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Chapter 4

Active Swimmers -- Passive Drifters:

The Oceanic Juvenile Stage of Loggerheads in the Atlantic System

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The life history of loggerhead sea turtles can be studied as a series of ontogenetic habitat shifts. These ecological and geographic shifts, sometimes spanning thousands of km, have at best been a challenge and at times an obstacle to our understanding of sea turtle biology. This is particularly true for post-hatchling sea turtles. Five-cm loggerhead hatchlings leave nesting beaches in the western Atlantic (primarily in southeastern USA), enter the ocean, and are not seen again in coastal waters of the western Atlantic until they are about half-grown at 50 cm in carapace length. This life stage from hatching to the 50 cm juvenile has been called the “lost year” (Carr 1986, Bolten and Balazs 1995) and is the focus of this chapter. I will concentrate on the North Atlantic loggerhead population(s) and will use examples from the Mediterranean, Indian Ocean, and Pacific when available.

We have made tremendous progress in our understanding of the “lost year” life stage since Archie Carr’s classic publication “Rips, FADS, and Little Loggerheads” in 1986. Our progress has been a result of both increased research efforts in the natural history of this life stage and development of new research tools. The most important tools have come from the fields of biotechnology (*e.g.*, genetic markers to identify populations and movements); biotelemetry (*e.g.*, remote tracking and sensing technologies to evaluate movements and distribution patterns); and computer science (*e.g.*, development of the personal computer has facilitated statistical modeling and demographic and ecological analyses).

Terminology

There is inconsistency in the use of oceanographic terms in the sea turtle literature. This is particularly evident in the discussions of the oceanic juvenile stage. I have been among those guilty of misuse of terms (*e.g.*, Bolten *et al.* 1993, Bolten and Balazs 1995, Bjorndal *et al.* 2000a). As more research is conducted in the ocean away from the nesting beach, researchers should be consistent in their descriptive terms and should use accepted oceanographic terminology.

To describe the early juvenile stage of sea turtles as the pelagic stage or the older juvenile stage as the benthic stage does not correctly communicate the ecological and physical oceanographic associations for these given life stages.

According to standard oceanographic terminology (Lalli and Parsons 1993), oceanic stage and neritic stage should be used.

The oceanic zone is the vast open ocean environment where bottom depths are greater than 200 m. The neritic zone describes the inshore marine environment (from the surface to the bottom) where bottom depths do not exceed 200 m. The neritic zone generally includes the continental shelf but in areas where the continental shelf is very narrow or nonexistent, the neritic zone conventionally extends to areas where bottom depths are less than 200 m (Lalli and Parsons 1993).

Organisms are pelagic if they occupy the water column, but not the bottom, in either the neritic zone or oceanic zone. Organisms are epipelagic if they occupy the upper 200 m in the oceanic zone. Organisms on the bottom in either the neritic zone or oceanic zone are described as benthic or demersal. Therefore, organisms can be pelagic in shallow coastal (= neritic) waters or in the deep open ocean (= oceanic). Likewise, organisms can be benthic in shallow coastal waters as well as in the deep ocean. Thus, we need to be consistent in our descriptions of sea turtle life stages and describe the early juvenile stage found in the open ocean as the oceanic stage, not the pelagic stage, and the later juvenile stage found in coastal waters as the neritic stage, not the benthic stage.

Life Stages

As with the terminology used to describe the association of sea turtles with the ocean realm, there has been inconsistency in the use of terms to describe the life stages of the loggerhead sea turtle. Some of this confusion has resulted from mixing the use of habitat descriptions with life stages and the use of imprecise terms to describe life stages.

The general life stages of the Atlantic loggerhead sea turtle and the habitats they occupy are diagrammed in Figure 4-1 and discussed below. A comparison of Figure 4-1 with earlier life history diagrams (Carr 1986, Musick and Limpus 1997) demonstrates how much has been learned about the early developmental stages of loggerhead sea turtles.

Eggs, Embryos, and Hatchling Stage – Terrestrial Zone

The life cycle begins with oviposition on the nesting beach – the habitat for the egg, embryo, and early hatchling stage. Characteristics of the nesting beach environment have been reviewed by Ackerman (1997) and Carthy *et al.* (this volume), and nest site selection has been reviewed by Miller *et al.* (this volume). Bjorndal (this volume) and Bouchard and Bjorndal (2000) present data on the flow of nutrients between the nest and the beach environment and on the effects of loggerhead nesting on the nesting beach ecosystem. After embryonic development, little turtles hatch from the egg, emerge from the nest (Moran *et al.* 1999), and actively orient and move rapidly to the sea (Lohmann and Lohmann, this volume).

Hatchling Swim Frenzy Stage – Neritic Zone

The hatchling stage (or neonate stage) continues in the nearshore waters and is of short duration (days). The hatchlings go through an active swimming period known as the "swim frenzy" (Wyneken and Salmon 1992), orient relative to wave direction, and maintain orientation relative to the earth's magnetic field (Lohmann and Lohmann, this volume). The "swim frenzy" is thought to bring the hatchlings to the major offshore currents.

The hatchling stage describes recently hatched individuals that are either in the nest chamber prior to emergence from the nest, on the beach or in the sea (hatchling swim frenzy stage). Hatchlings are nutritionally dependent on the remains of their yolk; this is primarily a pre-feeding stage. The hatchling stage ends when the turtles begin to feed.

Post-Hatchling Transitional Stage – Neritic Zone

The post-hatchling transitional stage begins when the turtles begin to feed, often while still in the neritic zone. Turtles in this stage live at or near the surface. This transitional stage ends when the turtles enter the oceanic zone. The post-hatchling transitional stage may not be marked by a major behavioral shift or functional change in their ecological roles but rather marked by a change in location – from the neritic to the oceanic zone. In the western Atlantic, this would be where the Gulf Stream Current/Azores Current System leaves the continental shelf. Off the coast of South Africa it is the Agulhas Current (Hughes 1974). This transitional stage can take days, weeks, or months depending on the stochasticity of surface currents and winds that either facilitate or inhibit the post-hatchlings from reaching the oceanic zone (Witherington 2002, in review a). Although the resultant geographic movements of the turtles may be primarily passive relative to the currents and winds, the post-hatchlings actively swim and orient within the currents increasing their chances of survival and increasing the probability of reaching the oceanic zone (Lohmann and Lohmann, this volume; Witherington in review a).

There may be a small percentage of the population that never leaves the neritic zone (Figure 4-1). The existence of this phenomenon is speculative. For one reason or another, probably by pure stochastic events, these individuals may never enter the major current systems and, if they survive, may go through their juvenile development entirely within the neritic zone. There is no direct evidence for this except that the size distribution of turtles that occasionally strand along the eastern US coastline (Musick and Limpus 1997, Turtle Expert Working Group 2000) and NW Gulf of Mexico (Plotkin 1996), suggests that some turtles may remain in the neritic zone. Also, the juvenile populations foraging on the Grand Banks off of Newfoundland, Canada, may be neritic zone populations.

Oceanic Juvenile Stage – Oceanic Zone

The oceanic juvenile stage (which will be referred to as the oceanic stage) is the focus of this chapter. The oceanic stage begins when the turtles enter the oceanic zone. Turtle movement in this stage is both active and passive relative to surface and sub-surface oceanic currents, winds, and bathymetic features (based on satellite telemetry and remote sensing studies, B. Riewald *et al.* unpublished data). These turtles are epipelagic, spending 75% of the time in the top 5 m of the water column but occasionally diving to depths greater than 200 m (B. Riewald *et al.* unpublished data). In the vicinity of seamounts, oceanic banks or ridges that come close to the surface, or around oceanic islands, loggerheads may become epibenthic/demersal by feeding or spending time on the bottom. In the Atlantic, turtles leave the oceanic zone over a wide size range, and as a result, the duration of the oceanic juvenile stage ranges between 6.5 and 11.5 years (Bjorndal *et al.* 2000a).

The causes for this variation in duration of this stage are not known, but may depend on the location of the turtles in the oceanic zone and available currents, food resources, or other cues.

Juvenile Transitional Stage – Oceanic and Neritic Zones

The ontogenetic shift from the oceanic to the neritic zone is a dramatic one, and, as such, there is probably a period of transition, perhaps, in both behavior and morphology. Kamezaki and Matsui (1997) discuss specific allometric relationships that change during the juvenile transitional stage that they suggest are related to changes in foraging behavior (epipelagic vs benthic).

The geographic regions where the transitional stages occur may be in regions where major oceanic currents approach or enter the neritic zone. The broad size range over which the turtles in the Atlantic leave the oceanic and enter the neritic zone (Figure 4-2, Bjorndal *et al.* 2000a, 2001) may also suggest that this transitional stage is of variable duration. I will discuss the factors that may drive this ontogenetic habitat shift later in this chapter.

Size frequency distributions of populations that fall between the oceanic stage and the neritic juvenile stage may support the existence of this transitional stage. The mean size of 53 cm CCL (n = 27; Tiwari *et al.* 2002) of a population off the Atlantic coast of Morocco is identical to the estimated mid-point of the size distributions for the juvenile transitional stage (see Figure 4-2) and may support the hypothesis that this population represents a transitional stage between the oceanic and neritic stages (Tiwari *et al.* 2002). A juvenile transitional stage for the Mediterranean populations has also been suggested (Laurent *et al.* 1998).

As Figure 4-1 indicates, if the oceanic-neritic transition is not complete, loggerheads may return to the oceanic zone. For example, a 78 cm loggerhead tagged along the east coast of Florida was recaptured in the Azores (Eckert and Martins 1989). Also, if juvenile loggerheads make multiple loops in the Atlantic gyre system rather than a single developmental loop, this could result in periodic movements between the oceanic and neritic zones.

Neritic Juvenile Stage and Adult Foraging Stage – Neritic Zone

The neritic juvenile stage and adult foraging stage occur in the neritic zone. The turtles are active and feed primarily on the bottom (epibenthic/demersal) although they do capture prey throughout the water column (Bjorndal this volume). In temperate areas, there may be seasonal movements among foraging grounds but in tropical areas the turtles may not show distinct temporal movement patterns. Depending on geographic region and population, the neritic juvenile stage and adult foraging stage may occupy the same habitats, or different size classes may be distributed differentially by water depth. This life stage is reviewed for the Atlantic by Schroeder *et al.* (this volume) and for the Pacific by Limpus and Limpus (Chapter 6, this volume).

Reproductively mature adults leave these foraging habitats to migrate to breeding habitats and may use specific migratory corridors. Depending on geographic region, these migratory corridors may take the turtles out of the neritic zone passing through the oceanic zone before returning to the neritic zone in the vicinity of the nesting beach. In other geographic regions, the migratory corridors may be entirely within the neritic zone.

Oceanic Juvenile Stage Loggerheads

Identification of Source Rookeries

The question asked by sea turtle biologists “where do the hatchling turtles go when they leave the nesting beach” is the reciprocal of the question asked by early explorers and sailors: “where do the little loggerheads found in the open ocean come from”. In the late 19th century, Prince Albert 1st of Monaco (1898) wrote that Azorean turtles (= oceanic stage) must have come from the “Antilles ou Floride” transported by the Gulf Stream. Brongersma (1972) also suggested that the little turtles in the eastern Atlantic came from the west Atlantic rookeries. Carr (1986) and later Bolten *et al.* (1993) used the comparison of size frequency distributions to suggest that the little loggerheads found in the oceanic zone around the Azores were an earlier life stage of the larger turtles in the neritic waters of the western Atlantic. The relationship between the little loggerheads in the oceanic zone and the larger-sized neritic loggerheads in the western Atlantic was further supported by a flipper tagging program managed by the Archie Carr Center for Sea Turtle Research at the University of Florida (Table 4-1; Bolten *et al.* 1992a,b; Bjorndal *et al.* 1994). A number of turtles captured and tagged in the oceanic zone have been recaptured in the neritic zone of the western Atlantic (Table 4-1B).

With the development of molecular genetic tools (*e.g.*, mitochondrial DNA sequence analyses), the relative contributions of rookeries to mixed stocks of oceanic-stage loggerheads could be evaluated (Bowen 1995, this volume). After the Atlantic rookeries were genetically characterized (Encalada *et al.* 1998), Bolten *et al.* (1998) were able to demonstrate that the oceanic-stage loggerheads in the waters around the Azores and Madeira were primarily from rookeries in the southeastern USA (90%) and Mexico (10%). Studies are currently underway with significantly larger sample sizes from the mixed oceanic-stage populations

(Bolten *et al.* unpublished data); more complete rookery sampling (*e.g.*, Cape Verde Islands, Luis Felipe *et al.* unpublished data); and increased sampling of southeast USA rookeries (Pearce 2001, Bjorndal *et al.* unpublished data). These additional data will likely result in changes to the percentages of contributions from the specific rookeries but the conclusion that the primary source rookeries for the Azorean – Madeiran populations are from the western Atlantic (primarily the southeastern USA) will probably continue to be supported (Bolten *et al.* unpublished data). In addition, recent developments in statistical models for analyzing mixed stock composition will likely result in broader, and more realistic, confidence intervals for the point estimates of rookery contributions to foraging populations (Bolker *et al.* in press). Studies in the Pacific (Bowen *et al.* 1995) and Mediterranean (Laurent *et al.* 1993, 1998) also demonstrate the use of genetic markers as a tool to estimate contributions from rookeries to mixed foraging stocks in the oceanic zone.

The classic diagram of the oceanic currents and the movements of loggerhead turtles in the North Atlantic (Carr 1986, 1987a) leaving the rookeries of the western Atlantic, becoming entrained in the Gulf Stream-Azores Current, travelling eastward to the Azores, Madeira, Canary Islands, and circling back to the western Atlantic in the North Atlantic Gyre is well known. However, this scenario is an over-simplification of what is known of movements of loggerheads. Oceanic-stage loggerheads spend 7 to 12 years in the waters around the Azores (see below, Bjorndal *et al.* 2000a) and may make only one transit rather than multiple loops. Also, based on flipper tag returns (Bolten *et al.* 1992a) and on molecular genetic studies (Laurent *et al.* 1993, 1998), movement of little loggerheads from western Atlantic rookeries and Azorean waters into the western Mediterranean is probably more common than originally thought. These loggerheads from the western Atlantic apparently leave the Mediterranean before they mature and reproduce (Laurent *et al.* 1998).

Genetic studies of other populations of oceanic-stage loggerheads in the Atlantic are currently underway and will soon provide additional details to Carr's classic diagram. For example, what are the rookery sources of the aggregation of small loggerheads in the Grand Banks off Newfoundland, Canada, and in the Canary Islands? What are the relationships of these populations to the Azorean-Madeiran population? In addition, studies are underway to identify the rookery sources for the hypothesized oceanic-neritic transitional population off the coast of Morocco (Tiwari *et al.* 2002, unpublished data).

Size-Frequency Distribution and Demography

Research conducted in the waters around the Azores during the last decade has provided the most thorough data on the size range, somatic growth rates, and duration of the oceanic stage. The size-frequency distribution of loggerheads in the waters around the Azores ranges from 8.5 to 82 cm curved carapace length (CCL) (Figure 4-2, Bjorndal *et al.* 2000a). The size distribution is not significantly different from another nearby oceanic-zone aggregation in the waters around Madeira (Bolten *et al.* 1993). Using length-frequency analyses with Multifan software, Bjorndal *et al.* (2000a) estimated the duration of the oceanic stage to be 6.5 to 11.5 years depending on the size of the turtles when they leave the oceanic zone (46 to 64 cm CCL). Based on a skeletochronology study of neritic-stage loggerheads, Snover *et al.* (2000) concluded that loggerheads are 52 cm SCL when they settle in the neritic zone off the east coast of the USA. This value of 52 cm SCL is similar to the value of 53 cm CCL at the intersection of the cubic smoothing splines of the length frequency distributions of the oceanic stage and the neritic stage (Figure 4-2), which is equivalent to 8.2 years duration in the oceanic stage (Bjorndal *et al.* 2000a).

The length-frequency analyses generated the following estimates of the von Bertalanffy growth model: K = 0.072 +/- 0.003 yr^{-1} and asymptotic CCL (Linf) = 105.5 +/- 2.7 cm (Bjorndal *et al.* 2000a). The size-specific growth rate function from length-frequency analyses is consistent with growth rates calculated from recaptures of tagged turtles (summarized in Bjorndal *et al.* 2000a).

Bjorndal *et al.* (in review a) have recently completed a skeletochronology analysis of oceanic-stage loggerhead turtles from the waters around the Azores and Madeira and have found that the growth rates closely match the results from the length-frequency analyses. An important contribution of their study is the presentation of a size-at-age relationship for oceanic-stage loggerheads. In addition, the skeletochronology analyses of the oceanic stage provide evidence for the first time of the phenomenon of compensatory growth in sea turtles. That is, turtles that are small for their age, grow more rapidly and “catch up,” resulting in reduced coefficients of variation for size-at-age with increasing age (Bjorndal *et al.* in review a). The authors conclude that compensatory growth may be a response to living in a stochastic environment.

Zug *et al.* (1995) evaluated the somatic growth rates of oceanic-stage loggerheads in the Pacific using skeletochronology. The age-specific growth function for the Pacific was similar in shape but with a slower growth rate than those for the Atlantic (Bjorndal *et al.* in review a). Using the same data set as Zug *et al.* (1995) but with a different modeling approach, Chaloupka (1998) presented a polyphasic growth function for the Pacific oceanic stage.

The duration of the oceanic stage in the Pacific may be longer than in the Atlantic based on the slower growth rates and the larger size of the loggerheads that begin to recruit to the western Pacific neritic zone (67 cm CCL, Limpus and Limpus, Chapter 6, this volume) compared with 46 cm CCL for the western Atlantic (Figure 4-2, Bjorndal 2000a, 2001). However, recent data from the eastern Pacific may suggest that the size at recruitment to the neritic zone may be similar to that in the Atlantic. Seminoff (2000) reports that loggerheads as small as 44 cm SCL begin to recruit to a neritic zone foraging ground in the Gulf of California. The size range reported by Seminoff (2000) is similar to the size range in which the Atlantic population begins to recruit to the neritic zone (46 cm CCL, Figure 4-2, Bjorndal *et al.* 2000a, 2001). Are differences in individual sizes at recruitment to the neritic zone between eastern and western Pacific populations real or do they reflect gaps in our knowledge of the Pacific loggerhead neritic juvenile populations? Extensive neritic foraging habitats in the western Pacific need to be surveyed to answer this question.

At present, there is not a good explanation for the differences in growth functions and growth rates for oceanic-stage loggerhead populations in the Atlantic compared with those in the Pacific. These differences, if real, may be based on nutritional differences in the two ocean basins. Interestingly, Atlantic-Pacific differences in growth functions and sizes at recruitment to neritic habitats have also been reported for green turtles (Bjorndal *et al.* 2000b).

Estimates for survival probabilities for the oceanic stage are vital for the development of demographic models. Survival probabilities for the oceanic stage have been generated as fitted values in demographic models rather than direct estimates (Chaloupka this volume, Heppell *et al.* this volume). Catch-curve analyses can be used to estimate survival probabilities, but emigration and mortality are confounded. Bjorndal *et al.* (in review b) used catch-curve analyses to estimate survival probabilities of oceanic-stage loggerheads in the waters around the Azores. At ages before loggerheads begin to emigrate from the oceanic zone (two to six years of age), the estimate of survival probability is 0.911; after emigration begins at seven years of age, the estimate of survival probability is 0.643.

In recent publications, Bjorndal *et al.* (2000a, in review a, b) have begun to derive some critical demographic values for the oceanic stage (*e.g.*, size-at-age, somatic growth, survival probabilities, and stage duration) that can be used in the development of population models of loggerhead turtles. Prior to these publications, the duration of the “lost year” was unknown and was a serious gap for model development. Both demographic chapters in this volume incorporate these recent results (Heppell *et al.* and Chaloupka). There is a great need for the quantification of sources of mortality from natural and anthropogenic (*e.g.*, longline bycatch) causes. There may be differences in mortality for turtles from the nesting beaches in the northern region of the east coast of the USA versus the southern region as hypothesized by Hopkins-Murphy *et al.* and Heppell *et al.* (chapters in this volume). To develop appropriate management and conservation plans, methods to assess relative population abundance and population trends for the oceanic stage are needed (Bjorndal and Bolten 2000).

Distribution, Movements, and Diving Behavior

In 1994, we began to use satellite telemetry to evaluate movement patterns of oceanic-stage loggerheads (Bolten *et al.* 1996, B. Riewald *et al.* unpublished data). The primary objective, at that time, was to determine if oceanic-stage loggerheads make multiple loops in the Atlantic gyre system or stay in the waters around the Azores until they reach the age or size to return to the neritic zone of the western Atlantic. We have not answered that question directly, but patterns of movement observed using satellite telemetry are consistent with residency in the oceanic zone around the Azores, not movement out of the region. In addition, long term recaptures (Table 4-1A) of tagged oceanic-stage loggerheads in Azorean waters suggests that in general, turtles do not make multiple loops in the Atlantic gyre during their oceanic stage but rather spend that developmental period in the waters around the Azores. The movement patterns reported for loggerheads in Madeiran waters (Dellinger and Freitas 2000) suggest that turtles in Madeira may be doing something different. This would not be surprising when one considers the differences in oceanic currents and bathymetric features of the two regions.

Since 1994 we have instrumented 38 turtles with transmitters to determine patterns of movement and distribution relative to environmental features observed from remote sensing data (*e.g.*, altimetry to evaluate currents, chlorophyll to assess areas of productivity, and sea surface temperature). In addition, using transmitters with depth sensors, we have been able to record diving behavior. Oceanic-stage loggerheads spend 75% of the time in the top 5 m of the water column; 80% of the dives are between 2 – 5 m with the remainder of the dives distributed throughout the top 100 m of the water column; occasionally dives are greater than 200 m (B. Riewald *et al.* unpublished data). Turtles in Azorean waters travel at sustained speeds of about 0.2 m / second (B. Riewald *et al.* unpublished data).

In 1998 a satellite telemetry program was begun in Madeira (Dellinger and Freitas 2000). Similar dive parameters were recorded as observed for turtles in Azorean waters by Riewald *et al.* (unpublished data, see above). No correlation was observed between maximum dive depth and body size (Dellinger and Freitas 2000); however, the scope of body size of the turtles instrumented with transmitters may not have been large enough to show this relationship.

The significant difference between the Dellinger study and the data collected by Riewald *et al.* is in the movement patterns of the turtles after release. Rather than demonstrate movements consistent with residency as observed in Azorean waters, in the Madeiran study the “turtles actively swam long distances against prevalent currents” and moved away from the point of release primarily to the north and west (Dellinger and Freitas 2000). However, their conclusion of turtles swimming against the current must be evaluated further because it is based on mean current movement patterns. Currents are highly variable at any location and mean movement patterns may not be indicative of the current direction for a given location at a given time. Additionally, altimetry data used to describe mean current patterns do not have the resolution to permit identification of smaller, local features, *e.g.*, countercurrents. Major currents are often associated with adjacent countercurrents which may influence turtle movement. Countercurrents associated with the Azores Current have been identified (Alves and de Verdiere 1999).

In the Pacific, George Balazs and colleagues have instrumented oceanic-stage loggerheads with satellite transmitters primarily to determine the behavior and survivorship of turtles caught in longline fisheries. In a recent report they conclude that nine juvenile loggerheads caught in the longline fishery in the central North Pacific all traveled westward against prevailing currents (Polovina *et al.* 2000). This conclusion requires further examination because, as discussed above, satellite altimetry data do not have the resolution that this conclusion requires. Major currents may have countercurrents associated with them, and because of the accuracy of turtle positions and the resolution of the remote sensing data, one can not rule out the possibility that the turtles were swimming/moving with the countercurrent.

Although there are differences in interpretation of results from satellite tracking data, it is clear that oceanic-stage turtles may behave differently in different areas. In the Azores, turtle tracking data and flipper tag returns suggest a long period of residency whereas turtles appear to be moving through Madeiran waters and are also non-resident in the regions of the Hawaiian study. This may not be surprising when one considers the physical oceanographic aspects of the regions. The Azorean region is characterized by a complexity of sea mounts, banks and the Mid-Atlantic Ridge which results in a complexity of eddies and convergent zones – prime habitats for the oceanic-stage loggerheads.

Ontogenetic Habitat Shifts: Why Do Loggerheads Leave the Oceanic Zone?

As the “mystery of the lost year” unravels, and we begin to understand where little loggerheads in the oceanic zone come from and how long they stay in that zone, we may now ask the question: “Why (and how) do they leave the oceanic zone?” Why does an animal that is finding food, growing, and surviving leave its habitat for a habitat with which it is almost totally unfamiliar – where it must learn to find new food sources and to avoid a new suite of predators?

Werner and Gilliam (1984) reviewed the theoretical basis for ontogenetic habitat shifts and hypothesized that a species will shift habitats to maximize growth rates. Can this hypothesis be applied to the Atlantic loggerhead population living in the oceanic zone? If the size-specific growth function for the oceanic stage (Bjorndal *et al.* 2000a) is extrapolated and compared to that of the size-specific growth function for the neritic stage (Bjorndal *et al.* 2001), the lines intersect (slopes of each line are significantly different, $p < 0.001$; Figure 4-3). That is, for a given carapace length greater than approximately 64 cm (a size by which almost all of the loggerheads have left the oceanic zone; Figure 4-2), growth rates will be greater in the neritic zone than in the oceanic zone. Additional support for this hypothesis comes from a skeletochronology study that demonstrated an increase in growth rates after the turtles moved from the oceanic stage to the neritic juvenile stage (Snover *et al.* 2000). Thus, reduced growth rates in the oceanic zone relative to those for turtles of the same size in the neritic zone may be an evolutionary explanation for why turtles leave the oceanic zone. Now it would be exciting to determine the "how" of this feedback system; research is needed to address this question.

We may also ask the reciprocal question of ontogenetic habitat shifts of why do hatchlings leave the neritic zone and enter the oceanic zone. This question is particularly interesting in light of the evidence that the Australian flatback turtle, *Natator depressus*, apparently does not have an oceanic stage (Walker and Parmenter 1990, Walker 1994). The tradeoff may be between increased food resources and increased predation risk in the neritic zone (see Walker 1994). For loggerheads, there must be strong selection for hatchlings to leave neritic waters, possibly to avoid increased predation risk which may be significantly lower in the open ocean.

The question of ontogenetic habitat shifts in the life history of sea turtles is fertile ground for speculation and research. A good place to pursue this question would be off Australian nesting beaches where there are flatback turtles that apparently stay in coastal waters and do not have an oceanic stage and where there are also loggerhead turtles that apparently do have an oceanic stage in the Pacific (*e.g.*, Queensland; Limpus 1995). Predation risks and food resources may be similar for both species, although the flatback hatchling is larger which may reduce its predation risk and/or facilitate exploitation of different food resources.

Anthropogenic Impacts on the Oceanic Stage

A major threat to the survival of loggerhead turtles during the oceanic stage is the risk of incidental capture in commercial fisheries. The bycatch of oceanic juveniles has been well documented for the high seas driftnet fishery (Wetherall *et al.* 1993). Incidental take of oceanic-stage loggerheads in the swordfish longline fisheries has recently received a lot of attention (Aguilar *et al.* 1995, Balazs and Pooley 1994, Bolten *et al.* 1994, 2000, Laurent *et al.* 1998).

The mean size CCL (+/- standard deviation) for loggerheads captured in the swordfish fishery in the Azores during an experiment conducted in 2000 was 49.8 +/- 6.2 cm CCL (n = 224; Figure 4-4, Bolten *et al.* unpublished data) which is significantly larger ($p < 0.001$, Kolmogorov-Smirnov Test, ks = 0.6528) than the baseline oceanic-stage population with a 34.5 +/-12.6 cm CCL (n = 1692, calculated from Bjorndal *et al.* 2000a). The largest size classes in the oceanic stage are the size classes impacted by the swordfish longline fishery (Figure 4-4). Earlier studies in Azorean waters documenting swordfish longline captures show similar size classes impacted by that fishery (Bolten *et al.* 1994, Ferreira *et al.* 2001). The demographic consequences relative to population recovery of the increased mortality of these size classes have been discussed (Crouse *et al.* 1987; see also Heppell *et al.* this volume and Chaloupka this volume).

Similar size classes are impacted by longline fisheries in other regions. In the western Mediterranean the mean size of loggerheads caught in drifting longline fisheries was 47.4 +/- 10.4 cm CCL (n = 62) and 45.9 +/- 7.5 cm CCL (n = 53) in the eastern Mediterranean (Laurent *et al.* 1998). Witzell (1999) reported a mean size of 55.9 +/- 6.5 cm CCL (n = 98) for loggerheads caught in the longline fishery from the western North Atlantic, primarily the Grand Banks, Newfoundland, Canada.

In the Pacific the mean size of loggerheads caught by longlines is 57.7 +/- 11.5 cm SCL (n = 163, Balazs and Parker unpublished data).

Results from satellite telemetry with satellite-linked time-depth recorders have demonstrated the potential negative impacts of longline hooking on dive behavior and movement patterns of oceanic juveniles. Following release, hooked turtles have a significantly reduced diving behavior (*e.g.*, shallower dive depths) and their movements appear to be influenced to a greater extent by ocean current movements – the turtles drift with the current (Riewald *et al.* unpublished data). Researchers in Hawaii report different results for movement patterns for longline hooked turtles (Polavino *et al.* 2000), but see the discussion above.

There are numerous fisheries that impact oceanic-stage loggerhead populations, and new ones continue to be developed. For example, the fishery for black scabbard (*Aphanopus carbo*) in Madeira has a significant bycatch of oceanic-stage loggerheads (Dellinger and Encarnacao 2000). This fishery is currently being developed in the Azores.

The open ocean is full of debris, and little loggerheads frequently ingest plastics, tar, styrofoam, and monofilament (Carr 1987b, Witherington in review b). This ingestion as well as entanglement is often lethal. The sublethal effects from marine debris ingestion may also have severe consequences but are difficult to quantify. Laboratory feeding trials have documented that post-hatchling loggerheads were not able to adjust their intakes to counter nutrient dilute diets similar to what turtles would experience when ingesting debris (McCauley and Bjorndal 1998). However, the authors suggest that with increasing size, turtles may be better able to adjust their intakes.

Conclusions – Where Do We Go from Here?

We have come a long way since “Rips, FADS, and Little Loggerheads” (Carr 1986), but we have only begun to unlock the “mystery of the lost year.” These are exciting times. Multidisciplinary approaches--with expertise in physical and biological oceanography, population genetics, statistical modeling, demography, and ecosystem analyses--are needed for the study of sea turtle biology, especially the study of the oceanic stage.

To develop more complete demographic and geographic models for oceanic-stage loggerhead sea turtles, we need to understand the relationships among the various populations within an ocean basin. For the Atlantic, we need to know the relationships between what we believe is the main oceanic stage population in the waters around the Azores and other populations on the Grand

Banks of Canada, in the Mediterranean, and along the west coast of Africa. Molecular genetic tools and more sophisticated statistical analyses of mixed stocks will be needed to help us answer these questions.

What is the fate of the little loggerheads that never become entrained in the main ocean currents? Are these “lost” in the evolutionary sense or do they have an entirely neritic development?

Developing methods for assessing population trends is another research area requiring high priority. Having spent many a day in the open ocean looking for little loggerheads, I can personally attest to the challenges of this goal. Population trends in this oceanic stage will allow us to predict trends in the nesting population 20 plus years ahead of time – maybe enough time to reverse/avert potential disasters!

Finally, quantifying the role of oceanic-stage loggerheads in their ecosystem(s) may be one of the most exciting directions for research. Collaborations with other disciplines will be necessary to understand these system processes. We have only begun to identify qualitatively the interactions of loggerheads with other species in the oceanic zone. For example, what are the prey and food items of loggerheads and what are the main predators of loggerheads? Quantifying these relationships is an important objective. Bjorndal (this volume) explores these interactions, but the data are sparse.

A number of ecosystem models are being developed for marine ecosystems. To incorporate oceanic-stage loggerheads into these models will require a better understanding of their trophic status and food web interactions. Simple gut content studies are needed as well as studies utilizing newer technologies (*e.g.*, stable isotope analyses) to evaluate the trophic status of oceanic stage loggerheads.

Acknowledgements

I have been extraordinarily fortunate to have had the opportunity to pursue the “mystery of the lost year.” Archie Carr stimulated my interest in this question and my collaboration with Karen Bjorndal made it happen. To Karen I will always be indebted for the development of ideas, companionship in the field and support during those frustrating times trying to solve a “mystery”. Our work in the Azores has given me the opportunity to develop a lasting friendship with Helen Martins, without whom this work would never have been accomplished. In addition, work in the Azores would not have been possible without the collaboration of my many friends and colleagues in “equipa tartaruga” and the collegiality of all of the faculty, staff, and students of the Department of

Oceanography and Fisheries, University of the Azores, Horta. In 1990 a collaboration developed with Joseph Franck and Greet Wouters from the M/V Shanghai that began an important working relationship with the sport fishing industry in Horta. I have benefited from the collaborations with Brian Riewald, who was developing a model of oceanic-stage movements and distribution patterns.

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Dedication

This chapter is dedicated to the memory of Brian Riewald (1972 – 2001), a brilliant student and great colleague. Brian was making significant contributions to our understanding of the distribution and movements of little loggerheads in the open ocean. Brian is greatly missed.

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Table 4-1. Locations of recaptured loggerheads. CCL 1 and 2 refer to curved carapace length at initial capture and recapture, respectively. Turtles are listed in order by initial capture date.

Tag Number[a]	**Capture location**	**Recapture location**	**Capture date DD-MM-YY**	**Recapture date DD-MM-YY**	**CCL 1 (cm)**	**CCL 2 (cm)**
A. Turtles initially captured and recaptured in the oceanic zone in the waters around the Azores						
BP701	Azores	Azores	12-06-89	27-08-89	45.8	--
BP624	Azores	Azores	15-06-89	21-09-91	41.0	52.0
A3913	Azores	Azores	20-07-90	16-11-90	52	52.5
BP683	Azores	Azores	28-08-91	21-12-94	60.4	70.9
BP2764	Azores	Azores	30-01-93	15-07-94	69.1	--
BP2774	Azores	Azores	06-08-93	04-08-95	53.5	--
A6001	Azores	Azores	08-07-94	12-08-96	35	--
N8082	Azores	Azores	30-06-97	28-08-97	53	--
BP3092	Azores	Azores	22-09-97	07-10-97	48.1	--

B. Turtles initially captured in the oceanic zone and recaptured in a different geographic location						
K5583[b]	Azores	Sicily	14-07-86	26-08-91	19.3	42.0
K5781[c]	Canaries	Cuba	13-06-87	14-11-87	--	--
BP2267[d]	Madeira	Canaries	29-06-90	04-02-93	40.5	49.8
AW3803	Mediter	FL – USA	28-07-90	15-05-94	--	--
A7951	Azores	NC – USA	14-05-91	17-11-95	45.0	74.0
A8006	Azores	Nicaragua	15-06-91	23-01-00[e]	56	--
A7710	Azores	Cuba	18-06-91	26-02-94	46	--
BP2151	Azores	Nicaragua	11-07-91	13-12-96[e]	50.5	--
A4821	Azores	NC – USA	10-05-92	23-06-96	28.0	48.0
A4837	Azores	Spain	30-06-92	15-11-95	26.0	42.0
N7869	Azores	Morocco	26-06-96	28-07-00	23	--
N5921	Azores	FL - USA	08-08-96	06-19-98	64.0	69.6

[a] The following institutions and individuals assisted with tag return information: Archie Carr Center for Sea Turtle Research, University of Florida, USA (K. Bjorndal, P. Eliazar); Azorean commercial fishing fleets; Centro Oceanografico de Canarias, Spain (C. Santana); Centro Oceanografico de Malaga, Spain (J. Caminas); Donana National Park, Spain; Fernandina Beach, Florida (stranding network); Fort Macon State Park, North Carolina, USA (R. Neuman); Greenpeace (Mediterranean Program); Instituto Espanol de Oceanografia, La Coruna, Spain (J. Mejuto); International Fund for Animal Welfare ("Song of the Whale", J. Gordon); Miskito Indians, Nicaragua; US National Marine Fisheries Service, Beaufort, North Carolina, USA (J. Braun, S. Epperly); University of the Azores, Department of Oceanography and Fisheries, Horta, Portugal (H. Martins, C. Leal); University of Central Florida Turtle Research Group (L. Ehrhart, D. Bagley); WWF, Progetto Tartarughe, Roma, Italy (M. Cocco, G. Gerosa); K. Abdelkhalek; J. and G. Franck ("Shanghai"); S. Forman ("Cajun Girls"); C. Lagueux (Caribbean Conservation Corporation); L. Steiner; and S. Viallelle.

[b] Bolten *et al.* 1992a.
[c] Bolten *et al.* 1992b.
[d] Bjorndal *et al.* 1994
[e] Exact recapture date is not known; these are the last possible dates

Figure Legends

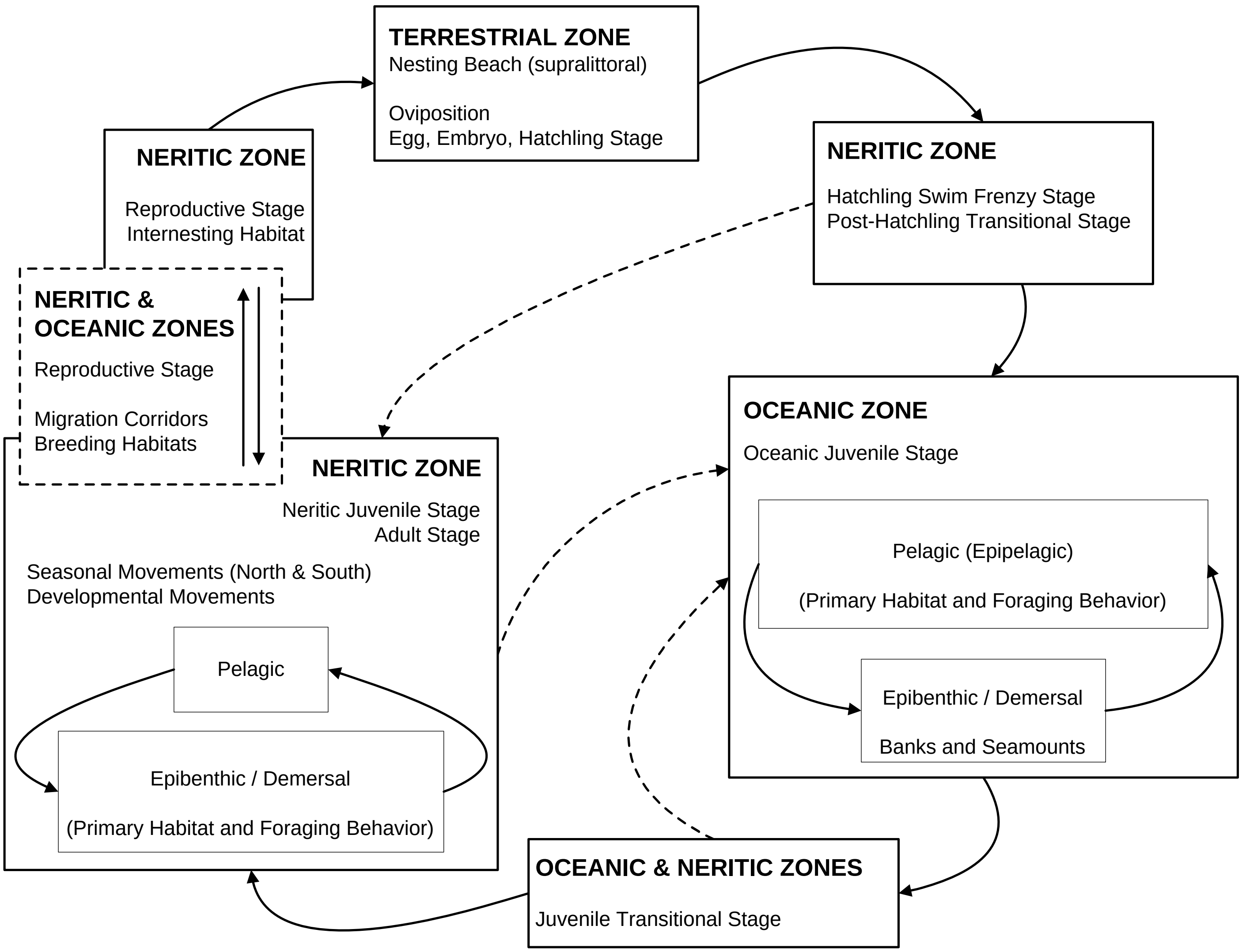
Figure 4-1: Life cycle diagram of the Atlantic loggerhead sea turtle. Boxes represent life stages and the corresponding ecosystems. Solid lines represent movements between life stages and ecosystems; dotted lines are speculative.

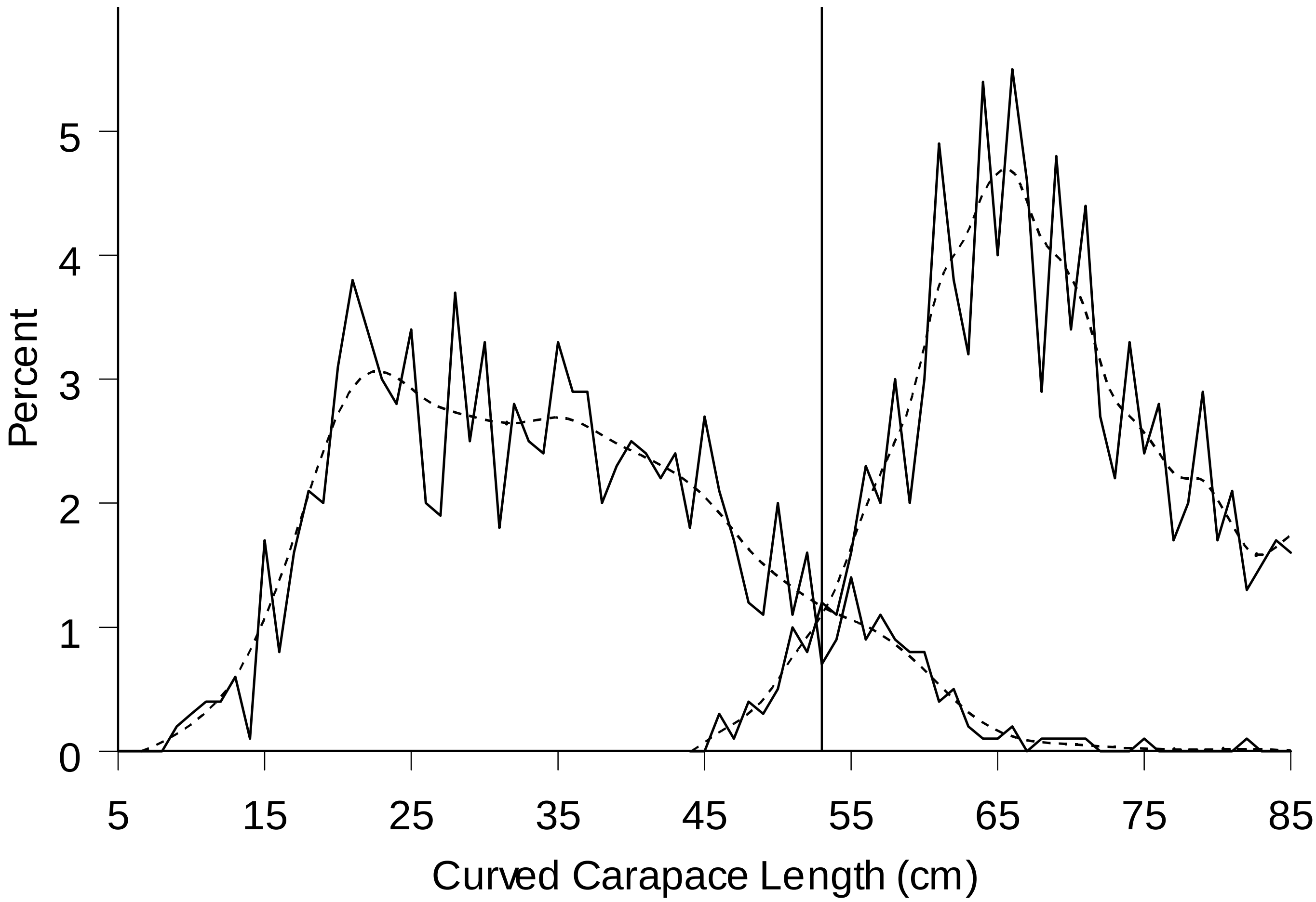
Figure 4-2: Size-frequency distributions of oceanic-stage loggerheads captured in waters around the Azores (left-hand curves, n = 1692) and neritic-stage loggerheads stranded in southeastern USA (right-hand curves, n = 1803) (modified from Bjorndal *et al.* 2000a, 2001). Percentages were calculated for each population. Dashed lines are the cubic smoothing splines (df = 15); vertical reference line at the intersection of the two smooths at 53 cm CCL.

Figure 4-3: Size-specific growth functions of oceanic-stage (solid circles) and neritic-stage loggerheads (open boxes) based on length-frequency analyses (data from Bjorndal *et al.* 2000a, 2001). Dashed line is an extrapolation of the growth function for the oceanic-stage loggerheads. The slopes of the lines are significantly different ($p < 0.001$).

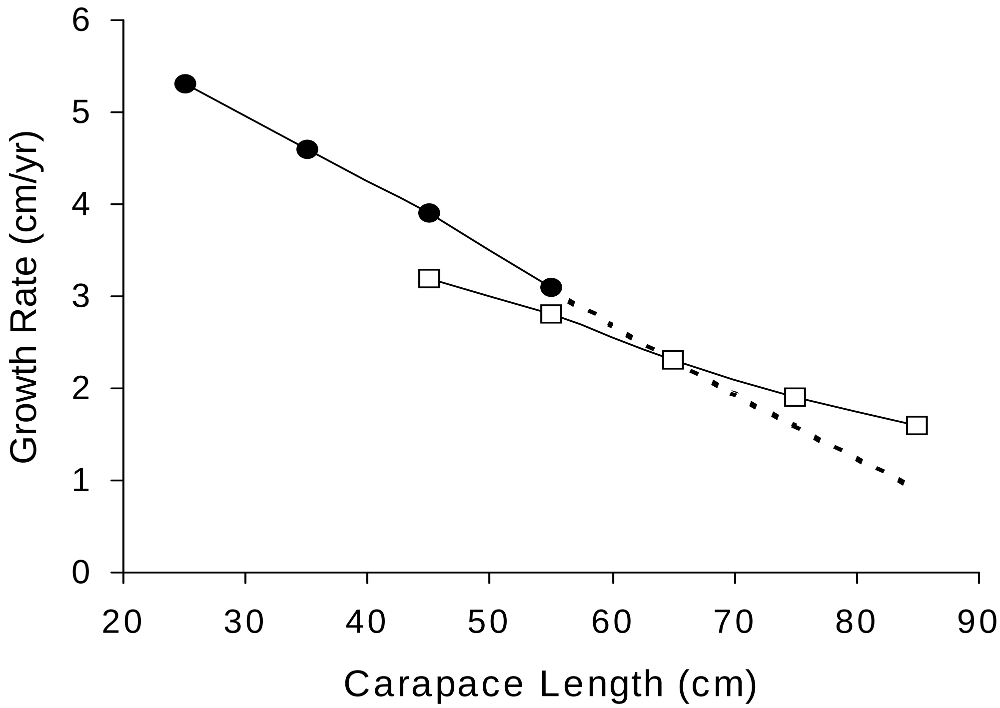
Figure 4-4: Size frequency distribution of oceanic-stage loggerheads (hatched bars; mean CCL 34.5 +/- 12.6 cm, n = 1692;

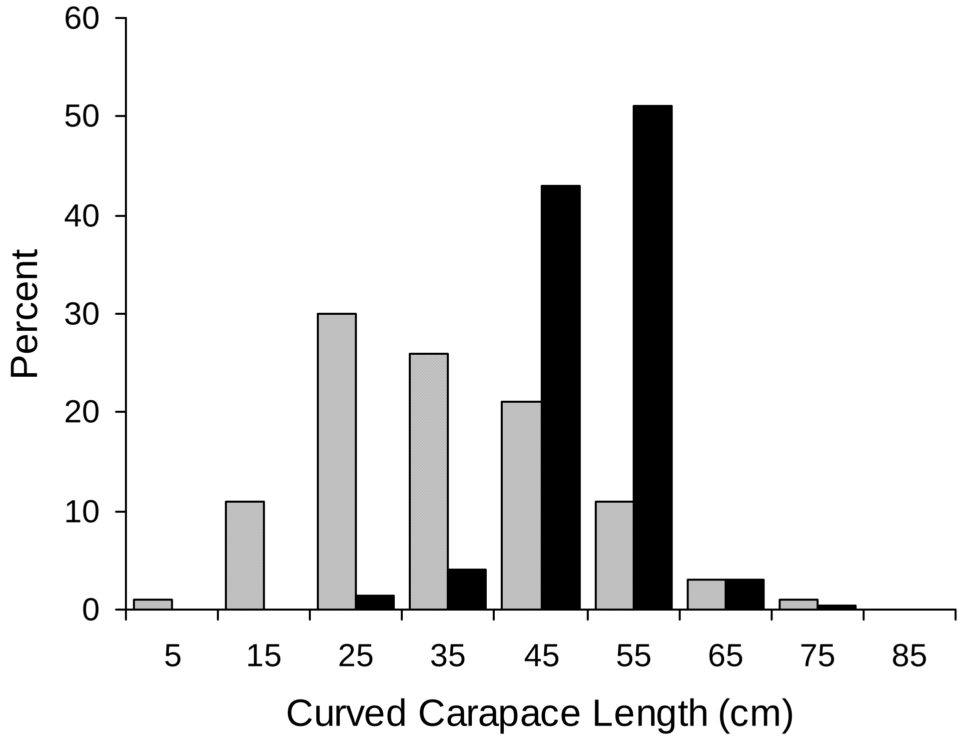
from Bjorndal *et al.* 2000a) and loggerheads caught in a swordfish longline fishery in the waters around the Azores July – December 2000 (solid bars; mean CCL 49.8 +/- 6.2 cm, n = 224; Bolten *et al.* unpublished data). The size distribution of the longline captures is significantly larger ($p < 0.001$, Kolmogorov-Smirnov Test, ks = 0.6528) than the baseline oceanic-stage population.


TERRESTRIAL ZONE
Nesting Beach (supralittoral)
Oviposition
Egg, Embryo, Hatchling Stage
NERITIC ZONE
Hatchling Swim Frenzy Stage
Post-Hatchling Transitional Stage
NERITIC ZONE
Reproductive Stage
Internesting Habitat
NERITIC & OCEANIC ZONES
Reproductive Stage
Migration Corridors
Breeding Habitats
NERITIC ZONE
Neritic Juvenile Stage
Adult Stage
Seasonal Movements (North & South)
Developmental Movements
Pelagic
Epibenthic / Demersal
(Primary Habitat and Foraging Behavior)
OCEANIC ZONE
Oceanic Juvenile Stage
Pelagic (Epipelagic)
(Primary Habitat and Foraging Behavior)
Epibenthic / Demersal
Banks and Seamounts
OCEANIC & NERITIC ZONES
Juvenile Transitional Stage



Percent
0
1
2
3
4
5
5
15
25
35
45
55
65
75
85
Curved Carapace Length (cm)


Growth Rate (cm/yr)
0
1
2
3
4
5
6
20
30
40
50
60
70
80
90
Carapace Length (cm)


60
50
40
30
20
10
0
Percent
5
15
25
35
45
55
65
75
85
Curved Carapace Length (cm)