

Life-History Variation in Marine Turtles

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We studied correlations among traits related to body size and reproductive behavior in marine turtles, using data from 96 different populations representing seven species. Our analyses focused on patterns of phenotypic covariation among species and among populations within species. At the species level, body size correlated positively with several reproductive traits, including egg size and overall reproductive effort. A trade-off between clutch size and egg size was confirmed for marine turtles, after factoring out the effects of body size. Patterns of variation within species were different from those among species. For example, in five out of six species there was a positive relationship between adult body size and clutch size, although this correlation was not found at the interspecific level. We also found important differences among species in the way life-history traits correlated with one another. Four species having a sufficient number of samples exhibited congruent worldwide patterns of body size variation. A comparative approach may prove useful for extending demographic models developed for loggerhead turtles to less well-known species, even though many of the model parameters have not been estimated for other species.

COMPARATIVE study of life-history variation is an important component of evolutionary and ecological research (Harvey and Pagel, 1991). Interest in the evolutionary origins of life histories stems from their close connection to fitness and their sensitivity to natural selection (Smith, 1991). Demographers include life-history traits such as age-specific fecundity and survival in life tables used for predicting changes in population size (Cole, 1954). Thus, life-history comparisons among populations or species may support predictions about population dynamics and provide insight into responses to evolution.

Marine turtles (Cheloniidae and Dermochelyidae) are well-suited for comparative analysis of life-history variation. Many studies have been carried out on nesting beaches around the world, and comparable measurements have been made from nesting females in each locality. Also, life-history traits of sea turtles differ in intriguing ways from those of freshwater and terrestrial turtles: marine species produce relatively large clutches of small eggs, in each of a large number of discrete nesting episodes (Wilbur and Morin, 1988). Finally, all marine turtles are endangered or threatened by human exploitation and environmental change, lending urgency to the effort to understand their biology.

All marine turtles share a similar life cycle. Hatchlings have a pelagic maturation period of poorly known duration (Carr, 1987), during which they feed and grow into the juvenile stage commonly encountered in shallow coastal waters. The time from hatching until first repro-

duction varies among species and populations but probably ranges from 7-30 years or more (National Research Council, 1990). Once they initiate breeding, mature females travel to breeding beaches every 2-5 years to lay from 2-10 clutches of eggs, 9-15 days apart. In many populations, males apparently make the journey as well, because mating is commonly reported in the waters adjacent to the breeding beaches (Ehrhart, 1982). The 2-5 year interval between reproductive episodes is considered an adaptation to the energetic costs of migrating between spatially distinct feeding and nesting locations (Hendrickson, 1980), although the pattern is retained in populations that show little migration (e.g., Limpus et al., 1984).

All species of marine turtle have large adult body size and long maturation period and lay large clutches of small eggs relative to other aquatic turtles, even after correcting for body size differences (Wilbur and Morin, 1988). Presumably, sea turtles evolved this reproductive pattern in response to high and unpredictable mortality during the egg and hatchling stages. Laying many small eggs in several different clutches avoids allocating a large proportion of a female's reproductive effort to any single offspring, which would be undesirable because each individual offspring has a high probability of perishing.

Within the sea turtle life-history plan, there is variation among species and populations in most reproductive traits. Our goal is to describe patterns of variation among species and among populations within species and to evaluate pos-

sible evolutionary consequences of life-history differences among species. In addition, we examine the consequences of life-history variation for determining appropriate conservation measures for marine turtles.

METHODS

Data collection.—We reviewed the literature and mailed personal inquiries to gather reproductive data on all species of sea turtles on their nesting beaches. We considered a population of turtles nesting on a particular beach or island to be the appropriate unit for comparison, and we combined results from separate studies of the same population.

Twelve measurements were extracted for each population, when available (Appendix). The carapace length of nesting females was measured as either the straight-line distance or the curved distance from the foremost point on the nuchal scute to the most posterior projection of the carapace. The Appendix gives the measurement originally reported, but we have used only straight carapace length in statistical analyses, calculated from known relationships between curved and straight measurements for each species from literature sources.

Clutch size was measured as the number of yolkeggs deposited by a female per nest. Egg diameter was the maximum diameter measured with calipers. Egg weight (wet mass) was measured immediately after oviposition. Egg volume was calculated by spherical volume: radius ratio, a good approximation for most species (e.g., Pinckney, 1990). Egg survival was the proportion of individuals that survived from oviposition until the hatchlings reached the beach surface, not including clutches transplanted to hatcheries. Reporting methods for egg survival were often ambiguous, but we attempted to exclude data from clutches lost to predators associated with human development, such as swine, dogs, and raccoons.

Incubation period was the number of days from oviposition until the first hatchlings reached the beach surface. Hatchling carapace length and hatchling weight were measured on the day the hatchlings emerged from the sand. Clutch frequency was the number of clutches of eggs laid by a single female during one active breeding season. Remigration interval was the number of years that elapsed between active breeding seasons for an average female. We define an estimate of reproductive effort, which is the total volume of eggs produced by a female per year. Our method of calculation was as follows: reproductive effort = (egg volume) ×

(clutch size) × (clutch frequency)/(remigration interval).

We gathered information on the quality and amount of data associated with each study. The Appendix gives sample sizes associated with estimates of female carapace length and clutch size, which reflect our level of confidence in those estimates. We rejected estimates that were presented without evidence of supporting data, which was especially common for statements about clutch frequency and remigration interval. We recognize that estimates of clutch frequency, remigration interval, and reproductive effort may be biased by tag loss and incomplete beach coverage, but we use the published data as the best available estimates for these reproductive traits. References for all studies in the Appendix are available upon request.

Data analysis.—We judged two values to be erroneous because of their inconsistency with other results and, therefore, omitted them from analysis. Egg diameter for the Ascension Island *Chelonia mydas* population (54.6 mm; Carr and Hirth, 1962) and egg weight of *Caretta caretta* from Dalyankoy Beach, Turkey (20.3 g; Geliday et al., 1982) both qualified as significant outliers from regressions on correlated traits ($P < 0.01$; Grubbs, 1969).

The results include a large number of statistical tests of significance, and we provide acceptable alpha-levels adjusted for multiple comparisons. In general, though, our analyses comprise a search for overall patterns of covariation among life-history traits rather than hypothesis tests for which conservative conclusions are necessary. Throughout this paper we interpret P -values as rough indicators of the degree of association between variables. Conservative significance tests for many of the patterns we discuss await better field data and experimental tests using other taxa.

Patterns of covariation among life-history traits are discernible at several levels, and different kinds of insight can be obtained at each level. We began at the level of the species by calculating species means for each reproductive parameter and then computing the correlations among traits. This level of comparison was used to study the way that body size influences reproductive traits and to uncover correlations reflecting constraints on patterns of diversification. Next, for species with a sufficient number of breeding localities, we used population means reported in the literature to calculate correlations among characters at the level of the population. This level of comparison illustrated the way reproductive traits vary on a geo-

TABLE 1. VALUES OF LIFE-HISTORY MEASURES FOR SEVEN SPECIES OF MARINE TURTLES. Entries in the table are mean and (standard error). The number of studies reporting each parameter may be found in the Appendix.

Species	Number of populations	Female carapace (cm)	Clutch size (eggs)	Egg volume (cc)	Egg survival (%)	Hatchling carapace (mm)	Clutch frequency (ns./yr)	Remigration interval (yr)	Reproductive effort (L of eggs/yr/fem)
<i>Dermochelys coriacea</i>	13	148.7 (1.7)	81.5 (3.6)	79.7 (2.4)	0.57 (.08)	60.1 (1.2)	6.17 (.47)	2.28 (.14)	23.82 (—)
<i>Chelonia mydas</i>	26	99.1 (1.9)	112.8 (3.7)	45.8 (1.2)	0.70 (.04)	50.1 (0.5)	2.93 (.28)	2.86 (.23)	5.28 (.54)
<i>Natatar depressa</i>	7	90.7 (0.9)	52.8 (0.9)	70.8 (1.1)	0.81 (.03)	60.0 (1.1)	2.84 (—)	2.65 (—)	3.98 (—)
<i>Lepidochelys kempi</i>	1	64.6 (—)	110.0 (—)	30.8 (—)	0.61 (—)	42.0 (—)	1.80 (—)	1.50 (—)	4.07 (—)
<i>Lepidochelys olivacea</i>	11	66.0 (1.1)	109.9 (1.8)	31.8 (1.1)	0.44 (.11)	43.3 (1.0)	2.21 (.79)	1.70 (.30)	4.27 (.32)
<i>Eretmochelys imbricata</i>	17	78.6 (1.7)	130.0 (6.8)	28.7 (1.3)	0.77 (.04)	41.3 (0.3)	2.74 (.22)	2.90 (.11)	4.40 (1.1)
<i>Caretta caretta</i>	21	87.0 (1.6)	112.4 (2.2)	36.2 (1.1)	0.53 (.07)	43.8 (0.6)	3.49 (.20)	2.59 (.15)	5.43 (.52)

graphic scale in response to environmental variation. Analyses at the level of individuals within populations are also possible in the context of detailed population studies (e.g., Pinckney, 1990) but are not covered in this report.

RESULTS

The Appendix gives values of reproductive traits for 96 populations of sea turtles that we located in the literature. Mean values of reproductive parameters for each species confirm widely held beliefs about marine turtle biology (Table 1). *Dermochelys coriacea* (leatherback turtle) is the largest species and lays the largest eggs; but its clutch size is small, and number of clutches per year is high. Body sizes and clutch sizes of *Caretta caretta* (loggerhead turtle) and *Chelonia mydas* (green turtle) are intermediate. *Natatar depressa* (flatback turtle) has a small clutch of relatively large eggs. *Eretmochelys imbricata* (hawksbill turtle) has a relatively small but variable body size and lays many eggs of small size. The two *Lepidochelys* (Kemp's ridley and olive ridley turtles) are the smallest species, and they lay small eggs.

Variation among species.—Species-level correlations illustrate that many reproductive traits vary with body size (Table 2). Large species tend to lay large eggs, which give rise to large hatchlings. Large species also lay more clutches per year and expend a greater reproductive effort than do small species. Interestingly, there is no correlation between clutch size and body size among the seven sea turtles (Fig. 1), although a strong positive relationship exists among all turtles (Wilbur and Morin, 1988). Species that lay large clutches have small eggs and small hatchlings. It is noteworthy that high reproductive effort is correlated not with large clutch size or large eggs or returning to breed more frequently but with higher frequency of clutches within a season (Table 2).

The correlations in Table 2 can be summarized by arranging the seven species along three independent axes derived from a principal components analysis of life-history traits (Fig. 2, Table 3). Reproductive effort was not included because it is a product of other traits. The first axis explains 68% of the variance in the original six variables and correlates primarily with size, clutch frequency, and clutch size. *Dermochelys coriacea* and *N. depressa* stand apart from other species on this axis because they have large body, egg, and hatchling sizes; high clutch frequencies; and relatively small clutches. The second axis correlates with remigration interval and

TABLE 2. PHENOTYPIC CORRELATIONS AT THE SPECIES LEVEL AMONG REPRODUCTIVE TRAITS OF MARINE TURTLES. The upper-right half of the table shows correlations among traits not corrected for body size; the lower-left half shows correlations among residuals from regressions of reproductive traits against carapace size. Each entry gives the Pearson correlation coefficient (above) and *P*-value (below). $n = 7$ species. In this table and all other correlation analyses that follow, significance values > 0.0018 should be viewed with caution because of the multiple comparison approach.

	Female carapace	Clutch size	Egg volume	Egg survival	Hatchling carapace	Clutch frequency	Remigration interval	Reproductive effort
Female carapace	X	-0.43 0.540	0.83 0.021	0.04 0.936	0.77 0.042	0.96 0.001	0.32 0.477	0.92 0.003
Clutch size	0.0 1.0	X	-0.85 0.014	-0.29 0.534	-0.88 0.009	-0.34 0.456	-0.02 0.962	-0.30 0.510
Egg volume	0.0 1.0	-0.99 0.000	X	0.24 0.598	0.99 0.000	0.74 0.057	0.22 0.634	0.69 0.083
Egg survival	0.0 1.0	-0.30 0.515	0.38 0.398	X	0.31 0.494	-0.13 0.787	0.64 0.118	-0.25 0.596
Hatchling carapace	0.0 1.0	-0.96 0.001	0.98 0.000	0.44 0.319	X	0.65 0.115	0.26 0.572	0.59 0.163
Clutch frequency	0.0 1.0	-0.29 0.530	-0.38 0.395	-0.60 0.156	-0.51 0.239	X	0.25 0.586	0.95 0.001
Remigration interval	0.0 1.0	0.14 0.772	-0.09 0.844	0.67 0.100	0.02 0.967	-0.24 0.609	X	-0.01 0.976
Reproductive effort	0.0 1.0	0.24 0.599	-0.30 0.527	-0.70 0.082	-0.43 0.332	0.64 0.118	-0.82 0.024	X

clutch size and distinguishes *N. depressa* and the *Lepidochelys* from other species because of their small clutches and short remigration intervals. The third axis correlates with remaining variation in remigration interval and clutch frequency; *Dermochelys coriacea* and the *Lepidochelys* score on one end of this axis, with *N. depressa* at the opposite end.

Similarities among species in life-history traits are reflected in a dendrogram derived from the PCA results (Fig. 3A). The two *Lepidochelys* species are very similar to one another in body size and reproductive behavior. *Caretta caretta*, *C. mydas*, and *E. imbricata* form a separate cluster on the basis of their similar body size, large clutch size, and relatively long remigration interval. *Natatar depressa* and *D. coriacea* are both distinct from each other and from all other sea turtles.

These analyses suggest that body size is confounded with other traits, so that the relationships among life-history measures must be studied by first accounting for size. We corrected for size by regressing each trait separately against female carapace length and saving the residuals for further analysis. The new variables represent the magnitude of the traits after first factoring out the apparent influence of body size.

Correlations among size-specific reproductive traits illustrate patterns of covariation that are independent of adult body size (Table 2).

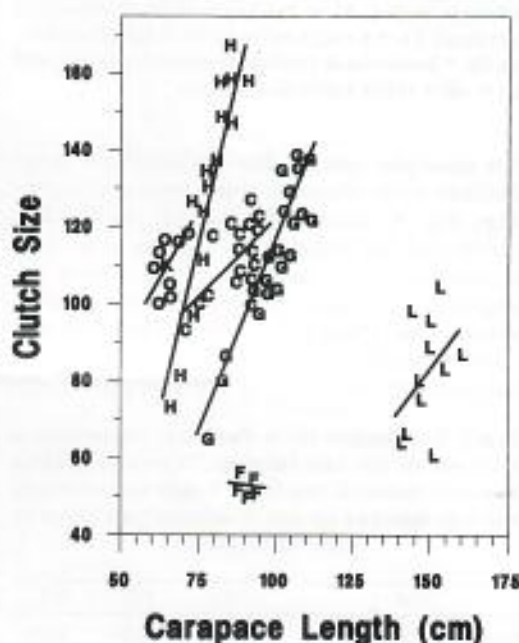


Fig. 1. Relationship between clutch size and female carapace size for seven species of sea turtle. Each point represents the mean value of a single population. Lines were fitted by least-squares regression. Abbreviated species symbols are as follows: C = loggerhead turtle, F = flatback turtle, G = green turtle, H = hawksbill turtle, K = Kemp's ridley turtle, L = leatherback turtle, and O = olive ridley turtle.

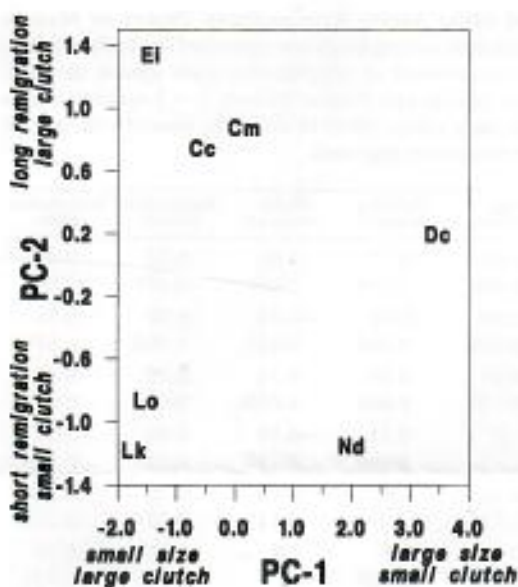


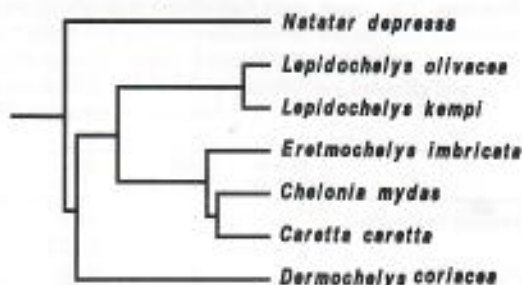
Fig. 2. Positions of seven marine turtle species in the space defined by the first two principal components derived from six measures of size and reproductive behavior (Table 3). Species symbols are as follows: Cc = loggerhead turtle (*Caretta caretta*), Nd = flatback turtle (*Natatar depressa*), Cm = green turtle (*Chelonia mydas*), Ei = hawksbill turtle (*Eretmochelys imbricata*), Lk = Kemp's ridley turtle (*Lepidochelys kempi*), Dc = leatherback turtle (*Dermochelys coriacea*), and Lo = olive ridley turtle (*L. olivacea*).

For example, species that lay relatively large clutches have relatively small eggs and hatchlings (Fig. 4). *Natatar depressa* has the smallest clutch and the largest eggs relative to its size; *E. imbricata*, *C. caretta*, and *C. mydas* have the largest clutches and the smallest eggs relative to body size. These data confirm a fundamental trade-off in allotment of resources to either many

TABLE 3. RESULTS OF A PRINCIPAL COMPONENTS ANALYSIS OF SIX LIFE-HISTORY TRAITS OF MARINE TURTLES, SHOWING THE FIRST THREE EIGENVECTORS AND THE PERCENT OF THE VARIANCE EXPLAINED BY EACH COMPONENT.

Trait	PC1	PC2	PC3
Female carapace	0.45	0.28	0.35
Clutch size	-0.38	0.53	0.35
Egg volume	0.49	-0.16	-0.05
Hatchling carapace	0.48	-0.18	-0.19
Clutch frequency	0.41	0.31	0.50
Remigration interval	0.16	0.70	-0.68
% of total variance	68.1	18.4	12.6
Cumulative % variance	68.1	86.5	99.1

A. Life History Traits



B. Correlation Among Traits

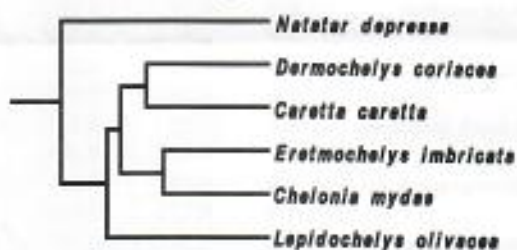


Fig. 3. Dendrograms expressing similarity among sea turtles in reproductive traits (A) and in the structure of their phenotypic correlation matrices (B). The cluster analysis in A was based on the first three components of a principal components analysis of six characters (Table 3). The PCA eliminated covariation between variables before clustering. In panel B, distance between species is measured as the mean squared difference between the elements of their correlation matrices.

small or few large offspring (Smith and Fretwell, 1974).

The negative relationship between egg survival and reproductive effort (Table 2, Fig. 5) suggests that species with high egg mortality expend more on reproduction relative to their body size. *Natatar depressa* and *C. mydas* exhibit relatively high egg survival and low reproductive effort, whereas the species with the poorest egg survival (*L. olivacea*) has high reproductive effort relative to its body size.

Interspecific variation in size-specific reproductive effort results mostly from adjustment in the number of clutches per season and the remigration interval (Table 2). In proportion to their body size, *D. coriacea*, *L. kempi*, and *L. olivacea* have high reproductive effort (average volume of eggs per year), which they accomplish by returning to breed after relatively short absences and depositing many clutches during the breeding season. Clutch size and egg size show no clear relationship with reproductive effort (Table 2).

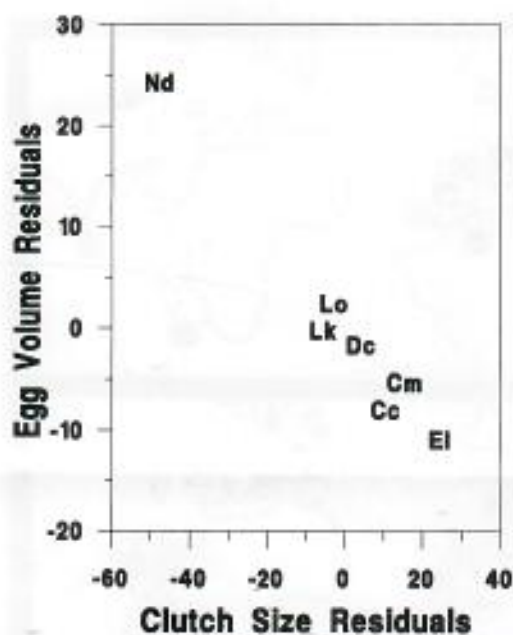


Fig. 4. Trade-off between egg volume and clutch size in seven species of sea turtle. Species with large clutches lay comparatively small eggs. Each point represents the mean value of the residuals after regression against body size for a single species. Species symbols are defined in Figure 2.

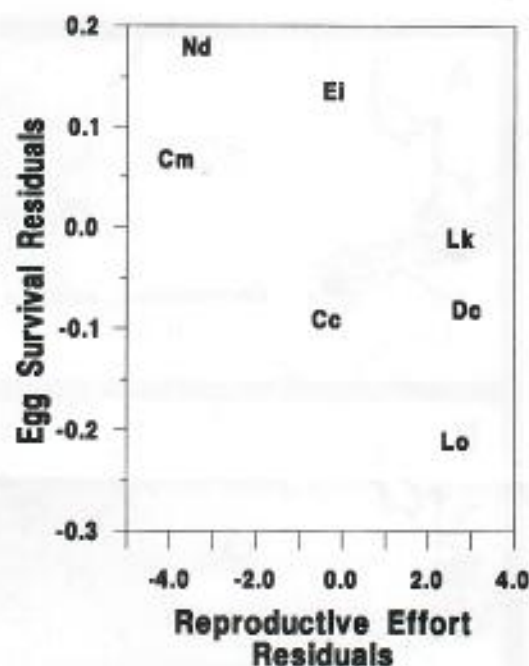


Fig. 5. Negative relationship between egg survival and reproductive effort in seven species of sea turtle. Each point represents the mean value of the residuals after regression against body size. Species symbols are defined in Figure 2.

Variation within species.—The geographic distribution of body size shows similar patterns in each of four species (Fig. 6). *Dermochelys coriacea* nesting in the eastern Pacific are small compared with Caribbean turtles. Eastern Pacific *C. mydas* are much smaller than those anywhere else in the world, whereas those in the Caribbean are large. There are striking size differences among *C. mydas* within the Indian Ocean: those in the north are small whereas those on oceanic islands surrounding Madagascar are large. *Eretmochelys imbricata* in Australia and the Indian Ocean are small except for those on Cousin Island; Caribbean populations are composed of large turtles. Finally, colonies of large *C. caretta* in the southeastern United States contrast with four colonies of small turtles in the Mediterranean. South African loggerheads are smaller than average, and Australians are a bit larger than average. We sorted nesting populations into six geographic regions and checked for correlations among species in the mean carapace size in these regions (western Pacific, Hawaii and eastern Pacific, Caribbean and western Atlantic, Mediterranean, Gulf of Oman and northern Indian Ocean, western Indian Ocean). All six pair-wise correlations among species were positive, with correlation coefficients ranging

from 0.21 to 0.94. The probability of all six tests giving coefficients with the same sign is 0.031 (two-tailed sign test). The general pattern in all four species is that Caribbean and western Atlantic populations contain large individuals, whereas eastern Pacific and northern Indian Ocean populations have smaller turtles (Fig. 6).

All species except *L. keampi* had a sufficient number of studies to calculate correlations among reproductive traits at the population level, and the four most complete matrices are shown in Tables 4–5. There is a positive relationship between clutch size and carapace size in five of six species (Fig. 1, Tables 4–5; *N. depressa*: $r = -.23$, $P = 0.71$; *L. olivacea*: $r = 0.60$, $P = 0.10$). Populations with large females produce larger eggs and larger hatchlings in *C. caretta* (Table 5) but not in any other species.

Tables 4–5 express some of the important differences among species in life-history correlations, but the degree of similarity in the overall structure of these matrices is not clear from casual inspection. We calculated the agreement between matrices as the mean squared difference between corresponding pairs of unique elements. If no elements were missing from two species' phenotypic correlation matrices, the measure of congruence between their

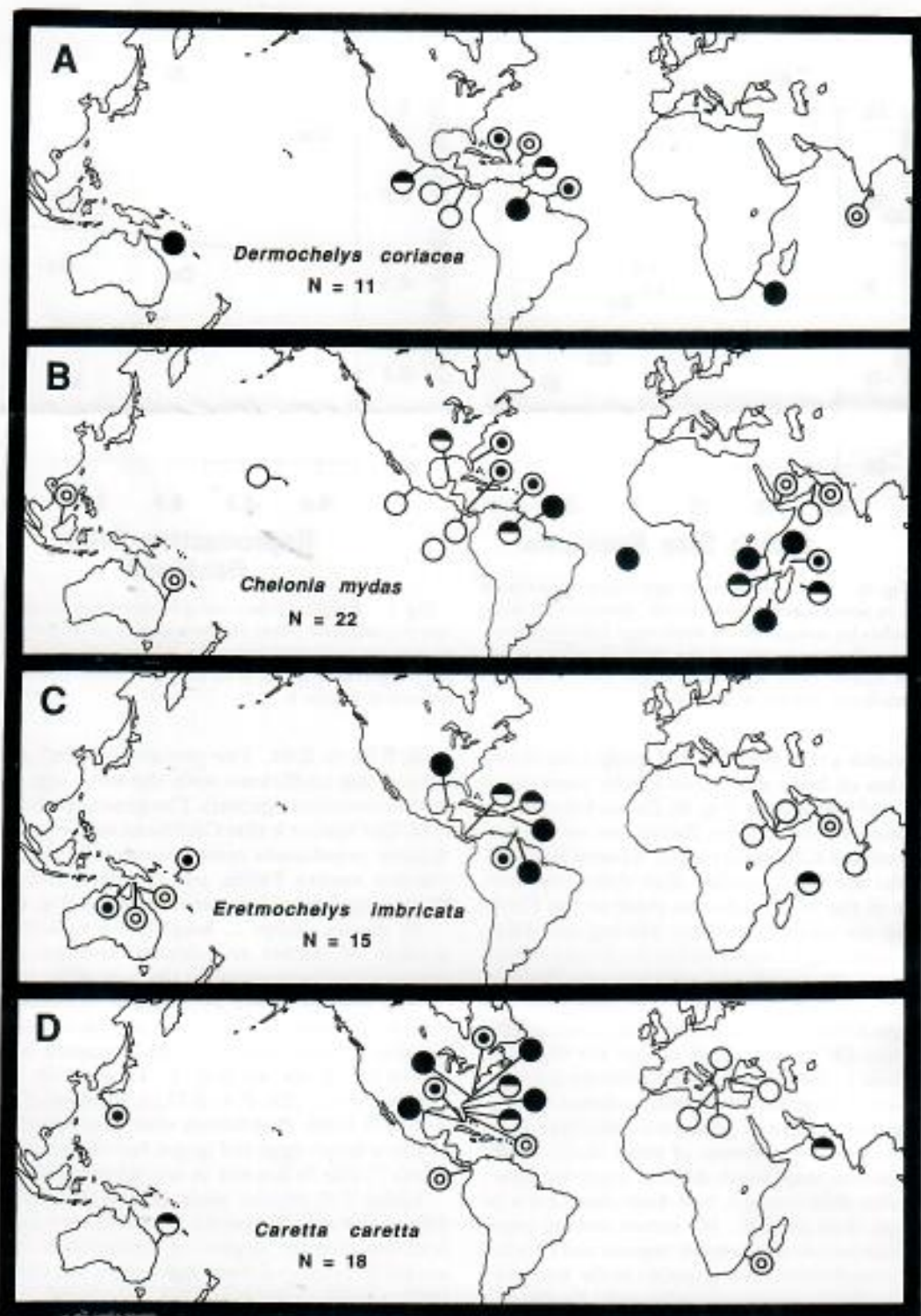


Fig. 6. Geographic distributions of nesting colonies and female body sizes for four species of marine turtle. Symbols signify the average size of nesting turtles: open circle = bottom 20% of all colonies, open donut = 20-40% of the colonies, dotted circle = 40-60%, split circle = 60-80%, filled circle = largest 20% of all colonies.

TABLE 5. CORRELATIONS AMONG REPRODUCTIVE TRAITS FOR 25 POPULATIONS OF *Chironia wyesae* (UPPER-RIGHT HALF OF TABLE) AND 21 POPULATIONS OF *Carrotia caryella* (LOWER-LEFT HALF). Entries in the table are the same as those in Table 4.

	Female carapace	Clutch size	Egg volume	Egg survival	Hatching carapace	Catch frequency	Remigration interval	Reproductive effort
Female carapace	X	0.93 (.000) 1.0 (0.0)	0.13 (.650) 1.0 (0.0)	0.23 (.530) 1.0 (0.0)	0.20 (.455) 1.0 (0.0)	0.27 (.479) 1.0 (0.0)	0.32 (.408) 1.0 (0.0)	0.49 (.328) 1.0 (0.0)
Clutch size	0.57 (.016) 1.0 (0.0)	X 21	0.04 (.885) -0.04 (.880)	0.20 (.585) -0.00 (.990)	0.14 (.617) -0.09 (.758)	0.20 (.631) -0.19 (.644)	0.09 (.834) -0.61 (.104)	0.77 (.074) 0.71 (.112)
Egg volume	0.78 (.016) 1.0 (0.0)	0.48 (.095) -0.11 (.721)	X 13	0.48 (.250) 0.49 (.221)	0.27 (.382) 0.27 (.367)	-0.11 (.818) -0.13 (.779)	0.28 (.548) 0.24 (.608)	0.41 (.422) 0.33 (.517)
Egg survival	0.16 (.017) 1.0 (0.0)	0.32 (.314) 0.28 (.378)	0.00 (.990) 0.08 (.830)	X 8	0.10 (.796) 0.20 (.612)	0.21 (.695) 0.22 (.670)	0.42 (.411) 0.48 (.339)	0.37 (.545) 0.42 (.487)
Hatching carapace	0.90 (.000) 1.0 (0.0)	0.62 (.052) -0.39 (.206)	0.31 (.001) 0.51 (.109)	0.04 (.936) 0.03 (.942)	X 9	-0.65 (.116) -0.61 (.145)	-0.47 (.292) -0.46 (.301)	-0.46 (.358) -0.46 (.357)
Clutch frequency	-0.74 (.256) 1.0 (0.0)	-0.28 (.722) 0.62 (.378)	-0.34 (.065) -0.80 (.197)	0.86 (.940) 0.99 (.067)	-0.16 (.839) -0.53 (.470)	X 4	0.71 (.031) 0.69 (.041)	0.46 (.357) 0.50 (.311)
Remigration interval	0.46 (.440) 1.0 (0.0)	0.72 (.168) 0.57 (.320)	-0.97 (.031) -0.83 (.174)	0.98 (.025) 0.83 (.174)	-0.59 (.411) -0.32 (.679)	0.20 (.800) 0.86 (.145)	X 9	0.06 (.910) -0.04 (.959)
Reproductive effort	-0.66 (.337) 1.0 (0.0)	-0.85 (.148) -0.46 (.544)	0.83 (.175) 0.71 (.291)	0.54 (.634) -0.50 (.664)	0.45 (.553) 0.12 (.876)	0.16 (.838) -0.66 (.338)	-0.93 (.071) -0.95 (.046)	X 4

matrices was based on 28 points. We assigned no statistical significance to the differences between matrices because the correlation coefficients within each matrix are not independent observations. Nevertheless, a dendrogram representing the similarity among species illustrates that several different patterns of life-history covariation are found in marine turtles (Fig. 3B). *Natatar depressa* shows a distinct pattern of correlation among reproductive traits, in part because of a negative correlation between body size and clutch size. *Eretmochelys imbricata* and *C. mydas* have similar patterns of life-history covariation, as do *C. caretta* and *D. coriacea* (Tables 4–5).

DISCUSSION

The results of our survey confirm earlier descriptions of the natural history of marine turtles (Hirth, 1980; Ehrhart, 1982; National Research Council, 1990). Figures 2 and 3A illustrate the close similarity in reproductive traits of the two *Lepidochelys* turtles, which were considered subspecies until recently (Loveridge and Williams, 1957). *Chelonia mydas* is distinct from other marine turtles in its herbivorous feeding ecology but is similar to *C. caretta* and *E. imbricata* in its size and reproductive ecology. *Dermochelys coriacea* is ecologically specialized as a pelagic jellyfish-feeder and is distinct from other sea turtles in its reproductive traits as well; *N. depressa* stands apart because of its comparatively few and large eggs and hatchlings.

We find it interesting that the three species with the greatest quantity of reproductive data also have similar life histories. *Chelonia mydas*, *E. imbricata*, and *C. caretta* apparently share a number of traits that permit investigators to carry out nesting beach studies, in addition to their similar life-history traits. These features may include worldwide distribution and seasonal, colonial nesting on accessible beaches.

Our approach emphasizes phenotypic correlations among species and populations. In general, these analyses do not permit conclusions about the underlying causes of relationships, which could arise in two ways. First, a phenotypic correlation could be caused by a genetic correlation, produced by natural selection, pleiotropy, or drift. If this were the case, we could make statements about constraints on future evolutionary change in the two traits, which must follow the pattern established by the genetic correlation. Alternatively, phenotypic correlations could be caused by variation in external factors that cause the traits to co-

vary, in which case conclusions about evolutionary constraints would not be possible.

The underlying causes of phenotypic correlations in sea turtles will always remain uncertain, because of our inability to perform experiments (Stearns, 1976). Nevertheless, patterns of covariation of life-history traits do permit speculation about the evolution of those traits and become increasingly convincing as they are confirmed in other taxa.

Interspecific comparisons.—Body size is correlated with life-history traits in many organisms (Peters, 1983). Our findings for marine turtles illustrate which reproductive traits are correlated with size and may in some sense be caused by body size and which traits are unrelated to size.

Two traits that may have causative relationships with body size are egg size and reproductive effort. Large species lay large eggs, in part because the ovaries and oviducts scale positively with body size, all else being equal. In this case, then, the interspecific phenotypic correlation between body size and egg size may reflect a positive genetic correlation and a constraint on turtle design.

The positive relationship between body size and reproductive effort may also reflect a genetic correlation between size and life history. Larger species can devote more resources to reproduction in absolute terms and are physically capable of carrying larger quantities of eggs. Indeed, large species produce more clutches within a breeding season than do small species, which implies a larger and more extended energetic commitment to breeding. The large clutches carried by small species are not nearly sufficient to compensate for their low clutch frequency and the small size of their eggs. Large species have larger eggs, and the egg volume within each clutch is larger ($r = 0.957$, $P = 0.0007$), as expected if clutch volume is limited by the size of the carapace.

The mechanism by which some species achieve high reproductive effort relative to their body size involves shortening the interval between remigration events and, to some extent, laying more clutches. Our results show that variation in egg volume or clutch size is not related to reproductive effort. It is tempting to conclude that future increases in size-specific reproductive effort of marine turtles could be achieved only by reducing the remigration interval or increasing clutch frequency. We look forward to the more reliable estimates of remigration interval and clutch frequency that will result from improved tagging techniques and more intensive beach coverage.

Several other traits are not consequences of body size at the species level. For example, one expects egg survival to vary with conditions on the nesting beach rather than because of the size of the female, and as expected we found no correlation between egg survival and female size. Remigration interval was also unrelated to size, suggesting that the unknown nutritional and behavioral factors that control remigration do not include body size.

We found that clutch size was uncorrelated with body size, although this relationship is strongly positive in more inclusive groups of reptiles (Moll, 1979; Dunham et al., 1988). In general, when egg and hatchling survival rates are low, selection will result in a small resource allocation to each of a large number of young (Smith and Fretwell, 1974; Brockelman, 1975; Wilbur, 1977). Sea turtles possess several alternative strategies for overcoming high juvenile mortality, all within the context of relatively large clutches in comparison with other turtles (Wilbur and Morin, 1988). *Dermochelys coriacea* compensates for its small clutch by laying many clutches per year, possibly to spread risk in the face of unpredictable all-or-none egg mortality (Mrosovsky, 1983). *Lepidochelys* turtles have large clutches relative to their body size (Fig. 1) but lay only about two clutches per active year of reproduction.

A different allocation pattern is exhibited by *N. depressa*, unique among sea turtles in that it has a small clutch that is compensated by egg size rather than remigration interval or clutch frequency. *Natatar depressa* lays only half as many eggs per year as most other species. The usual explanation for the large eggs in *N. depressa* is that marsupials do not prey upon turtle eggs in Australia, where this species nests, so the risk of losing the large and valuable eggs is low. Allocation to offspring in *N. depressa* may be designed instead to maximize escape of hatchlings from bird and crab predators, which experience difficulty killing large hatchlings (Limpus, 1971; Bustard, 1972). In fact, some support for this hypothesis comes from data on egg survival, which is higher in *N. depressa* than in any other marine turtle. Hatchling survival data are not available.

Intraspecific comparisons.—Analyses of life-history variation among populations of marine turtles yielded several unexpected results: (1) phenotypic correlations among traits were different at the population level than at the species level; (2) there were important differences among species in the pattern of correlation; and (3) geographic patterns in body size were similar in four species.

Most sea turtles show a significant positive correlation between body size and clutch size, whereas no such pattern exists among species. This situation might develop if variation arises from different sources at the intra- and inter-specific levels. Perhaps body size variation within species is caused by environmental and nutritional differences, whereas body size variation among species is the result of selection for a set of interrelated traits, including size, behavior, and resource allocation. According to this hypothesis, turtles that experience a nutritional advantage grow large and realize their increased reproductive potential by laying more eggs, rather than by adjusting behavioral traits such as remigration interval. In contrast, species differences in body size have evolved simultaneously with adjustments in many other traits. Thus, there is little reason to expect only clutch size to change with body size, at least within such a small set of similar species.

Our findings suggest that the covariance structure of life-history traits cannot be predicted based on the life-history pattern itself. Species that show similar patterns of correlation among traits may not be the same species that show similar average values of those traits (Fig. 3). In particular, *D. coriacea* is different from other species in its morphometric and reproductive measurements, but its phenotypic correlation matrix is most similar to that of *C. caretta*. There is clearly a distinction between a species' life-history traits and the way those traits covary.

There may be evolutionary implications of the different patterns of life-history covariation in different species. To the extent that phenotypic correlations reflect underlying genetic correlations, the different species may respond differently to similar selective regimes. For example, selection favoring increased egg size would cause an increase in the size of adult females in *C. caretta* but a decrease in size in *E. imbricata*. In truth, environmental and genetic causes for life-history correlations are equally plausible, and the evolutionary consequences of species differences in associations among traits must remain speculative.

The geographic distributions of body size in marine turtle breeding colonies showed similar patterns in each of the four species having adequate sample sizes. We suggest several environmental and evolutionary explanations for this result, which make different predictions about geographic patterns of predation and oceanic productivity. Colonies in the Caribbean and western Atlantic tend to contain large turtles, whereas those in the Mediterranean Sea, north Indian Ocean, and eastern Pacific are typically

small. We suspect that the pattern is not caused by size-biased methods of human harvesting, although this explanation is difficult to eliminate. Some regions with small turtles (e.g., north Australia and the Mediterranean) are not known for their heavy exploitation of adults. In other regions with large turtles (e.g., parts of the Caribbean), adults are extensively harvested.

The pattern of body size distribution may arise from nutritional differences that are consistent across species. For example, juvenile growth rates in *C. mydas* are consistently higher in the Caribbean and western Atlantic than in Australian and Hawaiian waters (Boulon and Frazer, 1990), suggesting that populations with large breeding females enjoy superior nutrition in the juvenile stage. This mechanism would be remarkable, however, because adults of the four species consume different foods (Hendrickson, 1980). Thus, one might predict that nutritional differences result from variation in overall productivity within turtle-feeding areas. Estimates of organic production in the oceans do not confirm the expectation that large turtles occur in regions of high productivity (Kennish, 1989). Open tropical oceans typically show low productivity (<50 g C/m²/yr); tropical nearshore waters in the Caribbean, Indian Ocean, and near Australia are slightly more productive (50–100 g C/m²/yr); and a region of high productivity occurs where turtles are especially small on the eastern Pacific continental shelf (200–400 g C/m²/yr). Clearly, the congruent pattern of body sizes in sea turtles cannot be explained simply by marine primary productivity, but some other consistent environmental difference could be responsible.

An alternative explanation for the body size pattern is that all four species have shown similar evolutionary responses to geographic variation in the environment. For example, heavy beach predation on eggs and hatchlings might favor females that produce large numbers of eggs, which could cause a correlated increase in body size, because body size is positively related to clutch size and clutch frequency within most species. Similarly, high predation on adults would reduce the reproductive value of adult females, causing an evolutionary shift toward earlier reproduction at a smaller body size (Williams, 1966; Stearns, 1976). Under this model, populations of large Caribbean turtles have faced higher egg predation or lower adult mortality than have populations of small turtles in several other parts of the world. It should be possible to exclude one or more of these hypotheses with better comparative data on the geographic distributions of survival during different life stages and productivity of turtle food resources.

Implications for demographic models of marine turtles.—We believe that our comparative approach may prove useful for extending demographic models developed for *C. caretta* (Crouse et al., 1987) to less well-known species. There is interest in using population models to evaluate competing conservation strategies for *E. imbricata* and *L. kempi*, because *E. imbricata* has been heavily harvested for the tortoise-shell industry and *L. kempi* has only one nesting population at Rancho Nuevo, Mexico. At this point, the major impediment to progress is that many model parameters have not been estimated for species other than *C. caretta*. Our analyses focus on a mixture of parameters, some of which are not included in the demographic models (e.g., female size and hatchling size) and some of which are incorporated in those models (e.g., clutch size, clutch frequency, and remigration rate). Size- and age-based survivorship estimates would be useful for our analyses here as well as for population modeling, but these data are difficult to acquire.

We propose that the degree of similarity among species in demographic and morphometric parameters summarized in Figures 2 and 3A may give a rough indication of the extent to which conclusions drawn from specific population models can be generalized. If this proves true, then predictions derived from the *C. caretta* model will be more appropriate for *C. mydas* and *E. imbricata* than for other species. Similarly, insights for the management of *L. kempi* might best be obtained by collecting data and formulating a population model for the more common *L. olivacea*. We hope that further comparative studies such as ours will enhance our ability to manage endangered species and populations in the absence of complete information.

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APPENDIX. SEA TURTLE LIFE-HISTORY DATA COLLECTED FROM FEMALES ON BREEDING BEACHES WORLDWIDE. A complete list of the data and literature sources is available upon request from JVB.

Location	Carapace length (cm)	n (or)	Clutch size (eggs)	n (Cl)	Egg diameter (mm)	Egg weight (g)	Egg survival (%)	Incubation period (days)	Hatch carapace (mm)	Hatch weight (g)	Clutch frequency (y/yr)	Reproduction rate (yr)
Green Turtle <i>Chelonia mydas</i>												
Ascension Island	109.8	678	121.4	472	54.6	—	—	59.5	51.7	—	3.0	3.83
Heron Island, Australia	102.4*	1192	113.0	>500	46.0	51.6	0.86	56.0	50.0	21.0	4.5	4.0
Ogasawara, Japan	—	0	110.7	15	46.0	—	—	63.0	—	—	—	—
Mayotte Island, Comoro Archipelago	110.8*	42	121.6	5	44.7	53.0	—	—	—	—	—	—
Moheli Island, Comoro Archipelago	112.3*	51	122.4	7	43.8	—	—	—	49.2	22.7	—	—
Playa Naranjo, Costa Rica	82.9	73	87.0	10	—	—	—	—	51.2	—	—	—
Tortuguero, Costa Rica	100.2	2107	113.1	2519	45.0	—	0.51	55.6	49.7	—	2.8	3.04
Galapagos, Ecuador	81.9	88	80.0	42	—	—	—	—	46.2	—	—	—
Shell Beach, Guyana	103.9	22	122.0	6	47.0	—	—	—	—	—	—	—
Sabah Island, Malaysia	—	0	—	0	—	40.3	—	61.0	49.0	22.1	—	—
Sarawak, Malaysia	97.5	2702	104.7	8000	40.0	36.0	0.47	57.0	50.0	21.2	4.0	3.0
El Cuyo, Yucatan, Mexico	108.0*	10	113.0	19	—	—	0.87	59.0	51.4	—	—	—
Michoacan, Mexico	77.3	—	64.9	1935	—	—	—	—	—	—	2.2	2.31
Quintana Roo, Mexico	—	0	116.0	33	—	—	—	—	—	—	—	—
Primeiras Islands, Mozambique	—	0	115.0	2	43.8	44.9	—	—	—	—	—	—
Masirah Island, Oman	93.2	90	97.0	16	—	—	—	—	—	—	—	—
Ras al Hadd, Oman	97.1	62	103.5	58	—	—	—	—	—	—	—	—
Aldabra Atoll, Seychelles	100.8	186	110.0	—	46.3	—	—	59.0	50.1	28.2	—	—
Europa Island, South Africa	108.7	323	141.2	—	43.5	46.9	0.78	70.0	50.4	25.5	—	—
Tromelin Island, South Africa	104.1	110	129.0	10	44.6	48.0	0.70	—	48.6	23.9	—	—
Sharma Beach, South Yemen	96.0	225	106.0	30	42.4	44.8	—	48.0	46.9	23.0	—	—
Bigi Sont, Surinam	109.0	60	138.0	566	45.0	—	0.69	56.4	51.0	—	2.96	2.52
Mazwi Island, Tanzania	112.9*	109	138.0	—	42.5	—	0.78	58.0	48.0	25.0	—	—
Melbourne Beach, Florida, USA	101.5	90	134.7	229	—	—	0.58	54.0	—	—	3.6	2.0
French Frigate Shoals, Hawaii, USA	92.2	379	104.0	50	44.0	50.0	0.71	64.5	53.0	31.0	1.8	2.47
Aves Island, Virgin Islands	107.7	—	—	0	44.4	45.1	—	—	54.6	27.0	2.61	2.60
Flatback Turtle <i>Natator depressa</i>												
Coberg Peninsula, Australia	—	0	53.0	14	52.1	64.6	—	50.2	—	35.2	—	—
Crab Island, Australia	89.3*	326	56.2	76	50.6	72.7	0.85	—	59.7	39.3	—	—
Curtis Island, Australia	93.9*	42	—	0	51.4	—	—	—	62.1	—	—	—
Mon Repos, Australia	92.3*	14	50.2	87	52.1	77.8	0.76	53.4	61.2	43.6	2.84	2.65
Peak Island, Australia	93.7*	212	54.5	44	—	—	—	—	—	—	—	—
Wild Duck Island, Australia	92.4*	18	51.0	—	51.9	—	—	—	—	—	—	—
Deliverance Island, Torres Strait	88.7*	19	51.9	12	50.8	—	0.83	—	57.0	—	—	—

APPENDIX. CONTINUED.

Location	Carapace length (cm)	n (car)	Clutch size (egg)	n (Cha)	Egg diameter (mm)	Egg weight (g)	Egg survival (%)	Incubation period (days)	Hatch carapace (mm)	Hatch weight (g)	Clutch freq (#/yr)	Reini-grabon ratio (yr)
Hawksbill Turtle <i>Eretmochelys imbricata</i>												
Pasture Bay Beach, Jumby Bay, Antigua	—	0	150.6	61	—	—	0.89	65.6	—	—	4.52	—
Campbell Island, Australia	83.2*	22	131.8	47	36.0	26.0	—	54.5	41.1	14.3	3.0	—
Raine Island, Australia	82.4*	15	111.7	29	36.4	26.4	0.91	—	41.2	14.6	—	—
Milman Island, Australia	81.7*	365	124.1	—	38.4	25.7	0.80	56.9	39.6	—	—	—
Barbados	84.1*	6	134.6	113	—	—	0.83	—	42.1	16.7	—	—
Tortuguero, Costa Rica	82.0	180	158.0	93	38.3	—	0.58	58.6	42.4	—	2.1	3.0
Shell Beach, Guyana	84.1	25	158.1	7	38.0	—	—	—	—	—	—	—
El Cayo, Yucatan, Mexico	96.0*	51	158.0	120	—	—	0.83	63.0	43.0	—	—	—
Palau Island, Micronesia	—	0	104.6	7	34.5	23.0	—	65.0	41.0	13.0	—	—
Masirah Island, Oman	73.3	48	97.0	9	—	—	—	—	—	—	—	—
Cousin Island, Seychelles	89.5*	20	167.5	80	40.0	29.8	0.73	60.6	40.5	—	2.76	2.79
Solomon Islands	80.5	40	137.5	164	—	—	—	64.0	40.0	—	—	—
Jabul Aziz Island, South Yemen	69.5	14	81.2	5	40.5	—	—	—	42.0	—	—	—
Sri Lanka	72.9	3	126.5	2	36.7	—	—	—	—	—	—	—
Seil Ada Kebir, Sudan	66.0	42	73.2	26	40.0	—	—	—	—	—	—	—
Mona Island, Puerto Rico	87.9*	30	148.4	30	38.0	—	0.60	53.5	41.1	15.4	—	—
Buck Island, Virgin Islands	90.1*	20	147.2	99	—	—	0.78	—	—	—	3.1	—
Loggerhead Turtle <i>Caretta caretta</i>												
Heron Island, Australia	95.8*	2207	127.0	1056	40.4	36.5	0.80	—	43.3	20.9	3.5	2.85
Buritaca Beach, Colombia	87.9	78	107.0	185	43.3	38.4	—	—	45.0	—	3.5	2.0
Cephalonia, Greece	77.0	46	102.3	54	38.8	31.4	0.47	—	41.4	—	—	—
Kiparissia Bay, Greece	83.1*	72	117.7	52	—	—	0.90	55.5	—	—	—	—
Zakynthos, Greece	80.4*	27	100.2	9	37.5	—	—	50.7	40.4	—	—	—
Sicily, Italy	—	0	—	0	41.1	25.5	—	—	41.8	20.1	—	—
Gamonda Beach, Japan	89.0	118	—	0	—	—	—	—	—	—	—	—
Quintana Roo, Mexico	—	0	107.6	144	—	—	—	—	—	—	—	—
Masirah Island, Oman	91.2	1378	107.0	161	42.1	—	0.60	50.7	—	—	—	—
Tongaland, Natal, South Africa	87.6	520	114.0	2988	40.9	—	0.78	62.0	44.7	21.0	3.98	2.8
Dalyankoy Beach, Turkey	70.0	—	93.0	50	39.0	20.3	—	57.0	39.9	16.1	—	—
Merritt Island, Florida, USA	92.3	331	110.0	44	42.2	41.8	0.72	—	45.8	21.0	—	—
Everglades, Florida, USA	92.0	75	100.0	79	41.0	—	0.13	—	—	—	—	—
Hutchinson Island, Florida, USA	90.9*	104	120.0	—	—	—	—	65.5	45.2	—	—	—
Melbourne Beach, Florida, USA	92.0	661	113.5	76,506	—	—	0.54	—	—	—	—	2.71
Sanibel Island, Florida, USA	90.4	31	108.0	46	41.1	—	—	56.0	46.7	19.6	—	—

APPENDIX. CONTINUED.

Location	Carapace length (cm)	n (arr)	Clutch size (eggs)	n (Clutch)	Egg diameter (mm)	Egg weight (g)	Egg survival (%)	Incubation period (days)	Hatch emergence (mm)	Hatch weight (g)	Clutch frequency (yr/yr)	Reproductive rate (yr)
Little Cumberland Island, Georgia, USA	95.9 ^a	110	119.8	2126	42.0	—	0.10	—	45.0	—	2.99	2.60
Cape Lookout, North Carolina, USA	92.5	13	119.5	20	—	—	0.74	60.5	—	—	—	—
Topstail Island, North Carolina, USA	—	—	128.4	177	—	—	—	61.2	—	—	—	—
Cape Romain, South Carolina, USA	92.7 ^a	18	118.4	464	42.2	34.9	0.73	55.0	45.0	21.2	—	—
Kiawah Island, South Carolina, USA	93.7	65	122.3	423	42.1	—	0.50	58.0	45.2	—	—	—
Olive ridley turtle <i>Lepidochelys olivacea</i>												
Goberg Peninsula, Australia	—	0	108.0	6	38.8	—	—	50.0	44.0	—	—	—
Playa Nancite, Costa Rica	62.9	453	110.5	10	—	—	—	48.5	—	—	—	—
Playa Naranjo, Costa Rica	65.2	55	105.0	20	—	—	—	50.0	—	—	—	—
Playa Ostional, Costa Rica	—	0	108.2	20	—	—	0.51	—	—	—	—	—
Honduras	66.6	4	102.0	5	37.5	—	—	—	—	—	—	—
Coromandel Coast, India	67.1 ^a	10	114.7	10	—	—	—	55.2	48.8	—	—	—
Hiwassa, Japan	—	—	113.7	10	40.0	—	—	60.0	42.7	—	—	—
Mexico	62.9	—	100.0	—	38.8	—	0.23	46.0	40.3	—	3.0	2.0
Masirah Island, Oman	71.5	100	118.0	22	—	—	—	—	41.9	—	—	—
Sri Lanka	63.5	2	112.5	—	40.5	35.7	—	50.0	42.8	17.0	—	—
Elianti Beach, Surinam	68.5	241	116.1	1154	40.0	—	0.59	55.0	42.0	—	1.42	1.4
Kemp's ridley turtle <i>Lepidochelys kempii</i>												
Rancho Nuevo, Mexico	64.6	203	110.0	271	38.9	30.0	0.61	54.0	42.0	17.3	1.8	1.5
Leatherback turtle <i>Dermochelys coriacea</i>												
Wreck Rock, Australia	162.4 ^a	9	82.8	14	53.2	81.95	0.15	—	58.8	46.9	—	—
Matina, Costa Rica	—	0	80.5	6	53.6	—	—	65.0	62.8	—	—	—
Playa Langosta, Costa Rica	149.0 ^a	94	64.0	225	—	—	—	—	—	—	—	—
Playa Naranjo, Costa Rica	141.0	18	65.6	6	51.0	—	—	—	55.0	—	—	—
Sibache Beach, French Guiana	157.4 ^a	192	88.1	?	—	—	—	—	65.0	—	—	2.12
Trengganu, Malaysia	—	0	82.3	627	—	—	0.63	56.0	57.3	38.2	5.5	2.0
Oaxaca, Mexico	150.0	98	60.1	124	53.0	66.0	0.50	57.0	—	—	—	—
Tongaland, Natal, South Africa	161.1 ^a	122	103.7	59	53.1	—	0.76	67.0	58.7	—	7.27	2.48
Sri Lanka	151.5 ^a	9	97.0	—	52.5	72.0	—	61.0	59.0	93.1	—	—
Bigi Sauti, Surinam	160.0	25	86.0	385	53.0	—	0.52	65.0	58.3	—	—	2.44
Matura Bay, Trinidad	158.0 ^a	20	95.0	—	57.0	—	—	—	67.0	57.5	—	—
Culebra Island, Puerto Rico	147.0	81	75.1	65	53.8	—	0.74	64.7	59.3	—	6.61	—
St. Croix, Virgin Islands	153.6 ^a	39	79.7	541	—	84.0	0.67	62.9	—	46.1	5.28	2.36

^a Over-the-curve carapace length.