

ONTOGENETIC HABITAT SHIFTS IN MARINE ORGANISMS: INFLUENCING FACTORS AND THE IMPACT OF CLIMATE VARIABILITY

Melissa L. Snover

ABSTRACT

Many marine animals must increase by several orders of magnitude in size as they grow from eggs or larvae to adults, and ecological scaling properties limit the size range over which certain habitats are exploitable. Many of these organisms therefore undergo one or more ontogenetic habitat shifts as they grow to maximize growth rates while minimizing predation risk. An understanding of the mechanisms that influence the timing and optimal sizes at these shifts is critical in managing both target and by-catch populations affected by fisheries. Here I summarize ecological processes that influence ontogenetic habitat shifts, including size-specific predation, size-specific limitations to habitat exploitation, and density dependence. I also consider how climate change may affect the variability in these processes. To illustrate the potential impact of climate variability, I present a simple model building on previous theoretical studies of ontogenetic habitat shifts. As a case study, I used the model to consider differences in the timing of the shift from pelagic to neritic habitats in populations of the loggerhead sea turtle (*Caretta caretta* Linnaeus, 1758), which are vulnerable to by-catch in different fisheries in the two habitats. Results of the model suggest that the optimal size at the pelagic-to-neritic habitat shift in loggerhead sea turtles may vary considerably over time. Generalizing these results, we must place our understanding of ontogenetic habitat shifts in the context of climate variability and recognize that the results of short-term observations and experiments may not be applicable at longer time scales.

The population dynamics of many marine organisms are influenced by their behavioral responses to ecological processes including biotic and abiotic variability. Ontogenetic habitat shifts are widespread in mobile marine species in which, for example, postlarvae may settle from the pelagic environment to benthic habitats that serve as early juvenile nurseries and eventually to adult habitats (see, e.g., Dahlgren and Eggleston, 2000; Etherington et al., 2003). Understanding the factors that drive ontogenetic habitat shifts is important for understanding the dynamics of populations that are target or by-catch species of fisheries. Population- and individual-level variability in the timing of these shifts can influence spatial and temporal variability in recruitment. Animals may be vulnerable to a fishery for only specific portions of their life cycles, but the durations of those life stages may vary depending on environmental conditions (Childress and Herrnkind, 2001; Snover et al., 2006) or density-dependent factors (Etherington et al., 2003) potentially requiring adaptive management strategies that, for example, change size restrictions on catch or the timing of seasonal openings and closures.

Werner and Gilliam (1984) present a theoretical treatment of the factors that drive ontogenetic habitat shifts. For prereproductive animals, fitness is maximized by minimization of the time to reproductive maturity (i.e., maximization of growth rates) and maximization of the probability of surviving to reproductive maturity (i.e., minimization of mortality risks). Werner and Gilliam (1984) demonstrate that the presence of trade-offs in which the habitat that would maximize growth rates does

not minimize predation rates, animals are predicted to select the habitat that minimizes the ratio of mortality risk to growth rate (i.e., minimizes μ/g). Empirical studies have found support for this hypothesis in aquatic systems (Werner and Hall, 1988; Dahlgren and Eggleston, 2000).

Here I review the state of knowledge regarding the factors that influence ontogenetic habitat shifts in marine organisms, discuss the potential implication of environmental variability and climate change, and offer a simple model to explore how environmental variability may influence the timing of a major ontogenetic habitat shift in loggerhead sea turtles.

FACTORS INFLUENCING HABITAT SHIFTS

Many potential factors, and combinations of those factors, can drive ontogenetic habitat shifts. A fundamental aspect of many of these factors is how they influence growth rates. In the simplest form, the body size of an individual that can be supported by a particular habitat may be subject to limits, and organisms that span a large range of body sizes during their ontogeny will then change to different habitats and diets as they grow in order to maintain optimal growth rates (Werner and Gilliam, 1984; Werner, 1988; Dahlgren and Eggleston, 2000). That such ontogenetic habitat shifts can reflect a growth advantage in the new habitat has been demonstrated empirically (Werner et al., 1983; Werner and Hall, 1988; Dahlgren and Eggleston, 2000), but numerous factors may control the availability of food resources that influence growth rates and affect the optimal size at the habitat shift.

SIZE-DEPENDENT PREDATION RISK.—In the absence of other considerations, an individual would shift to habitats that maximize growth rates, but differential mortality risks in different habitats may lead to a trade-off. Animals may use nutritionally suboptimal habitats to minimize the risk of predation until a size refuge is reached, at which point an ontogenetic habitat shift occurs (Werner et al., 1983; Werner and Hall, 1988; Dahlgren and Eggleston, 2000). Werner and Gilliam (1984) present a conceptual model for the growth consequences of ontogenetic habitat shifts. They demonstrate the link between optimizing growth and minimizing predation risk, suggesting that, in order to minimize mortality risk, animals may continue to use suboptimal habitats beyond the point where a shift would maximize growth rates. In field tethering and caging experiments, Dahlgren and Eggleston (2000) found that small juvenile Nassau grouper (*Epinephelus striatus* Bloch, 1792) experienced both lower growth rates and lower predation risk in nursery macroalgal habitats than in postalgal habitats. Furthermore, the ratio μ/g was significantly lower in the macroalgal habitats for small fish but significantly lower in the postalgal habitats for medium and large fish. These results provide evidence that these fish face a trade-off in maximizing growth rates and minimizing predation rates in the timing of the habitat shift.

Predation risk can also have sublethal effects such as reduced foraging rates that result in reduced growth rates (Holbrook and Schmitt, 1988; Steele and Forrester, 2002; Brown and Kotler, 2004). Brown and Kotler (2004) expanded on the minimizing- μ/g model of Werner and Gilliam (1984). Rather than considering growth rate, they suggested a foraging model that accounted for variability in predator and resource abundance and how these factors interacted with behavior.

HABITAT COMPLEXITY.—Numerous marine species, such as reef fishes, require habitat in the form of crevices or interstices of vegetation. Such habitats may offer refuges from predation (see, e.g., Dahlgren and Eggleston, 2000) or a means of defending a food source (Snover et al., 2005). Although I found no studies linking the availability of suitable complex habitats and size at habitat shifts, studies have demonstrated increased recruitment and survival with increasing habitat complexity (e.g., Stunz and Minello, 2001; Laurel et al., 2003), and in patch selection studies, habitat complexity was an important determinant in the presence of predation risk (Schmitt and Holbrook, 1985). Reasons for these positive interactions may include shelter from predation, increased food abundance, and higher water quality (Laurel et al., 2003). In a study on the post-settlement patterns of Atlantic cod (*Gadus morhua* Linnaeus, 1758) and Greenland cod (*Gadus ogac* Richardson, 1836), Laurel et al. (2003) altered eelgrass habitat, adding vegetation to some sites and removing it from others. They found increases in abundance at the former sites and decreases at the latter. The availability of complex habitats, such as eelgrass beds, may influence the size at ontogenetic habitat shifts, and individuals may shift at smaller sizes if suitable habitats exist that provide shelter and food resources.

SIZE-DEPENDENT LIMITATIONS TO HABITAT EXPLOITATION.—Smaller animals may not be able to exploit the resources in a habitat because, for example, they cannot dive to the necessary depths or lack the gape size to use a particular food (Schreer and Kovacs, 1997; McCormick, 1998). In this instance, although the adult habitat may provide superior resources and potentially similar predation rates, μ/g may be minimized for small animals in a nursery habitat with readily available, if inferior, food resources.

For example, Schreer and Kovacs (1997) found a significant positive relationship between maximum diving depths and durations and body mass for marine mammals and reptiles. Food resources for marine turtles, such as algae and invertebrates in benthic habitats, may therefore be unavailable to small individuals until they grow sufficiently to dive to the necessary depths. McCormick (1998) found an ontogenetic diet shift in the temperate reef fish *Cheilodactylus spectabilis* Hutton, 1872. Although fish of all sizes feed in the same habitat, diets of small juveniles were different from those of large juveniles and adults. McCormick (1998) found structural changes in feeding apparatus and morphology that allowed individuals to exploit different food resources as they grew.

Conversely, complex nursery habitats suitable for small individuals may reduce feeding rates of larger individuals. For example, Dahlgren and Eggleston (2002) found that despite, an abundance of preferred prey items in the macroalgal habitat preferentially used by small individuals, larger individuals showed lower growth and foraging rates, which the authors attributed to their inability to forage in the small interstices of the macroalgae.

The factors discussed above—habitat-specific growth rates, habitat availability, size-dependent predation risk, and size-dependent limitations to resource exploitation—are conditions that animals can face under which a decision must be made, depending on individual states, about which habitat will minimize μ/g and, ultimately, time to reproductive maturity. Understanding that species use ontogenetic habitat shifts as a part of their life history is basic to an understanding of their population dynamics and the development of stock assessments for species taken as target or by-catch in commercial and recreational fisheries. Beyond a basic understanding of

general habitat use and habitat switches within a population, however, will be the incorporation of variability in the timing of habitat shifts and the conditions that can drive this variability.

FACTORS INFLUENCING THE VARIABILITY IN TIMING OF HABITAT SHIFTS

DENSITY DEPENDENCE.—Variability in the density of conspecifics can influence the timing of and optimum size at an ontogenetic habitat shift. Density can limit the amount of available resources (food and/or habitat availability) and result in lower optimum size at the habitat shift if it decreases growth rates or habitat availability. The μ/g ratio may therefore be minimized at a smaller size when densities are high.

For example, Etherington et al. (2003) found a positive correlation between mortality and density for postsettlement juvenile blue crabs (*Callinectes sapidus* Rathbun, 1896) inhabiting sea-grass beds and suggested it is a mechanism driving habitat shifts from sea grass to unvegetated habitats.

Alternatively, high densities in the second habitat can encourage recruitment to it. For gregarious species, for example, the presence of conspecifics may decrease the perceived predation risk in the new habitat and result in transitions at smaller size. Childress and Herrnkind (2001) studied ontogenetic habitat shifts in Caribbean spiny lobsters [*Panulirus argus* (Latreille, 1804)]. Juveniles of this species shift from inhabiting dense vegetation to sheltering in crevices. Childress and Herrnkind (2001) found that the presence of conspecifics in the crevice shelters accelerated the timing of this shift for individuals inhabiting the vegetation.

INDIVIDUAL RESPONSES.—Individual animals respond to their environments differently. Animals with faster metabolisms may require more food and, to minimize μ/g , need to shift earlier than conspecifics with slower metabolisms. Snover et al. (2005, 2006) presented growth and fitness models for coho salmon demonstrating that individual genotype and phenotype may determine the age at which individuals mature and return to freshwater habitats to spawn. Their model suggests that individuals with rapid metabolism and territorial behaviors experience high at-sea growth rates when resources are plentiful and defensible (i.e., clumped). These individuals had longer at sea stages and spawned at larger sizes. Conversely, for these coho with rapid metabolism and territorial behaviors, sparse and/or uniformly distributed resources resulted in lower growth rates, shorter at-sea stages, and a smaller size at spawning. The results of their models demonstrate that environmental variability can differentially affect the timing of habitat shifts in individuals with different genotypes and phenotypes.

In an empirical study, Steele and Forrester (2002) found individual body size to be an important determinant of the impacts of predators and conspecific competitors on the blackeye goby [*Coryphopterus nicholsii* (Bean, 1882)]. They found that large, fast-growing individuals were more susceptible to predation, whereas smaller, slow-growing ones were negatively affected by increased competition. Although their study dealt with patch selection rather than ontogenetic habitat shifts, it demonstrates how individual condition or metabolism can influence movement between habitats.

TRANSITIONAL PHASES.—In some instances physiological transformations result in habitat shifts that are abrupt and discrete (e.g., anadromous salmon smolts moving from fresh water to seawater), but in other species, the shift may not be abrupt, and animals may sample the different habitats or continue to use both for a period of

time. In Caribbean spiny lobsters, Childress and Herrnkind (2001) noted that some individuals still spend time in the juvenile algae habitats after they first appear in the adult crevice shelters. This transitional phase lasts approximately 6–8 wks.

Another example is juvenile loggerhead sea turtles, which undergo at least one major ontogenetic habitat shift: the transition from an oceanic, pelagic habitat to a neritic, benthic habitat. In part because of the long migrations involved, this shift had previously been thought to be discrete (McClellan and Read, 2007), but McClellan and Read (2007) presented counter evidence, based on satellite tracking data for 23 loggerhead sea turtles in the Atlantic that had been caught and tagged in neritic habitats and had therefore presumably settled in this habitat. Of the turtles they tracked, 43% returned to pelagic habitats, indicating that at least some individual turtles may move back and forth between habitats for a period before settling definitively in the neritic habitat. The longest tracking period for a turtle returning to the pelagic was 381 d, after which the transmitter failed. The transitional period for loggerhead turtles can therefore last at least a year and may last even longer.

ENVIRONMENTAL VARIABILITY.—Numerous correlation studies have demonstrated relationships between climate variability indices such as the North Atlantic Oscillation (NAO), the Pacific Decadal Oscillation (PDO), and the El Niño–Southern Oscillation and factors influencing population dynamics in species important to fisheries (e.g., see Ottersen et al., 2001 and Lehodey et al., 2006, for review; see also Mantua et al., 1997; Bleckner and Hillebrand, 2002; Henderson and Seaby, 2005; Saba et al., 2007). Local physical changes brought about by climate fluctuations, e.g., in temperature, currents, and upwelling events, can strongly affect the abundance and distribution of animals (Stenseth et al., 2003). Temperature influences many individual-level biological processes important to population dynamics such as growth rate, time to maturity, timing of spawning, egg viability, and timing of food availability (see Ottersen et al., 2001, and references therein). Changes in current patterns can have obvious implications for larval transport and successful recruitment. Upwelling brings deep, nutrient-enriched waters to the surface. Shifts in currents that alter upwelling regions can have substantial effects on fisheries such as sardine and anchovy in the eastern Pacific (Barber et al., 2006). These shifts in production regimes require adaptive management strategies that respond to this natural climate variability.

Particularly important for the timing of ontogenetic habitat shifts is the way in which variability in these processes influences growth rates and recruitment from nursery habitats to adult habitats. Henderson and Seaby (2005), analyzing a 24 yr time series on abundance and growth of sole [*Solea solea* (Linnaeus, 1758)] in an estuarine nursery habitat, found a significant positive correlation between growth rates and the NAO winter index, monthly averages from December to March, for the previous winter. In positive NAO years (see section titled “Model for the Optimal Size at Habitat Shifts in Loggerhead Sea Turtles” for further discussion of positive and negative NAO years), much larger juvenile sole were still using the nursery habitat than had previously been noted, and sizes in that location that were considered exceptional during more negative NAO years were common in positive years. Juvenile sole in this estuary may therefore make the transition to adult habitats at a larger size (though probably not a greater age) under the conditions of high productivity that occur in positive NAO years. Henderson and Seaby (2005) also noted increases in abundance, suggesting increased survival and or higher spawning rates of adult sole.

For Pacific halibut that move from shallow, near-shore juvenile habitats to deeper adult habitats, Clark and Hare (2002) investigated the relationship between recruitment to the deeper waters and the PDO. They found that climate regime in the year of spawning is responsible for most of the observed variability in recruitment, more so than density-dependent factors.

The factors discussed here—density dependence, individual responses, transitional phases, and environmental variability—combine to affect how individuals and populations will use habitat shifts to minimize μ/g . Although understanding what biotic and abiotic mechanisms influence the timing of and size at an ontogenetic habitat shift is important, the relevant studies are often conducted over short time periods and provide only snapshots of the process. Observations about timing and size at habitat shifts must be placed in a broader context of interannual variability in biotic and abiotic conditions, and the ways these factors may affect process must be considered when these considerations are incorporated into fisheries management. Changes in observed growth rates or catchability can be symptoms of changes in ontogenetic habitat shifts. Understanding what the triggers are for observed changes is important to stock assessment and making good forecasts for species take allotments. I present a demonstration of the importance of considering interannual variability in environmental conditions using a simple model based on the minimizing- μ/g hypothesis presented by Werner and Gilliam (1984).

MODEL FOR THE OPTIMAL SIZE AT HABITAT SHIFTS IN LOGGERHEAD SEA TURTLES

Six of the seven species of sea turtles, including loggerheads, are listed as either threatened or endangered under the U.S. Endangered Species Act of 1973. Takes of loggerheads and other sea-turtle species have resulted in closures and modifications of fishing practices in several fisheries, including hook and bait modifications and closures of longline fisheries (Gilman et al., 2007), full and seasonal closures of gill-net fisheries (Caretta et al., 2004), and the use of turtle excluder devices and seasonal closures in trawl fisheries (Epperly and Teas, 2002). Takes of loggerhead turtles continue to have regulatory implications for fisheries management, and a better understanding of the dynamics of this long-lived and highly migratory species is critical to effective management of many fisheries.

Juvenile loggerhead sea turtles shift from an oceanic, pelagic habitat to a neritic, benthic habitat. The size at which this shift occurs differs considerably in different ocean basins. Juveniles of loggerheads nesting in the southeastern United States return to near-shore feeding habitats at 46–63 cm curved carapace length (CCL; Bjorndal et al., 2000). Those in the Pacific, Japan in the North Pacific and Australia in the South Pacific, return at much larger sizes, $> \sim 75$ cm CCL (Nichols et al., 2000; Limpus and Limpus, 2003). Lengths > 60 cm CCL are reported for loggerheads in the Indian Ocean (Hughes, 1974). The timing and sizes of these shifts are important considerations in the management of this species as they are taken as nontarget by-catch in numerous fisheries. In the pelagic habitat, loggerheads are vulnerable to drift gill nets (Parker et al., 2005) and longline fisheries (Lewison et al., 2004), although only larger loggerheads typically interact with the longline fishery (NMFS, 2001), so the longer the duration of this stage, the longer the turtles are vulnerable to this fishery. In the near-shore habitats, loggerheads are vulnerable to trawl, gill-net, and small artisanal fisheries (Nichols et al., 2000; Gardner and Nichols, 2001; NMFS,

2001). These near-shore fisheries affect all size classes, and the resulting mortality is directly related to the amount of time spent foraging in these habitats.

Although I attempted to incorporate as much biological realism as possible, the modeling effort presented here is a purely heuristic approach to assessing the interplay of factors controlling the optimal size at the habitat shift rather than an attempt at an accurate model of the given system. My objective was to present one way to model growth and survival in these two different habitats, to explore how interactions between these demographic parameters may influence the optimal size at the habitat shift, and to consider how climate variability may influence variability in the size at the shift. I used loggerhead sea turtles as a case-study species, but this model can be readily modified for other species of interest.

For growth I used the von Bertalanffy growth function (VBGF)

$$L_t = L_\infty(1 - e^{-kt}) \quad (1)$$

where L_t is the length (cm CCL) at time t (years), L_∞ is the asymptotic length (cm CCL), and k (yr^{-1}) is a rate constant commonly considered the growth coefficient. For size-specific growth rates (cm yr^{-1}) I used the derivative of the VBGF

$$g = \frac{dL_t}{dt} = k(L_\infty - L_{t-1}) \quad (2)$$

Snover et al. (2005, 2006) discussed a useful interpretation of L_∞

$$L_\infty = \frac{E}{k} \quad (3)$$

where E (cm yr^{-1}) is the coefficient of the anabolism term in the metabolic growth model from which the VBGF is derived. According to Snover et al. (2005), E is related directly to the amount of resources available to an individual and will vary with environmental conditions. In this model I considered only food resources, but other resources, such as habitat availability, can also be incorporated. I assumed a population mean value of k and varied values of E in the pelagic habitat to explore the impacts of interannual variability in food resource levels. I used the mean value of k , 0.056, determined from VBGFs developed for both pelagic and neritic loggerheads (Bjorndal et al., 2000, 2001).

Following Snover et al. (2005), I assumed that k is constant throughout an individual's life and that, although k will certainly include interindividual variation, the population mean value is the same in all habitats. Under this assumption, if one habitat has a lower level of food resources than another, it would logically be modeled by changes in E . For E values, I used 5.25 in the pelagic habitat and 6.5 in the neritic, thereby suggesting that more or higher-quality food resources are available in the neritic habitat. The values of E were selected such that, when they were combined with the value of $k = 0.056$, the resulting lengths and growth rates were consistent with our knowledge of loggerhead turtles.

E can be thought of as size-specific function, similar to size-specific predation. For example, near-shore food resources for sea turtles are primarily benthic, including crabs and molluscs (see Bjorndal, 1997, for review), and to exploit them the turtle

must be able to dive to reach them, both expending energy and suffering increased risk of predation. Conversely, pelagic food resources for turtles are primarily small epipelagic organisms such as the harp carinaria (*Carinaria cithara* Benson, 1835), snails (*Janthina* spp.), gooseneck barnacles (*Lepas* spp.), and the sail jellyfish (*Velella velella* [Linnaeus, 1758]) (Parker et al., 2005), which may be nutritionally suboptimal for large turtles.

I used a logistic function to control the percentage of available food resources that an individual is able to exploit in the neritic habitat. I imposed a size-dependent penalty on E for the near-shore benthic habitats that resulted in an asymptotic structure such that above a threshold size all turtles were able to exploit the food resources in that habitat fully. Below that size, individuals were only able to exploit a fraction, P , of the available food resources

$$P = \frac{\exp((L - 30)/15)}{1 + \exp((L - 30)/15)} \quad (4)$$

where L is length. With this relationship, animals above 46 cm CCL can use at least 90% of the habitat's food resources. This possible relationship is purely hypothetical, and I use it as an example of one way to model size-dependent limitations on habitat exploitation. Figure 1 depicts the resulting proportion of the neritic food resources available to an individual at size. To model growth rates in the neritic habitat, I combined Eqs. 2, 3, and 4

$$g_N = k \left(\frac{EP}{k} - L_{t-1} \right) \quad (5)$$

where N indicates neritic.

I used a size-dependent equation to model annual mortality rates at length L

$$\mu = 1 - e^{(-m_0 + m_i/L)} \quad (6)$$

The parameter m_0 is a size-independent mortality term, and the parameter m_i adjusts the size-dependent component of mortality. Survival rates are not well understood in sea turtle populations, and I simply used two parameterizations of Eq. 5 that resulted in different levels of size-dependent mortality in the pelagic habitat. For the neritic habitat, I assumed a high level of size-dependent mortality and let $m_0 = 0.0001$ and $m_i = 8$, whereas for the pelagic habitat, I assumed a lower level of size-dependent mortality and let $m_0 = 0.05$ and $m_i = 3.5$. Figure 2 depicts the resulting annual survival rates ($1 - \mu$) at size from these parameterizations.

To consider the influence of climate change on the timing of habitat shifts in loggerhead sea turtles, I drove variability in E using time series of the NAO and the PDO. The NAO is measured as the pressure difference between the subtropical atmospheric high-pressure zone centered over the Azores or Portugal and the atmospheric low-pressure zone over Iceland (Ottersen et al., 2001). During positive years, intense low pressure is centered over Iceland and intense high pressure in the subtropics, resulting in strong storms across the North Atlantic. Conversely, negative NAO years have fewer and weaker storms (Ottersen et al., 2001). The NAO is closely linked with sea surface temperature (SST), and during positive years the east-

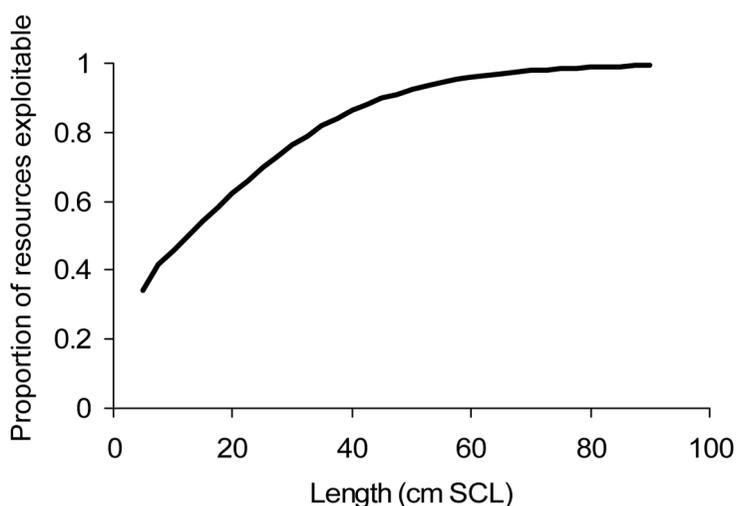


Figure 1. Proportion of food resources in the neritic habitat that can be exploited by a loggerhead of a given length. This is a hypothetical curve that accounts for the inability of small turtles to dive to depth and to handle hard-bodied benthic prey species.

ern Atlantic experiences higher SSTs and the western Atlantic lower ones. As many biological functions in poikilothermic animals are closely related to temperature, positive NAO values tends to have a positive influence on growth rates in marine environments of the eastern Atlantic (Bleckner and Hillebrand, 2002; Helama et al., 2007). As this is the forage area of pelagic-stage Atlantic loggerheads (Bjorndal et al., 2000), I scaled the NAO and E positively. Conversely, positive PDO values tend to have a negative influence on marine growth rates (Stenseth et al., 2003), so I scaled PDO and E negatively. The PDO is the leading principal component of SST anomalies north of 20°N (Mantua et al., 1997), and this is the region most commonly used by

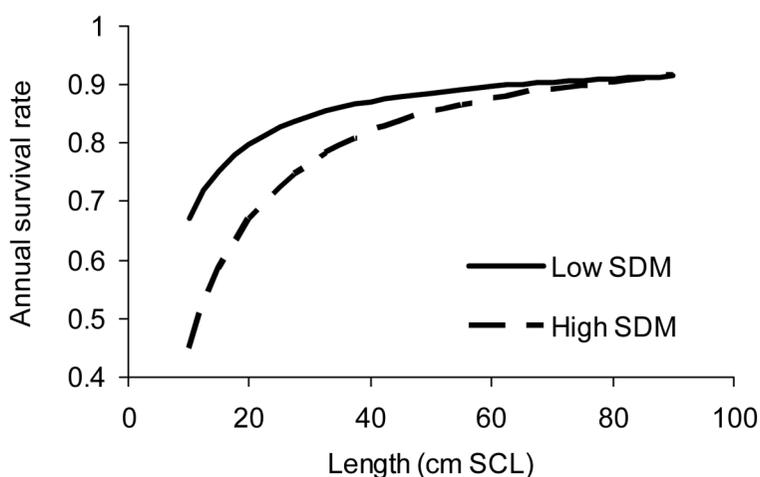


Figure 2. Annual length-based survival rates. Two survival curves were considered in the modeling approach, one with a high level of size-dependent mortality (SDM; dashed line) and one with a lower level of size-dependent mortality (solid line).

North Pacific loggerheads originating from Japanese nesting beaches (Polovina et al., 2006); I therefore chose this index rather than the El Niño–Southern Oscillation index used by Saba et al. (2007) for nesting leatherback sea turtles [*Dermochelys coriacea* (Vandelli, 1761)].

For the NAO data, I used the annual winter (December to March) means from 1901 to 2004 (Stenseth et al., 2003) from Hurrell (1995). This index of the NAO is a measurement of the difference in normalized sea-level pressure between Portugal and Iceland. I divided each value by the maximum absolute value in the data to produce an index from approximately -1 to 1 and added these values to the mean E of 5.25 to create a time series of E values. Keeping E values within this range resulted in realistic lengths and growth rates for loggerhead sea turtles. Similarly, for the PDO data, I used the annual December to March means from 1901 to 2004 (Mantua et al., 1997) and used the same method to create an index from -1 to 1 . In this case I subtracted these values from $E = 5.25$ to create the time series of E values.

MODEL IMPLEMENTATION.—To run the model, I used Eqs. 1 and 3 with $E = 5.25$ and $k = 0.56$ and $t = 1, 2, 3 \dots 20$ to model pelagic growth and Eqs. 2 and 4 to produce the annual growth rate. At the beginning of each time interval (equivalent to 1 yr), I used Eqs. 2, 3, and 4 to determine what the growth rate would be for that given length in the neritic habitat. The minimum absolute difference between the pelagic and benthic growth rates for a given length is the length at the habitat switch that maximizes growth rates. Similarly, length-based mortality rates were calculated for each length as described above, and the minimum absolute difference between μ/g for each habitat was the size at which a habitat switch minimized this ratio.

For climate variability, the same methods described above were used but with annually varying values of E based on the NAO and PDO indices, which were time series of length $i = 1, 2, 3 \dots 104$ yrs. Allowing 20 yrs for each cohort, I was able to model the size at habitat shift that minimized μ/g for 84 cohorts. For each cohort, x , E time series from $i = x \dots (x + 20)$ were used.

MODEL RESULTS

Using constant E values in the pelagic and neritic habitats of 5.25 and 6.25 , respectively, and Eq. 5 to model neritic growth produced the prediction that growth rates would be maximized with a habitat switch at 36 cm CCL (Fig. 3), but if mortality rates were considered as described above, with a stronger size-dependent mortality component in the neritic habitat than in the pelagic habitat, the ratio of mortality to growth rates (μ/g) was minimized with a habitat switch at 52 cm CCL (Fig. 3).

When E was varied annually and followed the climatic indexes of the NAO and the PDO, and all else remained the same (static mortality schedules), patterns emerged in the optimal size at the habitat switch. The PDO index revealed long cycles of predominantly high or low values with regime shifts estimated at 1948 and 1978. When E was negatively correlated with this index, the first 30 cohorts showed declining sizes at the habitat shift, as would be expected because the predominantly high PDO values suggest lower food resources (Fig. 4, upper panel). This trend was followed by a sharp increase in size at the habitat shift when cohorts began to experience the higher productivity associated with more negative PDO values. The NAO does not have the long cycles associated with the PDO, and the model results, when E was

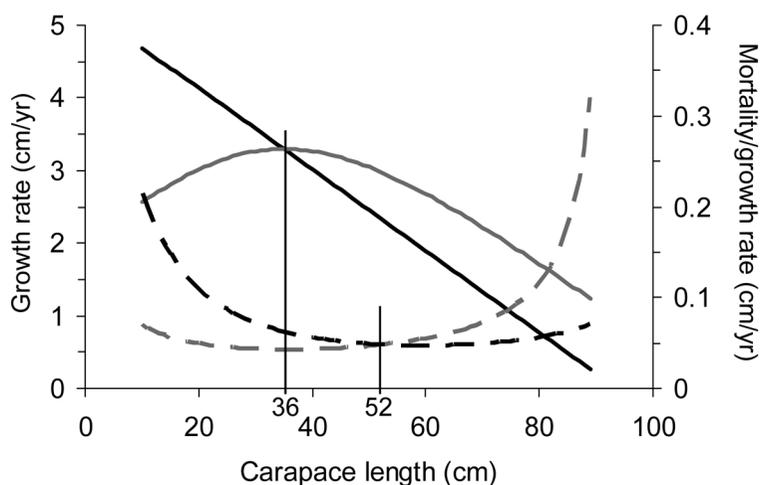


Figure 3. Growth rates (solid lines) and the mortality-to-growth rate ratio (dashed lines) as functions of length. Gray lines represent the neritic habitat and black lines the pelagic habitat. Growth rates are maximized when a turtle shifts from the pelagic habitat (solid black line) to the neritic habitat (solid gray line) at 36 cm curved carapace length (CCL). The ratio of mortality rate to growth rate is minimized when a turtle shifts from the pelagic habitat (dashed black line) to the neritic habitat (dashed gray line) at 52 cm CCL.

driven by this index, showed high variability but no clear trend in the early cohorts, followed by an increasing trend in the latter cohorts (Fig. 4, lower panel).

CONCLUSIONS

Our understanding of the mean sizes at the habitat shift of loggerhead turtles from pelagic to neritic habitats is generally based on relatively short and recent observations. What we understand today about the sizes of juveniles using pelagic habitats in the different ocean basins may only be the consequence of recent environmental conditions. Even with the simplifying assumptions used in the modeling exercise presented here, a great deal of variability in the optimal size at the pelagic to neritic habitat shift in loggerhead sea turtles (~40–70 cm CCL) was suggested over time. A more complicated model that considers fluctuations in the neritic habitats, environmentally driven variability in pelagic predation rates, and behavioral foraging decisions such as those presented by Brown and Kotler (2004) may reveal much more complicated dynamics and fluctuations in the optimal size at the habitat shift.

From the fisheries-management point of view, an understanding of what portion of the population resides where it is vulnerable capture by certain fisheries (e.g., longline fisheries in the pelagic and trawl and gill-net fisheries in the neritic), how long this residence lasts, and how environmental variability affects these proportions and stage durations is critical to assessments of allowable take for these fisheries. For example, if the duration of the pelagic stage increases, loggerheads taken by the longline fishery may be older and have higher reproductive value, and take limits may require modification designed to prevent a negative impact on these threatened populations.

Assessing the abundance of turtles in pelagic environments is difficult, and they are generally monitored only when observed in near-shore environments. Trends toward habitat shift at larger sizes, as indicated in Fig. 4 (lower panel), could easily be

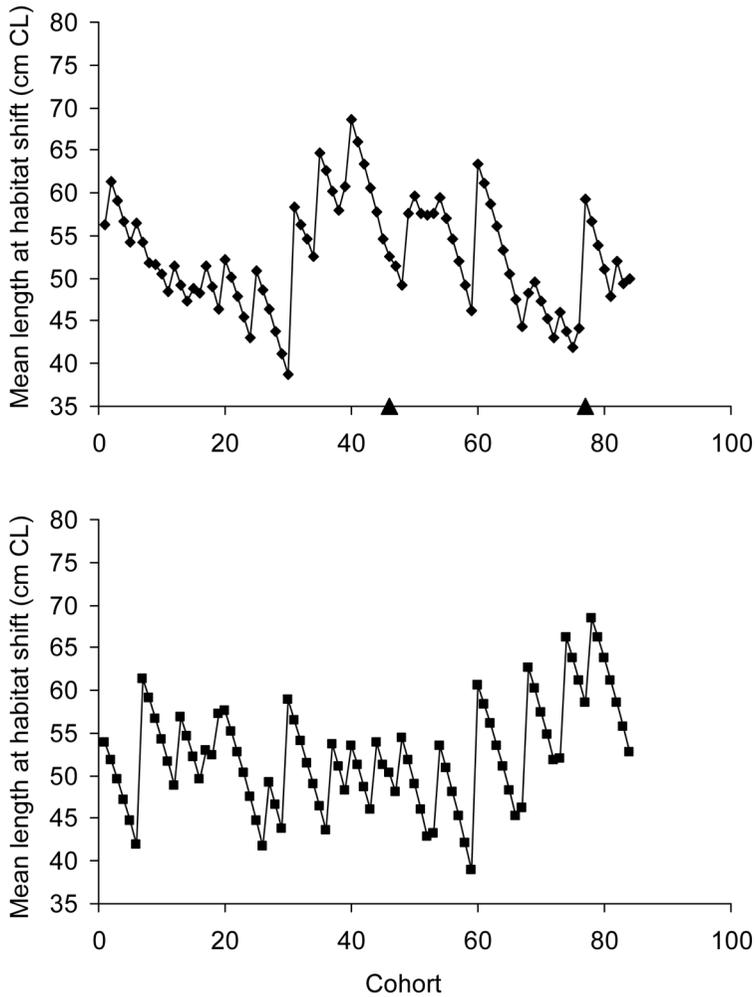


Figure 4. Potential variability in the length at which a habitat shift from the pelagic to the neritic would minimize the mortality rate-to-growth rate ratio under different environmental conditions. In the modeling exercise, each cohort was subjected to environmental variability driven by the Pacific Decadal Oscillation (upper panel) and North Atlantic Oscillation (lower panel). Filled triangles in the upper panel (A) denote the years corresponding to the 1946 and 1977 regime shifts in the PDO time series.

mistaken for a loss of recruitment, implying increased mortality in the pelagic stage or decreased productivity of the nesting beaches and a population decline. Alternative hypotheses such as a longer pelagic stage or increasing sizes at the habitat shift must therefore be considered as possible causal mechanisms when management options for this population are considered. The study by McClellan and Read (2007) suggesting that a large proportion of satellite-tagged turtles return to the pelagic is also a snapshot of a short time period, and the observed pattern may be a recent event and may indicate that Atlantic loggerheads sample habitats and remain in the pelagic longer.

Many marine organisms must increase in size by several orders of magnitude as they grow from eggs or larvae to adult size over the course of their life cycles, and complex life cycles involving habitat shifts are common (Werner and Gilliam, 1984; McCormick, 1998; Dahlgren and Eggleston, 2000), so an understanding of the processes that drive them are important to studies of population dynamics and fisheries management. Ontogenetic habitat shifts are directed at maximizing growth rates across the life history, and trade-offs are involved in obtaining the growth rates necessary to attain adult size. Most of the ecological processes discussed here will influence the trade-off between growth rates and mortality risk, and these processes will vary with individual condition, population or cohort size (i.e., density-dependent factors), and environmental variability. Future studies and modeling exercises should be designed to assess how environmental variability affects the timing and the size at habitat shifts to improve understanding of the population dynamics of marine animals. Better understanding of how these processes, and the variability in them, influence the spatial and temporal variability in habitat use by marine organisms may lead to better management of these populations.

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ADDRESS: NOAA/NMFS/Pacific Islands Fisheries Science Center, 2570 Dole Street, Honolulu, Hawaii 96822. E-mail: <melissa.snover@noaa.gov>.



