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CHAPTER 9

Variation in Sea Turtle Life History Patterns: Neritic versus Oceanic Developmental Stages

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9.1 INTRODUCTION

Sea turtles are slow growing and long-lived. Their complex life history patterns encompass a diversity of ecosystems from terrestrial habitats where oviposition and embryonic development occur to developmental and foraging habitats in coastal waters (neritic zone) as well as in the open ocean (oceanic zone). Of all the sea turtle life stages, the biology of post-hatchling and early juvenile stages is the least understood (i.e., the “mystery of the lost year,” [Carr 1986; Bolten and Balazs 1995]). For most sea turtle species, not even the location or duration of the early juvenile stage is known. Except for the loggerhead (*Caretta caretta*), little progress has been made in our understanding of the early juvenile stage beyond what was summarized in Musick and Limpus (1997) and Bjorndal (1997). Recent studies on the early life stages of the loggerhead sea turtle have improved our knowledge of the biology of the oceanic juvenile stage (for a review, see Bolten, in press; Bjorndal et al. 2000a, in review).

In this chapter, I identify three generalized sea turtle life history patterns and evaluate these patterns with respect to phylogenetic relationships and reproductive traits. Characteristics of the developmental stages (oceanic vs. neritic) and adult foraging stage (oceanic vs. neritic) are the primary differences that distinguish the three patterns. These variations are reviewed, the consequences of oceanic vs. neritic developmental stages are discussed, and finally, I speculate on how these differences may have evolved. The dramatic decline in sea turtle populations and the extensive degradation of their ecosystems make it difficult to determine the functional roles of sea turtles in their ecosystems (see Bjorndal and Jackson, this volume), and, therefore, difficult to evaluate the selective factors that led to the present day sea turtle life history patterns. It is particularly difficult, in the context of massive faunal declines and food web alterations, to speculate on the relative importance of the evolutionary pressures from competition for resources and predation that may have resulted in these observed life history patterns.

9.2 TERMINOLOGY

There has been inconsistency in the terminology used to describe the life histories of sea turtles, for both the oceanographic terms and the developmental stages (Bolten, in press). To be consistent with standard oceanographic terminology, the following terminology should be used (see Lalli and Parsons [1993] for review):

- The neritic zone describes the inshore marine environment (from the surface to the sea floor) where water 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 water depths are less than 200 m.

- The oceanic zone is the vast open ocean environment (from the surface to the sea floor) where water depths are greater than 200 m.
- Organisms are pelagic if they occupy the water column, but not the sea floor, 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 sea floor in either the neritic zone or oceanic zone are described as benthic or demersal.

Organisms can therefore be pelagic in shallow neritic waters or in the deep oceanic waters. Similarly, organisms can be benthic in shallow neritic waters as well as in the deep ocean. We should describe sea turtle life stages by the oceanic realm that they inhabit. Therefore, the early juvenile stage found in the open ocean should be described as the oceanic stage, not the pelagic stage, and the juvenile stage found in coastal waters as the neritic stage, not the benthic stage.

9.3 SEA TURTLE LIFE HISTORY PATTERNS

Although there are only seven extant species, sea turtles exhibit a surprising diversity of life history traits that make them good subjects for comparative life history studies. Aspects of this diversity are illustrated by reproductive extremes from arribadas to solitary nesting, dietary specializations from seagrasses to sponges to jelly organisms, and metabolic adaptations from hibernation to endothermy (*sensu lato*). Despite this high diversity in life history traits among sea turtle species, there have been few comparative analyses or syntheses of their life history patterns. Hendrickson (1980) was the first to attempt to summarize the ecological strategies of sea turtles. However, his conclusions were limited by the lack of information at the time of his synthesis in both life history characteristics of the different sea turtle species and their taxonomic relationships, which are now better understood through molecular techniques. In another analysis, Van Buskirk and Crowder (1994) developed a dendrogram to compare the reproductive characteristics among the seven species. In this chapter I will focus on an analysis of the variation in the juvenile developmental stages.

Once hatchlings emerge from their nests, crawl down the beach, and enter the sea, post-hatchlings embark upon 1 of 3 basic developmental life history patterns:

- complete development in the neritic zone (Type 1, Figure 9.1, top panel),
- early juvenile development in the oceanic zone and later juvenile development in the neritic zone (Type 2, Figure 9.1, middle panel), or
- complete development in the oceanic zone (Type 3, Figure 9.1, bottom panel).

9.3.1 Type 1: The Neritic Developmental Pattern

The Type 1 life history pattern is characterized by developmental and adult stages occurring completely in the neritic zone (Figure 9.1, top panel). The Australian flatback turtle (*Natator depressus*) apparently has a completely neritic developmental pattern (Walker and Parmenter 1990; Walker 1994) and is the only extant example of the Type 1 life history pattern. Walker (1994) suggests there may be increased food resources in the neritic zone but with a tradeoff of increased predation. Flatback hatchlings are larger than those of other cheloniid sea turtles (60 mm vs. 41-50 mm carapace length [Van Buskirk and Crowder 1994]; 39 g vs. 15-25 g hatchling mass [Miller 1997]). As would be expected from the evolutionary tradeoff between the size and number of offspring, clutch size is smaller in flatbacks (53 vs. 100-182 [Hirth 1980; Van Buskirk and Crowder 1994] although East Pacific green turtles [*Chelonia* *mydas*] have small clutch sizes from 65 to 90 [Hirth 1997]). Flatbacks thus produce fewer, larger progeny, a pattern typical of marine species with shorter dispersal distances relative to species that disperse more widely, such as Type 2 and 3 sea turtles. Researchers have speculated that the larger hatchling size of flatback turtles may reduce predation in the neritic zone (Hirth 1980; Walker and Parmenter 1990; Walker 1994; Musick and Limpus 1997). However, the size difference between flatback turtles and those species exhibiting Type 2 or 3 patterns does not seem to be great enough to make a significant difference with respect to marine predators. The larger hatchling size of the flatback may be a response to terrestrial predators and the need to survive the predator gauntlet from the nest to the water. The larger size of flatback hatchlings allows them to escape some bird and crab predators on Australian beaches that prey upon green turtle (*Chelonia mydas*) and loggerhead hatchlings (Limpus 1971). The fact that other sea turtle species have not also responded to terrestrial predators by increasing hatchling body size suggests that our understanding of the selective pressures leading to the increased size of flatback hatchlings is still not fully understood. Knowledge of the selective advantages of large hatchling size may be critical for understanding the success of the Type 1 life history pattern.

The early juvenile stage of Type 1 species (including post-hatchlings) probably feeds on the surface and within the water column and may later develop a benthic feeding strategy once they have gained buoyancy control and can dive to the sea floor. In the shallow waters that Type 1 species inhabit, their foraging behavior may be a mix of pelagic and benthic feeding throughout life. Support for this mixed foraging strategy is seen in the diet of both small and large flatback turtles (Limpus et al. 1988; Zangerl et al. 1988). However, the number of samples that have been evaluated are too small to be conclusive; more studies on the diet of flatbacks are needed.

9.3.2 Type 2: The Oceanic - Neritic Developmental Pattern

The Type 2 life history pattern is characterized by early development in the oceanic zone followed by later development in the neritic zone (Figure 9.1, middle panel). The best known example of this life history pattern is that of the loggerhead turtle (for review see Bolten, in press). Use of genetic markers has confirmed the relationships between oceanic foraging grounds and rookeries (Bowen et al. 1995; Bolten et al. 1998) that had been hypothesized based on length-frequency distributions (Carr 1986; Bolten et al. 1993) and tag returns (Bolten, in press). Although based on rather few data (summarized in Carr 1987a), this life history pattern is thought to be the pattern for the green turtle, hawksbill (*Eretmochelys imbricata*), and Kemp's ridley (*Lepidochelys kempi* [Collard and Ogren 1990]). Little is known about the ecology of juvenile olive ridleys (*Lepidochelys olivacea*); differences among populations from different ocean basins suggest that this species exhibits either a Type 2 or a Type 3 life history pattern, perhaps in response to differences in resource availability. In the West Atlantic (Pritchard 1976; Reichart 1993; Bolten and Bjorndal, unpublished data) and Australia (Harris 1994), olive ridleys appear to exhibit a Type 2 life history pattern, whereas East Pacific populations (Pitman 1990) appear to exhibit a Type 3 life history pattern.

Following the hatchling swim frenzy stage (Wyneken and Salmon 1992), loggerheads have a transition period when the post-hatchling begins to feed and moves from the neritic zone into the oceanic zone (Bolten, in press). The duration, movements, and distribution of the post-hatchlings during this transition have been reviewed by Witherington (2002, in review a). This transition is relatively passive in that oceanographic and meteorological factors (e.g., currents, winds) have the greatest influence on the movements and distribution patterns of these turtles, although the post-hatchlings may actively position themselves using magnetic orientation cues to maximize the likelihood of successful transport (Lohmann and Lohmann, in press). After a developmental period in the oceanic zone lasting from 7 to 11.5 years, when the turtles reach a size of 46 to 64 cm curved carapace length (Bjorndal et al. 2000a; Bjorndal et al., in review), juvenile loggerheads in the Atlantic leave the oceanic zone and complete their development in the neritic zone (Musick and Limpus 1997; Bjorndal et al. 2001; Bolten, in press).

Other Type 2 species recruit to neritic habitats at smaller sizes. Green turtles and hawksbills appear in neritic foraging grounds at about 20-35 cm carapace length (CL) and Kemp’s ridleys at 20-25 cm CL (Bjorndal 1997; Musick and Limpus 1997). Based on size at recruitment to neritic habitats, the durations of the oceanic stages in these species may be shorter than that of Atlantic loggerheads. Size at recruitment is apparently not a function of size at maturity. Adult size of loggerheads falls between those of Kemp’s ridleys and green turtles (Miller 1997).

Recruitment from the oceanic, where the turtles are primarily epipelagic, to the neritic, where they are primarily benthic, may involve another transition period before the juvenile turtles become fully neritic (Kamezaki and Matsui 1997; Laurent et al. 1998; Bolten, in press; Tiwari et al., in press). Adults of Type 2 species may leave neritic habitats during their reproductive migrations, which may involve oceanic migration corridors between the adult foraging areas (neritic) and internesting habitat (also neritic). Figure 9.2 presents the details of the loggerhead life history from the North Atlantic.

9.3.3 Type 3: The Oceanic Developmental Pattern

The Type 3 life history pattern is characterized by both developmental and adult stages occurring completely in the oceanic zone (Figure 9.1, bottom panel). Of course, post-hatchlings, once they leave the nesting beach, must traverse the neritic zone to reach the oceanic zone, and adults must return to the neritic zone for reproduction. The leatherback (*Dermochelys coriacea*) and olive ridley (East Pacific populations) are the two species that are believed to exhibit this life history pattern. Very little is known about the biology (e.g., oceanic distribution, diet, growth rates) of early developmental stages for olive ridleys and leatherbacks, but it is assumed that the juvenile stages occur in the oceanic zone.

Leatherbacks and olive ridleys are very different in many aspects, such as body size, thermal regulation, and foraging behavior. The leatherback is the largest sea turtle species with a mean adult size of 149 cm CL, whereas the olive ridley is one of the smallest species with a mean adult CL of 66 cm (Van Buskirk and Crowder 1994). Leatherbacks are able to maintain a body temperature 15°C above ambient and forage in waters with temperatures as low as 0-15°C (Spotila et al. 1997). The olive ridley maintains a body temperature at most a few degrees above ambient (Spotila et al. 1997) and appears to be limited to warmer, tropical waters (Pitman 1990, 1993; Polovina et al., in review). Leatherbacks are active predators and may not undergo a substantial diet shift as they grow because the ability to capture and consume gelatinous prey species is not size dependent (Bjorndal 1997). Olive ridleys apparently spend more time at the surface than leatherbacks (Pitman 1993) and may exhibit a “float and wait” foraging strategy, although Polovina et al. (in review) report that olive ridleys only spend 20% of their time on the surface and 40% of their time diving deeper than 40 m.

9.4 RELATIONSHIPS OF THE THREE LIFE HISTORY PATTERNS TO PHYLOGENIC PATTERNS AND REPRODUCTIVE TRAITS

9.4.1 Phylogenetic Patterns

A comparison of the life history patterns (Type 1, 2, or 3) of the seven species of extant sea turtles with their phylogenetic patterns are presented in Figure 9.3, left dendrogram (Bowen and Karl 1997). Sea turtles are generally recognized as a monophyletic group (Bowen and Karl 1997). The ancestor of sea turtles was probably a resident of coastal salt marshes, estuaries, and tidal creeks. Once these ancestors committed fully to the sea, a completely neritic developmental and adult life history (Type 1) would be the expected pattern because they would probably have stayed close to shore. The Type 1 pattern observed in the Australian flatback is secondarily derived based on the phylogenetic position of the flatback (Figure 9.3, left dendrogram). A change to the Type 2 pattern may have resulted from selective pressures to exploit new food resources with fewer competitors in the oceanic zone or to avoid the higher predation risks in the neritic zone.

A change from the Type 2 to Type 3 pattern would be a natural outgrowth of the Type 2 pattern. Once the transition has been made for early development to occur in the oceanic zone, it would be reasonable to continue development in that habitat. The phylogenetic pattern suggests that the olive ridley (Lo in Figure 9.3) has recently derived the Type 3 pattern from the Type 2 pattern. The hypothesis that the Type 3 pattern in olive ridleys is recent is supported by both Type 2 (West Atlantic, Australia) and Type 3 (East Pacific) life history patterns being expressed in this species. In contrast, the phylogenetic pattern suggests that the leatherback (Dc in Figure 9.3) has probably exhibited the Type 3 pattern for a long time with resultant physiological adaptations that have allowed leatherbacks to exploit both tropical and temperate oceanic realms.

9.4.2 Reproductive Traits

Van Buskirk and Crowder (1994) evaluated a number of reproductive traits (e.g., female size, clutch size, egg volume, hatchling size, clutch frequency, and remigration interval) and developed a dendrogram illustrating the relationships among the species (Figure 9.3, right dendrogram). The Van Buskirk and Crowder (1994) dendrogram is not congruent with the phylogeny of Bowen and Karl (1997) but has a greater similarity to the 3 life history patterns presented in Figure 9.1. This better fit would be expected between life history patterns (Figure 9.3, center) and reproductive behavior and demographic traits (Figure 9.3, right dendrogram). The two species with the greatest difference in reproductive traits (leatherbacks and flatbacks) are also the two species with the greatest difference in life history patterns.

9.5 A CLOSER LOOK AT THE TYPE 2 PATTERN – ONTOGENETIC HABITAT SHIFTS

Species exhibiting either the Type 1 or Type 3 pattern commit to either the neritic or oceanic zone, respectively, for their entire developmental stages as well as for the adult foraging stage. Only turtles with the Type 2 pattern have a major habitat change during their development. The Type 2 pattern is the most successful pattern if success is defined by the number of species with this life history pattern (5 of the 7 extant species exhibit the Type 2 pattern). As presented above in section 9.4.1, the Type 1 pattern is hypothesized to be the ancestral pattern that still exists today (although presumably secondarily derived) in the Australian flatback. Why post-hatchling turtles leave the neritic zone for the oceanic, and why, after an extended development period in the oceanic zone, the turtles return to the neritic to complete their development, are two intriguing questions.

The existence of an early developmental stage in the oceanic habitat may be a result of higher predator pressure in neritic habitats and/or intra- and interspecific competition for food in neritic habitats. Such competition may not be apparent now because of depleted sea turtle populations, but evidence for density-dependent effects on growth rates has been reported for a population of green turtles in a neritic foraging habitat (Bjorndal et al. 2000b).

Even more puzzling is the shift from oceanic to neritic habitats. Why do juvenile turtles leave the oceanic zone where they have spent the first years of their lives successfully finding food, growing, and surviving? When they leave the oceanic zone for the neritic zone, they enter a new habitat with which they are unfamiliar, and must learn to find new food sources and avoid a new suite of predators. A current hypothesis to explain why ontogenetic habitat shifts occur is that a species shifts habitats to maximize growth rates (Werner and Gilliam 1984). Bolten (in press) presents evidence for the Atlantic loggerhead population that supports the Werner and Gilliam hypothesis. The extrapolation of the size-specific growth function for the oceanic stage intersects the size-specific growth function for the neritic stage (Figure 9.4). Therefore, for a given carapace length greater than approximately 64 cm (a size by which almost all of the loggerheads have left the oceanic zone [Bjorndal et al. 2000a]), growth rates will be greater in the neritic zone than in the oceanic zone. Snover et al. (2000) present data from a skeletochronology study that also demonstrate increased growth rates of turtles that have left the oceanic zone and entered the neritic zone.

There is substantial variation among the species that have the Type 2 pattern, suggesting a fair amount of variation in lifestyles. Morphological differences in oceanic-stage turtles include variation in countershading (suggesting different predator avoidance behaviors) and front flipper length relative to body length (suggesting differences in swimming activity and resulting feeding behavior). The swimming behavior of post-hatchling green turtles appears to be different than that of loggerheads (Wyneken 1997). Another source of variation is the duration of the oceanic developmental stage that may be significantly different for the different species based on the size at which they recruit to neritic habitats (see section 9.3.2). In addition, resource partitioning along temperature gradients and among foraging strategies probably occurs among Type 2 species, but data are lacking. For example, loggerheads (Type 2 species) and olive ridleys (Type 3 species) apparently partition resources in the Pacific by water temperature; loggerheads inhabit cooler waters than do olive ridleys (Pitman 1993; Polovina et al., in review). Thus, as more is learned about this life stage, further divisions in the Type 2 pattern may be required.

9.6 ANTHROPOGENIC IMPACTS ON THE EARLY JUVENILE STAGE

The future is bleak. Early juvenile-stage sea turtles face a myriad of obstacles irrespective of whether they are in the neritic or oceanic zones. Directed take of very small turtles for food is not common. However, directed take for the souvenir trade in polished shells or whole stuffed turtles, such as the once-popular but now illegal tourist trade in Madeira, Portugal (Brongersma 1982), still exists in some regions.

Indirect take in fisheries, whether it is the high seas drift nets, longlines, or coastal trawlers, is a very serious problem for juvenile turtles (National Research Council 1990; Wetherall et al. 1993; Balazs and Pooley 1994; Witzell 1999; Bolten et al. 2000). Throughout the world's oceans, the size distribution of loggerhead turtles caught in longline fisheries is the largest size class for the oceanic development stage (Bolten et al. 1994; Ferreira et al. 2001; Bolten, in press), which has significant demographic consequences (Crouse et al. 1987; Heppell et al., in press).

The lethal and sub-lethal effects of debris ingestion and entanglement are also major concerns (Balazs 1985; Carr 1987b; McCauley and Bjorndal 1999; Witherington, in review b). Habitat loss, particularly in coastal areas, has been documented; habitat degradation in the oceanic zone is more difficult to document but nonetheless acute when the effects of pollution are considered (Lutcavage et al. 1997). Both oceanic and neritic ecosystems are changing as a result of overfishing and pollution. Changes to the suite of species interactions and food webs in these ecosystems are undoubtedly having a major negative impact on sea turtles.

9.7 CONCLUSIONS – RESEARCH DIRECTIONS

Our ability to solve the "mystery of the lost year" for those species for which the early juvenile stages remain unknown has been improved by the development of new research tools.

Biotechnology is providing molecular tags to identify populations and track movements; biotelemetry is allowing researchers to evaluate movement and distribution patterns. Stable isotopes may provide clues where to look for early juvenile stages and also provide information on their trophic relationships. For researchers to make rapid progress in the study of early juvenile stages, multidisciplinary teams should be developed with expertise in the fields of physical and biological oceanography, population genetics, statistical modeling, demography, nutrition, and ecosystem analyses.

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Figure Legends

Figure 9.1: Three distinct sea turtle life history patterns illustrating the sequence of ecosystems inhabited. See text for a description of each type.

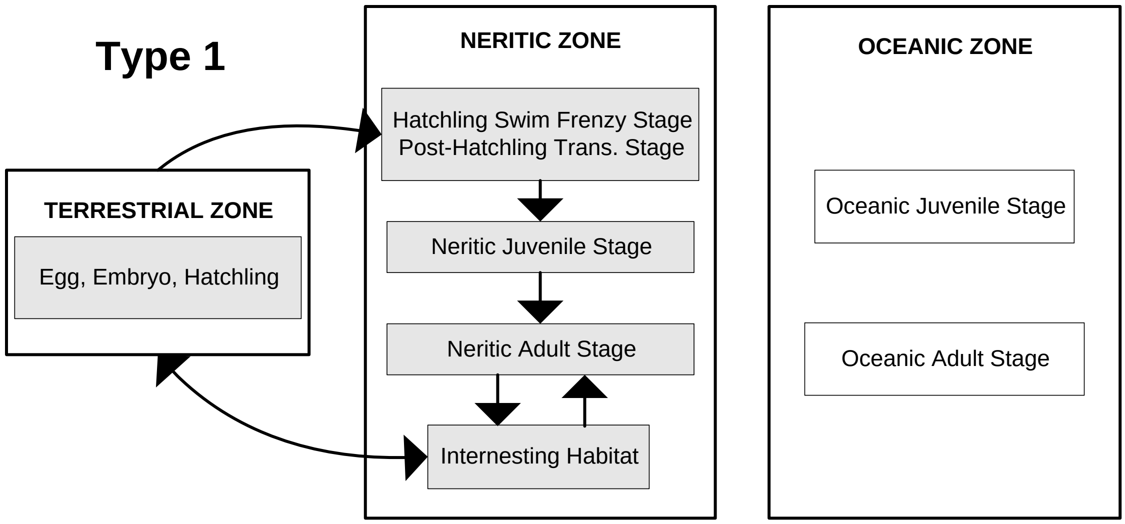
Figure 9.2: Life history diagram (modified from Bolten, in press) of the Atlantic loggerhead sea turtle. Boxes represent life stages and the corresponding ecosystems. Solid lines represent movements between life stages and ecosystems; dotted lines are speculative.

Figure 9.3: The relationships of the three types of life history patterns (see Figure 9.1) with a phylogeny based on mtDNA (left dendrogram of figure; modified from Bowen and Karl 1997) and a dendrogram of reproductive traits (right side of figure, modified from Van Buskirk and Crowder 1994). The branching of the phylogenetic and reproductive trait dendrograms are not to scale. The triangle indicates the Type 1 life history pattern, the circles indicate those species

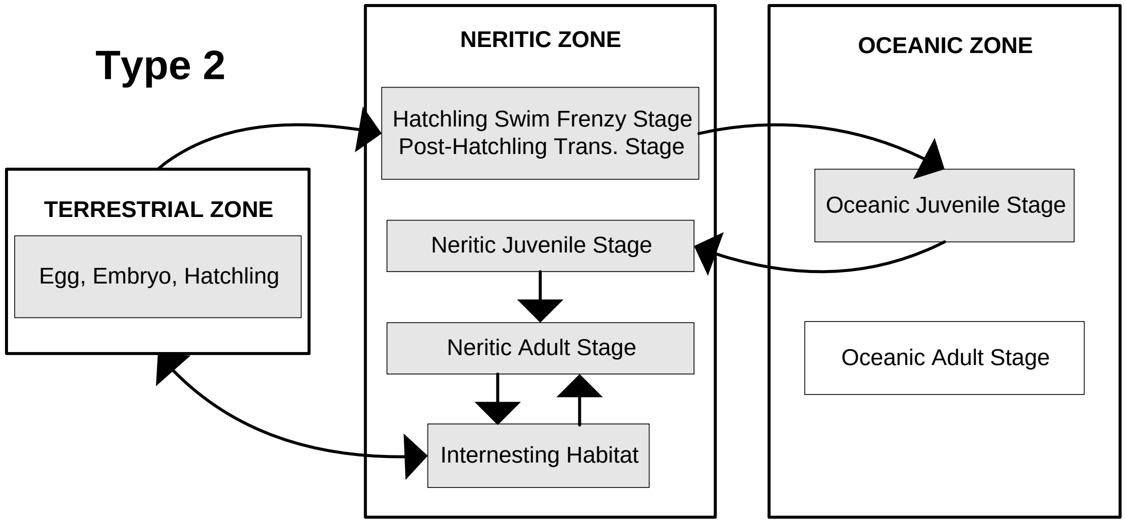
exhibiting the Type 2 pattern, and the squares indicate those species exhibiting the Type 3 pattern. The olive ridley (Lo) is diagrammed with both a circle (Type 2) to represent West Atlantic and Australian populations and a square (Type 3) to represent East Pacific populations (see text for discussion). Cc = *Caretta caretta*, Cm = *Chelonia mydas*, Dc = *Dermochelys coriacea*, Ei = *Eretmochelys imbricata*, Lk = *Lepidochelys kempi*, Lo = *Lepidochelys olivacea*, and Nd = *Natator depressus*.

Figure 9.4: Size-specific growth functions of oceanic-stage (solid circles) and neritic-stage (open boxes) loggerheads based on length-frequency analyses (data from Bjorndal et al. 2000a, 2001). Dashed line is an extrapolation of the growth function for oceanic-stage loggerheads. The slopes of the lines are significantly different ($p < 0.001$). Modified from Bolten (in press).

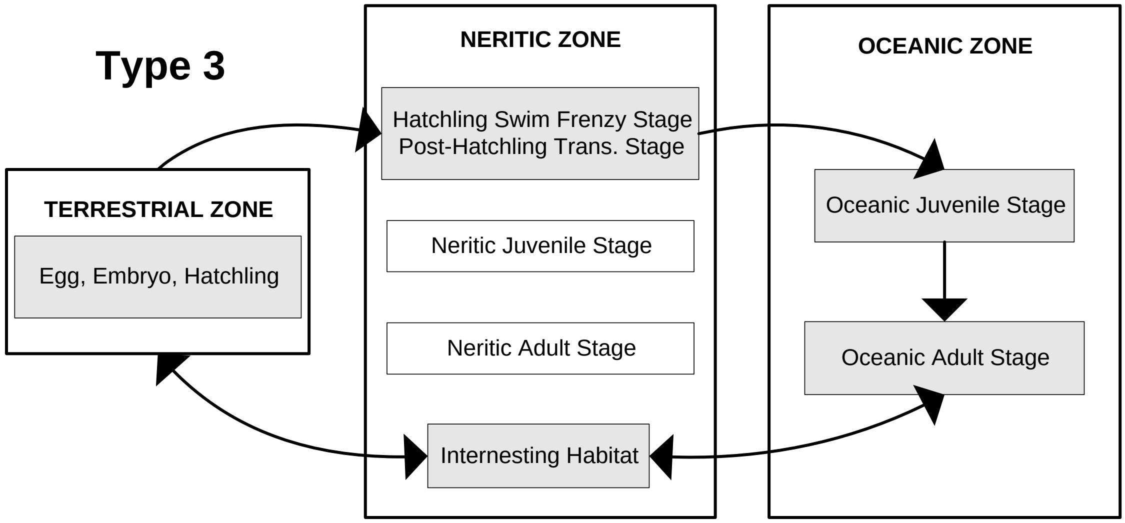
Type 1

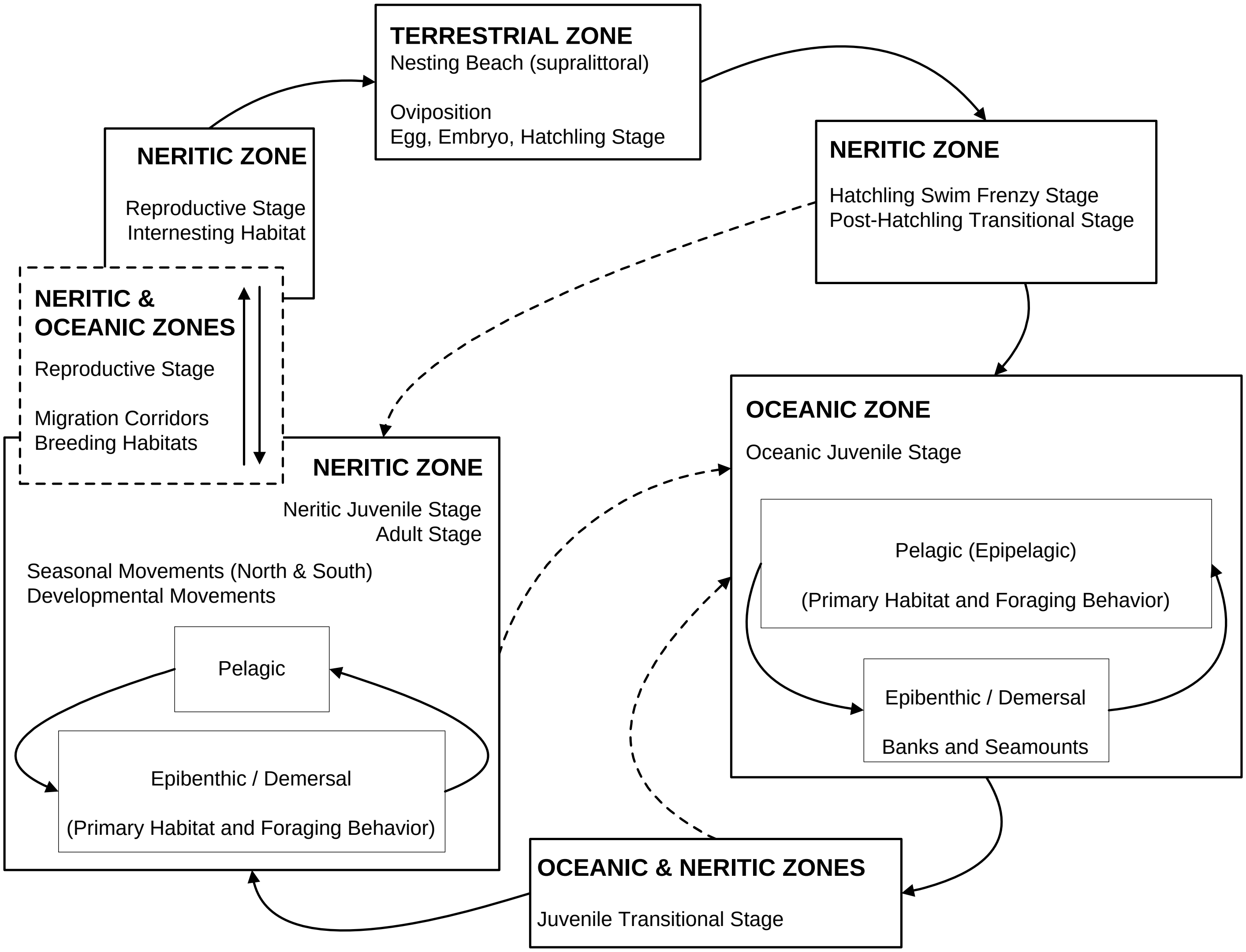


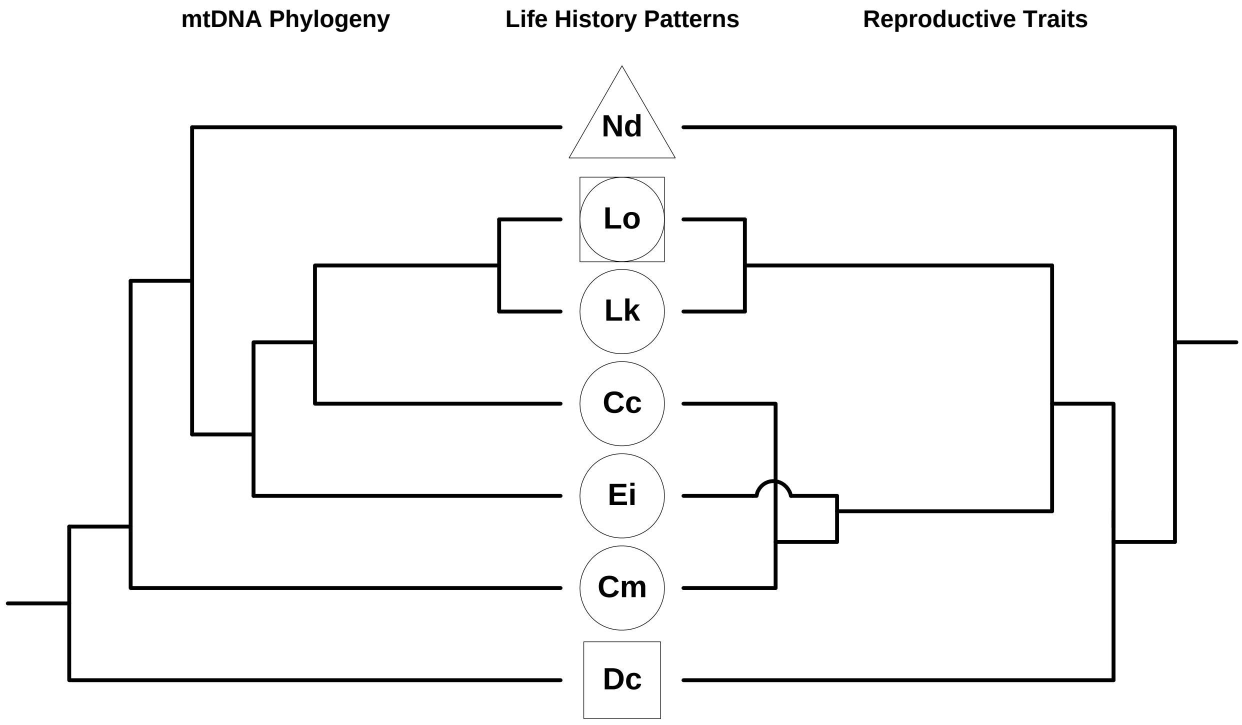
Type 2

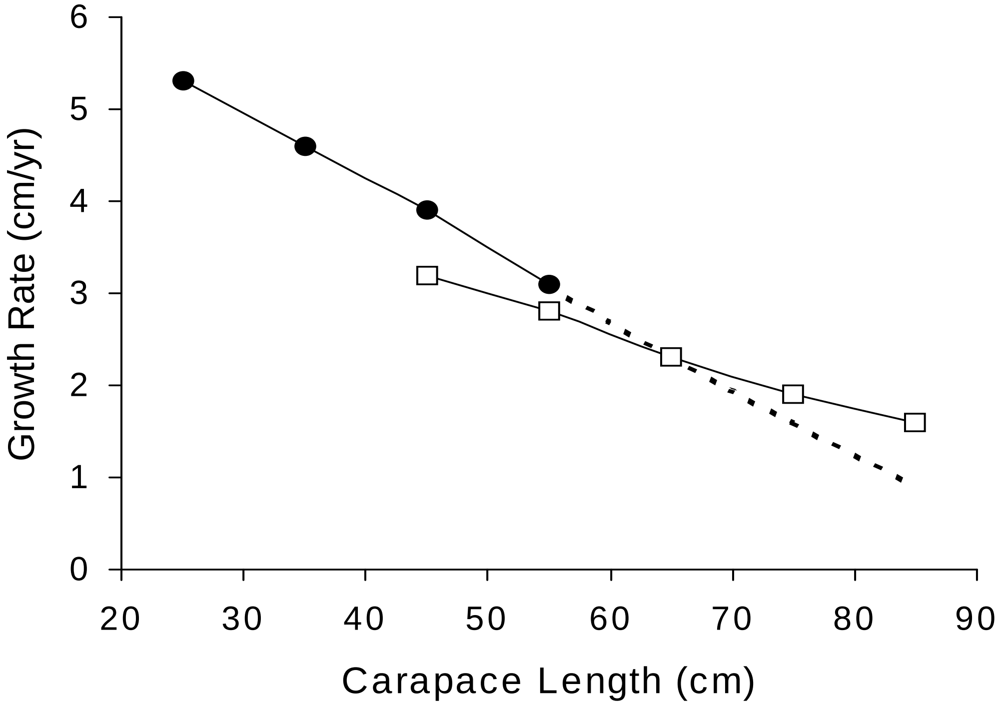


Type 3




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


mtDNA Phylogeny
Life History Patterns
Reproductive Traits
Nd
Lo
Lk
Cc
Ei
Cm
Dc



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