they begin the so-called ''lost year'' stage of life, although the ''lost year'' is now known to include a number of years, probably 3 to 5 (Carr 1986*a*), during which the hatchling grows into a subadult. The juvenile stage is most likely passed entirely in a pelagic existence riding on currents and gyres (Carr 1986*a*, 1986*b*, 1987). Records of juvenile loggerheads are scarce (summarized by Carr 1986*b*), although a surprisingly large number have been reported from the Azores (Carr 1986*b*). Juvenile loggerheads (section 1.2.5) are found stranded on the coasts of northern Europe (Fig. 7; Brongersma 1972).

After circulating on oceanic currents for a period of several years, juveniles reach about 40 cm SLCL and leave the pelagic ocean for subadult developmental habitats. In the western Atlantic, subadult developmental habitats include lagoons, estuaries, and the mouths of bays and rivers rich in food resources. Particularly favored areas include the Chesapeake Bay (Lutcavage 1981; Lutcavage and Musick 1985) and the Indian River Lagoon system of eastern Florida (Mendonça 1981; Mendonça and Ehrhart 1982; Ehrhart 1983). Hildebrand (1983) reported that the loggerhead is the most abundant turtle today on the Texas coast and that most animals are ''immatures.'' It is likely that loggerheads are found in many of the lagoons of the Texas and Mexican coasts.

Other literature records for subadult loggerheads include Long Island Sound, NY (Meylan and Sadove 1986), the Lesser Antilles (Meylan 1983), off the coast of Uruguay and Argentina (Frazier 1984*a*), the Baleares Islands (Carr 1986*b*), the French Mediterranean (Dumont 1974), Madeira and the Canary Islands (Brongersma 1968*b*), and the Gulf of California (Caldwell 1963; Marquez 1969; Cliffton et al. 1982). The locations of subadult developmental habitat for other populations is unknown. Data on loggerhead sea turtles not associated with a particular nesting beach, including juveniles and subadults, are shown in Table 6.

Adult loggerheads are best known from shallow coastal waters adjacent to nesting beaches. Little is known about habitat use away from nesting beaches, however, except for Limpus' (1985) studies on Australian loggerheads. Evidence suggests that the species is migratory, since there have been long-range tag returns from Australia and South Africa showing movement over considerable distances northward after the nesting season (Hughes and Mentis 1967; Bustard and Limpus 1970, 1971; Bustard 1974; Limpus 1982*a*; Limpus et al. 1984; Limpus and Parmenter 1986; Hughes 1977). Some loggerheads in the southeastern United States move northward in the spring (Bell and Richardson 1978; Meylan et al. 1983) and southward along the coast as autumn approaches, presumably to overwinter in the Bahamas or the Caribbean (Meylan 1982). Others, particularly subadults, remain year-round in Florida burying themselves in mud to escape cold conditions (Carr et al. 1982; Ogren and McVea 1982; Henwood 1987). Henwood (1987) suggested adult females are migratory whereas adult males are not, and remain in the vicinity of the nesting beaches throughout the year. Loggerheads buried in mud also have been reported in the Gulf of California (Cliffton et al. 1982). Iwamoto et al. (1985) reported the recovery of loggerheads tagged at Miyazaki, Japan, in the East China Sea over 377 km distant. Nothing is known of the migratory movements in other populations, or about seasonal movements of male turtles.

2.3 Determinants of Distributional Changes

Loggerhead distribution is centered in warm temperate and subtropical seas adjacent to nesting beaches, and in warm coastal regions providing appropriate feeding grounds. Warmwater temperature may limit the distribution of nesting, and warmwater currents probably allow hatchlings to disperse away from nesting grounds and use food sources in drift lines to grow to subadult size. Reproductive migrations of unknown distance from feeding areas to nesting beaches are suspected to occur at intervals of two or more years, although there are

Table 6. *Data on loggerhead sea turtles not associated with a particular nesting beach. Measurements in cm and kg.*

Location	How obtained	Measurement	Mean	Range	*N*	Source
New York	Cold-stunned	Carapace (SL)	48.7	36.0-58.3	9	Meylan and Sadove (1986)
North Carolina	Trawler	Carapace	74.4	67.3-104.1	8	Fahy (1954)
Florida	Netted/lagoon	Carapace (CL)	—	44.0-92.5	104	Mendonça and Ehrhart (1982)
Florida	Netted/lagoon	Mass	—	12.8-97.7	104	Mendonça and Ehrhart (1982)
Florida	Hibernating	Carapace (SL)	—	47.5-97.5[a]	139	Ogren and McVea (1982)
Florida	Netted/lagoon	Carapace (CL)	71.4	49-100	205	Ehrhart (1983)
Florida	Netted/lagoon	Carapace (SL)	65.8	44-93	205	Ehrhart (1983)
Florida	Netted/lagoon	Plastron	50.9	21-67	205	Ehrhart (1983)
Florida	Netted/lagoon	Mass	43.7	13-111	205	Ehrhart (1983)
Uruguay/Argentina	Stranded	Carapace	—	50-115	61	Frazier (1984*a*)
W. Atlantic	Sargassum	Carapace	—	5.2-18.0	—	Carr (1986*b*)
Azores	Fishermen	Carapace (SL)	22.9	11.0-38.0	82	Carr (1986*b*)
Baleares Is.	Not reported	Carapace (SL)	—	30-76	81	Carr (1986*b*)
Europe[b]	Stranded	Carapace	38.1	15.9-146.7	82	Brongersma (1972)
E. Australia	Stranded	Carapace (CL)	13.5	5.8-36.0	4	Limpus (1985)
SW. Australia	Stranded	Carapace (CL)	8.2	5.8-10.2	40	Limpus (1985)
Australia/ Moreton Bay	Feeding gr.	Carapace (CL)	97.5	91.0-103.0	20	Limpus (1985)
Australia/ Capricornia Reef	Feeding gr.	Carapace (CL)	94.5	84.5-101.0	14	Limpus (1985)
Australia/ Gulf of Carpentaria	Feeding gr.	Carapace (CL)	93.1	89.0-96.5	5	Limpus (1985)
Papua New Guinea	Feeding gr.	Carapace (CL)	98.8	96.0-103.5	5	Limpus (1985)
New Zealand	Stranded	Carapace (CL)	15.7	8.6-33.0	6	McCann (1966); Pritchard (1982*a*)

[a] Estimated from histogram.
[b] Summary of unanalyzed data.

records of single-year intervals (Hughes, personal communication). See sections 2.1, 2.2, 3.1.6, and 3.5.1.

2.4 Hybridization

Lewis (1940) reported that local Caymanian fishermen could describe what they believed was a hybrid between *Eretmochelys imbricata* and *Caretta caretta* called a "McQueggie" or a "McQuankie." Carr (1984) later showed that at least in some instances, McQueggies were referable to recognizable species and that the folklore probably had no basis. However, Kamezaki (1983) reported hybrids from an *Eretmochelys* x *Caretta* cross from eggs deposited on the Chita Peninsula, Japan.

3. BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.1.1 Sexuality

The comparative reproductive biology of sea turtles, including loggerheads, is discussed by Buitrago (1982). Loggerheads are bisexual, and sexual dimorphism is apparent in the adults; some references state that males are generally larger than females, although Hughes (1974*b*) could not demonstrate size dimorphism in Natal, South Africa, loggerheads and Pritchard and Trebbau (1984) stated that both sexes attain equal sizes. Hughes (1974*b*) reported that sexual differentiation was apparent in turtles 60.0 cm to 67.0 cm SLCL. Males have a longer tail than females (males:females, 3:1) and larger recurved claws (males:females, 3:1). Males also have a shorter plastron, presumably to accommodate their large muscular tail (Hughes 1974*b*; Geldiay et al. 1982). Females have a more domed carapace than males, but males appear to be wider, and have a more gradually tapering carapace (Deraniyagala 1939; Carr 1952). Males also show a tendency to have a wider head (Hughes 1974*b*; Pritchard and Trebbau 1984). Deraniyagala (1939) reported that there is a difference in pigmentation between the sexes, with males showing more yellow-ochre on the head. Sexual distinction of hatchlings, juveniles, and the smaller subadults is not possible through external examination, but only through dissection, laparoscopy, histological examination, or radioimmunological assays. Intersexuality has been reported in an adult from Australia (Limpus et al. 1982).

3.1.2 Maturity

Early estimates of age at maturity were based on captive individuals raised under ideal conditions, and were based on different minimum size estimates for sexually mature individuals. Thus, Caldwell (1962*c*) and Uchida (1967) estimated that loggerheads matured at 6-7 yr of age. Frazer and Schwartz (1984) provided an estimate of 16-17 yr in 2 loggerheads raised in captivity in North Carolina. Studies of wild turtles, based on measurements of recaptured individuals or growth annuli of humeral bones, gave estimates of 10-15 yr in Florida (Mendonça 1981); 12-30 yr in Florida, with the best estimate skewed toward the higher figure (Frazer and Ehrhart 1985); 14 yr (logarithmic regression estimate) to 19 yr (linear regression estimate) in Georgia (Zug et al. 1983); 13-15 yr in Georgia (Zug et al. 1986); 22 yr in Georgia (Frazer 1983*c*); and >30 yr in Australia (Limpus 1979).

The age at sexual maturity may vary between populations, or even within populations, since growth rates and size at sexual maturity show considerable variation within and between populations (e.g., Limpus 1985). Knowledge of the sizes of reproductively active turtles may assist in the determination of age of maturity, depending on which growth rate equation values are used. There is a considerable body of literature on the sizes of nesting females (Table 7) showing that the populations with the smallest mature females occur in the Mediterranean and Natal, South Africa. The largest average-sized females occur in the southeastern United States. Data on body mass are scarcer, but show only minor variation among United States, South African, and Australian populations (Table 8). The data in Geldiay et al. (1982) are presumed to include some nesters although this is not clear from the text. Sella's (1982*a*) data obviously are of subadult animals.

Data on male loggerheads are exceedingly scarce. Despite observations that males may be larger than females, only four studies and one casual observation report male carapace lengths (Table 9). Body mass has been reported by Sella (1982*a*) to average 37.5 kg; his sample presumably included, or consisted entirely of, subadults and the sample size was not reported. Hughes (1974*b*) gave an average of 68.0 kg for Natal males but his sample size was very small (N = 3, range = 62.0-74.6).

3.1.3 Mating

Mating of loggerheads is assumed to occur along the way to the nesting beach for several weeks prior to the onset of nesting, and may occur in specific aggregation areas or habitats (Caldwell 1959; Limpus 1985). For instance, an area near Sandy Cape, Australia, is an area of high density courtship for females that nest in rookeries 80-150 km distant (Limpus 1985). Mating also may occur as females pass through territories of resident males on their way to the nesting beaches (Limpus 1985). Mating has been recorded from late March to mid-May in South Carolina (Caldwell 1959), April and May during periods of peak male abundance off the coast of Cape Canaveral, FL (Henwood 1987), April and June off the southeastern U.S. coast (Fritts et al. 1983*a*), and from October to mid-December in Australia (Limpus 1985). Courtship usually does not take place, except for rare instances, off the nesting beach. In some cases where mated pairs have been observed near nesting beaches, such as at Heron Island, Australia, the mated females did not nest on the nearest nesting beach (Limpus 1985). Copulating pairs have been reported at a considerable distance from the nesting shore. Bearse (1985) provided a photograph of a mated pair 55 km south of Cape Hatteras, NC, at the western edge of the Gulf Stream in March 1985.

Mounted pairs are most frequently sighted at the surface, although there are reports of submerged copulations (Hughes 1974*b*; Limpus 1985). The male clings tightly to the female using his large recurved claws to hook onto the female's carapace above each of her shoulders. The claws of the hind flippers are also used to hold onto the female's carapace (illustrated in the photograph in Wood 1953). The male's long tail is curled directly down under the female to bring their cloacas together so that he may insert his penis. While the female may be responsive to external stimuli, the male appears preoccupied with copulation. If the female swims, he keeps his head on her carapace, presumably to reduce drag, and only raises it to increase drag and pivot the female to the surface when he needs a breath. Harry (1983 *in* Limpus 1985) reported that multiple inseminations by several males of a single female was normal, indicating that the loggerhead is polyandrous. Copulation may last several hours.

Instances of courtship rarely have been observed. Limpus (1985) described two instances of males circling females presumably prior to copulation. The male circles the female which may turn to face the male. After several minutes of circling, the male rapidly approaches the female from the rear and slides his head up on her

Table 7. *Carapace lengths (cm) of nesting loggerhead sea turtles. CL = over the curve measurement; SL = straight line measurement; NR = not recorded.*

Location	Measure	Mean	Range	*N*	Reference
Atlantic					
North Carolina	SL	92.5	85.0-98.0	13	Stoneburner (1980)
South Carolina	NR	92.7	84.5-102.9	18	Caldwell (1959)
Georgia	NR	95.9	79.4-114.9	110	Caldwell et al. (1959*a*)
Georgia	CL	105.1	94.6-114.9	25	Kraemer (1979)
Georgia	SL	92.4	80.5-107.0	52	Stoneburner (1980)
Florida	NR	92.5	77.5-106.7	164	Gallagher et al. (1972)
Florida	NR	90.3	71.1-114.3	—	Worth and Smith (1976)
Florida	SL	96.4	76.2-106.7	25	Davis and Whiting (1977)
Florida	SL	90.5	81-109	50	Davis and Whiting (1977)
Florida	CL	100.4	91-114	51	Ehrhart and Yoder (1978)
Florida	CL	99.5	86-111	111	Ehrhart and Yoder (1978)
Florida	CL	99.1	83-124	120	Ehrhart and Yoder (1978)
Florida	SL	90.9	82-103	84	Ehrhart and Yoder (1978)
Florida	SL	92.3	81-110	110	Ehrhart and Yoder (1978)
Florida	SL	93.1	83.0-105.0	137	Stoneburner (1980)
Florida	SL	—	87-114	33	Hirth (1982)
Florida	SL	92.0	74.9-109.2	661	Bjorndal et al. (1983)
Florida	CL	100.6	—	11	Mapes (1985)
Florida	CL	98.9	87.9-108.9	119	Witherington (1986)
Florida	SL	93.9	82.5-104.4	114	Witherington (1986)
Trinidad	NR	85.0	—	1	Bacon and Maliphant (1971)
Colombia	SL	92.7	70-102	96	Kaufmann (1973)
Colombia	SL	87.9	70-100	78	Kaufmann (1975*b*)
Colombia	SL	87.7	70-102	65	Kaufmann (1975*b*)
Indian					
Oman	SL	92.0	79-101	—	Ross (1979)
Oman	NR	93.6	81.8-107.0	29	Hirth (1980)
Natal	CL	84.7	71.0-94.0	23	Hughes (1974*b*)
Natal	SL	79.2	65.1-87.1	23	Hughes (1974*b*)
Tongaland	NR	107	—	—	McAllister et al. (1965)
Tongaland	NR	93.9	—	156	Hughes and Mentis (1967)
Tongaland	CL	93.6	79-105	134	Hughes et al. (1967)
Tongaland	CL	92.6	—	50	Hughes (1970*a*)
Tongaland	CL	94.1	87.0-102.5	30	Hughes (1971*d*)
Tongaland	SL	87.2	80.7-95.0	29	Hughes (1971*d*)
Tongaland	NR	93.7	—	154	Hughes (1972)
Tongaland	CL	94.0	—	276	Hughes and Brent (1972)
Tongaland	CL	93.7	82.0-106.5	254	Hughes (1975*a*)
Tongaland	SL	87.6	76-98	320	Hughes (1975*a*)
Mediterranean					
Greece	CL	80.4	69.5-95.0	27	Margaritoulis (1982)
Greece	NR	81.2	—	95	Sutherland (1985)
Pacific					
Queensland	CL	95.7	84-108	380	Limpus et al. (1984)
Queensland	CL	95.8	80.0-113.5	2,207	Limpus (1985)

Table 8. *Body mass (kg) of female loggerhead sea turtles. (Mass is for nesting animals unless otherwise indicated.)*

Location	Mean	Range	*N*	Reference
Atlantic				
Florida	118.2	89.7-170.9	47	Ehrhart and Yoder (1978)
Florida	116.3	71.7-148.9	93	Ehrhart and Yoder (1978)
Florida	114.7	79.6-180.7	121	Ehrhart and Yoder (1978)
Indian				
Tongaland	106.9	80.9-129.6	31	Hughes (1974*b*)
Oman	118.0	?-165.0	51	Ross (1979)
Mediterranean				
Israel[a]	27.7	—	—	Sella (1982)
Turkey[b]	57.5	40-75	—	Geldiay et al. (1982)
Pacific				
Queensland	100.7	70.3-146.1	112	Limpus (1985)

[a] Nonnesting animals.
[b] Presumed not to be nesting animals.

Table 9. *Carapace lengths (cm) of male loggerheads. CL = curved carapace length; SL = straight-line carapace length; NR = method not recorded.*

Location	Mean	Range	*N*	Reference
North Carolina (NR)	104.1	—	1	Fahy (1954)
Natal (CL)	86.7	79.0-98.5	14	Hughes (1974*b*)
Natal (SL)	81.6	75.2-90.5	13	Hughes (1974*b*)
Queensland (CL)[a]	96.6	89.0-104.0	43	Limpus (1985)
Queensland (CL)[b]	96.6	95.0-99.5	7	Limpus (1985)

[a] At feeding grounds.
[b] Courting at Heron and Wistari Reefs.

shoulder; he may bite her neck or shoulder in an effort to hold her. If the female is unreceptive, she will pivot and turn toward the male in an effort to dislodge or discourage him, and may angle her carapace upward. Males will continue to circle and pursue females, and they in turn will face the male to prevent copulation. Successful copulation after a courtship bout has not been observed. Circling behavior also has been observed involving two males and an adult male and subadult (Limpus 1985). Wood (1953) reported that a captive male had difficulty both in inserting his penis into the female's cloaca and in retracting it after copulation; Limpus (1985) observed no such difficulty.

3.1.4 Fertilization

Fertilization is internal.

3.1.5 Gonads

A description of the gonads of male and female hatchling loggerheads, including photographs and histological preparations, are provided by Yntema and Mrosovsky (1980). In gross examination, the ovary is an elongated structure extending from anterior to posteromedial on the ventral surface of the kidney. The ventral surface is marked by shallow grooves. The oviduct runs lateral to the ovary and is uniformly 0.05 mm in diameter. In gross appearance, the testis is not markedly different from the ovary, and the oviduct has not regressed. The testis is usually less serrated and smaller than the ovary.

Histologically, the germinal epithelium forms the outer surface of the ovary, and is relatively thick on the ventral surface. The epithelium may form extensions into the medulla, and the germinal epithelium is sharply delineated from the medulla. Small primary cords persist. In the testis, simple squamous epithelium may be on the surface. A delicate tunica albuginea underlies this. Convoluted primary cords form immature seminiferous tubules with diameters 2-4 times that of the regressing cords in females. Even at hatching, complete absorption of the oviduct does not occur.

3.1.6 Nesting Process

Beach description. Loggerheads nest primarily on continental beaches and secondarily on island beaches. With the exception of Masirah Island, Oman, islands in the Great Barrier Reef, Australia, and nesting grounds in southern Japan, all major nesting occurs on continental beaches; indeed, three of the four main continental nesting locations (southeastern United States, Australia, and South Africa) are located on the eastern side of their respective continents. The fourth area, southern Turkey, has nesting beaches on the south side of a continental/peninsular land mass. Scattered loggerhead nesting regularly occurs on some islands, such as those in the Mediterranean, the Bahamas, and Cuba. Loggerheads occasionally visit other island and continental beaches at very irregular intervals (Fig. 6). Loggerheads nest well up onto the beach above the high-tide line and often within vegetation behind the beach (Carr 1952). Caldwell (1959) noted that low dunes backing a high beach increased its desirability as a nesting site. Bustard (1968*a*) and Hughes (1974*b*) noted the tendency for loggerheads to nest on beaches fronted by or adjacent to outcrops of rocks and subtidal inshore reefs in Australia and South Africa, respectively. Descriptions of representative loggerhead nesting beaches are found in the following sources: Caldwell (1959), South Carolina; Kaufmann (1968), Colombia; Bustard (1968*a*), Bustard et al. (1971), Limpus (1985), Australia; McAllister et al. (1965), Hughes et al. (1967), Hughes (1974*a*, 1974*b*), Tongaland, South Africa; Bruno (1978), Mediterranean; and Mann (1977), Williams-Walls et al. (1983), Witherington (1986), Ehrhart and Witherington (1987), Florida. Photographs of typical nesting beaches were provided by LeBuff (1969) for Florida, Bustard (1972) for Australia, Hughes (1977) for South Africa, and Ross (1979) for Oman.

Nesting season. The nesting season of the loggerhead is confined to the warmer months of the year in the temperate zones, that is, from May through August in the Northern Hemisphere and from October through March in the Southern Hemisphere (Table 4). The closer one approaches the tropics, the more extended is the nesting season. Hence, in south Florida the nesting season extends from April through September. Even in the tropics, the nesting season is generally confined to summer at times of plentiful rainfall, although the season may shift to later in the year at some localities, such as Colombia. The only exception to the apparent summer nesting regime occurs in the Gulf of Mannar in southern India. Here, loggerheads are reported to nest in the fall and early winter during the northeast monsoon when this part of India receives its most rainfall. In nearby Sri Lanka, nesting occurs in midsummer.

In some areas, loggerheads have been reported to nest so infrequently that it is difficult to describe a nesting season. For instance, Schulz (1971, 1975, 1982) reported a loggerhead nesting in Surinam in May 1969, and this is still the only observation of loggerhead nesting in Surinam. Fretey (1987) recorded one nest in August 1983, in French Guiana. In the United States, loggerheads at the northern extent of their nesting range only have been observed nesting in July. The nesting season reflected in Table 4 may be too narrowly defined in some instances, such as reports from Brazil that show nesting only from November to January. It is probable that more extensive surveys would show an expanded nesting season at some locations.

Also, there may be questions about the accuracy of species identifications. As previously noted, there has been substantial confusion in the identification of *Caretta* and *Lepidochelys* in many areas. Misidentification may account for the rather extended nesting season reported in Panama (Cornelius 1982), since there are questions about the accuracy of reports of the species' presence in Panamanian waters of the eastern Pacific (J. Woody and S. Cornelius, personal communication). Some authors have included a number of species together in discussions of nesting seasons at a particular location (e.g., reports from Trinidad, Cuba, and Tokelau; Table 4); as such, the duration of the nesting season for loggerheads needs further clarification at these locations.

Behavior. Loggerheads do not form arribadas as do members of the genus *Lepidochelys*. At areas of concentrated nesting, it also would be imprecise to consider them solitary nesters like *Eretmochelys imbricata*. Instead, the rule is for many turtles to overlap in beach use, both spatially and temporally, but without implications of social behavior. Loggerheads also may nest as solitary individuals at some locations, but the significance of this behavior to the nesting biology of the species is unknown. Nesting most often occurs several hours after sunset (Caldwell 1959), but may occur at any time of the night. Daytime nesting has been reported by Caldwell et al. (1959*b*), Fritts and Hoffman (1982), Witherington (1986), and Ehrhart and Witherington (1987) in the United States, and by Bustard (1972) and Bustard et al. (1975) in Australia. Both Bustard (1972) and Fritts and Hoffman (1982) noted the tendency for diurnal nestings to be associated with high tides. If high tides occur near dawn, some females may beach during the early hours of daylight (Bustard 1972). Margaritoulis (1985) reported three females on the beach of Zakynthos, Greece, at dawn that returned to the water within 30 min. No details of nesting or tides were presented. Afternoon nesting has only been reported for two females in Florida (Witherington 1986; Ehrhart and Witherington 1987).

Some authors have reported that loggerhead emergences are associated with tidal cycles (Bustard 1979; Frazer 1981) while others could find no correlation (Caldwell 1959; Davis and Whiting 1977). Still others found that correlations with tidal cycles varied from year to year (Dean and Talbert 1975 *in* Frazer 1983*a*; Talbert et al. 1980). Bustard (1979) thought emergences were associated with tides when the tidal cycles were pronounced. In a review of the question, Frazer (1983*a*) concurred with Bustard (1979), noting that in areas with small tidal ranges (Caldwell 1959; Davis and Whiting 1977), such correlations do not occur. In essence, areas with high tide amplitudes show a correlation of emergence with high tides; beaches of similar slope but with lower tidal amplitudes show no such correlations (Frazer 1983*a*). Caldwell (1959) reported that excessive rainfall may discourage nesting, and that there was no correlation between nesting and phases of the moon. Routa (1968) and Iwamoto et al. (1985) also could not correlate nesting with moon phases although Uchida (1981) stated that nesting was strongly correlated with the period of the full moon.

As with other sea turtles, nest site selection is a complicated process that is not well-understood. Many beach workers have noted that female loggerheads plow sand with the underside of the neck followed by laying the head flat against the ground as they ascend the beach (''sand nuzzling''). Stoneburner and Richardson (1981) related sand nuzzling behavior to attempts by the female to assess thermal cues. When abrupt temperature differentials of 2.05°C to 3.55°C in the dry beach zone were encountered, the females proceeded to nest; if such were not encountered, the females returned to the sea. Stoneburner and Richardson (1981) noted that such temperature differentials occurred over a short distance (<0.5 m). The highest nesting densities in the Cape Canaveral, FL, area are associated with steeply sloped beaches and a gradual rather than abrupt increase in offshore depth (Provancha and Ehrhart 1987).

Nesting. General descriptions of loggerhead nesting may be found in Mast (1911), Florida; Carr (1952); Caldwell et al. (1959*b*), southeastern United States, including photographs of various nesting behaviors; Litwin (1978), Georgia; Kaufmann (1966, 1973), Colombia; Bustard et al. (1975), Australia; and Margaritoulis (1985), Greece, including diagram. Hirth (1980) reported that the average duration of nesting-related activities on land is 1.8 h for *Caretta*, but Geldiay, et al. (1982) only gave 45–60 min for loggerheads in Turkey, and Kaufmann (1973) stated that nesting required 60 min in Colombia. Bustard et al. (1975) gave an average total nesting duration of 2.5 h for Australian loggerheads, but noted that it may be completed in only 1.5 h.

Bustard et al. (1975) divided the nesting process into nine stages. These are briefly outlined as follows:

1. *Approach to the beach.* Loggerheads approach the beach to the shallow water, rest on the bottom, and extend the head to view the beach. They remain for a short but variable period of time, carefully scanning the beach. At this stage, the turtle is most sensitive to disturbance, and will rapidly turn and swim away if danger is present. They may be spooked by lights or moving objects silhouetted on the horizon.

2. *Ascent of the beach.* Ascent of the beach occurs in a series of forward movements interspersed with short pauses. The head is held low during forward motion and it often makes a furrow in the sand (''sand smelling'' or ''nuzzling''). During pauses, the head is raised as if surveying the surroundings. Flipper action is synchronous, employing a ''terrestrial gait'' such that the right front flipper moves in conjunction with the left rear flipper. At this time, the female's body temperature averages 1.9–3.2°C above the ambient water temperature, probably through muscular exertion (Sapsford and Hughes 1978).

3. *Wandering.* In some instances, the female will wander over considerable distances before nesting or returning to the sea. The head is often lowered to the sand, presumably testing for thermal cues (Stoneburner and Richardson 1981). Anonymous (1977) provided a diagram of the wanderings of 10 loggerheads prior to selecting a nest site and returning to the sea.

4. *Digging the body pit.* Body pits may be begun with a minimum of exploratory digging. In loggerheads, the body pit is shallow, poorly developed, and deeper at the rear, with the head and front flippers often not below the front of the pit. In all cases, the carapace is still well

above the surrounding sand. Both rear flippers work in opposition, that is, as one pushes posteriorly, the other moves forward. The front flippers are not used much during the nesting process, resulting in a pile of sand halfway toward the posterior of the shell. These piles remain until filling occurs. The front flippers clear sand in an arc of about 180°; the rear flippers in an arc of 70–80°. Construction of the shallow body pit usually takes 6–10 min but may take more or less time depending upon the consistency of the sand.

5. *Digging the egg chamber.* The rear flippers change from pushing sand posteriorly to a downward digging action comprising two distinct flipper actions. The first loosens the sand by a rotating movement, while the second digs into the sand and scoops it out and carries it to the side where it is dumped. The front flippers serve to anchor the turtle as the posterior of the body swivels from side to side to allow the digging flipper to be directly over the egg chamber. Digging is fairly rapid and continuous as the digging flippers are alternated from side to side. One rear flipper digs while the other anchors the turtle and prevents sand deposited from the previous cycle from tumbling back into the chamber. Each cycle of movement takes from 27–37 s (Margaritoulis 1985). Short rests (5–10 s in duration) are periodically taken. As the egg chamber deepens, the turtle pushes up with its front flippers to increase the inclination of the rear part of its body. When the flippers are unable to reach more sand from the bottom of the chamber, flipper action changes to remove sand from the bottom sides of the chamber. This results in a flask-shaped nest cavity. Kaufmann (1966) noted that the female only needed 10–15 min to dig the egg chamber.

6. *Egg laying.* Egg laying commences 15–20 s after completion of the egg chamber. Eggs are dropped singly or in groups of two or three. At the end of egg laying, eggs may fill from 50% to 100% of the egg chamber. Clear mucus often accompanies the eggs as they drop into the chamber, but the female does not urinate on the nest. Up to the point of egg laying, turtles may be easily frightened and abandon nesting and return to the sea. However, as egg laying progresses, the threshold to abandon the nesting sequence increases considerably (Margaritoulis 1985). Egg laying in Colombia took from 7 min (96 eggs) to 25 min (71 eggs) with an average of 14 min, 48 s (N = 38 turtles; Kaufmann 1973). Bustard et al. (1975) reported egg laying lasts 16–22 min for clutches of between 113 and 138 eggs. Margaritoulis (1985) reported eggs were laid at the rate of 8.5 per min, while Cribb (1978) stated eggs or groups of eggs were dropped at 5–10 s intervals.

7. *Covering and packing the egg chamber.* After egg laying, the female rests from 1–3 min before beginning to cover the eggs. The rear flippers move one at a time medially under the body in a 45° arc. The female stabilizes herself on one knee, then gently sweeps sand over the eggs with the knee and flipper of the other leg. Each flipper makes one or several strokes before the other one takes over. After a few minutes, the flippers begin to make wider arcs and the action becomes more vigorous. Sand is packed down over the chamber through the action of the knees rocked from side to side. The front flippers are used to stabilize the body but are not used in the covering process. Packing requires 10–15 min.

8. *Filling the body pit and concealing the nest site.* After packing is completed, the front flippers begin to throw sand backwards as the turtle slowly moves forward, filling in behind as she goes. Margaritoulis (1985) noted that the front flippers can throw sand a considerable distance (termed "sand spraying") onto the female's carapace and to the area behind the nest. This action carries the shallow body pit forward, thus disguising the actual location of the nest chamber. An elongated area of disturbed sand 3.4 m × 1.3 m results, but the area may be larger. Flippers may be operated concurrently or they may be alternated in an unpredictable manner. Eventually the female relies more on the front flippers than the rear flippers. From 26–45 min may be spent covering and disguising the nest.

9. *Return to the sea.* Turtles will suddenly stop their filling actions, raise their heads, and look around the beach. The journey down the beach is usually then completed rapidly. Bustard et al. (1975) stated that the female will travel at the rate of 10 m in 30–45 s, and Mast (1911) estimated the rate of movement at 0.5 mi per h. The turtle may pause briefly as she travels to the water, and again at the water's edge. After swimming several meters, the female raises her head and takes a single inspiration before disappearing beneath the waves.

Margaritoulis (1985) noted that the digging cycle is a very stereotyped behavior. Injured turtles will still go through the digging motions even when flippers are missing or deformed, or when impenetrable objects such as large stones are encountered. Caldwell (1962*b*) noted that one female with a deformed rear flipper laid her eggs on a flat beach below the dunes after several unsuccessful attempts to dig a nest chamber. Loggerheads also occasionally deposit part of a clutch, begin covering, then deposit additional eggs (Caldwell et al. 1959; Caldwell 1962*b*). Caldwell (1962*b*) suggested these might be inexperienced females.

One difference from the generalized nesting sequence above is the number of eggs deposited at a time. Most authors report 1-3 eggs, while Kaufmann (1966) reported 2-4 eggs per sequence with single eggs deposited rarely. However, Kaufmann (1973) later noted that 25% of the eggs were deposited singly, 43% in twos, 23% in threes, 8% in fours, and <1% in fives. Kaufmann (1966) also reported that the ovipositor swings back and forth so that no egg drops on others previously laid, and speculated that the mucus secreted during egg-laying may function to avoid encrustation of the cloacal opening with sand. Both Kaufmann (1966) and Caldwell et al. (1959*b*) noted that females produce copious tears while nesting and that they may produce an audible "huff" or snort with each egg-producing effort. Cribb (1978) noted that the female breathed deeply as she extruded eggs. While Carr (1952) reported that loggerheads may pound the site to pack loose sand, this behavior has not been observed by other authors.

Aborted nesting attempts ("false crawls") are a common feature of loggerhead nesting, and have been observed at all nesting beaches with the exception of those in Queensland, Australia. False crawls include emergences that result in the female making no nesting attempts, digging one or more body pits without nesting, and even digging a nest chamber without depositing eggs. Nesting may be aborted from human disturbance, improper beach substrate characteristics such as may occur on artificially restored beaches (Raymond 1984*b*), improper temperature cues (Stoneburner and Richardson 1981), or other factors known only to the turtle. Raymond (1984*b*) reported that from 46% to 49% of emergences (*N* = 1,898) resulted in false crawls (34%-36% with no body pit; 12% with one body pit; 1% with more than one body pit) on nonrestored beaches. Talbert et al. (1980) stated that 532 of 1,290 (40.5%) emergences between 1972 and 1976 were false crawls, and that they ranged from 28.7% in 1972 to 47.7% in 1975. Nearly all body pits contained nests (range 86.4%-95.6%, average = 90.4%). Andre and West (1981) reported 71% of emergences resulted in false crawls, while Crouse (1984*a*) reported that about half of the emergences resulted in nests. Stoneburner (1981) gave the following percentages of false crawls for the 1979-1980 seasons: 30.8% (*N* = 1,317) at Canaveral National Seashore, FL; 41.2% (*N* = 721) at Cumberland Island National Seashore, GA; and 50.4% (*N* = 119) at Cape Lookout National Seashore, NC. Lund (1986) only noted 10.5% false crawls (*N* = 3,110) on a protected beach in Florida. In South Africa, Hughes et al. (1967) reported 45% false crawls (*N* = 645), and that there was a tendency for more false crawls to occur in bad weather. In contrast, Limpus (1985) stated that loggerheads in Queensland decide the suitability of the nesting beach prior to emergence, and that there were no false crawls; unsuccessful nesting attempts were attributed in all cases to a specific disturbance.

Most females that are unsuccessful in nesting during an emergence return later the same night or following night, or at most within a few days, to make another nesting attempt. Limpus (1985) reported a mean of 1.082 days (*N* = 319) and that 87.5% of the females were reported back on the same beach they previously had attempted to nest on.

Multiple nesting. Loggerheads are known to nest anywhere from one to six times in a nesting season (e.g., Lund 1986), with a record of seven nests in a season by a female in Georgia (Lenarz et al. 1981). Limpus (1985) also noted that Australian loggerheads nested from one to six times per season, although Hughes (1974*a*) suggested that Tongaland loggerheads normally nested four to five times per season. Kaufmann (1975*b*) reported Colombian loggerheads could nest at least four times a season and possibly more. Margaritoulis (1983) could only confirm 1-3 nests per season, and suggested that loggerheads did not remain the entire nesting season at a nesting site. Talbert et al. (1980) noted that South Carolina loggerheads generally nested from 2-3 times per year, with a range of 1-6. Richardson and Richardson (1982) estimated 2.5 nests per female per season in Georgia, although Stoneburner (1981) only estimated 1.84-1.97 nests per female per year for the same area. Frazer and Richardson (1985*b*), again working on Little Cumberland Island, GA, reported yearly variation in estimated clutch frequency from 2.81 in 1982 to 4.18 in 1979 between the years 1974 and 1983. Iwamoto et al. (1985) verified two nestings per season in Japan. Lund (1986) reported that experienced females (i.e., remigrants) produced more clutches per year than presumed novice nesters (1.61 vs. 1.37 nests per female per year).

The internesting interval of loggerheads varies, but is generally about 14 d depending on location (Table 10). The longest internesting interval is that of 18-28 d ($\bar{x}$ = 23.4) reported by Geldiay et al. (1982) for Turkish loggerheads, and the shortest is 9 d reported by Limpus (1985) in Queensland, Australia. With the exception of Limpus' (1985) study, most sample sizes are small, and often the internesting interval appears to be based on casual observations rather than detailed analysis of tag returns. Both Hughes and Brent (1972) and Williams-Walls et al. (1983) noted that an influx of cool water during the onset of the nesting season can

Table 10. *Internesting interval reported for female loggerhead sea turtles.*

Location	Mean	Range	*N*	Reference
Atlantic				
South Carolina	13.0	—	44	Talbert et al. (1980)
Georgia	—	12–15	26	Caldwell et al. (1959*b*); Caldwell (1962*b*)
Florida	—	12–14	—	Gallagher et al. (1972)
Florida	14	11–17	18[a]	Worth and Smith (1976)
Florida	12	—	34[a]	Davis and Whiting (1977)
Florida	13.9	11–20	—	Williams-Walls et al. (1983)
Florida	13–15	—	[c]	Lund (1986)
Colombia	15.0	—	2	Kaufmann (1973)
Colombia	14.7	13–17	7[a]	Kaufmann (1975*b*)
Mediterranean				
Greece	14.6	13–20	14	Margaritoulis (1983)
Turkey	23.4	18–28	—	Geldiay (1980 *in* Margaritoulis 1983)
Indian				
Tongaland	16–17	—	—	Hughes et al. (1967)
Tongaland	14–15	—	89	Hughes and Mentis (1967)
Tongaland	14.7	—	—	Hughes (1970*a*)
Tongaland	15.2	—	—	Hughes and Brent (1972 *in* Margaritoulis 1983)
Oman	—	14–16	—	Ross (1979)
Pacific				
Japan[b]	16.2	14–21	—	Iwamoto et al. (1985)
Queensland	15.0	12–17	—	Bustard (1972)
Queensland	13.9	9–23	2,959	Limpus (1985)

[a] Values inferred from information in text or figures.

[b] Figures based on peaks of nesting rather than data on individual turtles renesting within a season.

[c] Difficult to determine from text, but possibly *N* = 843.

increase the internesting interval. During the internesting period, the female remains offshore in the general vicinity of the nesting beach (Limpus and Reed 1985). Limpus (1973*a*) reported feeding during the internesting interval, but has since concluded that within-season weight gains are due to other causes (Limpus, personal communication to A.B. Meylan). Limpus (1973*a*) suggested an abundant food source during the internesting period might be a major criterion in the establishment of a loggerhead rookery, but this is apparently not the case.

Renesting turtles generally return to the same beach or a nearby area to lay successive clutches, although they are less site-specific than other sea turtles (but see Limpus 1985, who argues that this has yet to be proven). Hughes (1974*a*) suggested that loggerheads were not site-specific per se, but did orient toward a stretch of coastline averaging 9.6 km. He also noted a tendency to shift southward in the early part of the season and northward in the latter part of the season. Lund (1986) could find no such shift in east-central Florida.

In Florida, Gallagher et al. (1972) indicated most tag returns occurred between 0.8 km and 6.8 km from previous tag sites, while Worth and Smith (1976) recorded distances averaging 4.6 km, but ranging to 21.5 km. During 3 years, Williams-Walls et al. (1983) reported that the average intraseasonal renesting distance ranged from 4.6 km through 5.0 km, but that 80% of the distances were under 5.0 km. Lund (1986) recorded the average distance moved as 3.0 km (*N* = 803; range 0–14.0 km). In South Carolina, Talbert et al. (1980) reported that 22 multiple return females averaged 3.2 ± 1.8 km between successive emergences. These authors suggested that loggerheads in South Carolina might show less site fidelity than green turtles because beaches in South Carolina undergo yearly unpredictable fluctuations as a result of erosion. Thus, less site fidelity might be selectively advantageous in subsequent nest site selection. In Australia, Limpus (1985) noted that

Table 11. *Remigration frequency in nesting loggerhead sea turtles.*

Location	Mean	Range	*N*	Reference
Georgia	2.6	1-6	151	Richardson et al. (1978)
Tongaland	2.5	1-5	95	Hughes (1976*b*)
Queensland	3.0	1-9	699	Limpus (1985)
Queensland[a]	3.5	1-9	1,405	Limpus (1985)

[a] Revised estimate after adjusting for tag loss.

the average distance between successive intraseasonal emergences was 381 m (range = 25–1,450; *N* = 265); successful nesting turtles were less likely to move between beaches than turtles disturbed during nesting. In Oman, the average distance between consecutive landings was 0.88 km and the mode was 0.4 km (*N* = 522) at Surf Beach on Masirah Island (Ross 1979).

However, some loggerheads move considerable distances between successive nestings (summarized by Bjorndal et al. 1983). The record appears to be held by a female that nested 9 July 1979 in North Carolina and again 28 July in Florida, a distance of 725 km (Stoneburner and Ehrhart 1981). Bjorndal et al. (1983) recorded 38 instances of intraseasonal renestings from 26 km to 182 km distant. Iwamoto et al. (1985) reported a female that nested 26 June 1979 in Nagasaki and again 29 July at Miyazaki, a distance of 377 km. Hughes (1974*a*) mentioned one female that, when disturbed, moved 12 km before nesting the same night.

There is much confusion about nesting cycles in sea turtles in general. Although widely reported to nest on a 2-, 3-, or 4-yr cycle (Table 11), the vast majority of nesting females are never seen again, even taking into consideration tag loss (Henwood 1986) and inadequate beach coverage (Hughes 1982*a*). The significance of this is unknown. A small percentage may be seen in consecutive years (Hughes 1976*b*, 1982*a*; Richardson et al. 1978; Bjorndal et al. 1983; Limpus 1985; Lund 1986) or after an extended period of time (Table 12). The 2- to 3-yr cycle seems to predominate (Table 12) although it may be more appropriate to speak of irregular nesting cycles. Hughes (1974*a*) and Limpus (1985) have shown that females may switch from a 2-yr cycle to a longer or shorter one over an extended period of time. The particular periodic nesting cycles observed on any given beach are dependent, in part, on the annual survival rates of the nesting females (Frazer 1984). The assessment of periodic nesting cycles, and the determination of their significance, requires additional data.

Loggerheads nesting in a particular area show a high degree of philopatry when remigrating in subsequent years. Limpus (1985) noted that 98.3% of Australian remigrants were captured at the original tagging location (*N* = 1,433 remigrants over 9 seasons). About 4.5% of remigrants changed local nesting beaches between nesting seasons. Females may shift nesting sites, but they are more likely to move to a relatively nearby area than progress further afield. Some authors have stated that loggerheads do not show strict site philopatry (Hughes 1974*a*), although Hughes went on to say that 93.1% (in 1971–72 with a mode of 800 m) and 91.1% (in 1972–73 with a mode of 400 m) of Tongaland remigrants returned to within 9.6 km of their original tagging site. Thus, the argument about site philopatry might revolve more about what is to be termed "close" rather than whether loggerheads remigrate to the same general area. However, there are exceptions (Bjorndal et al. 1983). Of 647 loggerheads tagged on Little Cumberland Island, GA, between 1964 and 1976, 22 of 43 tag returns occurred within 16.6 km, 3 within 50 km, and 18 at greater distances (Bell and Richardson 1978). Most were from Jekyll Island and

Table 12. *Literature records for loggerhead sea turtle remigration intervals.*

Location		1 yr	2 yr	3 yr	4 yr	5 yr	6 yr	7 yr	Reference
Florida	N	3	75	56	21	5	0	1	Bjorndal et al. (1983)
	%	1.9	46.6	34.8	13.0	3.1	—	0.6	
Georgia	N	7	135	75	17	4	4	0	Richardson et al. (1978)
	%	2.9	55.8	31.0	7.0	1.7	1.7	—	
Tongaland	N	110	332	151	239	32	19	6	Hughes (1982*a*)
	%	12.3	37.3	16.9	26.8	3.6	2.1	0.6	
Queensland	N	63	408	383	156	74	20	4	Limpus (1985)
	%	5.7	36.7	34.4	14.0	6.7	1.8	0.4	

Cumberland Island, the nearest beaches to the north and south, respectively. Also, the tag returns reported by Bell and Richardson (1978) included turtles caught in trawls as well as turtles found dead or nesting on other beaches. Bjorndal et al. (1983) reported interseasonal shifts of 46 loggerheads seen on other Florida beaches that span a distance of 255 km. One female tagged in west Florida in 1968 was recaptured in 1972 on Melbourne Beach on the east-central coast of Florida, a distance of 550 km (LeBuff 1974).

3.1.7 Eggs

Freshly laid loggerhead eggs are generally spherical and white with soft papery or leathery shells coated with a mucous secretion. The secretion dries in a few hours and the shell takes on a parchment-like texture. Caldwell (1959) reported that eggs laid last were generally smaller than eggs deposited at the start of nesting. Limpus (1985) noted that the first few eggs were more ellipsoidal than the rest of the clutch, and that eggs deposited in different parts of the clutch had significantly different diameters. Eggs laid at the beginning of the clutch also were generally larger than those deposited in the latter part of the clutch. Hughes et al. (1967) thought no such relation existed, although they admitted their sample size was small. Caldwell (1959) reported that the size of the egg was inversely correlated with the carapace length of the female. Ehrhart (1982) stated that there was a weak positive correlation between female size and egg size, while Frazer and Richardson (1986) stated that egg size did not change substantially with female size. They called for more work to assess the relation between egg size and clutch frequency in sea turtles.

The appearance of small eggs, generally incorrectly termed ''yolkless'' eggs because they may contain from zero to more than two small yolk masses (Miller 1982), has been noted in a number of areas. They were first reported by Caldwell (1959) in South Carolina as being 28–30 mm in diameter; he speculated they were the last eggs deposited since they generally were at the top of the nest. Caldwell (1959) also reported occasional exceptionally large eggs (one shaped like a hen's egg measured 43 × 51 mm) and an egg with two yolks measured 47 × 66 mm. Other abnormally sized and shaped eggs were reported by LeBuff and Beatty (1971), Miller (1982), Limpus et al. (1984), and Limpus (1985). Unlike *Dermochelys* and *Eretmochelys* which often lay a large number of abnormally small eggs, Limpus (1985) found that ''yolkless'' eggs occurred in only 5.1% of the samples he examined; these measured 7.0 mm to 29.9 mm and averaged 18.9 mm ($N = 28$).

Loggerhead clutch data, such as clutch depth, egg diameter and mass, and number of eggs per clutch have been reported for numerous locations. Loggerhead nest dimensions have been recorded mostly from the southeastern United States and Australia although sample sizes are often small, and important parameters, such as the range, often are not reported (Table 13). The diameters and masses measured for eggs from nests throughout the world have been summarized in Tables 14 and 15, respectively. Egg diameters are nearly identical regardless of population; the high value reported by Hughes et al. (1967) in Tongaland is obviously in error since it does not match the range of values reported in the text. Egg mass also is rather similar except for the reports from Turkey showing an average egg mass about half that of all other populations (Geldiay et al. 1982). For both sets of data, however, most sample sizes are small. As with other sea turtles, the clutch size varies greatly from population to population (Table 16) with the highest average clutch sizes in Australia. There is a great deal of intrapopulational variation in clutch size as well (Table 16), although Frazer and Richardson (1985*a*) noted that the mean clutch size varied significantly in only 2 of 19 consecutive years at Little Cumberland Island, GA. The overall range of clutch size varies from 23 to 198. Hirth (1980) reported that there was no relation between clutch size and average carapace length of nesting females in six populations: Cape Romain, SC; Cape Kennedy, FL; Hutchinson Island, FL; Buritaca, Colombia; Tongaland, South Africa; and Masirah Island, Oman. Caldwell et al. (1959*b*) also reported no such relation at Jekyll Island, GA ($N = 25$).

Ehrhart (1979*a*) reported a positive relation between clutch size and female carapace length for the population in east-central Florida, as did Limpus (1985) in Australia. Contrary to the findings of Caldwell (1959) previously, Frazer and Richardson (1986) reported a positive relation in loggerheads nesting at nearby Little Cumberland Island, GA. They attributed the lack of correlation seen in some studies to a small sample size. Witherington (1986) and Ehrhart and Witherington (1987) also reported a positive relation in Florida, but a negative correlation between clutch size and date of deposition. However, these authors reported that larger females nested earlier in the season, which accounted for the correlation. Caldwell (1959), LeBuff and Beatty (1971), and Davis and Whiting (1977) reported that clutch size decreased as the nesting season progressed, while Kaufmann (1975*b*) felt it increased. However, none of these studies provided rigorous supporting data, and sample sizes were small. Frazer and Richardson (1985*a*) reported that successive clutches were not

Table 13. *Loggerhead nest dimensions (cm).*

Location	Mean	Range	*N*	Reference
Depth to top of nest				
New Jersey	20.0	—	1	Brandner (1983)
Maryland	36.0	—	1	Graham (1973)
North Carolina	32.8	30-38	6	Coker (1906)
North Carolina	29.2	18-41	17	Ferris (1986)
South Carolina	—	12.7-55.9	317	Caldwell (1959)
Florida	27.9	—	1	Mast (1911)
Queensland	33.1	0-59	277	Limpus (1985)
Depth to bottom of nest				
New Jersey	45.0	—	1	Brandner (1983)
Maryland	79.0	—	1	Graham (1973)
North Carolina	—	51-66	6	Coker (1906)
North Carolina	57.4	43-71	17	Ferris (1986)
Georgia[a]	41.9	34.9-47.0	25	Kraemer (1979)
Florida	44.5	—	1	Mast (1911)
Australia	50	—	—	Bustard et al. (1975)
Australia	58.6	44-85	—	Limpus et al. (1979*b*)
Queensland	57.9	36-85	505	Limpus (1985)
Maximum diameter of nest				
New Jersey	20.0	—	1	Brandner (1983)
Maryland	20.0	—	1	Graham (1973)
Florida	22.9	—	1	Mast (1911)
Tongaland	20	—	—	McAllister et al. (1965)
Australia	—	20-25	—	Bustard et al. (1975)

[a]Measured from the nest bottom to the female's plastron.

Table 14. *Diameter (mm) of loggerhead sea turtle eggs.*

Location	Mean	Range	Clutches	Eggs	Reference
Atlantic					
New Jersey	38	—	1	129	Brandner (1983)
South Carolina	41.5	35-49	44	827	Caldwell (1959)
Florida	42.3	40.2-44.8	6	702	Ehrhart (1979*c*)
Florida	42.2	37.0-55.2	44	4,804	Ehrhart (1979*c*)
Colombia	43.3	39.7-47.5	3	370	Kaufmann (1968)
Indian					
Oman	42.1	38-46	29	—	Hirth (1980)
Tongaland	38	—	—	—	McAllister et al. (1965)
Tongaland	49.9[a]	36-44	26	260	Hughes et al. (1967)
Mediterranean					
Sicily	—	40-44	—	—	Bruno (1970)
Greece	—	35-40	2	12	Margaritoulis (1985)
Turkey	39	37-42	50	500	Geldiay et al. (1982)
Pacific					
Queensland	40.1	37.6-42.3	29	290	Limpus (1973*a*)
Queensland	40.7	38.3-49.8	—	100	Miller (1982)
Queensland	41.2	39.1-43.4	17	170	Limpus et al. (1984)
Queensland	40.4	34.7-45.7	343	3,430	Limpus (1985)

[a]These are the figures as reported; the mean does not match the range of data provided in the accompanying histogram.

Table 15. *Mass (g) of loggerhead sea turtle eggs.*

Location	Mean	Range	Clutches	Eggs	Reference
Atlantic					
South Carolina	34.9	—	1	119	Caldwell (1959)
Florida	41.7	36.5–46.0	6	702	Ehrhart (1979*c*)
Florida	42.0	28.2–52.9	44	4,840	Ehrhart (1979*c*)
Colombia	38.4	29.7–46.8	3	370	Kaufmann (1968)
Mediterranean					
Turkey	20.3	—	50	500	Geldiay et al. (1982)
Pacific					
Queensland	39.0	35.7–42.3	—	100	Miller (1982)
Queensland	39.2	34–46	17	170	Limpus et al. (1984)
Queensland	36.5	26.2–43.1	24	240	Limpus (1985)

Table 16. *Clutch size of loggerhead sea turtle nests.*

Location	Mean	Range	*N*	Reference
Atlantic				
New Jersey	129	—	1	Brandner (1983)
Maryland	133	—	1	Graham (1973)
North Carolina	135.0	118–152	6	Coker (1906)
North Carolina	119.5	86–159	20	Ferris (1986)
South Carolina	126	64–198	71	Caldwell (1959)
South Carolina	111.4	—	28	Stancyk et al. (1980)
South Carolina	117	—	393	Andre and West (1981)
Georgia	121.1	—	701	Frazer and Richardson (1985*a*)
Georgia	119.8	—	2,126	Frazer and Richardson (1985*b*)
Florida	110	44–172	46	LeBuff and Beatty (1971)
Florida	120	—	—	Worth and Smith (1976)
Florida	100	48–159	—	Davis and Whiting (1977)
Florida	117	81–149	6	Ehrhart (1979*c*)
Florida	110	43–154	44	Ehrhart (1979*c*)
Florida	149	70–165	26	Witherington (1986)
Colombia	106	58–163	52	Kaufmann (1968)
Colombia	105	58–163	69	Kaufmann (1973)
Colombia	107.0	58–163	185	Kaufmann (1975*b*)
Indian				
Oman	107	55–150[a]	—	Ross (1979)
Oman	101	72–130	29	Hirth (1980)
Tongaland	118	81–141	—	McAllister et al. (1965)
Tongaland	112.0	55–160	98	Hughes et al. (1967)
Tongaland	118	—	68	Hughes and Mentis (1967)
Tongaland	118	—	86	Hughes (1970*a*)
Tongaland	117	—	19	Hughes (1971*d*)
Tongaland[b]	115	76–155	10	Hughes (1972)
Tongaland	94.6	39–161	24	Hughes (1972)
Tongaland	113	—	41	Hughes and Brent (1972)
Tongaland	105.3	39–154	72	Hughes (1974*a*)
Mediterranean				
Sicily	—	120–150	—	Bruno (1970)
Greece	100.2	—	9	Margaritoulis (1985)
Greece	114.4	—	52	Sutherland (1985)
Turkey	93	23–134	50	Geldiay et al. (1982)

Table 16. *Continued.*

Location	Mean	Range	*N*	Reference
Pacific				
Queensland[c]	133.0	83-174	31	Limpus (1973*a*)
Queensland	124.4	89-164	27	Limpus et al. (1984)
Queensland	127.0	48-190	1,056	Limpus (1985)

[a] Estimated from histogram.

[b] Values for clutches moved to a hatchery assumed to be separate from reports for nests left in the beach.

[c] Based on renesting of 10 females within a nesting season.

significantly different over the course of a season, although the last clutch was significantly smaller than the first clutch. With a large sample size ($N = 940$), these authors felt no trends could be discerned relating clutch size to the time of the season clutches were laid.

Loggerhead clutch incubation periods and hatching success, including natural and transplanted clutches, have been recorded for a number of populations. It should be noted, however, that hatching precedes emergence by 2-7 d (Miller 1982) and it is not often clear in many studies whether this has been taken into consideration. Given this caution, the incubation period is similar between populations (Table 17), presumably reflecting similar thermal regimes on nesting beaches. McGehee (1979) showed that nest temperature was inversely correlated with the duration of incubation (see also Miller 1982); at the extremes, eggs incubated at a constant 32°C took 48.4 d to hatch while eggs incubated at 24°C took 87.3 d to hatch. Less than 20% of the eggs hatched successfully at 24°C while >70% hatched at 27, 30, and 32°C. Similar results were presented by Yntema and Mrosovsky (1979, 1980) who also noted that hatching success decreased at temperatures >32°C. McGehee (1979) also noted that optimal nest conditions included a moisture content of

Table 17. *Incubation periods (days) for loggerhead sea turtle nests. (The figures are for nests as deposited by the female unless otherwise indicated.)*

Location	Mean	Range	*N*	Reference
Atlantic				
South Carolina	55.0	49-62	55	Caldwell (1959)
North Carolina	60.5	56-65	19	Ferris (1986)
Georgia	62.6	50-76	918	Kraemer (1979)
Florida[a]	65.5	—	20	Worth and Smith (1976)
Florida	55.0	—	—	Davis and Whiting (1977)
Florida[b]	69.0	63-75	—	Ehrhart (1979*c*)
Florida[b]	60.5	—	15	Demmer (1981)
Florida	53.1	49-58	67	Witherington (1986)
Indian				
Tongaland	67.0	—	4	McAllister et al. (1965)
Tongaland	67.3	55-80	10	Hughes (1972)
Tongaland[c]	56.8	53-59	10	Hughes (1975*a*)
Oman[d]	51.2	—	18	Ross (1979)
Oman[e]	50.2	—	15	Ross (1979)
Mediterranean				
Greece	50.7	—	3	Margaritoulis (1985)
Greece	57.5	49-69	6	Sutherland (1985)

[a] Artificially incubated by unknown method.

[b] Clutches incubated within a building near the nesting beach.

[c] Clutches incubated in a protected hatchery on a nesting beach.

[d] Data for 1977.

[e] Data for 1978.

around 25% saturation and a salinity content less than 25%. On her control beach, moisture averaged 18.3% saturation with a salinity content of 3.5% seawater. McGehee (1979) suggested that temperature was the most important factor in limiting the geographic range of sea turtle rookeries, while Kraemer (1979) suggested that ambient sand temperature temporally limits the nesting season. Mrosovsky and Yntema (1980) noted that, under controlled conditions, increasing the incubation temperature 1°C decreases the duration of incubation 5 d within the thermal limits of development.

The hatching success (i.e., percentage of emerged hatchlings) of various loggerhead populations on natural nesting beaches is shown in Table 18. Nesting success on these beaches is similar, although there is a great deal of variation from one nest to the next. Nests relocated to protect them from predation or other forms of destruction can enjoy high rates of hatching success (McGehee 1979; Blanck and Sawyer 1981; Miller 1982), provided they are moved soon after deposition, and in certain cases the hatching success may be considerably improved (Wyneken et al., 1987). McGehee (1979) showed that movement up to 12 h after deposition caused no problems, while Limpus et al. (1979*a*, 1979*b*) found even gentle inversion from 12 h to 14 d after deposition significantly reduced hatching success. Blanck and Sawyer (1981) suggested that eggs not be moved after 36 h since the extra-embryonic membranes encompass the embryo and attach it to the top of the shell at about this time. Miller and Limpus (1983) suggested that cooling eggs immediately after deposition would reduce movement-induced mortality. Low or 0% hatching success also may result from deposition of infertile eggs. Seyle (1987) provided data from a female nesting at Wassaw Island, GA, that produced fertile clutches in 1981 and 1986. Her four clutches in 1984 were all infertile. Hatching success may be greater in sands 0.25-0.125 mm in diameter than coarser grained sands (Schwartz 1982), although more rigorous tests need to

Table 18. *Percentage of loggerhead sea turtle eggs resulting in emerged hatchlings. (Unless otherwise indicated, the figures are for nests as deposited by the female on a natural beach, and not disturbed by predators.)*

Location	Mean %	Range %	Nests	Reference
Atlantic				
North Carolina	74.4	3.14-98.4	20	Ferris (1986)
South Carolina	73.4	29.0-98.0	62	Caldwell (1959)
South Carolina	66.8	—	11	Stancyk et al. (1980)
South Carolina	72.5	—	7	Stancyk et al. (1980)
South Carolina	80.0	—	3	Stancyk et al. (1980)
Florida[a]	63.8	2.0-95.0	48	Worth and Smith (1976)
Florida	72.0	—	43	Ehrhart (1979*c*)
Florida	55.7	0.0-99.1	97	Witherington (1986)
Indian				
Tongaland	82.6	—	26	Hughes et al. (1967)
Tongaland	83.4	—	91	Hughes and Mentis (1967)
Tongaland[b]	66.1	31.3-83.1	859	Hughes (1971*d*)
Tongaland	82.4	31.0-98.7	20	Hughes (1972)
Tongaland[b]	68.7	42.1-94.2	10	Hughes (1972)
Tongaland	77.8	0.0-98.7	72	Hughes (1974*a*)
Oman[d]	57.3	—	18	Ross (1979)
Oman[e]	53.1	—	15	Ross (1979)
Oman[f]	67.8	—	11	Ross (1979)
Pacific				
Queensland	83.8	10.6-100	90	Limpus et al. (1979*b*)
Queensland[c]	81.9	—	422	Limpus (1985)
Queensland[c]	80.4	—	578	Limpus (1985)

[a] Artificially incubated in sand or vermiculite.
[b] Values for nests moved to a protected hatchery on a natural beach.
[c] Values for different nesting seasons.
[d] Data for 1977.
[e] Data for 1978, estimated from nests marked when laid.
[f] Data for 1978, estimated from nests excavated after hatchling emergence.

be made to determine the effects of sand grain size on hatching success.

The temperature of natural loggerhead nests monitored in Florida averaged 28.7°C (range 26.1-29.8°C; McGehee 1979), while nests in Japan ranged from approximately 24-28°C (Uchida and Kajihara 1977). Caldwell (1959) reported the average temperature fluctuated from 27.8°C to 31.1°C, with extremes of 25.0°C to 33.9°C. The temperature of the egg mass, originally equal to the sand temperature, rises from 1.8°C to 2.3°C during the course of development (McGehee 1979; Kraemer 1979). Kraemer (1979) also showed that the rise in metabolic heat occurred gradually from 1-5 weeks, sharply from 5-8 weeks, followed by a sharp decline until emergence. Some authors (e.g., Limpus et al. 1983; Limpus 1985) have measured the sand temperature at the depth of an average nest in an attempt to monitor the thermal variation eggs would be exposed to on a beach. However, McGehee (1979) has shown that a clutch of eggs is slightly warmer (average 0.9°C) than sand at the same depth. In any case, Australian beaches generally fluctuated from 25-32°C for the bulk of the nesting season. Island beach sand was typically 1-2°C cooler than mainland beach sand (Limpus et al. 1983). Greater hatching success may occur in fine sands (0.25-0.125 mm diameter) when compared with more coarse sands (Schwartz 1982).

During incubation, oxygen consumption increases sigmoidally (Ackerman 1977, 1980), and Ackerman (1980) has suggested that the construction of the sea turtle nest chamber functions to equalize gas exchange for all eggs buried in the clutch. He further suggested that the number of hatchlings produced relative to the number of eggs deposited by the female is related to nest gas exchange. Oxygen consumption increases rapidly during the second half of incubation and slows just prior to hatching. The oxygen consumed is about one half per g the amount consumed per g of an avian egg mass (Ackerman 1981*b*). At similar egg masses, the oxygen cost of incubation increases as incubation time increases. Impeded gas exchange can prolong incubation time and increase egg mortality (Ackerman 1981*a*).

Predation on loggerhead eggs has been reported from ghost crabs, ants, varanid lizards, crows (already partially depredated nests), rats, raccoons, pigs, foxes, dogs, and even bears (Table 21). In the southeastern United States, raccoons are responsible for nearly all of the >90% nest mortality on certain beaches (e.g., Ehrhart 1979*b*). The literature also contains speculation about possible predators without documentation of actual predation; such references are not included in Table 21. Wyneken et al. (1988) noted that high species diversity of bacteria in eggs or the occurrence of the same bacteria in both eggs and the laying female was correlated with lower hatching success. Bacteria included: *Serratia* sp., *Klebsiella* sp., *Acinetobacter* sp., *Moraxella* sp., *Aeromonas* sp., *Enterobacter* sp., *Pseudomonas* sp., and *Vibrio* sp. These authors also noted the presence of a fungus (possibly *Mucor* sp.) in some eggs but it was not associated with any particular nonviable category of eggs. Nematodes may be found on broken eggs (Caldwell 1959).

Additional mortality of loggerhead nests may be due to beach erosion (Caldwell 1959; Hopkins et al. 1978), especially during tropical storms (e.g., Witherington 1986), disturbance by other nesting loggerheads or different species of sea turtles (Limpus 1985; Witherington 1986), invasion of clutches by plant roots (Witherington 1986: 3% of clutches invaded and destroyed, particularly by morning glory vine, *Ipomoea pes-caprae*), and off-road vehicles crushing nests (Mann, 1977). Hopkins et al. (1978) reported that 65 of 458 (14.2%) nests were destroyed by a combination of erosion and salt water inundation during the 1977 nesting season. Flooding due to sea water overwash is considered the major cause of nest failure at Masirah Island (Ross 1979). In 1977, a hurricane at Masirah destroyed an estimated 42% of the total season's egg output; flooding was less intense in 1978 but still destructive due to overwash from very high tides (Ross 1979). Ferris (1986) reported that low nest success (<50% hatching) was significantly correlated with overwash of the nest site. Excessive rainfall can also destroy nests by suffocating developing embryos and hatchlings (Ragotzkie 1959; Kraemer and Bell 1980). Fritts and McGehee (1982 *in* Coston-Clements and Hoss 1983) reported that fresh crude oil causes significant embryonic mortality but that weathered crude may not. DDE levels of 9 loggerhead eggs from 9 clutches on Merritt Island, FL, averaged 0.047 ppm (range 0.024-0.090 ppm) in 1976 (Clark and Krynitsky 1980) and 0.091 ppm in 1979 (N = 15 eggs; range 0.084-0.099 ppm; Clark and Krynitsky 1985). Fletemeyer (1980) noted 0.034 ppm (N = 4) in loggerhead eggs from southeast Florida. None of these values is considered deleterious to development.

3.2 Embryonic and Hatchling Phase

3.2.1 Embryonic phase

Although Agassiz (1857) was the first to describe the development of the loggerhead, few studies have discussed the development of this species since (e.g., Mitsukuri 1894, 1896-98; Jordan 1917*a*, 1917*b*; Fujiwara 1966). Ewert (1985) reviewed the embryology of turtles in general with some reference to the literature on *Caretta*, and Miller (1985) reviewed the early work on the developmental biology of the loggerhead. Table 19 summarizes references to the developmental biology of embryos and the anatomy of *Caretta* hatchlings.

The most comprehensive work to date is that of Miller (1982, 1985) who studied the embyology of five indigenous species of sea turtles in Australia, including *Caretta*. He divided the developmental period into 6 preovipositional stages and 25 post-ovipositional stages, provided descriptive accounts and photographs of each stage, gave measurements of embryos at each stage, and provided a chart comparing relative sizes of embryos incubated at different temperatures. He noted that these developmental stages are similar in all marine turtles except *Dermochelys*.

The developmental stages are summarized briefly as follows (Miller 1985):

Pre-ovipositional stages (1–6)
Stage 1. Single furrow forms initial cleavage.
Stage 2. Embryonic area contains about 100 blastomeres surrounded by deep cleavage furrows.
Stage 3. Embryonic area contains about 300 blastomeres surrounded by deep cleavage furrows.
Stage 4. Embryonic area contains small blastomeres surrounded by large blastomeres.
Stage 5. Embryonic area contains equally sized small blastomeres; peripheral cleavage furrows reduced or absent.
Stage 6. Dorsally, embryonic area situated eccentrically and posterior to ovoid pellucid area; blastopore present as transverse slit.

Post-ovipositional stages (7–31)
Stage 7. Head fold shallow transverse groove; area of notochord forms elevated triangle; extra-embryonic mesoderm extending along lateral borders.
Stage 8. Embryonic shield oval; head fold semicircular furrow at apex of neural groove; embryonic plate thickens.
Stage 9. Blastodisk is an elongated oval with the chordomesodermal canal located at posterior end; neural groove and neural folds are distinct. Miller (1982) also noted the frequency of various shapes of the blastopore in 38 *Caretta* blastodisks during gastrulation.
Stage 10 Two to three pairs of somites; head fold a deep inverted U-shape; head process slightly raised.

Table 19. *Descriptions of the anatomy of embryonic and hatchling* Caretta caretta.

Organ/system	Aspect	Group[b]	Reference
Adrenal	Origin	E	Kuntz (1912)
Chordomesodermal canal	Development	E	Fujiwara (1971*b*)
Esophagus	Development	E	Jordan (1917*a*)
Embryonic membranes	Description	E	Blanck and Sawyer (1981)
Eye	Structure of orbit, eyeball & retina	H to A	Underwood (1970)
Germ layers	Development	E	Jordan (1917*b*); Fujiwara (1966); Fujimoto et al. (1979); Kuwana et al. (1980)
Gonads	Sex differentiation	E	Yntema and Mrosovsky (1980); Reed (1980)
Hindgut	Development	E	Fujiwara (1973*a*)
Kidney	Development	E	Fujiwara (1973*b*); Fujihara (1972)
Lacrimal gland	Histochemistry/fine structure	H to A[a]	Abel and Ellis (1966)
Lymph sacs	Origin/development	E	Van Der Jagt (1931, 1932)
Lymphatic system	Development	E	Stromsten (1912)
Nervous system	Development of sympathetic	E	Kuntz (1911)
Nose	Histology of egg tooth	H	Ogawa and Nagahama (1971); Fujiwara (1971*a*)
Pineal-paraphyseal complex	Structure	H	Owens and Ralph (1978)
Pituitary	Development	E	Pearson et al. (1983)
Stomach	Development	E	Sjongren (1945)
Whole animal	Description/stages	E to H	Miller (1982, 1985)
Whole animal	Description	E to H	Agassiz (1857); Ewert (1985)

[a] Described as "young" *Caretta* but no measurements provided.
[b] E = embryo; H = hatchling; A = adult.

Stage 11. Five to six pairs of somites; neural folds fused behind head, but remain open for the length of the body; optic vesicles lie lateral to prosencephalon.
Stage 12. Eight to ten pairs of somites; optic vesicles just visible; heart as endocardial tubes; amnion covers one-half total length.
Stage 13. Twelve to thirteen pairs of somites; anterior neuropore closed; optic vesicles prominent; heart S-shaped; lateral body folds.
Stage 14. Fifteen to seventeen pairs of somites; neural folds fused anteriorly; lenses forming; first pharyngeal cleavage evident; heart beating; amnion covers neurenteric canal.
Stage 15. Nineteen to twenty-one pairs of somites; first pharyngeal cleavage open, 2nd and 3rd as grooves; mouth open; lenses recognizable.
Stage 16. Twenty-three to twenty-seven pairs of somites; two pharyngeal clefts open; small limb buds; tail process extends beyond base of hindlimbs; blood islands visible; cranial and cervical flexure.
Stage 17. Twenty-nine to thirty-four pairs of somites; 3rd, 4th, 5th pharyngeal clefts fusing; retinas pigmented; lateral body walls well-defined; tail long and straight; small allantois.
Stage 18. Thirty-five to forty pairs of somites; pharyngeal clefts partially obscured; limb buds forming distally; choroid fissure a conspicuous streak; urinogenital prominence.
Stage 19. More than 45 pairs of somites; 15 somites visible in tail; all pharyngeal clefts closing; limb buds at paddle stage; tail curled anteroventrally.
Stage 20. Somites difficult to see; limb stalk of forelimbs obvious; allantois larger than head.
Stage 21. All pharyngeal clefts covered; carapace evident as a marginal ridge; inframarginal area not defined.
Stage 22. No digital ridges visible; lateral edge of plastron evident; radii of irides distinct; tail longer than hindlimbs.
Stage 23. Foreflippers elongated; digital ridges; posterior border of carapace a low postcentral ridge; scutes not differentiated; nasolabial groove fused; choroid fissure absent.
Stage 24. Digital ridges well-developed; hindflippers mostly rounded; central scutes faintly differentiated; rugose beak; irides fully pigmented; scleral ossicles in ventral half of eyes.
Stage 25. Foreflippers long and unpigmented; claws on first digit; phalanges well-defined; periphery of carapace complete; scleral ossicles; intestine herniated.
Stage 26. Scales may be present on flippers; all scales on carapace, plastron, and bridge distinct; scales on head visible; plastron pigmented.
Stage 27. Volume of yolk greater than volume of embryo; scales of head pigmented; periocular scales distinct; transverse fold of plastron a trough.
Stage 28. Volume of yolk equals volume of embryo; eyelid encroaches on lenses; urinogenital papilla withdrawn into cloaca.
Stage 29. Embryo 1.5 to 4 times the volume of yolk; hatchling pigmentation present.
Stage 30. Pipping occurs; embryo 5 to 11 times volume of yolk; yolk partly withdrawn into abdomen.
Stage 31. Hatching; yolk mostly to completely withdrawn into abdomen and covered by pigmented tissue; umbilical scar.

Blanck and Sawyer (1981) discussed the formation of embryonic membranes in *Caretta* (with photographs of histological cross-sections), and compared gross morphology of development with that of the freshwater turtle *Chelydra serpentina*. The chorioamnion begins to fold over the embryo at day 2 of development. By day 3, the chorion and amnion are distinct and by day 4, the amnion is distinctly two-layered. The outer layer of the amnion eventually fuses with the yolk sac membrane and the chorionic mesoderm; the chorion adheres to the shell membrane. Miller (1982) noted the lack of a vitelline membrane in yolkless eggs.

Organogenesis has been summarized for marine turtles by Miller (1982, 1985). Primordial germ cells are imbedded in the yolk sac endoderm at the anterolateral sides of the blastopore at day 5 to day 6 of development (Kuwana et al. 1980). Jordan (1917*b*) described the migratory route of the primordial germ cells and noted similarities with freshwater turtles; the period of greatest movement is between day 7 and day 12 and is essentially completed by day 16.

Stromsten (1912) described the peri-aortic lymphatic plexus and noted that it forms from days 23 through 30 of development. The anterior lymph sac is well-developed by day 24 of development. It arises from a vacuolation of mesenchyme in the region of the cardinal tributaries, a process described by Van Der Jagt (1931, 1932). Kuntz (1912) described the origin of the adrenal from coelomic epithelium. Pearson et al. (1983) noted that the pituitary and the apex of the hypophyseal angle are derived from the stomodeal epithelium and epithelium of mixed origin; they provided histological cross-sections of the complex during development. Owens and Ralph (1978) described the complex pineal–paraphyseal interrelationship in hatchlings. Yntema and Mrosovsky (1980) compared the gonads of male and female hatchlings and provided histological photographs illustrating differences.

Much of the work on the biochemistry of *Caretta* embryos was performed by Japanese workers in the late 1920's through the early 1930's. Summaries are provided by Miller (1985) and in Table 20. Karashima (1929*a*) and Bustard et al. (1969) presented divergent results on the fate of magnesium during development. One additional paper discussed enzymes during development in sea turtles, presumably loggerheads (Sagara 1929). Enzymes discussed include diastase, lipase, nuclease, and trypsin, but since symbols in the table are not explained and the text does not clarify the table, it is impossible to determine the fates of these enzymes during development.

McGehee (1979) and Miller (1982) provided reviews of deformities during the development of *Caretta* embryos. McGehee (1979) recorded more deformities in embryos incubated at lower temperatures (<30°C) than those at higher temperatures although Miller (1982) speculated that lower temperatures per se might not be responsible for the deformities. Deformities may arise from environmental influences or hereditary factors.

Irregularities of the scutes are the most common deformities in loggerhead hatchlings, and have been reported from a wide array of studies: Agassiz (1857), Coker (1905, 1910), Babcock (1930), Caldwell (1959),

Table 20. *Biochemical changes during development of the loggerhead embryo (adapted from Miller 1985).*

Function/chemistry	Activity during incubation	Reference
Free glucose	decreases	Tomita (1929)
Lactic acid	decreases <15 d increases >15 d	Sendju (1929*a*)
Free cholesterol	shifts to ester forms	Kusui (1930)
Total cholesterol	decreases	Kusui (1930)
Glutathione	increases late incubation	Tomita (1929)
Inorganic phosphorus	increases in embryo decreases in yolk	Karashima (1929*a*)
Organic phosphate	present as 2,3-DPG in erythrocytes	Isaacks et al. (1978)
Inositol pentaphosphate	absent in red blood cells	Isaacks et al. (1978)
Free fatty acids	constant	Karashima (1929*b*)
Water-soluble and insoluble fatty acids	constant	Karashima (1929*b*)
Total fatty acids	decreases	Karashima (1929*a*)
Tryptophane	decreases	Sendju (1929*b*)
Tyrosine	decreases	Sendju (1929*b*)
Cystine	decreases	Sendju (1929*b*)
Arginine	decreases	Sendju (1929*b*)
Histidine	increases	Sendju (1929*b*)
Lysine	varies	Sendju (1929*b*)
Purine-based amino acids	increases	Sendju (1929*b*)
Urea production	greater than uric acid	Tomita (1929)
Total nitrogen	decreases	Nakamura (1929)
Total ash in egg	constant	Karashima (1929*a*)
Ash in yolk and albumin	decreases	Karashima (1929*a*)
Ash in amniotic and allantoic fluids	increases	Karashima (1929*a*)
Ash content of yolk	0.9 ± 0.1%	Kraemer and Bennett (1981)
Ash content of hatchling	16.43 ± 2.93%	Kraemer and Bennett (1981)
Magnesium	> in embryo than egg	Karashima (1929*a*)
Magnesium	< in embryo than egg	Bustard et al. (1969)
Calcium	increases in embryo	Karashima (1929*a*); Bustard et al. (1969)
Calcium	62% from egg shell	Bustard et al. (1969)
Ash-free dry mass in yolk	7,949 ± 132 cal/g	Kraemer and Bennett (1981)
Ash-free dry mass in hatchling	6,712 ± 29 cal/g	Kraemer and Bennett (1981)
Moisture content of yolk	44.9%	Kraemer and Bennett (1981)
Moisture content of hatchling	72.0%	Kraemer and Bennett (1981)
Posthatching yolk metabolism	50% between hatching and emergence	Kraemer and Bennett (1981)
Water absorption during incubation	50%	Cunningham and Hurwitz (1936)

Hughes et al. (1967), Hughes and Mentis (1967), Nishimura (1967), Hughes (1970*a*, 1974*b*), Fujiwara (1972), McGehee (1979), and Miller (1982). The scutes involved include the marginals, inframarginals, costals, head shields, and mandibular scales. Both Coker (1910: carapacial scutes) and Nishimura (1967: carapace, inframarginals, head shield, and mandibular) provided numerous illustrations of such variation. Gadow (1899) also reported scute abnormalities in *Thalassocheys caretta* from New Britain but, according to Nishimura (1967), these were misidentified *Lepidochelys olivacea*. Much of the older literature, especially from the western Pacific and Indian oceans, confuses *Lepidochelys* with *Caretta* (Nishimura 1967); as such, data from these studies must be assessed with caution.

Anomalies such as supernumerary or decreased numbers of costals and marginals need not be detrimental to the turtle. Subadults (Brongersma 1968*a*) and adults occasionally have odd numbers or patterns of these scutes. However, more serious deformities are almost always fatal either prior to pipping or, if pipping occurs, prior to emergence from the nest (Miller 1985). Such deformities include malformations of the eyes and jaws, especially in connection with albinism (see Section 1.3.1); dicephaly; reduction or absence of limbs; and gross deformities of the body and carapace (Caldwell 1959; Hughes et al. 1967; McGehee 1979; Miller 1982; Limpus 1985; Ferris 1986; Witherington 1986; Ehrhart and Witherington 1987).

Miller (1982; Tables 60 and 61) listed 13 categories of abnormalities seen in his and McGehee's (1979) studies, excluding albinism with no other deformity and atypical scale patterns, and including encephalocele, anopthalmia, monopthalmia, synopthalmia, micrognathia, prognathism, diprosopus, perocormus, celosomia, amelia, ectomelia, micromelia, and phocomelia. He also provided photographs of specimens exhibiting several of these deformities (Miller 1982; Figs. 47 and 48).

In any case, such deformities are relatively rare (0.6% of 5,666 eggs, McGehee 1979; <1.0% of 2,811 unhatched eggs, Blanck and Sawyer 1981; 0.17% of 90,000 eggs, Miller 1982; 46 abnormalities per 100 clutches [postemergence clutch examination], 3.7 abnormalities per 100 clutches [emerged hatchlings], Limpus 1985; <1.0% of unhatched eggs, Ferris 1986).

Twinning has been reported in *C. caretta* from South Carolina (Caldwell 1959, one set that died prior to hatching), Japan (Fujiwara 1964, seven pairs separated, one bifurcated apically), Florida (McGehee 1979, details not provided), Australia (Miller 1982, six pairs separated completely, eight pairs incompletely separated; Limpus 1985, three pairs), and North Carolina (Ferris 1986, two sets of twins). Miller (1982) described the external and internal anatomy of various sets of twins. It is unknown whether twins ever complete development, hatch successfully, and enter the sea.

3.2.2 Hatchling phase

The maturation of the sea-approach behavior occurs during development around day 30 when the reactions essential for swimming and terrestrial locomotion appear (Smith and Daniel 1946). After pipping, the hatchlings lie quietly for up to 26.6 h to allow their carapaces to straighten (Demmer 1981). Prior to hatching, the nest chamber undergoes volumetric reduction (Kraemer and Richardson 1979). Hatchling loggerheads, like other sea turtles, move the buried egg chamber to the surface en masse by periodic outbursts of group thrashing. The frenzied thrashing scrapes sand from the side of the egg chamber and builds up the chamber floor until it reaches the surface (Demmer 1981). Hatchlings begin the scramble toward the surface, described as social facilitation, in response to a negative geotaxis (Demmer 1981) and emergence occurs 1-7 d (mean = 2.5 d) after hatching (Demmer 1981; Miller 1982). Emergence generally occurs simultaneously as the top hatchlings move off after being pushed above the surface of the sand by the hatchlings underneath. Most emergences occur at night as sand temperatures are falling (Demmer 1981), although a small percentage may emerge in the early morning hours or even later in the day. Hughes (1974*a*) reported only 3 daylight emergences in 10 yr of fieldwork, while Limpus (1985) reported 3 of 85 (4%) emergences during daylight hours. Hatchling activity decreases in response to an increase in sand temperature which facilitates emergence at night. In some instances, not all hatchlings emerge at the same time; in these cases, stragglers will emerge in subsequent nights (Limpus 1985). Loggerhead hatchlings rely substantially on anaerobic metabolism both during emergence and the subsequent hatchling frenzy (Dial 1987).

Upon emergence, hatchlings immediately begin a rapid crawl down the beach toward the ocean; pauses are very brief and last only a second or so. Hooker (1908*a*, 1908*b*, 1911) thought loggerheads to be negatively geotropic; that is, they would always go down a slope unless there was no way to go but up. Parker (1922*a*) also noted this phenomenon, but considered it a positive geotropism since the animals were going with, rather than against, gravity. Parker (1922*a*) discounted light as a factor in orientation, but instead thought an unblocked horizon caused turtles to orient toward it. Loggerhead hatchlings now are known to be positively phototropic, or using Mrosovsky and Kingsmill's (1985) phrase, to exhibit a complex phototropotactic reaction to light, which is presumed to be an innate behavior to guide them to the sea (see also Daniel and Smith 1947*a*, 1947*b*). As such, they orient in the direction of the ocean because of moonlight reflecting on the open water. Circling behavior in response to unilateral blindfolding suggests that the reaction may be more complex than simple phototropic behavior (Kingsmill 1980; Kingsmill and Mrosovsky 1982). Loggerhead hatchlings also positively orient toward light in the blue wavelengths (Hooker 1908*c*, 1911; Parker 1922*a*; Fehring 1972). Artificial lighting behind beaches can disorient hatchlings and lead to extensive mortality (McFarlane 1963; Mann 1977; Ross 1979; Raymond 1984*a*; Witherington 1986). Even a lighthouse 1.6 km away on an otherwise unlit beach can cause hatchling disorientation (Ferris 1986).

Once in the water, the hatchlings plunge through the surf and begin swimming offshore rapidly. It appears that hatchlings use light to initially orient away from the beach, although wave direction may serve as a supplementary cue; it is not the primary cue, however (Salmon and Wyneken 1987). Turtles show periods of orientation that last past the first day of swimming. Two types of swimming behavior have been observed, termed powerstroking and dogpaddling (Salmon and Wyneken 1987) or submarine flight swimming and surface paddling (Parker 1922*b*). In dogpaddling, both sets of flippers are used alternately as if the turtle were crawling. During dives, however, powerstroke swimming relies only on the simultaneous down stroke of the front flippers; the rear flippers serve as rudders (Parker 1922*b*). These patterns are alternated, with relatively long periods of powerstroking (mean = 11.53 s) followed by short periods of dogpaddling (mean = 2.81 s; Salmon and Wyneken 1987). At rest, the front flippers are folded back onto the carapace while the rear flippers are held vertically near the sides of the body (Parker 1922*b*; Smith and Daniel 1946).

For about the first 20 h, the swimming is virtually nonstop and has been called the swimming frenzy. Salmon and Wyneken (1987) reported that hatchlings in the ocean swam at an average of 21.34 m/min (range 18.29-22.88; $N = 3$) which would, assuming they maintained this pace for the entire swimming frenzy, take them 22-28 km offshore. This is not quite enough distance to reach the Florida Current, their presumed destination (30 km offshore where Salmon and Wyneken conducted their observations). Laboratory observations indicate an increase in water temperature lowers the swimming speed (O'Hara 1980). During the first few days of swimming, hatchlings do not eat (Hughes 1974*a*; Salmon and Wyneken 1987), but then abruptly begin eating after about day 3 (Smith and Daniel 1946).

Hatchling mortality is assumed to be substantial after emergence and during the first few days of swimming. Reports of predation are summarized in Table 21. Crabs (*Ocypode*), raccoons, dogs, nearshore fishes, and sharks are probably the chief predators. Loggerhead hatchlings are not strongly countershaded as has been reported for green turtles as an adaptation against oceanic predation. In addition to natural predators, hatchlings may be disoriented by beach lighting causing them to wander overland where they are crushed by vehicles, desiccate, or are otherwise exposed to additional sources of mortality (see previous references). Mann (1977, 1978) reported that vehicles could compact the sand above a nest preventing successful hatchling emergence. However, Raymond (1984*b*) detected no influence of compaction on emergence on restored beaches since the nesting process substantially altered the sand directly over the nest allowing normal emergence. Limpus (1985) noted that some hatchlings became entangled in grass roots or seemed to be left behind in the bottom of the nest chamber and thus unable to escape. Hatchlings may get trapped in ruts left on the beach by off-road vehicles (Hosier et al. 1981; Witherington 1986). Loggerhead hatchlings also may be trapped in oil slicks on the beach (P.R. Witham, personal communication).

Mean carapace length (Table 22), carapace width (Table 23), head width (Table 24), and body mass (Table 25) of hatchlings around the world are very similar. Graham's (1973) measurements of hatchling length appear to be in error. Very small hatchlings are occasionally reported (Limpus 1985), but not from an entire clutch. The body masses reported by Graham (1973) indicate normal sized hatchlings. Also, Kaufmann's (1968) body mass data for 6-day-old hatchlings are suspect. Considering hatchlings do not eat for 2-3 d after emergence, Kaufmann's (1968) hatchlings would have doubled their weight in 3 d. This seems unlikely since the carapace lengths he reported are in the range of normal hatchlings (Table 22).

The sex ratio of hatchling loggerheads is unknown. However, loggerheads have environmental sex determination (ESD) and lack sex chromosomes (Standora and Spotila 1985). Eggs from Little Cumberland Island, GA, incubated at temperatures greater than 30°C produced all females whereas males were produced at 29°C

Table 21. *Nonhuman predators of loggerhead sea turtles. A = adult; J = juvenile; H = hatchling; E = egg; U = unknown or unreported.*

Predator	Location	Life stage	Reference
General review	—	E, H, A	Bustard (1972); Brongersma (1972); Rudloe (1979); Stancyk (1982)
Invertebrates			
Ants			
Dorylus sp.	S. Africa	E, H	McAllister et al. (1965); Hughes (1974*a*)
Unspecified	Florida	E	Witherington (1986)
Crabs			
Eriphia laevimana	Australia	H	Bustard (1972)
E. sebana	Australia	H	Limpus (1985)
Ocypode albicans	N. Carolina	H	Ferris (1986)[a]
	S. Carolina	E, H	Caldwell (1959)
O. ceratopthalmus	S. Africa	H	Hughes (1974*a*)
	Australia	H	Bustard (1974); Limpus (1985)
O. cordimanus	Australia	H	Limpus (1985)
O. kuhlii	S. Africa	H	Hughes (1974*a*)
O. quadrata	S. Carolina	E	Hopkins et al. (1978)
	Florida	E, H	Witherington (1986)
Unspecified	S. Africa	H	McAllister et al. (1965)
	Florida	E	LeBuff (1969)
	Georgia	E	Anderson (1981)
Flies			
Aedes taeniorhynchus	Florida	A	Day and Curtis (1983)
Vertetrates			
Fish			
Carcharhinus leucas	S. Africa	J, A	Hughes (1974*a*)
C. longimanus	Florida	J	Caldwell et al. (1959)
C. menisorrah	Australia	H	Limpus (1985)
C. spallanzani	Australia	H	Bustard (1974); Limpus (1985)
Carcharodon carcharias	N. Carolina	A	Coles (1915)
Centropristes striatus	S. Carolina	H	Caldwell (1959)
Coryphaena hippurus	Florida	H	Witham (1974)
Galeocerdo cuvieri	N. Carolina	A	Coles (1919)
	N. Carolina	U	Bell and Nichols (1921)
		J, A	Nichols (1921)
	Florida	U	Gudger (1949)
	W. Africa	U	Cadenat (1957)
	S. Africa	J, A	Hughes (1974*a*)
	Hawaii	J	Balazs (1979)
	Australia	A	Limpus (1985)
"Hammerhead shark"	Australia	U	Bustard (1972)
Unspecified fish	S. Carolina	H	Caldwell (1959)
Unspecified shark	Not stated	A	Larcher (1916)
	Florida	U	Caldwell (1959)

Table 21. *Continued.*

Predator	Location	Life stage	Reference
Reptiles			
Varanus exanthematicus algigularis	S. Africa	E	McAllister et al. (1965)
V. varius	Australia	E	Bustard (1972)
Birds			
Corvus corax	Greece	H	Margaritoulis (1985)
C. orru	Australia	H	Limpus (1973*b*, 1985)
C. ossifragus	Florida	E	Witherington (1986)
Dacelo gigas	Australia	H	Limpus (1985)
Egretta sacra	Australia	H	Limpus (1985)
Falco cenchroides	Australia	H	Limpus (1973*b*, 1985)
Haliaeetus leucogaster	Australia	H	Limpus (1985)
Haliastur indus	Australia	H	Limpus (1973*b*, 1985)
H. sphenurus	Australia	H	Limpus (1973*b*, 1985)
Larus argentatus	S. Carolina	H	Andre and West (1981)
	Greece	H	Margaritoulis (1985)
L. atricilla	S. Carolina	H	Andre and West (1981)
	Florida	H	Witherington (1986)
L. novaehollandiae	Australia	H	Limpus (1973*b*, 1985); Bustard (1974)
Milvus aegyptius	S. Africa	H	Hughes et al. (1967); Hughes (1974*a*)
''crows''	S. Carolina	H	Caldwell (1959)
''gulls''	S. Carolina	H	Caldwell (1959)
Unspecified	Georgia	E	Anderson (1981)
	N. Carolina	H	Ferris (1986)
Mammals			
Atilax paludinosus	S. Africa	H	Hughes (1974*a*)
Canis aureus	Libya	E	Schleich (1987)
C. familiaris	Not stated	A	Ernst and Barbour (1972)
	S. Carolina	A	Caldwell (1959)
	S. Africa	E, H	McAllister et al. (1965); Hughes et al. (1967); Hughes (1970*a*, 1974*a*)
	Greece	E	Margaritoulis (1985)
Felis catus	Australia	H	Limpus (1985)
Genetta rubiginosa	S. Africa	H	Hughes (1974*a*)
Procyon lotor	Florida	E	Routa (1968); LeBuff (1969); Gallagher et al. (1972); Worth and Smith (1976); Davis and Whiting (1977); Williams-Walls et al. (1983); McMurtray (1986*a*,*b*); Witherington (1986); Ehrhart and Witherington (1987)
	Georgia	E	Anderson (1981)
	N. Carolina	H	Ferris (1986)
	S. Carolina	E	Hopkins et al. (1978); Stancyk et al. (1980); Talbert et al. (1980); Andre and West (1981)
	S. Carolina	E, H	Caldwell (1959)
	Mexico	E	Flores-Villela (1980)
Rattus rattus	Australia	E	Limpus (1985)
Sus scrofa	Australia	E	Bustard (1972)
	Georgia	E	Anderson (1981)
Ursus americanus	Florida	E	Romans (1775)
Vulpes vulpes	Australia	E, H	Bustard (1972); Limpus (1985)

[a] Recorded elsewhere in the publication as *O. quadrata*.

Table 22. *Carapace length (mm) of hatchling loggerhead sea turtles.*

Location	Mean	Range	*N*	Reference
Atlantic Ocean				
Maryland[a]	18.1	17.5-19.0	20	Graham (1973)
South Carolina	45.0	38-50	398	Caldwell (1959)
Georgia	—	46.7-52.0	5	Caldwell (1962*c*)
Georgia	44.5	35.4-49.0	200	Kraemer (1979)
Florida	45.5	44-47	4	Caldwell et al. (1955)
Florida	46.1	39.2-49.9	6	Ehrhart (1979*c*)
Florida	45.5	33.5-49.5	42	Ehrhart (1979*c*)
Colombia	44.6	—	—	Kaufmann (1967)
Colombia[b]	46.0	42.9-50.0	—	Kaufmann (1968)
Indian Ocean				
Sri Lanka	44.1	42-45	21	Deraniyagala (1930)
Tongaland	44	—	—	McAllister et al. (1965)
Tongaland	44.7	37-48	183	Hughes et al. (1967)
Tongaland	45.0	—	499	Hughes and Mentis (1967)
Tongaland	44.4	—	50	Hughes (1970*a*)
Tongaland	44.5	41.4-46.6	30	Hughes (1971*d*)
Tongaland	45.2	42.0-48.4	58	Hughes (1972)
Tongaland	44.7	38.7-48.8	1,004	Hughes (1974*b*)
Mediterranean Sea				
Greece	40.4	—	20	Margaritoulis (1982)
Greece	40.0	—	221	Sutherland (1985)
Pacific Ocean				
Queensland	43.7	40.0-49.6	127	Limpus et al. (1984)
Queensland	43.3	39.0-46.9	710	Limpus (1985)
Japan	45.8	40.0-55.0	60	Nishimura (1967)
Solomon Islands	44.9	43-46	10	Carr (1952)

[a] Most probably an inaccurate measurement.
[b] Based on 6-day-old hatchlings.

Table 23. *Carapace width (mm) of hatchling loggerhead sea turtles.*

Location	Mean	Range	*N*	Reference
Atlantic Ocean				
Maryland[a]	7.0	6.4-7.1	20	Graham (1973)
South Carolina	35.5	31-40	398	Caldwell (1959)
Georgia	34.8	26.8-38.8	200	Kraemer (1979)
Florida	34.7	30.2-38.0	6	Ehrhart (1979*c*)
Florida	34.0	29.0-38.4	42	Ehrhart (1979*c*)
Indian Ocean				
Sri Lanka	35.7	34-38	21	Deraniyagala (1930)
Tongaland	35	—	—	McAllister et al. (1965)
Tongaland	36.2	29-39	183	Hughes et al. (1967)
Tongaland	36.7	—	499	Hughes and Mentis (1967)
Tongaland	36.5	—	50	Hughes (1970*a*)
Tongaland	36.3	31.9-38.1	30	Hughes (1971*d*)
Tongaland	36.3	31.6-38.3	58	Hughes (1972)
Mediterranean Sea				
Greece	33.9	—	20	Margaritoulis (1982)
Pacific Ocean				
Japan	40.4	34-51	60	Nishimura (1967)
Solomon Islands	38.0	36.5-39.0	10	Carr (1952)

[a] Most probably an inaccurate measurement.

Table 24. *Head width (mm) of hatchling loggerhead sea turtles.*

Location	Mean	Range	*N*	Reference
Solomon Islands	15.9	15-16	10	Carr (1952)
Tongaland	15.7	14.5-16.4	30	Hughes (1971*d*)
Tongaland	16.1	14.4-16.7	58	Hughes (1972)

Table 25. *Mass (g) of hatchling loggerhead sea turtles.*

Location	Mean	Range	*N*	Reference
Atlantic Ocean				
Maryland	—	17.0-19.0	20	Graham (1973)
South Carolina	21.2	—	104	Caldwell (1959)
Georgia	18.9	13.5-23.8	200	Kraemer (1979)
Florida	21.7	16.1-25.8	6	Ehrhart (1979*c*)
Florida	20.8	12.2-27.6	42	Ehrhart (1979*c*)
Colombia[a]	49.4	42.1-63.3	—	Kaufmann (1968)
Indian Ocean				
Tongaland	19.7	16.5-22.4	30	Hughes (1971*d*)
Tongaland	22.0	17.6-24.8	58	Hughes (1972)
Pacific Ocean				
Queensland	19.3	15.5-22.0	127	Limpus et al. (1984)
Queensland	20.9	14.6-26.5	690	Limpus (1985)

[a] Based on 6-day-old hatchlings.

or less; at 30°C, both sexes resulted (Yntema and Mrosovsky 1980, 1982). In Australia, the pivotal temperature is 1.3°C lower than that of the United States (Limpus et al. 1983), and there appears to be intrapopulational variation as well (Limpus et al. 1985). Limpus et al. (1985) speculated that loggerhead populations in other geographic regions also may show intrapopulational variation in ESD. The results of these controlled experiments show that some clutches on natural beaches have the potential to produce all males or all females depending upon incubation temperature, which in turn is influenced by the location of the nest on the beach. Limpus et al. (1983) noted that mainland beaches in Australia had the greatest potential for producing female hatchlings. Females also can be produced on northerly-aspect beaches on coral cays in the Southern Hemisphere.

During a nesting season in Georgia and South Carolina, 100% males resulted from eggs deposited in late May. Clutches deposited in early July produced 80% females. The sex ratio dropped to only 10% females for eggs laid in early August (Mrosovsky et al. 1984). The seasonal time of deposition probably affects incubation temperature which in turn affects the sex ratio of the hatchlings, since sand temperatures are cooler earlier in the season than they are during midsummer. However, on a natural beach in Australia, Reed (1980) found a significant hatchling bias toward females from all clutches produced by two females during the 1979-1980 nesting season, indicating either consistency in selecting female-producing nesting locations or a degree of heritablity in ESD.

After reviewing the data, it may be premature to automatically assume a 1:1 sex ratio in loggerhead hatchlings coming from a particular beach in any particular year.

3.3 Juvenile, Subadult, and Adult Phase

3.3.1 Longevity

There are no documented longevity estimates for wild loggerhead turtles. Frazer (1983*c*) estimated the reproductive life span of loggerheads on Little Cumberland Island, GA, an area of heavy shrimping activity, to be 32 yr with an annual constant survivorship of adult females of 0.81. Assuming these females take 15-30 yr to reach maturity (Frazer 1986), the maximum female life span would be 47-62 yr. In the absence of human effects, natural longevity could be greater (Frazer, personal communication). Other populations may reach maturity at an earlier or later date (Table 26), and nothing is known of male survivorship or longevity.

In records of captive animals, Flower (1925) mentioned a *Caretta* in a New York aquarium for 14 yr and another in Monaco for 12 yr. Flower (1937) added two additional records: 33 yr at the Vasco da Gama Aquarium in Portugal and 25 yr for a female in the Berlin Zoological Garden Aquarium.

3.3.2 Hardiness

Loggerheads may be considered a hardy and adaptable species within their natural environment (Carr 1952). However, they are susceptible to cold-stunning in areas that normally do not experience extremely cold weather, such as in Florida during the freezes in the late 1890's (Brice 1896) and the December 1983 and January 1985 freezes (Ehrhart, personal communication; Provancha et al. 1986). Stragglers also may be cold-stunned in northern waters in the autumn prior to returning south (Meylan and Sadove 1986) or as they ride the Gulf Stream waters to Europe (Brongersma 1972). Hildebrand and Hatsel (1927) considered the loggerhead quite sensitive to cold weather, noting the death of captive individuals during the winter of 1916-1917. Schwartz (1978) reported that loggerheads died after 9-12 h of exposure to water temperatures of 5.0-6.5°C. At 9.5°C, adults became ''floaters'' although smaller turtles were able to swim normally at lower temperatures. Hughes (1974*a*) found that loggerheads could survive sharp drops in sea water temperature. He placed hatchlings kept at water temperatures of 14-18°C suddenly in water 6-7°C or 9-10°C. The hatchlings survived. Feeding continued in water as cold as 17°C, and hatchlings survived at least 14 d in water 14°C. Turtles dunked in cold water recovered immediately upon return to warmer water.

Loggerheads are susceptible to drowning in fishing nets (Hillestad et al. 1982; Weber 1987; Thompson 1987), especially shrimp nets that are trawled for extended periods of time. Parker (1925) observed sea turtles in an aquarium and noted that they generally spent less than 40 min submerged. He also observed a loggerhead in the Berlin Aquarium that submerged voluntarily for 64 min but noted it was in a quiescent state. Ingle and Smith (1949) reported that captive loggerheads remained submerged up to 3 h in the winter. Loggerheads apparently can hibernate in some areas (Carr et al. 1981; Ogren and McVea 1982) so they may be able to remain submerged over an extended

Table 26. *Growth rates and estimated age at maturity of loggerhead sea turtles. C = captive turtles; W = wild turtles. Some values were derived from Part 3 of the Appendix in Zug et al. (1986).*

C/W	Estimated age at maturity (yr)	Estimated growth rate (cm/yr)	Reference
C	—	16.17	Parker (1926)
C	—	11.03	Hildebrand and Hatsel (1927)
C	—	8.21	Caldwell et al. (1955)
C	6-7	12.8-15.0	Caldwell (1962*c*)
C	8	12.5	Uchida (1967)
C	—	17.68, 11.14	Kaufmann (1972)
C	—	18.29	Rebel (1974)
C	—	13.64	Witham and Futch (1977)
W	30 +	0.625-1.375 0.0-0.26	Limpus (1979)[a]
W	10-15	5.90 (1.8-10.1)	Mendonça (1981)
W	—	5.70	Bjorndal et al. (1983)
C	16-20	—	Frazer and Schwartz (1984)
W	12-30	—	Frazer and Ehrhart (1985)
W	>27	0.2, 1.0[b]	Limpus (1985)
W	15-30	—	Frazer (1986)
W	13-15	2.1-19.8[c]	Zug et al. (1986)

[a] Range for subadults (first line) and adults (second line).
[b] Mean for adults (first value) and immatures (second value).
[c] Excludes outliers and those with excessively high age estimates.

period. However, the increased oxygen demand associated with attempts to escape a net probably hastens drowning or asphyxiation.

Although not generally the object of mariculture, loggerheads have been successfully reared in captivity. However, they are susceptible to a wide variety of diseases and rearing difficulties, including pulmonary mycobacteriosis, constipation, asymptomatic hatchling death, papillar eruption, emaciation, erosive dermatosis, focal granulosus dermatosis, and white-sutured carapace (Leong 1979). Some of these diseases may be successfully treated using a combination of chemotherapeutics (Leong et al. 1980). For instance, Witham (1973) noted that fungal infections are successfully treated using a 5%-10% solution of gentian violet. Bacterial disease may be a more serious problem. Necrotic spreading lesions, primarily due to *Bacteriodes* sp., seriously affected a small group of hatchling loggerheads reared at the House of Refuge in Florida (Witham 1973). Other bacteria found included *Pseudomonas aeruginosa* and *Staphylococcus epidermis*. Although successfully treated with high dosages of a penicillin-streptomycin mixture, Witham (1973) suggested chloramphenicol be used in future bacterial outbreaks. Uchida (1970) reviewed disease problems of loggerheads raised at the Himeji City Aquarium. Ehrhart (1987) noted a ''diseased turtle syndrome'' in loggerheads stranded in the spring of 1980, 1981, and 1982 in the Port Canaveral, FL, area. Symptoms included a profusion of small barnacles on the head, neck, shoulders, and front flippers, a massively depressed and concave plastron, eyes sunken in their sockets, and rotting, peeling skin. Diagnosis of disease problems prior to overt symptoms has been aided by the development of radiologic techniques (McLellan and Leong 1981). For instance, excretory urography using sodium diatrizoate has been attempted to detect kidney disease; while absorption occurred through injection in the neck without apparent tissue damage, no opacification of the kidneys was seen on serial films made up to 2.5 h after injection (McLellan and Leong 1982).

3.3.3 Competitors

The loggerhead seems to be an opportunistic carnivore (section 3.4), foraging in a wide variety of coastal and, in the case of hatchlings and juveniles, epipelagic habitats. There are no known vertebrate competitors. Loggerheads often use nesting beaches frequented by other marine turtles, but nest site competition is not known to occur.

3.3.4 Predators

Predation on loggerheads is largely unquantified, although juvenile and subadult stages would seem particularly vulnerable, especially to shark attacks. Adult loggerheads are frequently seen missing flippers or portions of the rear of the carapace. The most commonly mentioned shark is *Galeocerdo cuvieri*, a large coastal predator occurring worldwide (Table 21). Rudloe (1979) noted that a sea turtle could defend itself from attack by fleeing to the surface and beating its flippers making a thunderous slapping noise that seems to deter a shark. Carr (*in* Rudloe 1979) reported that turtles can block shark attacks by folding the flippers under the plastron, bending their head down, and presenting the carapace as a shield. In captivity, adult loggerheads may occasionally attack sharks; Rudloe (1979) noted that his captive loggerhead attacked a lemon shark in his tank, ripping out the shark's gills. Other than sharks, only dogs have been reported to attack and kill adult nesting females (Caldwell 1959). A peculiar form of predation occurs on adult nesting females; that is, predation on loggerhead blood by the mosquito *Aedes taeniorhynchus* (Day and Curtis 1983).

3.3.5 Parasites and commensals

Published information concerning species of parasites, diseases, and commensals of the loggerhead is summarized in Table 27. As can be seen in this table, *Caretta* is parasitized by a wide variety of cestodes, nematodes, and, especially, trematodes. A surprising amount of data has been recorded from loggerheads off the Egyptian coast, especially since so little is known of loggerheads in this area (Frazier and Salas 1984). A substantial amount of information also is known from Australian loggerheads. However, much of the data from other locations is based on small sample sizes, often of animals stranded far from known nesting and foraging grounds. Loggerheads are also heavily parasitized by the leech *Ozobranchus margoi* (Table 27). The chief commensals are stalked and encrusting barnacles, and various types of algae, bryozoans, and tunicates. Sucker fish (remoras) are rarely reported but undoubtedly are frequently associated with adult loggerheads. Heavy infestations of encrusting barnacles are associated with diseased turtles in Florida (Ehrhart 1987).

There are no literature records on the methods loggerheads might use to deal with parasites or commensals. Wedging into crevices undoubtedly scrapes some barnacles off the shell; whether this is intentional is unknown. N. Rouse (personal communication) reports that logger-

Table 27. *Commensals and parasites of* Caretta caretta.

Species	Location	Reference
Protozoa		
Bertariella carinii	Brazil	Cerruti (1931); Correia de Meyrelles (1938)
Entamoeba invadens	Captive	Frank et al. (1976)
Platyhelminthes		
Cestoda		
Ancistrocephalus imbricatus	Not stated	Ernst and Barbour (1972); Looss (1901)
Tentacularia coryphaenae	Not stated	Ernst and Barbour (1972)
Trypanorhynchan sp.	Egypt	Sey (1977)
Nematoda		
Cucullanus carettae	Egypt	Baylis (1923); Ernst and Ernst (1977)
	Australia	Lester et al. (1980)
Echinocephalus sp.	Australia	Lester et al. (1980)
Kathlania leptura	Egypt	Baylis (1923); Sey (1977); Ernst and Ernst (1977)
	Australia	Lester et al. (1980)
Sulcascapis sulcata	General	Lichtenfels et al. (1980)
	Egypt	Baylis (1923); Sey (1977); Ernst and Ernst (1977)
	Mediterranean	Sprent (1977)
	Australia	Lester et al. (1980); Berry and Cannon (1981)
Tonaudia tonaudia	Egypt	Baylis (1923); Ernst and Ernst (1977)
Trematoda		
General review		Hughes et al. (1941); Yamaguti (1958); Ernst and Ernst (1977)
Adenogaster serialis	Not stated	Ernst and Barbour (1972)
	Egypt	Looss (1901, 1902); Sey (1977)
Bicornuata caretta	N. Carolina	Pearse (1949)
Calycodes anthos	Japan	Braun (1899)
	Egypt	Looss (1901, 1902); Sey (1977)
Carettacola bipora	Not stated	Ernst and Barbour (1972)
	Florida	Manter and Larson (1950)
Cricocephalus albus	Not stated	Ernst and Barbour (1972)
	Egypt	Looss (1901, 1902)
C. americanus	Florida	Linton (1910)
C. delitescens	Not stated	Ernst and Barbour (1972)
Cymatocarpus solearis[a]	Not stated	Braun (1901)
	Egypt	Looss (1899)
	Not stated	Ernst and Barbour (1972)
	Florida	Linton (1910); Pratt (1913); Luhman (1935)
	Australia	Blair and Limpus (1982)
Desmogonius loossi	India	Chattopadhyaya (1972)
Diaschistorchis ellipticus	Not stated	Ernst and Barbour (1972)
	Gulf of Mexico	Pratt (1913)
D. pandus	Not stated	Ernst and Barbour (1972)
	Italy	Johnston (1913 *in* Yamaguti 1958)
	Egypt	Sey (1977)
Distoma pachyderma	Not stated	Ernst and Barbour (1972)
D. testudinus	Not stated	Ernst and Barbour (1972)
Elytrophallus carettae	Australia	Blair (1984)
Endodiotrema carettae	Australia	Blair and Limpus (1982)
Enodiotrema acariaeum	Not stated	Ernst and Barbour (1972)
E. instar	Not stated	Ernst and Barbour (1972)
	Egypt	Looss (1901, 1902)
E. megachondrus	Not stated	Ernst and Barbour (1972)
	Egypt	Looss (1901, 1902)
	Mediterranean	Euzet and Combes (1962)

Table 27. *Continued.*

Species	Location	Reference
E. reductum	Not stated	Ernst and Barbour (1972)
	Egypt	Looss (1901); Sey (1977)
Epibathra crassa	Not stated	Ernst and Barbour (1972)
	Egypt	Looss (1901, 1902)
Haemoxenicon sp.	Not stated	Wolke et al. (1982)
Hapalotrema loossi	Not stated	Ernst and Barbour (1972)
	Egypt	Looss (1899, 1902)
H. mistroides	Not stated	Ernst and Barbour (1972)
	Italy	Monticelli (1896)
H. synorchis	Not stated	Ernst and Barbour (1972)
	Florida	Luhman (1935)
Learedius europaeus	Not stated	Ernst and Barbour (1972)
	Egypt	Looss (1899 as *Haplotrema constrictum*)
Lophotaspis vallei	Not stated	Ernst and Barbour (1972)
	Egypt	Looss (1901, 1902)
	Florida	Luhman (1935)
Metacetabulum yamagutii	India	Chattopadhyaya (1972)
Monticellius sp.	Not stated	Wolke et al. (1982)
Neospirorchis pricei	Not stated	Ernst and Barbour (1972)
	Florida	Manter and Larson (1950)
Orchidasma amphiorchis	Not stated	Ernst and Barbour (1972)
	Italy	Braun (1901)
	Egypt	Looss (1901, 1902); Sey (1977)
	England	Baylis (1928)
	Florida	Luhman (1935)
	Australia	Blair and Limpus (1982)
Pachypsolus irroratus	Not stated	Ernst and Barbour (1972)
	Oceanic	Looss (1901)
	England	Baylis (1928)
	Mediterranean	Euzet et al. (1972)
	Australia	Blair and Limpus (1982)
P. ovalis[b]	Not stated	Ernst and Barbour (1972)
	Florida, Panama	Linton (1910); Pratt (1913)
P. tertius[b]	Not stated	Ernst and Barbour (1972)
	Florida	Linton (1910); Pratt (1913)
Paralepoderma acariaeum	Egypt	Looss (1902)
Plesiorchis cymbiformis[c]	Not stated	Ernst and Barbour (1972)
	Egypt	Looss (1901, 1902); Sey (1977)
	Florida	Luhman (1935)
	Adriatic	Ernst and Ernst (1977)
	Australia	Blair and Limpus (1982)
Pleurogonius carettae	India	Chattopadhyaya (1972)
P. longiusculus	Not stated	Ernst and Barbour (1972)
	Egypt	Looss (1901, 1902)
	Florida	Luhman (1935)
	Brazil	Ernst and Ernst (1977)
P. trigonocephalus	Egypt	Looss (1901, 1902); Sey (1977)
	Brazil	Ernst and Ernst (1977)
Polyangium linguatula	India	Chattopadhyaya (1972); Blair (1986)
Polystomoides mydae	Not stated	Ernst and Barbour (1972)
	Europe	Ernst and Ernst (1977)
P. ocellatus	Not stated	Ernst and Barbour (1972)
Pronocephalus mehrai	India	Chattopadhyaya (1972)
Pyelosomum longicaecum	Not stated	Ernst and Barbour (1972)
	Florida	Luhman (1935)

Table 27. *Continued.*

Species	Location	Reference
Rhytidodes gelatinosus	Not stated	Ernst and Barbour (1972)
	Egypt	Looss (1901, 1902); Sey (1977)
	Mediterranean	Euzet and Combes (1962); Euzet et al. (1972)
	Australia	Blair and Limpus (1982)
R. secundus	Not stated	Ernst and Barbour (1972)
	Florida	Pratt (1913); Luhman (1935)
R. similis	India	Ernst and Ernst (1977)
Schizamphistomum scleroporum	Not stated	Ernst and Barbour (1972)
	Oceanic	Looss (1912)
	Brazil	Ernst and Ernst (1977)
Styphlotrema solitaria	Not stated	Ernst and Barbour (1972)
	Egypt	Looss (1899, 1902)
	Florida	Luhman (1935)
Cnidaria		
Hydrozoa		
Obelia dichotoma	SE U.S.	Caine (1986)
Tubularia crocea	SE U.S.	Caine (1986)
Anthozoa		
Anemonia sargassiensis	SE U.S.	Caine (1986)
Anemone sp.	SE U.S.	Caine (1986)
Leptogorgia virgulata	SE U.S.	Caine (1986)
Porites porites	SE U.S.	Caine (1986)
Mollusca		
Gastropoda		
Anomia simplex	SE U.S.	Caine (1986)
Costoanachis avara	Florida	Frazier et al. (1985)
C. floridana	Florida	Frazier et al. (1985)
Crepidula fornicata	Georgia	Frazier et al. (1985)
	SE U.S.	Caine (1986)
C. plana	Georgia	Frazier et al. (1985)
	SE U.S.	Caine (1986)
Mitrella lunata	SE U.S.	Caine (1986)
Thais haemastoma	Florida	Frazier et al. (1985)
Bivalvia		
Anadara sp.	Georgia	Frazier et al. (1985)
Anadara transversa	Florida	Frazier et al. (1985)
Argopecten gibbus	SE U.S.	Caine (1986)
Atrinia sp.	SE U.S.	Caine (1986)
Brachidontes exustus	Georgia	Frazier et al. (1985)
B. modoilus	Georgia	Frazier et al. (1985)
Chama macerophylla	Georgia	Frazier et al. (1985)
Crassostrea virginica	SE U.S.	Caine (1986)
Gouldia cerina	SE U.S.	Caine (1986)
Hiatella arctica	Georgia	Frazier et al. (1985)
Musculus lateralis	Georgia	Frazier et al. (1985)
Mytilus edulis	Greece	Frazier et al. (1985)
Ostrea edulis	Greece	Frazier et al. (1985)
O. equestris	Georgia	Frazier et al. (1985)
	SE U.S.	Caine (1986)
Rupellaria typica	Georgia	Frazier et al. (1985)
Sphenia antillensis	Georgia	Frazier et al. (1985)
	SE U.S.	Caine (1986)
Venus sp. or *Venerupis* sp.	Greece	Frazier et al. (1985)

Table 27. *Continued.*

Species	Location	Reference
Annelida		
Hirudinea		
Ozobranchus margoi	Uruguay	Cordero (1929)
	Italy	Sanjeeva Raj (1954, 1959)
	S. Africa	Hughes et al. (1967); Hughes (1974*a*)[d]
	Pacific	Ernst and Barbour (1972)
	Captive	Davies and Chapman (1974)
	N. Carolina	Schwartz (1974)
	Florida, Georgia	Sawyer et al. (1975)
	Hawaii	Balazs (1979)
Polychaeta		
Filograna vulgaris	SE U.S.	Caine (1986)
Pomatoceros sp.	Greece	Frazier et al. (1985)
Sabellaria vulgaris	SE U.S.	Caine (1986)
Serpula sp.	Greece	Margaritoulis (1985); Frazier et al. (1985)
S. vermicularis	SE U.S.	Caine (1986)
Unspecified polychaetes	Greece	Frazier et al. (1985)
	SE U.S.	Caine (1986)
Crustacea		
Cirripedia		
Unspecified	Australia	Bustard (1972)
Family Lepadidae		
Lepas sp.	Norway	Willgohs (1952)
	S. Africa	Hughes (1974*a*)
	Greece	Margaritoulis (1985); Frazier et al. (1985)
	Australia	Limpus (1985)
L. anserifera	Not stated	Ernst and Barbour (1972)
	S. Africa	Hughes (1970*a*)
	Australia	Monroe and Limpus (1979)
L. anatifera	England	Brongersma (1972)
	Australia	Monroe and Limpus (1979)
	SE U.S.	Caine (1986)
L. hillii	Scotland	Ritchie (1924)
	Australia	Monroe and Limpus (1979)
	Greece	Frazier et al. (1985)
Conchoderma virgatum	Scotland	Ritchie (1924)
	S. Africa	Hughes (1974a)
	Australia	Monroe and Limpus (1979); Limpus (1985)
C. auritum	Australia	Monroe and Limpus (1979)
Family Balanidae		
Balanus sp.	S. Africa	Hughes (1974*a*)
Balanus amphitrite	SE U.S.	Caine (1986)
B. trigonus	Australia	Monroe and Limpus (1979)
	Virginia	Lutcavage and Musick (1985)
B. variegatus	Australia	Monroe and Limpus (1979)
Unspecified	S. Africa	Hughes (1970*a*)
Family Coronulidae		
Chelonibia sp.	Seychelles	Frazier (1971)
	S. Africa	Hughes (1974*a*)
	Turkey	Geldiay et al. (1982)
	Greece	Frazier et al. (1985)

Table 27. *Continued.*

Species	Location	Reference
Chelonibia testudinaria	Not stated	Ernst and Barbour (1972)
	New Jersey	Richards (1930)
	Australia	Monroe and Limpus (1979)
	California	Guess (1981)
	Virginia	Lutcavage and Musick (1985)
	SE U.S.	Killingley and Lutcavage (1983); Caine (1986)
	Greece	Margaritoulis (1985)
C. caretta	Not stated	Ernst and Barbour (1972)
	Scotland	Ritchie (1924)
	Netherlands	Holthuis (1952)
	Australia	Monroe and Limpus (1979)
	SE U.S.	Caine (1986)
Coronula regina	Not stated	Ernst and Barbour (1972)
	Gulf of California	Caldwell (1963)
Platylepas sp.	S. Africa	Hughes (1974*a*)
	Greece	Frazier et al. (1985)
Platylepas decorata	Australia	Monroe and Limpus (1979)
P. hexastylos	Not stated	Ernst and Barbour (1972)
	Netherlands	Holthuis (1952)
	Australia	Monroe and Limpus (1979)
	Virginia	Lutcavage and Musick (1985)
P. multidentata	Australia	Limpus (1985)
Stephanolepas sp.	S. Africa	Hughes (1974*a*)
Stephanolepas muricata	Australia	Monroe and Limpus (1979)
Stomatolepas elegans	Not stated	Ernst and Barbour (1972)
	Japan	Hiro (1936)[e]
	Europe	Smaldon and Lyster (1976)
S. praegustator	Florida	Pilsbry (1910)
	Australia	Monroe and Limpus (1979)
Tubicinella cheloniae	Australia	Monroe and Limpus (1979)
Tanaidea		
Zeuxo robustus	SE U.S.	Caine (1986)
Amphipoda		
Caprella sp.	Greece	Frazier et al. (1985)
Caprella andreae	SE U.S.	Caine (1986)
C. equilibra	SE U.S.	Caine (1986)
Cyrtophium chelonophilum	Azores	Chevreux and de Guerne (1888)
Paracaprella tenuis	SE U.S.	Caine (1986)
Ampithoe ramondi	SE U.S.	Caine (1986)
Elasmopus rapax	SE U.S.	Caine (1986)
Erichthonius braziliensis	SE U.S.	Caine (1986)
Hyale sp.	SE U.S.	Caine (1986)
Podocerus brasiliensis	SE U.S.	Caine (1986)
P. cheloniae	SE U.S.	Caine (1986)
Stenothoe minuta	SE U.S.	Caine (1986)
Isopoda		
Eurydice sp.	Australia	Bustard (1976)
Sphaeroma quadridentatum	SE U.S.	Caine (1986)
Brachyura		
Neopanope texana	SE U.S.	Caine (1986)
Pachygraspus sp.	SE U.S.	Caine (1986)
Panopeus herbstii	SE U.S.	Caine (1986)
Planes cyaneus	California	Guess (1981)
P. minuta	SE U.S.	Caine (1986)

Table 27. *Continued.*

Species	Location	Reference
Bryozoa		
Bugula neritina	SE U.S.	Caine (1986)
Membranipora sp.	Australia	Limpus (1985)
M. membranacea	S. Africa	Hughes (1974*a*)
Unspecified	Florida	Caldwell (1968)
	S. Africa	Hughes (1970*a*)
	Australia	Limpus (1985)
Chordata		
Urochordata		
Molgula manhattensis	SE U.S.	Caine (1986)
Pisces		
Echeneis naucrates	Australia	Limpus (1985)
Remora sp.	Seychelles	Frazier (1971)
Plants		
Algae		
Chaetomorpha linum	Greece	Frazier et al. (1985)
Cladophora sp.	Greece	Margaritoulis (1985); Frazier et al. (1985)
Giffordia virescens	England	Parke and Dickinson (1947)
Polysiphonia sp.	Greece	Frazier et al. (1985)
Sphacelaria sp.	Greece	Margaritoulis (1985)
S. tribuloides	Greece	Frazier et al. (1985)
"green"	Seychelles	Frazier (1971)
	S. Africa	Hughes (1974*a*)
"red"	S. Africa	Hughes (1974*a*)
Unspecified	Australia	Bustard (1976)
	Greece	Frazier et al. (1985)

[a] Synonymous with *C. undulatus*.
[b] Synonymous with *P. irroratus*.
[c] Synonymous with *Phyllodistomum cymbiforme*.
[d] As *O. maggoi*.
[e] Turtle misidentified as *C. olivacea*.

heads off Palm Beach, FL, regularly use cleaning stations allowing small fish to eat epidermal parasites. The turtles fully extend their head and flippers to allow access to the axial and inguinal appendicular areas.

3.4 Nutrition and Growth

3.4.1 Feeding

The loggerhead is primarily carnivorous, feeding on a wide variety of food items (section 3.4.2), especially molluscs. The broad head and substantial jaw muscles seem particularly well-adapted for crushing hard-shelled prey (Hendrickson 1980). Thompson (1980) concluded that the anatomy and histology of the alimentary canal of the loggerhead differed from a "general reptile" only by the cornified papillae in the esophagus. Hatchling loggerheads did not differ substantially from hatchlings of *Chelonia*, *Dermochelys*, or *Eretmochelys* in the ratio of the intestine length to carapace length (IL:CL average value of 3.32) whereas the ratio was substantially smaller in adults and subadults compared with the herbivorous *Chelonia*—IL:CL values of 8.55 vs. 12.6 and 13.9—(Thompson 1980; summarized in Bjorndal 1985). There are no studies indicating whether the loggerhead is an opportunistic feeder, or whether it selects certain prey in higher proportions than the prey occurs in the benthic fauna. Whether there is resource partitioning between other partially or wholly molluscivorous sea turtles, such as *Lepidochelys kempii*, that spatially overlap the loggerhead's range is also unknown. Hendrickson (1980) speculated that there has been a twofold partitioning of resources (in terms of diet and spatial distribution) between the loggerhead and the ridley although no supporting data were supplied.

While adult loggerheads are primarily bottom feeders, they will feed on jellyfish at the surface. Carr (1952) and

Rudloe (1979) reported that loggerheads swim among concentrations of *Physalia* jellyfish feeding with their eyes closed to avoid the stinging cells. Even then, their eyes were red, puffy, and almost swollen shut. Hatchling and juvenile loggerheads also feed at the surface on macroplanktonic prey concentrated in drift lines (Carr 1987). Hildebrand and Hatsel (1927) noted that captive hatchlings appeared unable to dive; that is, they were positively buoyant (Davenport and Clough 1986), thus necessitating surface feeding. Davenport and Clough (1985) showed that 50 g turtles from Cyprus were able to use pseudoclaws—modified pointed scales located on the anterior edge of the flipper—to handle food items. They did this by using the sharp row of scales as a saw to tear food held in the mouth. Small pieces of food adherent to the pseudoclaws were then eaten by turning the head in the appropriate direction. Some small loggerheads do not have these pseudoclaws, so their significance to the feeding ecology of the species is unknown.

Layne (1952) observed that captive juvenile loggerheads readily bit off the legs of horseshoe crabs (*Limulus*) but were unable to crack the carapace of the crab despite vigorous shaking. Parrish (1958) noted the feeding behavior of captive adult sea turtles, but did not distinguish between *Caretta* and *L. kempii*, *Eretmochelys*, and *Chelonia* in making his observations. Only one adult used its flippers to help maneuver food into its mouth. Most turtles went directly for a food item, thrust their head straight forward, and snapped at the food. Food entered the mouth by opening the mouth while thrusting the head forward, perhaps creating a vacuum. The turtles frequently tilted their heads while feeding. Captive loggerheads crushed whole clams "with the greatest ease" (Hildebrand and Hatsel 1927).

3.4.2 Food

A summary of known loggerhead food items is presented in Table 28. Nearly all of their food consists of animal matter, mostly benthic invertebrates and coelenterates. Loggerheads also take algae on occasion, perhaps ingesting it while feeding on invertebrates. Various species of turtle grass also have been reported in the gut. Surprisingly, comprehensive lists of items in the diet are available only for hatchling, subadult, and adult loggerheads in Tongaland, South Africa (Hughes 1974*a*), and for juveniles in Australia (Moody 1979), and the eastern Atlantic, particularly the Azores (Table 28). Most other reports of food are from animals stranded far from nesting and feeding grounds, and were made incidental to reporting the stranding.

Hatchling loggerheads probably feed on the macroplankton that accumulates in drift lines off the coasts and in the open ocean (Carr 1987), but a detailed analysis of gut contents has been reported only by Hughes (1974*a*) and Carr and Meylan (1980). Hughes (1974*a*) found jellyfish, algae, grit, feathers, bark, a piece of plastic sheet, and plastic beads in 37 hatchlings stranded on Cape Agulhas, South Africa. Carr and Meylan (1980) found food in 5 of 15 hatchlings stranded during a hurricane in Florida; these contained *Sargassum* floats and leaf parts, snails (*Litiopa melanostoma* and *Diacria trispinosa*), and fragments of crustacean appendages. Carr (personal communication) reported that terrestrial insects were found in the stomachs of small loggerheads off the coast of Georgia, but the species were not identified. The results of Grassman and Owens (1982) do not support the food imprinting hypothesis for hatchling loggerheads. While some preference is shown for certain types of food, in this case fish and pellets, the young readily fed on other types of food as they grew older.

From the contents listed in Table 28, it would appear that juvenile loggerheads are particularly fond of coelenterates. Most observations on juvenile gut contents occur from turtles captured in the Azores and Madeira, and it is unknown to what extent juvenile loggerheads in other parts of their range rely on jellyfish. It is likely that they also feed heavily on other forms of macroplankton that accumulate in pelagic drift lines.

While subadult and adult loggerheads also feed on jellyfish, they are primarily feeders on a wide variety of benthic invertebrates (Table 28). Loggerheads may exploit a regionally abundant prey. For instance, one of the preferred foods of loggerheads in the southeastern United States is the horseshoe crab (*Limulus*), a very abundant species in this region but not found off other nesting grounds. The extent of regional specialization, if it indeed occurs, is unknown. Fish may be ingested intentionally, scavenged, or eaten incidentally to the intake of jellyfish. However, Schwartz and Carter (1984) noted that loggerheads rejected pipefish (*Syngnathus louisianae*) as food.

All stages of loggerheads eat a variety of nonfood items that they apparently mistake for food. As early as 1886, Pouchet and de Guerne (1886, 1940) recorded birch bark, straw, cinders, cork, and wood chips in the guts of juvenile loggerheads from the Azores. Other items reported since then include pieces of plastic, Azores (Brongersma 1968*b*); synthetic and other debris including plastic strips, bags, pieces of glass, sugar cane, bark, South Africa (Hughes 1974*a*); plastic, rope, tar,

Table 28. *Food of the loggerhead sea turtle,* Caretta caretta. *A = adult; H = hatchling; J = juvenile and subadult; U = unknown or not stated.*

Item	Location	Life Stage	Reference
General	U	U	Carr (1952); Ernst and Barbour (1972); Bjorndal (1985)
	Queensland	J	Thompson (1980)
Porifera			
Cliona celata	N. Atlantic	A	Layne (1952)
Suberites sp.	Adriatic	U	Steuer (1905)
Tethya lyncurium	Adriatic	U	Steuer (1905)
Cnidaria			
Unidentified	Nova Scotia	J	Bleakney (1967)
	Queensland	U	Limpus (1973*a*); Bustard (1974)
	Madeira	J	van Nierop and den Hartog (1984)
Agalma sp. (?)	Madeira	J	van Nierop and den Hartog (1984)
Apolemia uvaria	Azores	J	van Nierop and den Hartog (1984)
Cyanea sp.	Nova Scotia	J	Bleakney (1967)
Geryonia proboscidalis	Madeira	J	van Nierop and den Hartog (1984)
Pelagia noctiluca	Madeira	J	van Nierop and den Hartog (1984)
Physalia physalis	Not specified	A, J	Babcock (1938); Wangersky and Lane (1960); Lane (1960)
	S. Africa	H, J (?)	Hughes (1974*a*)
	Florida	A	Rudloe (1979)
Porpita sp.	S. Africa	A	Hughes (1974*a*)
Velella velella	S. Atlantic	A	Murphy (1914)
Virgularia sp.	Texas	U, J (?)	Plotkin (personal communication)
"fungid coral"	Queensland	J	Moody (1979)
Annelida			
Polychaeta			
Chloeia flava	W. Australia	A	Lester et al. (1980)
Mollusca			
Unspecified	Indian Ocean	A	Deraniyagala (1939)
Cephalopoda			
Unspecified	Azores	J	Richard (1934)
	Queensland	U	Limpus (1973*a*)
Chaunoteuthis mollis	Madeira	J	van Nierop and den Hartog (1984)
Japatella sp.	Madeira	J	van Nierop and den Hartog (1984)
Leachia sp.	Azores	J	Richard (1934)
Onychoteuthis banksi	Nova Scotia	J	Bleakney (1967)
Spirula sp.	S. Africa	A	Hughes (1974*a*)
Todarodes sagittatus	Baleares Is.	J	Salavador (1978)
Gastropoda			
Action sp.	S. Africa	A	Hughes (1974*a*)
Anachis moleculina	Uruguay	U	Gudynas (1980)
Anitica sp.	S. Africa	A	Hughes (1974*a*)
Astrea andersoni	S. Africa	A	Hughes (1974*a*)
Babylonia crumenoides	S. Africa	A	Hughes (1974*a*)
Bittium sp.	Queensland	J	Moody (1979)
Bufonaria crumenoides	S. Africa	A	Hughes (1974*a*)
Bullia similus	S. Africa	A	Hughes (1974*a*)
Bursa granularis	S. Africa	A	Hughes (1974*a*)
Cavolinia tridentata	Madeira	J	Brongersma (1968*b*)
	Azores	J	van Nierop and den Hartog (1984)
Cerithium echinatum	Queensland	J	Moody (1979)
C. tenuifilosum	Queensland	J	Moody (1979)
Charonia lampas	S. Africa	A	Hughes (1974*a*)
Chrysostoma paradoxum	Queensland	J	Moody (1979)

Table 28. *Continued.*

Item	Location	Life Stage	Reference
Conus sp.	S. Africa	A	Hughes (1974*a*)
Cymatium labiosum	S. Africa	A	Hughes (1974*a*)
Cymbiolacca pulchra	Queensland	J	Moody (1979)
Cypraea sp.	Queensland	J	Moody (1979)
Diacria trispinosa	Florida	H	Carr and Meylan (1980)
Dupliclaria sp.	S. Africa	A	Hughes (1974*a*)
Ficus ficus	S. Africa	A	Hughes (1974*a*)
F. subintermedius	S. Africa	A	Hughes (1974*a*)
Glycimeris queketti	S. Africa	A	Hughes (1974*a*)
Harpa amouretta	S. Africa	A	Hughes (1974*a*)
H. davidus	S. Africa	A	Hughes (1974*a*)
H. major	S. Africa	A	Hughes (1974*a*)
Hyalaea tridentata	Azores	U	Pouchet and de Guerne (1886)
Ianthina pallida	Madeira	J	van Nierop and den Hartog (1984)
Janthina janthina	Azores	J	Richard (1934)
	S. Africa	H, J (?)	Hughes (1974*a*)
J. prolongata	S. Africa	J (?)	Hughes (1974*a*)
Kelletia kelleti	Gulf of California	J	Caldwell (1963)
Latirus abnormis	S. Africa	A	Hughes (1974*a*)
Limaria fragilis	S. Africa	A	Hughes (1974*a*)
Litiopa melanostoma	Florida	H	Carr and Meylan (1980)
Lophiotoma acuta	Queensland	J	Moody (1979)
Lyria ponsonbyii	S. Africa	A	Hughes (1974*a*)
Marginella pipenata	S. Africa	A	Hughes (1974*a*)
Mayena australasia	S. Africa	A	Hughes (1974*a*)
Murex falax	S. Africa	A	Hughes (1974*a*)
Nassarius kraussianus	S. Africa	A	Hughes (1974*a*)
Natica duplicata	N. Jersey	A	Fowler (1914)
N. gualtieriana	Queensland	J	Moody (1979)
N. onca	Queensland	J	Moody (1979)
Pintada radiata	S. Africa	A	Hughes (1974*a*)
Polinices albumen	W. Australia	A	Lester et al. (1980)
P. didyma	S. Africa	A	Hughes (1974*a*)
Pterotrachea sp.	Madeira	J	van Nierop and den Hartog (1984)
Pupa nitidula	Queensland	J	Moody (1979)
Rapana rapiformis	S. Africa	A	Hughes (1974*a*)
Rhinoclavis apser	Queensland	J	Moody (1979)
R. fasciatum	Queensland	J	Moody (1979)
R. vertagus	Queensland	J	Moody (1979)
Strombus sp.	SE U.S.	U	True (1884)
S. campbelli	W. Australia	A	Lester et al. (1980)
Strombus gigas	Not specific	U	Babcock (1938)
S. gibberulus	Queensland	J	Moody (1979)
Tonna variegata	S. Africa	A	Hughes (1974*a*)
Trochus sp.	Queensland	J	Moody (1979)
Turbo bruneus	Queensland	J	Moody (1979)
T. perspeciosus	Queensland	J	Moody (1979)
Umbanium vestarius	Queensland	J	Moody (1979)
Vepricardium asiaticum	S. Africa	A	Hughes (1974*a*)
Xancus rapa	Indian Ocean	A	Deraniyagala (1939)
Zidona dufresnei	Uruguay	U	Gudynas (1980)
Pelycepoda			
Unspecified	Indian Ocean	A	Deraniyagala (1939)
Atrina sp.	W. Australia	A	Lester et al. (1980)
Callista planatella	W. Australia	A	Lester et al. (1980)

Table 28. *Continued.*

Item	Location	Life Stage	Reference
Circe sulcata	W. Australia	A	Lester et al. (1980)
Dardanus sp.	Aldabra	J	Frazier (1971)
Eucrassatella pulchra	W. Australia	A	Lester et al. (1980)
Fragum fragum	Queensland	J	Moody (1979)
F. retusum	W. Australia	A	Lester et al. (1980)
Hyotissa sp.	W. Australia	A	Lester et al. (1980)
Mactra janueriensis	Uruguay	U	Gudynas (1980)
Megacardita incrassata	W. Australia	A	Lester et al. (1980)
Paphia sulcosa	W. Australia	A	Lester et al. (1980)
Pecten sp.	S. Africa	A	Hughes (1974*a*)
Perna perna	S. Africa	A	Hughes (1974*a*)
Pinctada vulgaris	Indian Ocean	A(?)	Deraniyagala (1953)
Pinguitellina robusta	Queensland	J	Moody (1979)
Pinna sp.	S. Africa	A	Hughes (1974*a*)
Psammobia vespertina	Canary Is.	J	Brongersma (1968*b*)
Tapes literatus	W. Australia	A	Lester et al. (1980)
Tellina sp.	Queensland	J	Moody (1979)
Timoclea sp.	W. Australia	A	Lester et al. (1980)
Tridacna chametrachae	Queensland	A	Limpus (1973*a*); Bustard (1974)
T. fossor	Queensland	A	Bustard (1976)
T. maxima	Queensland	J	Moody (1979)
Venus laqueata	W. Australia	A	Lester et al. (1980)
V. verrucosus	Canary Is.	J	Brongersma (1968*b*)
Merostomata			
Limulus polyphemus	Florida	A	Rudloe (1979)
	Virginia	J, A	Lutcavage (1981); Lutcavage and Musick (1985)
Crustacea			
Unspecified	S. Africa	A	Hughes (1974*a*)
Amphipoda			
Euthemisto compressa	Nova Scotia	J	Bleakney (1967)
Hyperia medusarum	Azores	U	Pouchet and de Guerne (1886)
	Nova Scotia	J	Bleakney (1967)
Phronima sedentaria	Madeira	J	van Nierop and den Hartog (1984)
Cirripedia			
Unspecified	Madeira	J	Brongersma (1968*b*)
Lepas sp.	Madeira	J	van Nierop and den Hartog (1984)
Lepas anatifera	Azores	U, J, A	Pouchet and de Guerne (1886); van Nierop and den Hartog (1984)
	Nova Scotia	J	Bleakney (1967)
	Madeira	J	van Nierop and den Hartog (1984)
L. fascicularis	Nova Scotia	J	Bleakney (1967)
Decapoda			
Unspecified	Australia	A	Limpus (1973*a*); Lester et al. (1980)
	Georgia	A	Shoop and Ruckdeschel (1982)
Brachiodontes variabilis	Aldabra	J	Frazier (1971)
Calappa sp.	Indian Ocean	A	Deraniyagala (1939)
Calappa hepatica	Queensland	J	Moody (1979)
Callinectes sapidus	Virginia	J	Lutcavage (1981)
Cancer irroratus	Virginia	J	Lutcavage (1981)
Dardanus euopsis	Queensland	J	Moody (1979)
Dromia sp.	Indian O.	A	Deraniyagala (1939)
Eucrate sp.	W. Australia	A	Lester et al. (1980)
Funchalia villosa	Madeira	J	van Nierop and den Hartog (1984)
Hepatus epheliticus	Texas	U	Plotkin (personal communication)

Table 28. *Continued.*

Item	Location	Life Stage	Reference
Libinia sp.	N. Atlantic	A	Layne (1952)
	Texas	U	Plotkin (personal communication)
Libinia spinosa	Uruguay	U	Gudynas (1980)
Melitta sp.	Not specific	A	Babcock (1919)
Paguristes sp.	S. Africa	A	Hughes (1974*a*)
Pagurus sp.	S. Africa	A	Hughes (1974*a*)
Pagurus arresor	S. Africa	A	Hughes (1974*a*)
P. pollicaris	N. Jersey	A	Fowler (1914)
Panulirus sp.	S. Africa	A	Hughes (1974*a*)
Persephona punctata	Texas	U	Plotkin (personal communication)
Planes minutus[a]	Azores	A	Pouchet and de Guerne (1886)
Platyxanthus cuenulatus	Uruguay	U	Gudynas (1980)
Thalamita integra	Queensland	J	Moody (1979)
T. sima	W. Australia	A	Lester et al. (1980)
Isopoda			
Idotea metallica	Madeira	J	van Nierop and den Hartog (1984)
Insecta			
Unspecified terrestrial insects	SE U.S.	H	A. Carr (personal communication)
Bryozoa			
Flustra sp.	Adriatic	U	Steuer (1905)
Echinodermata			
Unspecified	Indian Ocean	A	Deraniyagala (1939)
	Texas	U	Rabalais and Rabalais (1980)
Clypeaster humilis	Indian Ocean	A	Deraniyagala (1939)
Prionocidaris baculosa	S. Africa	A	Hughes (1974*a*)
Spiny sea urchin	S. Africa	A	Hughes (1974*a*)
Unspecified Holothuroidea	Queensland	J	Moody (1979)
Chordata			
Urochordates			
Unspecified	Nova Scotia	J	Bleakney (1967)
	Madeira	J	Brongersma (1968*b*)
Phallusia depressiuscula	W. Australia	A	Lester et al. (1980)
Pyrosoma sp.	N. Zealand	J	McCann (1966)
Pyrosoma atlanticum	Madeira	J	van Nierop and den Hartog (1984)
Pyura sp.	S. Africa	A	Hughes (1974*a*)
Salpa sp.	N. Zealand	J	McCann (1966)
Pisces			
Unspecified	Azores	U	Pouchet and de Guerne (1886)
	Queensland	A	Limpus (1973*a*)
Brevoortia tyrannus	Virginia	J(?)	Bjorndal (1985)
Ceratoscopelus maderensis	Azores	J	van Nierop and den Hartog (1984)
Diodon sp.	S. Africa	A	Hughes (1974*a*)
Entelurus aequoreus	Azores	U	Pouchet and de Guerne (1886)
Hippocampus hudsonius	Nova Scotia	J	Bleakney (1967)
Macrorhamphosus gracilis	Madeira	J	Brongersma (1968*b*)
Sardinops ocellata	S. Africa	A	Hughes (1974*a*)
Scombre scombrus	Nova Scotia	J	Bleakney (1967)

Table 28. *Continued.*

Item	Location	Life Stage	Reference
Reptilia			
Caretta caretta hatchling	S. Africa	A	Hughes (1974*a*)[b]
Plants			
Algae			
Unspecified	Indian Ocean	A	Deraniyagala (1939)
Ascophyllum sp.	Nova Scotia	J	Bleakney (1967)
Sargassum sp.	Texas	U	Rabalais and Rabalais (1980)
	Florida	H	Carr and Meylan (1980)
	Virginia	J	Lutcavage (1981)
Sargassum fluitans	Nova Scotia	J	Bleakney (1967)
S. natans	Nova Scotia	J	Bleakney (1967)
S. vulgare	Azores	J	van Nierop and den Hartog (1984)
Ulothrix flacca	Nova Scotia	J	Bleakney (1967)
Urospora penicilliformis	Nova Scotia	J	Bleakney (1967)
Angiosperms			
Cymodocea nodosa	Madeira	J	van Nierop and den Hartog (1984)
Thalassia sp.	Not specific	U	Ernst and Barbour (1972)
Zostera sp.	Not specific	U	Ernst and Barbour (1972)

[a] As *Nautilograpsus*.
[b] Carapace shields.

onion, Balearic Islands (Salvador 1978); plastic bags, Florida (Rudloe 1979); paper, nylon thread, ball of thread, pieces of polyethylene, oil clots, transparent plastic, Madeira (van Nierop and den Hartog 1984); iron bolt, monofilament line, weathered petroleum, plastic bottle, feathers, plastic champagne cork, glass, plastic pieces, nylon thread, United States (Balazs 1985); plastic debris, plastic sheet, plastic bag, synthetic line, Japan (Balazs 1985); pellets of tar, plastic beads, styrofoam, pelagic habitats (Carr 1987). It is clear that floating debris, particularly plastics and oil, forms a serious threat to sea turtles in their pelagic, developmental, feeding, and migratory habitats (Balazs 1985). Loggerheads will also eat human food scraps and fish remains from fishing trawlers (Limpus 1973*a*) and fish processing houses (Shoop and Ruckdeschel 1982).

In captivity, hatchlings have been fed oysters (Coker 1906); fish (Hildebrand and Hatsel 1927); stingrays, octopods, and squid (Vollbrecht 1947); raw beef (Cadenat 1957); octopus, shrimp, and marine fish (Sachsse 1970); ground crab, fish, and commercial trout pellets (Stickney et al. 1973); jellyfish and molluscs (Hughes 1974*a*); shrimp and fish, including shark (Kaufmann 1975*a*); cooked crab supplemented by jellyfish (Witham and Futch 1977); horse mackerel (Nuitja and Uchida 1982); fish supplemented with squid, clams, scallops, and shrimp (Frazer and Schwartz 1984); and pelleted fish food and herring (Hendrickson and Hendrickson 1986). Juveniles and subadults have been fed fish, blue crabs, and clams (Hildebrand and Hatsel 1927); and fish, squid, lobster, mussels, whelks, other molluscs, and horseshoe crabs (Layne 1952). Adults have been kept on fish scraps (Parrish 1958), crabs, horseshoe crabs, and other benthic invertebrates (Rudloe 1979).

3.4.3 Growth rate

Much of the early work on growth rates of loggerheads was based on captive individuals. Often, sample sizes were small and the diet, feeding conditions, or holding conditions were not reported. Hence, the value of some studies to understanding growth rates in loggerhead populations is questionable. Growth rates during the first year in captivity have been plotted for five published studies (Fig. 8) by Frazer (1982): Caldwell et al. (1955), Kaufmann (1967), Stickney et al. (1973), Rebel (1974), and Witham and Futch (1977). Growth rates beyond the first year in captivity (Fig. 9) were plotted by Frazer (1982) for the studies of Hildebrand and Hatsel (1927), Parker (1929), Uchida (1967), Hughes et al. (1967), and Schwartz (1981). Parker (1926) followed the growth of four loggerheads, noting that one grew to 53 cm SLCL and 19 kg only 3 yr after hatching. Three nearly 5-month-old loggerheads weighed 565, 625, and 1,300 g, respectively. Parker

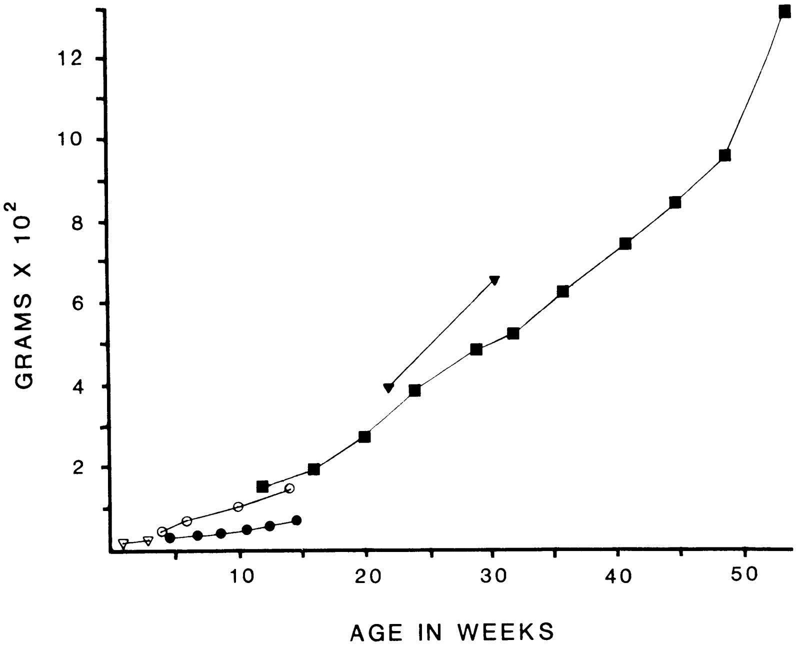

Fig. 8. Growth rates for loggerheads during the first year of activity. Figure from Frazer (1982).

(▼) Mean from Kaufmann (1967);
(▽) Mean from Caldwell et al. (1955);
(●) Grand mean from Stickney et al. (1973);)
(○) Mean from Rebel (1974);
(■) Mean from Witham and Futch (1977).

(1926) concluded that adult weight might be reached faster than previously suspected, given these growth rates. At 4.5 yr old, the turtle mentioned by Parker (1926) measured 63 cm and weighed 37 kg, while the three younger turtles weighed between 8.5 kg and 18 kg (Parker 1929). The lower growth rates were similar to those reported by Hildebrand and Hatsel (1927) for two loggerheads raised for 6 yr; at release, these animals weighed 25 kg and 27.5 kg. Uchida (1967) raised two loggerheads for 4.5 yr, at which time they were 67–73 cm; based on this growth rate, he estimated the age at sexual maturity to be 6–7 yr. Hughes et al. (1967) raised four young for 2.5 yr, at which time they weighed 1.95 kg. Sachsse (1970) raised two specimens, which

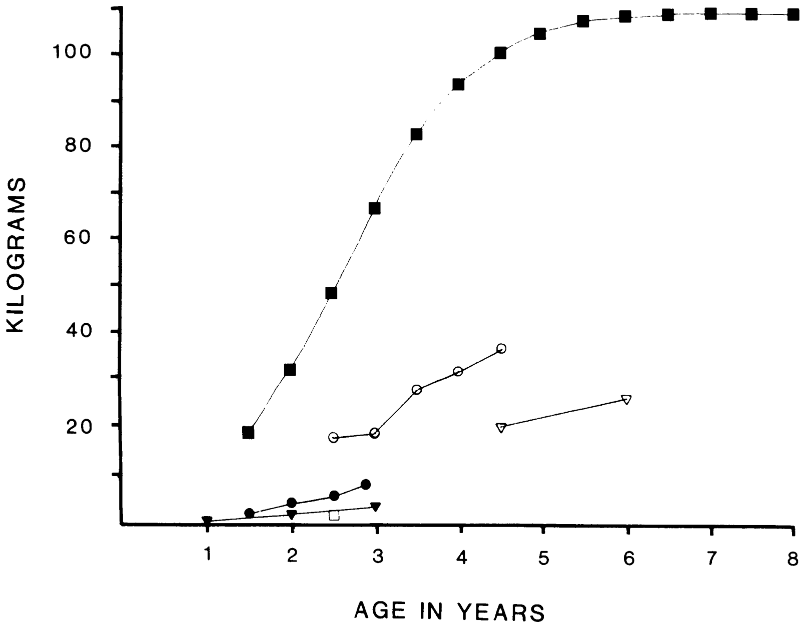

Fig. 9. Growth rates for loggerheads beyond the first year in captivity. Figure from Frazer (1982).

(■) Calculated from Uchida (1967);
(○) Data for Parker's (1929) fastest-growing turtle;
(●) Mean for three other turtles of Parker's (1929);
(▽) Mean from Hildebrand and Hatsel (1927);
(□) Mean from Hughes et al. (1967);
(▼) Grand mean from Schwartz (1981).

reached 17.8 cm and 18.1 cm after 1 yr. Kaufmann (1967) reported that captive *Caretta* grew from an SLCL of 4.46 cm and weight of 18.1 g at hatching to 13.5 cm SLCL and 393.7 g at 5 mo and 15.9 cm SLCL and 653.0 g at 7 mo. After 2 yr, these figures increased to 18.28 cm SLCL and 754.8 g at 15 mo and 39.83 cm SLCL and 855.9 g at 2 yr (Kaufmann 1972). Witham and Futch (1977) reported that loggerheads grew to 18.1 cm SLCL and 1.28 kg (N = 25) after 1 yr. Schwartz (1981) raised three batches of hatchlings which weighed 5.99 kg, 3.14 kg, and 4.85 kg, respectively, after 3 yr.

Diet differences and varied rearing conditions may account for some of the differences in the figures reported in the previous paragraph. Over a 3-mo period, Stickney et al. (1973) reported average weight gains of 11.7 g on a commercial pellet diet, 65.4 g on a half-pellet–half-fish diet, 60.5 g on a fish diet, and 24.5 g on a crab diet. Increased food rations led to increased growth rates (Nuitja and Uchida 1982). Frazer and Schwartz (1984) applied both the logistic and von Bertalanffy equations to the growth of two captive loggerheads (Table 29), and showed that the logistic equation provided a better estimate of carapace length. They thus supported Uchida's (1967) findings on Japanese loggerheads (Table 29).

There have been fewer studies of the growth rates of wild loggerheads because of the difficulty in recapturing animals previously marked. There also are additional potential problems in determining growth rates from recaptured animals, since Shoop and Ruckdeschel (1986) have pointed out that even experienced individuals may obtain quite different measurements of a particular sea turtle carapace. There are no estimates on hatchling and juvenile growth rates based on marked and recaptured animals. In a preliminary report, Limpus (1979) reported values <1.5 cm/yr for subadults, and even smaller values (<0.26 cm/yr) for adults (Table 26). He later estimated that Australian adults grow an average of only 0.2 cm/yr while subadults grow an average of 1.0 cm/yr (Limpus 1985). The only other growth rate estimates are those of Mendonça (1981) for a lagoonal population of *Caretta* in Florida: 13 subadults grew an average of 5.90 cm/yr. Both Mendonça (1981) and Limpus (1985) noted that growth rates decline dramatically as sexual maturity is reached. Contrary to the findings on captive loggerheads, Frazer and Ehrhart (1985) reported that growth in straight-line carapace length fits the von Bertalanffy growth model better than the logistic model for Florida lagoonal subadults (Table 29). When compared with other species, Australian green and loggerhead turtles appear to grow at similar rates (Limpus 1979), whereas lagoonal *Caretta* in Florida grow at twice the rate of lagoonal *Chelonia mydas* (Mendonça 1981).

The humerus bones of *Caretta* show distinct rings assumed to contain a record of annual growth. Zug et al.

Table 29. *Logistic, von Bertalanffy equation, and regression values for carapace length growth in the loggerhead sea turtle.*

Location	N	a(cm)	K	b	Reference
Logistic $L = \dfrac{a}{(1 + be^{-kt})}$					
Japan	2	104.1	0.703	1.13	Uchida (1967)
		97.2	0.710	1.08	
N. Carolina	2	91.8	0.325	13.0	Frazer and Schwartz (1984)
		99.2	0.264	12.2	
Florida	20	94.6	0.143	0.95	Frazer and Ehrhart (1985)
von Bertalanffy $L = a(1 - be^{-kt})$					
N. Carolina	2	1,228.0	0.0041	0.997	Frazer and Schwartz (1984)
		541.8	0.0081	0.990	Frazer and Schwartz (1984)
Florida	20	94.6	0.120	0.952	Frazer and Ehrhart (1985)
Regression			Equation		
Florida	13		$Y = 0.48 \times -0.04$[a]		Mendonça (1981)

[a]Regression of carapace length at recapture versus number of months since first capture.

(1983, 1986) have used such skeletochronological marks to obtain an estimate of 13–15 yr for sexual maturity in Georgia loggerheads. Ages were determined by dividing half the humerus diameter by the average width of the extant growth rings. Age estimates derived from the long axis of the humerus were usually 10 or more years higher than those obtained from the short axis; short axis estimates were considered more reliable (Zug et al. 1986). These authors noted the absence of growth rings in some specimens; irregular, interrupted, or accessory arrested growth lines; and the loss of growth lines because of bone remodeling, which could hamper age determination of individual specimens.

Other growth parameters are the length–weight relations presented by Hughes et al. (1967) and Ehrhart (1978 *in* Hirth 1982) using log-log transformed data. Uchida (1967) and Anonymous (1984*a*) used the allometric growth equation to express the relation between carapace length or width and a variety of meristic characters in captive loggerheads. These studies are summarized in Tables 30 and 31.

3.4.4 Metabolism

There is only one published study on the metabolic rates of loggerhead sea turtles, and this focused on hatchlings (Dial 1987). Hatchling frenzy results in a 22-fold increase in lactate concentration ($\bar{x}$ = 0.919 mg/g) over resting concentrations. Dial (1987) concluded that anaerobic metabolism during the hatchling frenzy represents a physiological adaptation for energetic support to quickly traverse the beach and thus minimize exposure to predators.

Loggerheads are reported to wedge themselves into crevices, and some observers have inferred that they sleep at this time. However, Šušić (1972) concluded that loggerheads do not sleep, but instead alternate between periods of inactivity and activity that are simultaneous with a nonaltered level of responsiveness. Loggerheads appear to hibernate in some areas (Carr et al. 1981; Ogren and McVea 1982), although brumation may be a better term since it does not imply the physiological and metabolic changes associated with hibernation by endotherms. It is unknown what metabolic changes, if any, occur during the period of inactivity described by Šušić (1972) or the hibernation (i.e., brumation) that occurs during winter on the southeast coast of the United States.

Schmidt-Nielsen and Fange (1958) described and illustrated the salt gland of the loggerhead. It is a large gland, located in the orbit of the eye, divided into about 100 lobes separated by blood vessels and connective tissue. The gland consists of closely packed branching glandular tubules radiating from central ducts in the lobe. These post-orbital glands regulate levels of the majority of solutes in the body fluid, and can concentrate salts to twice that of body fluids (Prange 1985). Osmotic concentration also occurs in the urine, but Prange (1985) believed such concentration was primarily involved with waste excretion, and that the ionic and osmotic regulation of body fluids in sea turtles did not necessarily imply homeostasis.

Sapsford and Hughes (1978) measured the cloacal temperatures of 11 nesting female loggerheads in Tongaland, South Africa. These nesting females had body temperatures that averaged 2.85°C (range 1.1–4.5°C) above the sea temperature. These authors attributed the increased temperature to absorption of solar radiation rather than muscular activity associated with leaving the ocean or metabolic heat. Sapsford and Van der Riet (1979) noted that a captive loggerhead raised its body temperature up to 3.75°C above the water temperature through basking on clear days. On cloudy days, the temperature rise did not occur. Sapsford and Van der Riet (1979) suggested that pulmonary circulation was important in heat transfer to the internal body organs.

3.5 Behavior

3.5.1 Migrations and local movements

Because they nest in mostly temperate and subtropical regions, loggerheads are assumed to migrate between reproductive habitats and wintering areas; little is known about migrations of males. Group migration is unknown in *Caretta*. As previously noted (section 2.2.2), loggerheads may remain year-round in offshore waters. In Florida, some individuals go to the soft bottom of the Canaveral Ship Channel or the bottom off West Palm Beach, where they are found encased in mud (Carr et al. 1981; Ogren and McVea 1982; Rouse 1984). Whether they actively burrow into the mud, or whether it forms around them as they settle onto the bottom is questioned (L. Ehrhart, personal communication), although Rouse (personal communication) believed they actively bury into the mud. Henwood (1987) reported three distinct groups of loggerheads in the vicinity of Cape Canaveral, FL, based on recaptures of tagged loggerheads (*N* = 25 males, 199 females, 475 subadults). The first consisted of adult males who were most abundant between April and May and were considered to be possible residents throughout the year. The second group was the adult females that arrived from May through July from winter foraging habitats. Adult males and females did not travel together. The third group consisted of subadults that dominated the population from July through March; subadults thus also constituted a resident population, but one that disperses in spring and early summer as weather conditions improve (Henwood 1987).

Localized movements of loggerheads have been reported for a few turtles with the use of a variety of tracking techniques. In early experiments, Carr (1962) followed six adult females initially caught nesting on Florida's east coast but released on the west coast. He was unable to draw any firm conclusions concerning orientation, but noted that two females seemed to have directed movement to the south. Stoneburner (1982), using satellite telemetry, followed the movements of eight females after nesting on Cumberland Island National Seashore. These turtles swam in a northerly direction after nesting and entered estuarine waters behind a barrier island where they remained for 1–3 d. Afterwards, they moved to small isolated areas of stable substrate where they remained until the next nesting attempt. Stoneburner (1982) showed that such movements were not random wanderings, but directed movements. Using radio and acoustic tracking, Kemmerer et al. (1983) noted 8 of 10 loggerheads removed from the Canaveral Ship Channel in Florida and released 8 km south returned to the area of original capture within 13 d; these observations indicate the potential for homing by *Caretta*. An adult loggerhead ("Dianne") fitted with a satellite transmitter was released in October 1979 east of Louisiana and followed until June 1980. During this time, she wandered west and southwest in coastal waters to a region north of Brownsville, TX, whereupon she turned northward back up the coast to near Port Arthur, TX (Timko and Kolz 1982). Killingley and Lutcavage (1983) attempted to reconstruct the movement patterns of one adult female and five subadult loggerheads from the Chesapeake Bay in Virginia using isotopic profiles from barnacle shells. They found that the turtles all had different movement patterns: turtle 1 moved from a low saline environment to a marine environment, but had not migrated to warmer waters the previous winter; turtle 2 had traveled north from tropical regions on a long migration prior to entering the Bay; turtle 3 showed two distinct patterns of living in brackish waters separated by a period in warm ocean waters; turtle 4 moved from warm to cool ocean water prior to entering brackish waters; turtle 5 was similar to turtle 3 but had only one complete cycle of brackish-ocean water occupation; turtle 6 was similar to turtle 2 except for a longer period in brackish waters. These data suggest considerable variation in movement patterns between individual turtles. Keinath (1986) reported that two loggerheads released within Newport Harbor, RI, swam away from land and exited the harbor within several hours. They appeared to be heading south when tracking was terminated because of a weak signal.

Loggerheads tagged on the coast of the southeastern United States have been reported from other areas in U.S. waters in the northeast and Gulf of Mexico (Meylan 1982; see also section 3.1.6). International recoveries have been reported in the Bahamas (Grand Bahama, Abaco, and Eleuthera), the Dominican Republic and Cuba (Meylan 1982; Meylan et al. 1983), and Yucatan and Belize (*in* Meylan 1982). The method of orientation, whether chemosensory, celestial, acoustic, or through social facilitation, is unknown. Kirschvink (1980) noted that loggerheads appear to have magnetic material within their heads which may aid in orientation as has been shown in other migratory animals. His sample size was small and limited to hatchlings, however.

Outside U.S. waters, there are few data on localized movements of loggerheads, although general long distance migratory routes are known for the populations in Australia and South Africa. In most studies, patterns have been pieced together based on relatively few recaptures, and it is largely unknown whether differences exist between the sexes or what percentage of the turtles migrate each year. Based on tagged recaptures, Hughes (1971*c* [*N* = 29], 1971*d*, 1974*a* [*N* = 35], 1977) noted that Tongaland loggerheads dispersed northward along the African coast as far as Tanzania with a few returns from the northern and southern coasts of Madagascar. The majority of returns originally came from the area around the city of Moçambique but more recent data have the majority of returns further north (Hughes, personal communication). Presumably, these loggerheads migrate between Tongaland nesting grounds and feeding grounds further north. Tagged Tongaland females have not been captured nesting at nesting grounds in Mozambique (Hughes 1971*d*).

Bustard and Limpus (1970) noted that a female loggerhead nesting at Mon Repos Beach in Queensland, Australia, was recaptured in the Trobriand Islands 63 d later. A tag from a turtle nesting on Mon Repos also was found in the Gulf of Carpentaria near Weipa (Bustard and Limpus 1971). Since these early reports, additional recoveries have been made along the northeastern coast of Queensland, southern New Guinea, and New Caledonia (Bustard 1974, 1976). According to Limpus (1982*a*, 1985) and Limpus and Parmenter (1986), loggerhead turtles nesting in southern Queensland come from feeding grounds that extend northward along the Queensland coast, around Cape York into the Gulf of Carpentaria, to New Guinea including the Trobriand Islands. Large populations inhabit the waters of the Great Barrier Reef. As in the southeastern United States, some loggerheads live year-round in the vicinity of nesting beaches (Limpus 1985). Limpus and Reed (1985) reported that a single female remained with a single underwater refuge adjacent to her nesting beach during the entire reproductive season.

In Japan, seven nesting females tagged at Miyazaki have been recaptured in the East China Sea indicating possible migration between feeding and nesting grounds (Iwamoto et al. 1985). Kajihara et al. (1969) noted that 9 of 20 30-cm loggerheads fitted with a beacon were recaptured at periods of up to 4 mo after release. These turtles were recovered off the Japanese coast in areas inhabited by the adult nesting population. These authors also attempted to track four turtles using a radio-wave oscillator, but the experiment proved unsuccessful because of the leakage of seawater into the housing. The localized movements of a single female that was radio-tracked 136 h after release at Omaezaki Beach were reported by Soma and Ichihara (1977*a*, 1977*b*, 1978) and Soma (1985). She concentrated her activity in two offshore areas approximately 25 km straight-line distance apart and never ventured farther than 15 km offshore.

3.5.2 Schooling

There is no indication that loggerhead turtles form "schools" or "flotillas" in the classical sense. They may, however, form local concentrations at sea or in the vicinity of nesting beaches. There have been reports of massed numbers of loggerhead juveniles or small subadults in the Atlantic. Maigret (1983) reported thousands of small turtles off the coast of Gibraltar (Section 2.1). These turtles were originally misidentified as *Lepidochelys kempii* but later reidentified as *Caretta*. What they were doing or where they were going is unknown. Woody (personal communication) reported large numbers of subadult loggerheads 42 km off the coast of Baja California, but no further details are available. Murphy (1914) reported "numbers" of adult loggerheads between 670 km and 830 km east of Uruguay. Rivas (*in* Meylan et al. 1983) sighted hundreds of reddish-brown turtles, presumably loggerheads, along the outer reefs of the Florida Keys and Cay Sal Bank in May 1977, including six copulating pairs. Previous surveys in April and early May sighted only an occasional turtle. A similar group was seen by Barker (*in* Meylan et al. 1983) in the same area in mid-May 1976. Further data are necessary to evaluate the significance of these concentrations of loggerheads and to determine if aggregations form in other areas.

3.5.3 Responses to stimuli

The loggerhead is often represented as aggressive and feisty (Carr 1952; Ernst and Barbour 1972), which may be an unfair characterization for individuals molested in their natural environment or removed from it after being netted or otherwise harassed. For instance, Bruno (1970) called them "apathetic" except when fishermen grab them to haul on board; then they fight fiercely to regain freedom. Hildebrand and Hatsel (1927) reported that loggerheads were initially docile, but became so aggressive that they had to be released. Deraniyagala (1939) stated that loggerheads emit a faint musky odor when captured, and that Tamil fishermen call it the "nai amai" (dog turtle) because it bites "savagely" and "is even aggressive when hauled aboard." He noted that fishermen clubbed the turtles in the head prior to bringing them on board to subdue them. However, Carr (1942) stated that loggerheads could be handled with relative immunity compared with *Lepidochelys kempii*, and Layne (1952) considered his captives to be quite docile; they would bite only as they competed for particular food items. Likewise, Parrish (1958) stated that captives seldom showed signs of aggressiveness. Both Layne (1952) and Parrish (1958) reported that one loggerhead might bite another if the intruder occupied a favored location in the tank. On the other hand, Parrish (1958) noted one instance where an intruder chased a resident from its favored place. Rudloe (1979) noted that a captive loggerhead was not aggressive toward humans but viciously attacked a lemon shark, biting it through the gills. In Australia, a large female was not aggressive toward divers despite being repeatedly pulled from her internesting cavity over a period of several months (Limpus and Reed 1985). Rouse (personal communication) also reported that loggerheads off the coast of West Palm Beach, FL, are not aggressive toward divers.

In the wild, loggerheads may occupy crevices or holes either as residents or during the internesting period (Rouse, personal communication; Limpus and Reed 1985). Limpus and Reed (1985) recorded a female using one specific hole during the entire 2.5 mo spent between nestings at Heron Island, Australia. Local resident *Caretta* usually abandoned a site after being pulled from a crevice to read a tag number, but the internesting female returned directly to the hole both after being pulled from it and after surfacing to breathe. Rouse (personal communication) also noted that loggerheads can be consistently located at specific crevices during the time they remain on the reef off the coast of West Palm Beach.

In captivity, daily activity is about equally divided between swimming and resting. While resting, loggerheads lie completely motionless with the head in a protected area (e.g., a corner), the eyes open or half shut, and the flippers extended (Layne 1952). Layne (1952) suggested that loggerheads slept in this position since they were found at night in a similar position but with their eyes closed. At night, they were slower to arouse than they were in the daytime. Parrish (1958) recorded four basic resting positions: hatchlings fold the front flippers back onto the carapace with the rear flippers held close together; juvenile turtles extend the front flippers while the rear flippers are held close together; juveniles may also fold the front flippers back on the carapace but extend the rear flippers; and a completely spread-eagle position. The last-mentioned posture was the one most frequently observed. During resting, the eyes are kept open and the turtles appear alert and aware of external stimuli.

Loggerheads are known to sleep (Layne 1952; Carr 1952; Parrish 1958; but see Šušić 1972, for a different view of sleeping). Sleeping occurs underwater except in the open ocean where turtles sleep while floating at the surface (Carr 1952). In captivity, sleeping begins at sundown and occurs gradually over a 5-10 min period. After surfacing to breathe at night, turtles also appear slower to return to sleep (Parrish 1958). Loggerheads have been observed to scratch themselves vigorously and thoroughly in captivity (Parrish 1958). Virtually any solid object may be used. The longest a loggerhead was seen scratching was 20 min.

The swimming behavior of loggerheads has been described by Carr (1952), Parrish (1958), and Walker (1971) for adults, and Salmon and Wyneken (1987) for hatchlings (section 3.2.2). Parrish (1958) noted two types of locomotion for captive animals—a crawling gait in which alternate flippers (e.g., left front, right rear) were moved forward simultaneously and in contact with the substrate, and swimming. Crawling was used to move distances over the bottom or as a preliminary movement to begin swimming from a resting position. In swimming the propulsion of the foreflippers was directed downward and backward at 10-15° from the vertical. The propelling stroke produces a slight upward movement of the turtle in the water. Parrish (1958) reported that there were normally 10-30 complete strokes per minute. Walker (1971) gave a more detailed and technical account of the swimming motion of sea turtles, including *Caretta*, with diagrams based on motion picture analysis and a discussion of angles and forces. The power stroke is the downstroke, although some propulsion also is generated on the upstroke; movements of the humerus are the main force propelling the flipper. The rear flippers act as rudders and elevators, and aid in steering and depth changes. Hatchling loggerheads are unable to dive (Hooker 1908*a*; questioned by R. Byles, personal communication) and only develop buoyancy control after the first year of life (Milsom 1975). Adult loggerheads are either slightly lighter or heavier than seawater depending on the amount of air inhaled during the last breath on the surface (Jacobs 1939). Buoyancy is controlled by the amount of air in the lungs. At normal buoyancy, the animal is horizontal, but with a very large lungful of air, the rear part of the body becomes lighter than the front. Swimming compensates for the imbalance (Jacobs 1939). Normally, the right and left lungs are equally inflated, but the turtle is capable of moving air from one lung to the other (Jacobs 1939). The volume of the lung is established by smooth muscle within the lung, and the relation between the mechanics of ventilatory movements and lung volume regulation is complex (Milsom 1974).

Surfacing behavior has been noted for captive loggerheads and for wild loggerheads tracked by radiotelemetry. Three loggerheads in captivity at the South Boston Aquarium in Woods Hole, MA, surfaced every 2.1 min (range 15 s to 24 min) while actively swimming, and every 12.7 min while resting (Layne 1952). In Marineland, FL, captive loggerheads surfaced every 10-56 min while resting or every 30 s to 10 min while swimming (Parrish 1958). At night, surfacing occurred every 35-45 min. Two wild subadult loggerheads tracked by Keinath (1986) off Newport, RI, had rather different surface-submersion patterns. One turtle averaged only 2.2 s on the surface (range 0.7-7.4 s) and 264.1 s per dive (range 12.6-844.7 s). This turtle had 10-27 surfacings per hour. The other turtle averaged 44.8 s on the surface (range 0.7-547 s) and 313 s per dive (range 3.2-1,664 s). It had 2 to 69.3 surfacings per hour, and spent 79% of its time submerged. In contrast to these times, Soma (1985) reported the average time on the surface for a loggerhead in Japan prior to egg deposition was 79 s during the day and 53 s at night. After egg deposition, these averages changed to 105 s and 80 s, respectively. The average duration of dives prior to egg-laying was 1,314 s during the day and 471 s at night. After deposition, these changed to 1,200 s and 1,261 s, respectively. The average depth of dives was 20.3 m during the day and 12.8 m at night prior to deposition, and 11.5 m during the day and 15.5 m at night after deposition. Kajihara et al. (1969) reported that a loggerhead spent only 25% of its time submerged; generally a short surface time was followed by a short dive time. These short periods of surfacing and diving were interspersed by long surface times averaging 10-20 min. In sea turtles, the lung is the primary oxygen store during dives (Lapennas and Lutz 1982).

The reaction of loggerheads to light has been discussed (section 3.2.2). Loggerheads are sensitive to electrical fields, especially to AC fields, and such fields have been used effectively to deter loggerheads from the intake pipes at Florida Power & Light Company's St. Lucie plant (J. O'Hara, personal communication). The voltages required to turn turtles back were inversely proportional to the size of the turtle.

Little is known concerning the chemosensory behavior or abilities of loggerhead turtles (Owens et al. 1986), although such cues may be important in the imprinting hypothesis used to explain why turtles might return to their natal beach for their own egg deposition (Hughes 1974*a*; Carr 1984). Grassman and Owens (1981*a*, 1981*b*) demonstrated that hatchling loggerheads oriented toward a chemical that had been placed in the nest during development over other control chemicals in a laboratory situation. Their results tentatively support the hypothesis that the nest environment harbors important sensory cues for later orientation. Grassman and Owens (1982) also implicated chemosensory information in the location of food by loggerhead hatchlings.

It is unlikely that loggerheads hear airborne sounds since they lack an inner ear structure. However, a young loggerhead exhibited a startle reaction to underwater stimuli of 0.25 kc/s and 0.50 kc/s. This "hearing" appears to be mediated through bone, with the shell and skull acting as receiving surfaces (Lenhardt et al. 1983). These authors suggest that marine turtles are capable of receiving the low-frequency spectrum of sounds emanating from the natal beach, and that such sensory input may serve as one cue to females returning to a beach to nest.

4. POPULATION

4.1 Structure

4.1.1 Sex ratio

The sex ratio of adult loggerhead populations is unknown because of lack of information on males. At Heron Reef, Australia, Limpus (1985) found a male-biased sex ratio of resident turtles of seven males for every three females. On Wistari Reef and North West Island Reef, males also dominated the resident population giving an overall sex ratio at these three reefs of 0.41 females per male. Of 586 adult turtles moved during trawling in the Cape Canaveral area of Florida from 1978 through 1984, there was 1 female per 1.16 males (Henwood 1987). However, Wibbels et al. (1987*b*) recorded 1 male for every 1.94 females in subadult loggerheads from Cape Canaveral. Whether these results reflect true populational sex ratios is unknown, but is unlikely. The sex ratio of hatchling loggerheads, based on studies in conjunction with environmental sex determination, is reviewed in section 3.2.2.

4.1.2 Age composition

There is no information available on the overall age composition of loggerhead turtle populations. However, Henwood (1987) has shown that the age composition of turtles inhabiting the Cape Canaveral area of Florida varies seasonally (section 3.5.1). Estimates to age of maturity are presented in section 3.1.2; maximum age is discussed in section 3.3.1.

4.1.3 Size composition

There are no reliable estimates of size composition of loggerhead turtle populations. Indeed, it is difficult to characterize what constitutes a loggerhead population. Henwood (1987) gives a length frequency distribution of loggerheads captured during trawling operations off the coast of Cape Canaveral, FL, from 1978 to 1984 ($N = 3{,}679$). The largest group included turtles with an SLCL of 60-80 cm, with a smaller peak between 90 cm and 105 cm. Turtles <45 cm were unrepresented. To what extent these frequencies reflect those of loggerheads elsewhere in the vicinity or in other areas of the southeastern U.S. coast is unknown. In addition, Henwood (1987) noted that the composition of the population varied seasonally which further complicates the determination of a population's size composition. Lutcavage (1981) and Lutcavage and Musick (1985) provided a size-frequency histogram for the subadult loggerhead population, based on stranding and incidental catch data, which feeds in the Chesapeake Bay, VA, during summer. Most turtles fell into the 60-90 cm curved carapace length (CCL) categories, and such distribution probably reflects the frequency distribution of turtles using the Bay. Size ranges of nesting females vary considerably between populations (Table 7) and various growth parameters are discussed in section 3.4.3 and presented in Tables 26, 29, 30, and 31.

Table 30. *Regression of log weight (Y) in kg on log carapace length (X) in cm in the sea turtle* Caretta caretta *using the equation log Y = a + b log X from selected studies.*

Locality	N	Sex	Slope	Intercept	Source
South Africa	33	F	1.642	- 1.233	Hughes et al. (1967)
Florida	33	F	2.341	- 2.613	Ehrhart (1978 *in* Hirth 1982)

4.2 Abundance and Density

4.2.1 Average abundance and density

The average abundance and density of populations of loggerhead sea turtles is unknown, except for crude estimates or direct counts of the number of nesting females on particular nesting beaches. Many estimates are based on unpublished data and assumptions about the dynamics of loggerhead populations that, as yet, have not been verified; others appear to be "best guesses" without discussion about how the figure was calculated. The estimation of abundance and density is hampered by lack of information on population structure and sex ratios, as well as difficulties in identifying spatial limits of biological populations of sea turtles.

The largest nesting population of loggerhead sea turtles may be that nesting on Masirah Island, including the small colony in the Kuria Muria Islands, off the coast of Oman. Ross (1979) estimated the number of females nesting in 1977 to be between 19,000 and 60,000; in 1978 the estimate varied between 28,000 and 35,000. Ross (1979, 1982) considered the best estimate to be approximately 30,000 females nesting annually. However, Ross' (1979) report did not discuss the methods by which these estimates were obtained and, as such, the figures need substantiation.

The second largest, or perhaps even the largest, population of nesting loggerheads occurs in the southeastern United States, with 31,000 nests reported in Florida alone in 1986 (W.J. Conley, personal communication). Conley and Hoffman (1987) summarized nest counts reported to the Florida Department of Marine Resources from 1979 to 1985. The number of loggerhead nests per kilometer has varied from 35.7 to 61.4, although the amount of beach coverage has increased each year resulting in yearly increases in the total number of loggerhead nests recorded. These figures indicate well over 20,000 loggerhead nests are oviposited in Florida each year. Using aerial survey techniques, Crouse (1984*a*) estimated that between 497 and 585 nests were deposited in North Carolina in 1981. Between 1980 and 1982, S. Murphy (personal communication) counted 3,270 tracks on beaches in South Carolina, again using aerial survey procedures. Between 1979 and 1984, from 30 to 106 loggerhead nests per kilometer have been recorded in the vicinity of Cape Canaveral, FL (Provancha and Ehrhart 1987). On one day in July 1982, there were an estimated 5.45 fresh nesting crawls per kilometer from Melbourne Beach south to Sebastian Inlet, and from Hobe Sound National Wildlife Refuge to Lake Worth Inlet in Florida (Shoop et al. 1985). These authors also reported 4.09 fresh nesting crawls per kilometer during 1 d of aerial surveys on Cape Island, SC. These areas represent the highest known density of loggerhead nesting in the United States. The beach from Melbourne south to Sebastian Inlet may support 9,000–10,000 nests per season

Table 31. *The relationship between various meristic characters in several studies of captive loggerheads, using the allometric growth equation $Y = aX^b$.*

Locality	Y	X[b]	a	b	Source
Japan	carapace width	CL	0.1709	1.4189	Uchida (1967)
	carapace width	CL	1.0608	0.9678[a]	
	shell depth	CL	0.4706	1.0081	
	head length	CL	0.9643	0.7787	
	head width	CL	1.1306	0.6821	
	body weight	CL	0.00049	2.8317	
	body weight	CW	0.00044	2.9147	
Japan	body weight	CL	0.00034	2.89	Anonymous (1984*a*)

[a] Expressed after inflection point.

[b] CL = carapace length; CW = carapace width.

(334 nests per kilometer), and thus contains the largest number of nesting loggerheads in the Western Hemisphere (Ehrhart and Raymond 1987). With the recognition of the importance of the Melbourne Beach loggerhead nesting assemblage, the population of *Caretta* inhabiting the southeastern United States may rival Masirah Island as the largest nesting population in the world. In addition to the nesting population, Musick et al. (1983 *in* Lutcavage and Musick 1985) estimated that 4,500 to 5,000 loggerheads, mostly subadults, inhabit Chesapeake Bay, VA, in summer foraging habitat.

A large number of loggerheads apparently nests in southern Turkey (Geldiay et al. 1982). These authors estimated that 1,683 nests were deposited on 5 beaches: Dalyankov (47 nests/km), Alanya (30 nests/km), Kumluca (29.4 nests/km), Belek (10 nests/km), and Side (10 nests/km). These estimates were based on surveys conducted around research stations, and the densities were extrapolated to the entire beach. Thus, there is margin for error. Geldiay et al. (1982) noted that only 100 km of Turkey's 2,000-km Mediterranean coastline had been surveyed. Another substantial population of nesting females occurs in southeastern Africa. Hughes (1974*b*) estimated the total population of nesting females in southern Africa as 10,000, with 4,000 in Tongaland, 3,000 in Madagascar, and 3,000 on the remainder of the African coastline, although the method of estimation was not stated. In Tongaland, Hughes (1974*b*) reported 301-502 nesting females per year (1969/70–1972/73), although the largest number of nesting females handled in any year was only 408 (1963/64–1982/83; Hughes 1984). In Madagascar, 300 females nest per year (Hughes 1971*e*).

Other estimates of density or numbers of nests and females nesting annually are as follows (in order of decreasing importance): Wreck Island, Australia, 1,000 females/yr (Limpus *in* Ross 1982); Quintana Roo, Mexico, 500 (Marquez 1976); Quintana Roo, Mexico, <1,000 nests/yr (J. Woody, personal communication); Bundaberg beaches, Australia, roughly 275-625 females/yr (1969/70-1980/81; Limpus 1985); Santa Marta, Colombia, 300 nests/yr, but declining (Kaufmann 1973); Miyazaki, Japan, 79-532 (average = 278) "landings" per year (1976-1983; Iwamoto et al. 1985); Heron Island, Australia, <100 females/yr (1974/75-1980/81; Limpus 1985).

Thus, the largest nesting populations of *Caretta caretta* are found in the southeastern United States and Oman, with South Africa and Australia also containing substantial populations. The full extent of nesting in Turkey, Japan, Brazil, and Mexico needs further evaluation before estimates can be made concerning population size and density. The estimates above may be unreliable because of the dynamic nature of sea turtle populations.

4.2.2 Changes in abundance and density

Although loggerheads may be seen year-round in some areas, there are some changes in abundance and density due to reproductive movements (Henwood 1987; sections 2.2, 2.3, and 3.1.6). There also may be natural population fluctuations due to variation in survivorship and annual reproduction. In some areas, loggerhead numbers appear to be declining (Abascal 1971; Ross 1982; Frazer 1986; Crouse et al. 1987) because of habitat destruction (Mann 1977, 1978; Coston-Clements and Hoss 1983; section 4.3.2) and incidental take, particularly in shrimp trawls (Hillestad et al. 1982; Shoop and Ruckdeschel 1982; Crouse 1984*b*; Weber 1987; Thompson 1987). The relative status of loggerhead populations around the world was reported by Ross (1982).

4 . 3 Natality and Recruitment

4.3.1 Reproduction rates

The factors affecting reproductive rates of loggerhead sea turtles appear to vary geographically, and there is considerable intrapopulational variation as well (section 3). This variation makes it difficult to assess reproductive output on particular beaches by a population of nesting females. A crude calculation follows: Loggerheads produce, on the average, 100–130 eggs per clutch (Table 16), with an average success rate of 60%-85% hatching (Table 18). Assuming a female lays 2 or 3 times per season, then an individual may produce 120 to 332 hatchlings in a season. Most authors ascribe a 2- or 3-yr reproductive cycle for *Caretta* females while acknowledging the pitfalls of the data supporting such cycles (Hughes 1976*a*; 1982). Frazer (1983*b*) estimated a reproductive lifespan of 32 yr for loggerheads on Little Cumberland Island (LCI), GA. Assuming his estimate applies to other loggerhead populations, on a 2-yr cycle, an average female might be expected to have 16 reproductive seasons, and produce 1,920–5,312 hatchlings. On a 3-yr cycle, a female would produce 1,320–3,652 hatchlings.

Frazer (1984) produced a model to determine age-specific fecundity in LCI loggerheads based on a maximum 32-yr reproductive lifespan. Using the model, he predicted that a female would produce 14,864 eggs if she produced eggs each year. Assuming a 2-yr cycle, LCI females might produce 7,432 eggs during their reproductive life; a 3-yr cycle would produce 4,954 eggs. Again assuming a 60%-85% hatching success, LCI females would have a reproductive output of 4,459-6,317 successful hatchlings on a 2-yr cycle and 2,972-4,211 hatchlings on a 3-yr cycle. While the upper values are slightly higher than would be obtained by using mean values alone, these data show that a female produces a relatively small number of hatchlings during her long lifespan even assuming maximum egg production, highest production of successful hatchlings per clutch, and maximum number of reproductive years. Most females probably rarely approach these maximum values even considering the high survivorship of adults under natural conditions (Frazer 1983*b*, 1983*c*), since only 53% of the adults would be alive after their first reproductive season and only 1 of 1,000 females survives to attain a 32-yr reproductive lifespan. Frazer (1986) has shown survivorship from egg to adulthood to be only 0.0025 in a stable population, and from 0.0009 to 0.0018 in the declining population at Little Cumberland Island. Thus, an "average" female has a reproductive life of only 4 yr. Clearly, the number of successful hatchlings (i.e., those surviving from egg to adult) produced by an individual female is rather small.

4.3.2 Factors affecting reproduction

General environmental factors prevailing during the nesting season (heavy rains, floods, destructive storms, wave surge, temperature), as well as immediate specific environmental factors affecting nesting emergence (tide, time of day, moon phase), affect reproduction (section 3.1.6). The condition of the feeding grounds (i.e., amount and quality of food available to the female) also affects reproduction since it determines the female's ability to yolk-up several clutches of eggs. Factors affecting incubation and nest success (rain, gas exchange, predators, chemical content of sand, intraspecific and interspecific nest destruction) also affect reproductive success (section 3.1.7).

Loggerhead females are disturbed by lights and moving shadows as they approach and land on nesting beaches and during the early stages of nesting. Such females return quickly to the sea (Caldwell et al. 1959*b*; Margaritoulis 1985). Such behavior is readily evident on beaches frequently disturbed by human activity, such as the presence of people on the beach, or the presence of residences, resorts, commercial and military operations, and highways near nesting beaches (Mann 1977, 1978; Coston-Clements and Hoss 1983; Witherington 1986; Ehrhart and Witherington 1987). A variety of management options have been proposed to deal with these problems (section 6), especially with regard to the modification of beachfront lighting (Raymond 1984*a*).

4.3.3 Recruitment

Little is known concerning actual recruitment to loggerhead populations. Based on a summary of 7 yr of tag return data, Hughes (1974*a*) estimated that the recruitment rate was relatively high—between 20%-30%—for the Tongaland population. At the Heron Island Reef resident population in Australia, recruitment was estimated at 13.1%-17.4%, although this included turtles moving from one resident population to another (Limpus 1985). Most of the turtles which were never previously tagged elsewhere and were recorded as recruits, were immature with a CCL at the lower end of the population (Limpus 1985). Frazer (1986) mathematically demonstrated that a survival rate (egg-to-reproductive adult) of 0.0025 is necessary to maintain a stable population of nesting females.

4.4 Mortality

4.4.1 Mortality rates

Adult mortality (1 - survival rate) can be estimated from Frazer (1983*c*) as 0.19/yr at Little Cumberland Island, GA. Juvenile mortality for this population was estimated as 0.305/yr (Frazer 1987). These are the only mortality rate estimates available. Frazer (1983*c*, 1986) estimated that the loggerhead population nesting on Little Cumberland Island, GA, was declining at a rate of 3.0% per year. The survival rate from egg to reproductive adult was estimated at only 0.0009 to 0.0018, below that which is necessary to maintain a stable population (Frazer 1986).

4.4.2 Factors causing or affecting mortality

Loggerhead hatchlings are preyed upon primarily by ghost crabs, sharks, predatory bony fishes, and a variety of mammals, including the water mongoose, genets, raccoons, foxes, dogs, and cats. A variety of birds also take hatchlings that emerge during daylight hours (section 3.3.2; Table 21). Mortality from nonpredatory animals, including disease, starvation, and cold-stunning, undoubtedly occurs but nothing is known about effects on particular populations. Mortality of hatchlings also occurs from the ingestion of tar, oil residues, and plastic and styrofoam objects (Balazs 1985).

Juvenile, subadult, and adult loggerheads are preyed upon primarily by sharks, particularly tiger sharks (*Galeocerdo cuvieri*). These size classes also are prone to cold-stunning during periods of particularly cold weather, and may ingest tar and plastic leading to injury and death. A small number of loggerheads die from trauma associated with boat collisions, and some are maliciously killed by humans for unknown reasons (e.g., Kaufmann 1966). Seventy-one loggerheads were killed during the dredging of the Port Canaveral Ship Channel, FL, in 1980 (Rudloe 1981; Joyce 1982); 1,250 loggerheads were relocated after it became apparent that serious mortality was occurring. Procedures, including use of the California-type draghead and the limitation of trawling to autumn when few turtles are present, have been implemented to reduce mortality in the future (Studt 1987).

Mortality from incidental catch in pound nets, trawls, and long-line operations may also take considerable numbers of loggerheads. Loggerheads are particularly prone to mortality from drowning in shrimp trawls since they try to outswim the trawl and thus exhaust themselves (Ogren et al. 1977; Hillestad et al. 1982). Bullis and Drummond (1978) reported 41 loggerheads caught in 7,625 h of trawling by National Marine Fisheries Service (NMFS) research vessels, but these figures were based on trawls in areas where turtles might not be expected to be abundant. South Carolina shrimpers caught 1-3 turtles per week with an estimated mortality rate of 18.2% in 1976 and 43.3% in 1977 (Ulrich 1978 *in* Hillestad et al. 1982). Richardson and Hillestad (1978) reviewed incidental catch of Georgia loggerheads. Of trawler captures in Georgia and South Carolina from 1978 to 1979, most (259 of 274) were subadults (Hillestad et al. 1982). Ruckdeschel and Zug (1982) reported an increase in loggerhead mortality at Cumberland Island, GA, between 1974 and 1979, and noted that strandings coincided with the shrimping season. However, these authors believed that not all mortality could be attributed to commercial fishing alone, as pollutants and sea detritis could contribute to mortality through disease and starvation. Ehrhart (1987) noted that loggerhead strandings ($N = 602$) were highly correlated with heightened shrimping activities between 1977 and 1984 in the Port Canaveral area of Florida. As many as 45,000 loggerheads now are caught by shrimpers annually in the southeastern United States, of which 12,600 are estimated to drown (Weber 1987). Thompson (1987), based on NMFS estimates, stated that 47,973 turtles were caught of which 11,179 died. From 1980 through 1986, the NMFS reported 8,317 turtles stranded on U.S. coasts, the vast majority of which were loggerheads. Shrimping also occurs off loggerhead beaches in Mexico, Australia (Limpus 1973*a*), South America, South Africa (Hughes 1974*a*), and Japan. The extent of this mortality is unknown.

Loggerheads are caught and drowned incidentally in pound nets in the Chesapeake Bay, VA (Lutcavage 1981; Lutcavage and Musick 1985). Since monitoring began in 1979, between 100 and 225 dead loggerheads per year have been reported (Cook 1982). From 1979 to 1981, 527 dead *Caretta* were recorded, although all mortality cannot be attributed solely to drowning in pound nets (Lutcavage and Musick 1985). C.R. Shoop (*in* Crouse 1984*b*) also reported pound net mortality in Rhode Island and New York, although Meylan (personal communication) knew of no cases of drowning due to pound nets in Long Island Sound, NY. Other nets that might ensnare loggerheads include large-mesh gill nets, purse seines, and shoreline set nets (Hughes 1974*a*; Limpus 1975; Hillestad et al. 1982; Crouse 1984*b*). In South Africa, most of the turtles caught in shark nets were subadults, and Hughes (1974*a*) suggested that larger turtles remained outside the littoral waters where nets are set. Shark fishermen, using baited hooks, also are reported to take large numbers of subadults in the Azores (Carr 1986*b*) and Baleares islands (J. Mayol, personal communication to A. Carr).

4.5 Dynamics of Population

The population dynamics, or more properly the life history characteristics, of sea turtles, using nonmathematical data, have been briefly reviewed by Bustard (1979). The only population models available for any loggerhead population are those developed for the Little Cumberland Island nesting population (Richardson and Hillestad 1978; Richardson 1982; Richardson and Richardson 1982; Frazer 1983*a*, 1983*b*, 1984, 1986, 1987), including a preliminary life table (Frazer 1983*b*). Development of these models was facilitated by more than 20 yr of nesting data, during which virtually every female that nested was recorded and tagged. These data indicate a 3.0% rate of population decline (Frazer 1986). Richardson and Richardson's (1982) model predicts 39% annual recruitment, 3 yr as the mean longevity of nesting adults, and a turnover of nesting females every 6 yr. These authors constructed a survivorship curve in which a cohort replaces 50% of itself the first 3 nesting seasons and 90% during the first 13 nesting seasons. Richardson and Richardson (1982) further estimated that survivorship from egg to adult would have to be 0.0013 to maintain a stationary population. Frazer (1986) noted that Richardson and Richardson (1982) did not adjust fecundity for sex ratio, and he recalculated the survivorship value to be twice that of Richardson and Richardson (1982). Frazer (1986) further noted that Hughes' (1974*a*) estimates were somewhat lower than his, but that Hughes (1974*a*) used a 1:2 sex ratio. Crouse et al. (1987) have used a stage-based population model to examine the sensitivity of Frazer's life table, and concluded that management practices currently focus on the least responsive life-stage, the eggs on the nesting beach. Survival of the juvenile and subadult stages has the largest effect on population growth. The strength or longevity of a loggerhead population does not come from sheer numbers alone, but from a combination of survival, fecundity, and growth throughout the life cycle.

4.6 The Population in the Community and the Ecosystem

The loggerhead sea turtle is a large marine reptile inhabiting a wide variety of marine habitats in temperate, subtropical, and tropical seas. As with other marine turtles, populations appear to be separated into discrete breeding populations (section 3.1). The loggerhead inhabits offshore areas, lagoons, estuaries, and reefs adjacent to, or at some distance from, nesting beaches (section 2). It is primarily carnivorous, feeding on a wide variety of marine invertebrates (section 3.4). Although loggerheads share the marine environment with several other species of marine turtles, there are no known serious competitors.

Loggerhead turtles are not group nesters in the sense of turtles of the genus *Lepidochelys*, although many turtles could potentially be on a nesting beach simultaneously. They usually renest two to three times within a nesting season, although there is a great deal of individual variation. Loggerheads frequently nest on the same beaches as other sea turtles, although they are usually numerically the dominant nester on their major nesting beaches. Intergeneric mating appears to be extremely rare (section 2.4).

Loggerhead eggs and hatchlings are eaten by a wide variety of predators (sections 3.1.7 and 3.2.2), while juveniles, subadults, and adults appear to be preyed upon primarily by sharks (section 3.3.4).

Some loggerhead populations appear to be, or are, declining, or are certainly threatened (southeastern United States outside Florida, Mexico, Caribbean, Colombia, Mediterranean, Madagascar, Mozambique, Japan) due to habitat destruction or alteration, incidental take, and the directed take of eggs and adults. Others are stable (Florida, see Conley and Hoffman 1987) and appear reasonably protected (South Africa, Australia). The status of the remainder is unknown (Oman, West Africa, New Caledonia, Brazil, China).

5. EXPLOITATION

5.1 Fishing Equipment and Methods

At many nesting beaches, loggerhead turtles are protected from capture (e.g., Australia, Oman, South Africa, United States) and as such there is no directed fishery. Also, the meat is not considered very good to eat by many people (Hartt 1870; Ingle and Smith 1949; Villiers 1958; Caldwell 1960; Murthy and Menon 1976; Frazier 1984*b*; Moll 1985; Schleich 1987). This may explain why loggerhead remains are so rarely found in Paleo-Indian sites adjacent to large nesting colonies (Johnson 1952; Wing et al. 1968). Englehardt (1912) noted that the loggerhead was of little economic importance at the turtle market in Key West, FL, because of their "inferior quality as food." True (1884) describes loggerhead meat as leathery and oily, smelling strongly of musk. However, he considered young loggerheads as "tolerably esculent." Carr (1952) called it tough and stringy, but noted that it is eaten by some people as "turtleburgers" or in soup. Only Cuba and Mexico appear to have a commercial industry focusing on the loggerhead (Cardona and de la Rúa 1971; Rainey and Pritchard 1972; Marquez 1976*b*), although substantial numbers also are taken in Madagascar (Hughes 1971*e*).

The most common methods of directed capture include "turning turtle" (i.e., flipping a turtle on its back while it is on a nesting beach), harpooning, diving, and the use of nets. Harpoons typically have a wooden shaft with a detachable point of wood or metal. The point has a long line tied to it which the fisherman holds and uses to eventually pull the tired turtle to the boat or canoe. In the late 1800's in North Carolina, loggerheads were speared with harpoons called "gauges;" diving was used to supplement harpooning and to avoid damaging the turtle (True 1887). In Madagascar, fishermen balanced themselves in canoes called "lakampiara" and harpooned turtles (Vaillant and Grandidier 1910). The harpoons, called "fondaka," were tipped with a detachable hard wooden spear, called a "teza." The teza had a cord about 150–200 m long attached to it by which the turtler could pull in the turtle when it tired. Variations on this method have been used worldwide. For instance, Audubon (1926) described a similar harpoon used by turtlers in the Caribbean.

In Mexico, Ramos (1974) reported loggerheads are captured using mesh nets, harpoons called "pegas," and by diving on the turtles in the water. Abascal (1971) and Rebel (1974) discussed the nets used by fishermen to catch sea turtles in Caribbean waters. These nets, set primarily for green and hawksbill turtles, were constructed of cotton line of about 33 threads with a mesh of 20.3–30.5 cm diameter. They were up to 61 m long and 6.1–12.2 m deep, and sometimes were supported by wooden floats carved and painted like turtles. These wooden floats have given way to modern floats of plastic and styrofoam. Abascal (1971) provided photographs of fishermen setting nets and removing a loggerhead from a net. Set nets, diving, hook and line fishing, harpoons and "turning turtle" are all used by Cuban fishermen (Cardona and de la Rúa 1971). Cuban loggerheads are consumed locally, and the skin is used to make leather goods (Gonzalez 1982). Food and Agriculture Organization (FAO) catch statistics for loggerheads taken in Cuba during 1971 amounted to 0.4 t (Bacon 1975).

Although relatively few loggerheads appear to be taken by directed fisheries at present, especially compared with fisheries for the other marine turtles, this has not always been the case. True (1887) reported that small loggerheads found ready sale in the interior markets of North Carolina. In 1895, 11,364 kg of loggerheads entered the market at Key West, FL (Brice 1896). In 1944, 12,572 kg of loggerheads were sold at Grand Bahama (Ingle and Smith 1949). Nearly 3,300 kg of *Caretta* were sold within British Honduras (now Belize) in 1945 (Smith and Ingle 1949). The loggerhead nesting colony in Colombia has nearly disappeared because of wholesale slaughter of females and removal of all eggs deposited (Kaufmann 1966). During market surveys in 1965 and 1966, 54 loggerheads (19% of all turtles in the market) were reported in Cartagena, Colombia (Medem 1983), and more than 1,000 loggerheads presently enter the Colombian markets each year. Between 1951 and 1971, 66,674 kg of loggerheads were landed in Florida (Rebel 1974). As recently as 1970 through 1974, between 1,464 kg and 10,303 kg of loggerheads were landed in Brevard County, FL (Witzell 1987). Prior to protection within the United States, 90% of the loggerheads caught off Quintana Roo, Mexico, were exported to U.S. markets (Ramos 1974; Marquez 1976*b*).

While not the main focus of a fishing industry, loggerheads may be taken in some areas whenever they are encountered, and the numbers taken may be substantial. Although the meat is eaten in Venezuela, few loggerheads enter these waters so the market is not very substantial (Roze 1955). Small specimens are rarely caught in large drag-nets in the Canary Islands, although they are sold stuffed as curios in Madeira (Brongersma 1968*b*). Brongersma (1968*b*) estimated that 1,000 or more are taken per year. Hughes (1971*e*; also cited by Frazier 1980) reported an estimated gross mass of 181,300 kg of loggerheads taken in Madagascar per year. Despite certain religious bans on take, nearly every loggerhead encountered by fishermen in Mozambique is killed for food (Hughes 1971*a*). Loggerheads were identified in commercial catches around Krusadai Island in the Gulf of Mannar, India, but no figures were provided on the number caught (Kuriyan 1950). However, Jones and Fernando (1973) reported nearly 20% (i.e., about 700) of the marine turtles caught in the Gulf of Mannar are loggerheads and are consumed locally. Di Palma (1978) estimated that 100 loggerheads were caught each year by each fishing family on Isole Eolie in the Mediterranean, or 500–600 total per year. From 1978–1981, long-line fisheries off the Italian coasts took from 10–46 subadult (12 kg–37 kg) loggerheads per year in the swordfish fishery, and from 226–964 subadults (9 kg–22 kg) per year in the albacore fishery (De Metrio et al. 1983).

Although the loggerhead is not subject to substantial take in comparison with the green, hawksbill, and ridley turtles for its flesh, shell, and leather, the eggs are consumed worldwide wherever they are encountered. Poaching may occur even when strict regulations are in force to protect eggs and nests, especially due to misconceptions about the alleged aphrodisiac qualities of turtle eggs.

5.2 Fishing Areas

Loggerheads may be captured whenever they are encountered throughout the year in most parts of their tropical to temperate range, except in areas with strictly enforced prohibitions (e.g., Australia, South Africa, the United States). In most areas, *Caretta* is not the target species; the more desirable species are the green turtle (*Chelonia mydas*) and the hawksbill (*Eretmochelys imbricata*), and loggerheads may be taken incidentally to the fishery for these other species. Nets are fished in lagoons and channels, while harpooning usually takes place in deeper waters. Diving is also more common in shallower water.

5.3 Fishing Seasons

Loggerheads may be taken opportunistically at any time of the year when restrictions are lacking or when regulations are not enforced. The majority of turtles may be captured in connection with reproductive activities in temperate areas—Mexico, India, and Madagascar.

Migrating and foraging turtles are most likely encountered elsewhere in the tropics and subtropics at virtually any time of the year.

5.4 Fishing Operations and Results

Loggerhead meat is eaten in many areas throughout its range, although a substantial number of people will not eat *Caretta* because of its alleged disagreeable taste (section 5.1). They are readily consumed by coastal peoples in India (Jones and Fernando 1973), Madagascar (Hughes 1971*a*, 1982*b*), Mexico (Ramos 1974; Flores-Villela 1980; Hildebrand 1982), and Mozambique (Hughes 1971*a*; 1982*b*), and are probably eaten by coastal peoples throughout the tropics when caught incidentally to other fisheries activities. Meylan (personal communication) reported loggerhead turtle heads stuffed and mounted for sale in Guadeloupe, and polished carapaces for sale at a number of locations in the eastern Caribbean. Despite the potential for greater trade, its economic importance is far less than other sea turtles because of its limited distribution in tropical and subtropical regions with depressed economies, and because its shell and leather are either unworkable or unsuitable for many craft articles.

Except in areas where restrictive regulations are strictly enforced, loggerhead eggs are eaten without ill effects whenever found. Because substantial nesting colonies are located in regions with enforced restrictions on egg harvest (e.g., Australia, United States, South Africa, Japan), loggerhead eggs do not supply any substantial percentage of protein intake in areas adjacent to these colonies. In some areas, take of loggerhead eggs has been substantial, and has led to the decimation of the population (e.g., Colombia; Kaufmann 1966). While the eggs supplied a portion of the protein intake for coastal residents for a while, the unregulated take of eggs caused the rapid depletion of the population, forcing residents to seek other protein sources. Eggs are also consumed without regard for the effects on the population in Mozambique, despite protective regulations (Hughes 1982*b*), and in Madagascar (Hughes 1982*b*). Only in Oman has the take of loggerhead eggs been deemed significant in the diets of coastal inhabitants. Ross (1979) estimated 6% of the eggs deposited at Masirah Island (i.e., about 400,000) were consumed per year.

6. PROTECTION AND MANAGEMENT

6.1 Regulatory Measures

The literature contains many articles calling for the protection of sea turtles, including loggerheads, and their habitat (e.g., Hughes 1971*e*; Lipske 1977; Anonymous 1978*a*; Fletemeyer 1979; Morales 1981; Frazier and Salas 1983; Huang and Mao 1984; Alvarado et al. 1985; Veniselos 1986; Anonymous 1987), either out of concern for the loggerhead per se or concern for sea turtles in general. As the status and importance of the species has been recognized, regulatory measures have been imposed on the capture and marketing of loggerhead eggs, meat, and parts, such as carapaces. Because these laws are numerous and often complex, they are not individually discussed here. Legislation and regulations designed to protect habitat alteration and destruction have been slow to be enacted, and even when such are created, enforcement is often lacking. Major legislative actions involving loggerheads are described for the following locations: Australia (Bustard 1969*a*), Cuba (Gavilan and Andreu 1983), French Antilles (Kermarrec 1976), and Mexico (Flores-Villela 1980). The United States Endangered Species Act of 1973, as amended, makes it unlawful to take, import or export loggerhead turtles or products thereof (Anonymous 1978*b*; National Marine Fisheries Service 1978; Mager 1985). Regulatory measures for many nations in the western central Atlantic Ocean are summarized by Rebel (1974), Bacon (1975, 1981), Carr et al. (1982), Meylan (1983), and Bacon et al. (1984). Additional regulations for sea turtles in various countries around the world are described by Honegger (1978), Groombridge (1982), and Bjorndal (1982).

The loggerhead is listed on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). As of late 1987, this convention had been signed by 90 nations. As an Appendix I species, commercial trade is banned among signatory nations. It is listed as an Annex II species under provisions of the Convention on Migratory Species. An Annex II species is one for which international protection is necessary for its conservation. Although without statutory authority, the International Union for the Conservation of Nature and Natural Resources (IUCN) classifies the loggerhead as a "vulnerable" species (Groombridge 1982).

Enforcement of various national and international regulatory measures is difficult, and loggerheads of all size classes are harvested in many areas. In some cases, policing agencies are logistically unable or unwilling to enforce regulations. In other areas, budget cuts have seriously hampered the ability of enforcement agencies to regulate trade and protect turtles and their habitat.

6.2 Management Strategies

In order to manage and conserve loggerhead sea turtle populations, it will be necessary to focus on all important habitats, including nesting, developmental, migratory, and foraging areas. Conservation must also be based on the best available biological data, since the ultimate success or failure of conservation and management activities will be assessed within the biological constraints imposed by loggerhead life history characteristics. To these ends, fostering scientific inquiry and study of all facets of loggerhead biology should be encouraged and supported with a minimum of red tape. The development of a detailed recovery plan may help to focus the direction of the activities deemed necessary to conserve and manage sea turtle resources within an area (e.g., Hopkins and Richardson 1984). A manual is now available to assist biologists and resource managers with a guide to sea turtle measurement, census, and conservation techniques (Pritchard et al. 1983). General considerations for the conservation of sea turtles are in Pritchard (1980, 1982*b*), Ehrenfeld (1982), and King (1983). Richardson (1981) reviewed the Georgia management plan for dealing with sea turtle mortality in the early 1980's, and made recommendations for future research.

Pritchard (1980) divided management alternatives into five categories: statutory regulation of commerce, especially international commerce; protection of nesting females on the beach; the movement of eggs to protected incubators or hatcheries; head-starting; and stocking eggs or hatchlings to areas now depleted, but which at one time had a viable resident population. To these measures might be added measures to protect hatchlings, turtles, and their habitat when they are away from nesting beaches, and the introduction of modified fishing gear to reduce mortality from incidental catch. Each of these options has been tried with varying degrees of success in the protection of loggerheads.

Statutory regulation of commerce. Inasmuch as there is no great demand for loggerhead shell or leather, such international trade as occurs is probably insignificant. While loggerhead meat has occasionally entered international trade (e.g., Ramos 1974), most meat and eggs now are consumed locally. As long as they are enforced, provisions of CITES may be effective in preventing overt detrimental international trade in loggerhead turtle parts and products. Trade within nations is controlled with varying degrees of success by national law. For instance, national law has been effective in controlling the take of eggs within the United States and Australia, although poaching still occurs. However, unrestricted take of eggs has proved disastrous in Colombia (Kaufmann 1966) and is likely seriously impacting the populations in other areas (e.g., Mozambique and Madagascar). Complete enforced protection may be necessary to allow these populations to recover. In other areas (e.g., Oman), it may be desirable to regulate but not completely ban egg removal by instituting quotas on the percentage of deposited eggs allowed to be taken for consumption. Such quotas should only be assessed after a rigorous analysis of the nesting population, and only in areas where eggs constitute a major source of protein that might otherwise not be available to coastal inhabitants.

Protection of the female on the beach. Because they are most vulnerable during nesting, and because of their reproductive importance, female turtles on the beach should receive protection from disturbance. This can be accomplished by minimizing human access to important nesting beaches during the nesting season and reducing artificial lighting so that turtles can nest with a minimum of disorientation (Raymond 1984*a*). Development near nesting beaches need not automatically inhibit nesting if careful planning is conducted prior to construction to minimize impacts (Wilcox 1979). For instance, the construction and operation of the St. Lucie Power Plant in Florida has not had long-term negative impacts on the nesting loggerheads on nearby beaches. This is because bright lights, noise from equipment, beach access, and thermal discharges were strictly controlled by using dunes and dune vegetation to serve as a light screen and as a buffer to noise, limiting beach access, and using diffusers to reduce the temperature of cooling waters (Proffitt et al. 1986).

Nests and nesting females may need to be protected from off-road vehicles by prohibiting access to nesting beaches since they are known to either compact the sand thereby inhibiting emergence (Mann 1977), or they make ruts which hatchlings have great difficulty negotiating (Hosier et al. 1981; Ferris 1986). Night use of such vehicles might also disturb females as they attempt to nest.

In the southeastern United States, many beaches have been ''restored'' because of excessive erosion. In beach restoration, offshore sand is pumped onto the existing beach to build it up and prevent property loss. Restored beaches have a significantly lower nesting success percentage than beaches not restored, because of substrate compaction (Raymond 1984*b*). However, restored beaches appear to become less compact through time, and nesting success percentages again approach normal. Beach restoration should obviously not be conducted during the nesting season. The use of heavy mechanized beach cleaning equipment on heavily-used nesting beaches should be avoided since the use of this equipment can lead to excessive mortality (Mann 1977).

Protected hatcheries. On beaches that are difficult to protect from poachers, predators, and erosion, freshly deposited nests have been moved to protected hatcheries where they are either reburied within a compound or kept in moist beach sand, usually within styrofoam boxes, in a building near the beach. If moved shortly after deposition, these methods may prove effective although waiting too long may disrupt extra-embryonic membrane formation causing the egg to die (Blanck and Sawyer 1981; Miller 1982). The use of hatcheries is attractive in that the hatchery can be relatively easily guarded and hatching success monitored. However, hatcheries require constant manpower to protect against poachers and predators. In addition, destruction of the hatchery (by a storm, vandalism, etc.) could destroy an entire season's hatchling production in a very short time. The use of styrofoam boxes to incubate eggs has its own pitfalls. The eggs must be guarded against desiccation, and the temperature needs to be monitored. Mrosovsky and Yntema (1980) have pointed out that the use of styrofoam boxes to incubate eggs may have led to the masculinization of hatchlings, since the incubation temperatures were often lower than that on a natural beach; such hatchlings were probably 100% male. Pritchard et al. (1983) provided a design plan for construction of a hatchery. Illustrations of hatcheries are in Bustard (1968*b*), Cardona and de la Rúa (1971), and Pritchard et al. (1983).

An alternative to moving eggs to a protected hatchery is simply to move a clutch of eggs some distance from where they were deposited and rebury them on the natural beach. Apparently, this removes some olfactory cues by which predators, particularly raccoons, find a freshly deposited clutch. When the clutch is reburied, it can be screened to further inhibit digging predators while still allowing hatchlings to escape. However, early trials of this technique were not very successful (Rhame et al. 1982; S. Murphy, personal communication). The use of aversive chemicals, such as human and bobcat urine, and lithium chloride, applied over nests has not proved successful in deterring predators (Rhame et al. 1982; S. Murphy, personal communication; Hopkins and Murphy 1978).

Head-starting. Head-starting is the practice of rearing hatchlings to a size large enough to reduce predation when they are released. It is an experimental technique that has yet to be proven to work, and most sea turtle biologists stress that habitat protection should take priority over head-start programs (Pritchard et al. 1983). Head-starting has been, or is being, used to augment populations of green turtles (*Chelonia mydas*), hawksbills (*Eretmochelys imbricata*), and Kemp's ridleys (*Lepidochelys kempii*) in various parts of the world. For *Caretta*, there have been few attempts to head-start young animals. In the United States, loggerheads were reared at the National Marine Fisheries Service sea turtle facility at Galveston, TX, during the early stages of the Kemp's ridley project in order to better understand problems that might be faced while rearing the highly endangered Kemp's ridley. This phase of the program only lasted about 1 yr (L. Ogren, personal communication). Young loggerheads also have been raised and released after a study of graft-marking procedures conducted at the Miami Seaquarium (Hendrickson and Hendrickson 1986). These animals should be identifiable upon recapture, but, as yet, no results have been obtained. Cardona and de la Rúa (1971) recommended holding hatchlings 2 mo prior to release in appropriate offshore habitats. Loggerheads also have been raised for head-starting and aquarium exhibition in Japan (Anonymous, 1984*a*). Both fungal and bacterial diseases are common in hatchlings raised in captivity (section 3.2.2).

Experimental stocking of populations. As far as is known, there has been only one attempt to restock a "depleted" loggerhead population. This involved moving eggs from Cape Romain National Wildlife Refuge, SC, to National Wildlife Refuges in Virginia in the mid 1970's. However, there is no evidence Virginia ever had a substantial nesting loggerhead population, and hatchlings would have had a hard time surviving since they would be hatching late in the season and the warm water of the Gulf Stream is a considerable distance offshore at this latitude. Also, because of low sand incubation temperatures, it is likely that hatchlings would have been predominantly, or entirely, male.

Protection of hatchlings. Hatchling sea turtles need special protection to reduce predation, prevent disorientation from beach lighting, and minimize pollutants and plastics in the water and drift lines that sea turtles mistake for food items. The easiest way to reduce predation may simply be to eliminate the predators. For instance, predation has been substantially decreased on certain beaches in the southeastern United States by live-trapping or shooting raccoons. Raymond (1984*a*) has reviewed the effects of disorientation of hatchling sea turtles and recommended four things that must be done to minimize mortality: identify existing problem lights and eliminate or modify them, set guidelines and standards for acceptable beachfront illumination, establish coastal lighting ordinances that restrict shoreline lighting, and educate the public in coastal areas concerning the problem of hatchling disorientation. Research in the study of hatchling orientation to different light wavelengths and in the development of shields and screens to shade existing lights is recommended (Raymond 1984*a*). Finally, the pollution of the oceans, manifested by tar, oil slicks, and detritis, especially plastic and styrofoam objects that litter beaches and accumulate at drift and convergence lines, must be addressed to prevent ingestion by turtles and subsequent mortality (Carr 1987).

Modifications of fishing gear. Growing recognition and documentation of the substantial mortality of sea turtles, particularly loggerheads, drowned incidentally in shrimp trawls (section 4.4.2) has led to the development of Turtle Excluder Devices (or Trawler Efficiency Devices, nicknamed TEDs) by the United States National Marine Fisheries Service (NMFS; Lipske 1979, 1980; Weber 1987; Thompson 1987). The TED is a lightweight, collapsable device that fits in the front of a trawl (illustrated in Anonymous 1982, 1986; Thompson 1987; photograph in Weber 1987). It has an excluder panel which deflects sea turtles, jellyballs, and species of large finfish, out of the net yet does not result in decreased shrimp catch. Trials run by NMFS indicate the TED is extremely efficient at excluding sea turtles and significantly reduces mortality, and in some cases may increase shrimp catch. Despite opposition from some segments of the fishing industry, the use of TEDs is now required in certain U.S. waters during parts of the year when sea turtle abundance is highest (Thompson 1987). Interest in TEDs has been expressed by the governments of Belize, Colombia, Honduras, Indonesia, Mexico, Panama, and Trinidad (J. Woody and M. Weber, personal communication). With the adoption of TEDs, drowning in shrimp trawls, particulary in the critical subadult life stage (Crouse et al. 1987), will be reduced and nearly eliminated.

7. MARICULTURE

Because loggerhead sea turtles are not esteemed for their flesh, and because their skin is unsuitable for leather and their shell for artisan crafts, there appears to be no commercial mariculture incentive for this species. Loggerheads have been reared in captivity for varying amounts of time in different areas (section 6.2) and released in limited head-start operations. Captive loggerheads eat a wide variety of food items (section 3.4.2). Disease is a common problem with sea turtle rearing operations, generally due to poor water circulation and fungal infections because of abrasion and the aggressiveness of many turtle hatchlings. The most common disease is a fungal infection which erodes the shell, eyes, flippers, and skin. The infection spreads quickly and is fatal unless treated early. Diseases of hatchlings reared in captivity and possible treatments are reviewed in section 3.2.2.

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50272-101

REPORT DOCUMENTATION PAGE	**1. REPORT NO.** Biological Report 88(14)	**2.**	**3. Recipient's Accession No.**

4. Title and Subtitle

Synopsis of the biological data on the loggerhead sea turtle *Caretta caretta* (Linnaeus 1758)

5. Report Date

May 1988

6.

7. Author(s)

Dodd, C. Kenneth, Jr.

8. Performing Organization Rept. No.

9. Performing Organization Name and Address

U.S. Fish & Wildlife Service
National Ecology Research Center
412 N.E. 16th Avenue, Room 250
Gainesville, FL 32601

10. Project/Task/Work Unit No.

11. Contract(C) or Grant(G) No.

(C)

(G)

12. Sponsoring Organization Name and Address

U.S. Fish & Wildlife Service
Federal Assistance and Fisheries, P.O. Box 1306
Albuquerque, NM 87103

13. Type of Report & Period Covered

14.

15. Supplementary Notes

16. Abstract (Limit: 200 words)

This report is the first to collate and synthesize the published data on the biology and management requirements of the loggerhead sea turtle. More than 850 literature references were covered. Topics discussed include taxonomy, morphology, life history, population biology, exploitation, protection, and management.

17. Document Analysis a. Descriptors

No thesaurus available

b. Identifiers/Open-Ended Terms

Literature synopsis, sea turtle, *Caretta caretta*, Cheloniidae, endangered species, Reptilia, marine biology, taxonomy, morphology.

c. COSATI Field/Group

18. Availability Statement	**19. Security Class (This Report)** Unclassified	**21. No. of Pages** 110
	20. Security Class (This Page) Unclassified	**22. Price**

(See ANSI–Z39.18) **See Instructions on Reverse** **OPTIONAL FORM 272 (4–**
(Formerly NTIS–35)
Department of Commerce

U.S. Government Printing Office: 1988—573 205/80029

TAKE PRIDE
in America

March 3, 1849

U.S. DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE