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Spatial Distribution of Green Turtle (*Chelonia mydas*) Nests at Tortuguero, Costa Rica

KAREN A. BJORNDAL AND ALAN B. BOLTEN

We monitored spatial distribution of nests of green turtles, *Chelonia mydas*, for three years at Tortuguero, Costa Rica. The beach was divided into three zones from water's edge to supralittoral vegetation depending on the extent of vegetation cover. The extent of shade affects the temperature of the nest and, ultimately, the sex of the offspring in that nest through environmental sex determination. Patterns of nest distribution among beach zones within and among years were evaluated both for the population and for individual turtles. Distribution of nests among the three zones varied among years. Individual turtles that nested three or more times within a season more often deposited clutches in more than one zone than in just one zone. Individual green turtles are more likely to conform to the population's pattern of nest distribution each year than to maintain their own individual pattern between years. Thus, annual factors apparently have a greater effect on nest placement than do individual nesting patterns. The lack of any consistent pattern of nest distribution may result from environmental uncertainty and low predictability of nest success. Because patterns of nest placement are not consistent either for the population or for individuals, we predict that primary sex ratios will vary from year to year for both the Tortuguero population and for the offspring of individual turtles. The distribution of nests of hawksbills, *Eretmochelys imbricata*, at Tortuguero within each year is not different from that of the green turtle.

Hemos vigilado por tres años la distribución espacial de los nidos de las tortugas verdes, *Chelonia mydas*, en Tortuguero, Costa Rica. La playa fue dividida en tres zonas desde el borde del agua hasta la vegetación supralitoral dependiendo del alcance de la protección ofrecida por la vegetación. La cantidad de sombra afecta la temperatura del nido y en última instancia, el sexo de la prole del nido a través de la determinación ambiental del sexo. Las tendencias de distribución de los nidos entre zonas playeras entre épocas del año y de año a año fueron evaluadas para la población y para tortugas individuales. La distribución de los nidos entre las tres zonas varió de año a año. Las tortugas individuales que anidaron tres veces o más dentro de una temporada depositaron puestas mas a menudo en más de una zona que en sólo una zona. Las tortugas verdes individuales se amoldan más probablemente a la tendencia de distribución de nidos de la población cada año que a mantener su tendencia individual de año a año. Por lo tanto, los factores anuales aparentemente tienen un efecto mayor en la colocación del nido que en las tendencias de nidada individuales. La falta de una tendencia consistente en la distribución de los nidos puede ser el resultado de la incertidumbre ambiental y de una baja capacidad de predecir el éxito del nido. Debido a que las tendencias de colocación de los nidos no son consistentes ya sea para la población o para los individuos, podemos predecir que las proporciones primarias de sexo variarán de año a año para la población de Tortuguero y la prole de tortugas individuales. La distribución de los nidos de la tortuga Carey, *Eretmochelys imbricata*, en Tortuguero dentro de cada año, no es diferente de aquella de la tortuga verde.

FOR any egg-laying organism, nest placement has important consequences for reproductive success. When a sea turtle emerges on an oceanic beach to nest, she usually enters

a relatively large, heterogeneous environment in which she must select her nest site. Where she places her nest can affect her reproductive success and fitness through her own survival,

through the survival of her offspring, and through the sex of her offspring.

The largest green turtle (*Chelonia mydas*) colony in the Atlantic nests at Tortuguero, Costa Rica, and has been monitored annually since 1955 (Carr et al., 1978). The beach at Tortuguero has areas of open sand and areas with low-growing plants such as seapurslane (*Sesuvium portulacastrum*), railroad vine (*Ipomea pes-caprae*), and rush grass (*Sporobolus virginicus*). The beach is backed by a dense stand of vegetation, primarily cocoplum (*Chrysobalanus icaco*) and seagrape (*Coccolobis uvifera*). Hirth (1963) describes the beach habitat in more detail.

Within a nesting season at Tortuguero, individual green turtles deposit several clutches at 12-day intervals (Carr et al., 1978), each with a mean of 112 eggs (Bjorndal and Carr, 1989). A number of gradients affecting reproductive success and fitness operate perpendicular to the shoreline. Females that nest at greater distances from the sea may increase the probability of their own mortality from terrestrial predators or entanglement in beach debris, although neither of these sources of mortality is common at Tortuguero (Carr, 1967). Nest loss from tidal inundation or erosion decreases with distance from the surf, but nests deposited near the supralittoral vegetation suffer increased predation (Fowler, 1979). Hatchlings that emerge from nests placed further from the ocean have a longer journey to the sea, during which they are exposed to predation, misorientation, and entanglement. Because green turtles exhibit environmental sex determination (Mrosovsky and Yntema, 1980; Morreale et al., 1982), nest placement can affect sex ratio of hatchlings. At Tortuguero, nests laid in areas shaded by vegetation produce significantly fewer females than nests laid in open areas (Spotila et al., 1987).

We monitored nest placement by green turtles at Tortuguero for three years to determine whether nests were distributed among zones in a pattern that was consistent among years. The beach was divided into three zones: the open, full-sun zone; the border zone between open and vegetation zones, where there is some shading from vegetation; and the vegetation zone, where there is complete shade.

All three zones are used by nesting turtles. Hirth and Samson (1987) compared nesting behavior of green turtles nesting in the three zones at Tortuguero. They found no significant difference in time spent in five nesting stages, except that turtles nesting in vegetation spent less

time covering and camouflaging their nests. They suggested that this abbreviated covering resulted from interference from vegetation and may be one factor in the higher predation rates suffered by nests laid in the vegetation zone.

In this paper, we evaluate distribution of nests among beach zones within and among years both for the population and for individual turtles. We relate these results to (1) the consistency of the primary sex ratio from year to year, and (2) our ability to predict the sex ratios of hatchlings based on patterns of nest distribution among zones by the population and by individual turtles. We do not evaluate the mechanism(s) of nest site selection by female green turtles.

METHODS

At Tortuguero, green turtles are tagged on their front flippers, after they have completed nesting, by tagging teams that patrol the northern-most 8 km of the 35 km beach at hourly intervals every night from early July to mid-Sept. The tags bear identification numbers and identify turtles that return to nest again within that nesting season and turtles that return to nest in later years.

During the 1986, 1987, and 1988 nesting seasons, members of the tagging team recorded the zone where each female nested. Three zones were defined, based on the extent of vegetation cover, which would affect the temperature of the nest. The open zone extended from water's edge and included the area of the beach in which vegetation did not shade the sand. The vegetation zone was the dense stand of supralittoral vegetation where sand was shaded all day. The border zone was between the open and vegetation zones and comprised the area that was partially shaded by vegetation. For all zones in all years, nest distribution was not limited by available space.

Changes in nest distribution within each year were evaluated by dividing each nesting season into six, sequential, 12-day intervals. We used a 12-day interval because that is the average interval between successive clutches in individual green turtles at Tortuguero (Carr et al., 1978).

The data were analyzed using one-sample and k-sample chi-square tests and, in cases where expected cell size was less than five, with Fisher exact probability tests (Siegel, 1956; Statistical Analysis Systems [SAS], 1982; Zar, 1984). Although data are presented as percentages in the

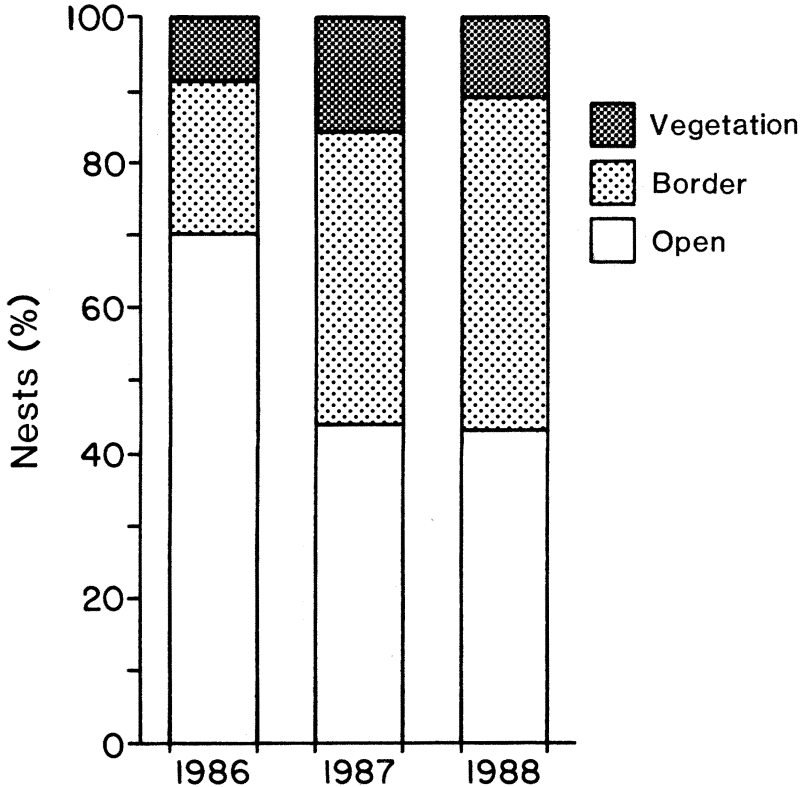


Fig. 1. Distribution of green turtle nests among three beach zones in 1986 ($n = 6624$), 1987 ($n = 1395$), and 1988 ($n = 4563$) at Tortuguero, Costa Rica.

figures to facilitate visual comparison, all statistical tests were run on actual values. Unless otherwise stated, $\alpha = 0.05$.

RESULTS

Nesting density varied considerably among the three years. The numbers of nests recorded in 1986, 1987, and 1988 were 6624, 1395, and 4563, respectively. Wide fluctuations in nesting density in successive years have been observed at Tortuguero since 1975 (unpubl. data).

The distribution of nests in the three zones in each year (Fig. 1) varied significantly among the three years (two-sample chi-square, $df = 2$, $P < 10^{-6}$ for each pair of years). In 1986, over three times as many clutches were deposited in the open zone as in the border zone, but in 1987 and 1988, the proportions of nests in the open and border zones were nearly equal.

Within each year, the distribution of nests laid in each of the three zones varied significantly among the six, sequential, 12-day inter-

vals (Fig. 2; six-sample chi-square, $df = 10$, $P < 0.0001$ for each year). However, there is no consistent trend in the relative distribution of nests among the three zones during the nesting season (Fig. 2).

We analyzed multiple nesting within a year for 2795 green turtles to evaluate patterns and consistency of nest distribution of individual turtles. We recorded 1657 turtles nesting twice, 736 turtles nesting three times, 280 turtles nesting four times, 105 turtles nesting five times, 16 turtles nesting six times, and one turtle nesting seven times. Numbers of turtles that placed all clutches in the same zone (consistent) were compared against the numbers of turtles that placed clutches in more than one zone (inconsistent). For the two-clutch nesters, there was no significant difference between the number of consistent and inconsistent nesters (chi-square, $df = 1$, $P = 0.12$). For the three-, four-, five-, and six-time nesters, there were significantly more inconsistent than consistent nesters (chi-square, $df = 1$, $P < 0.001$ for each group).

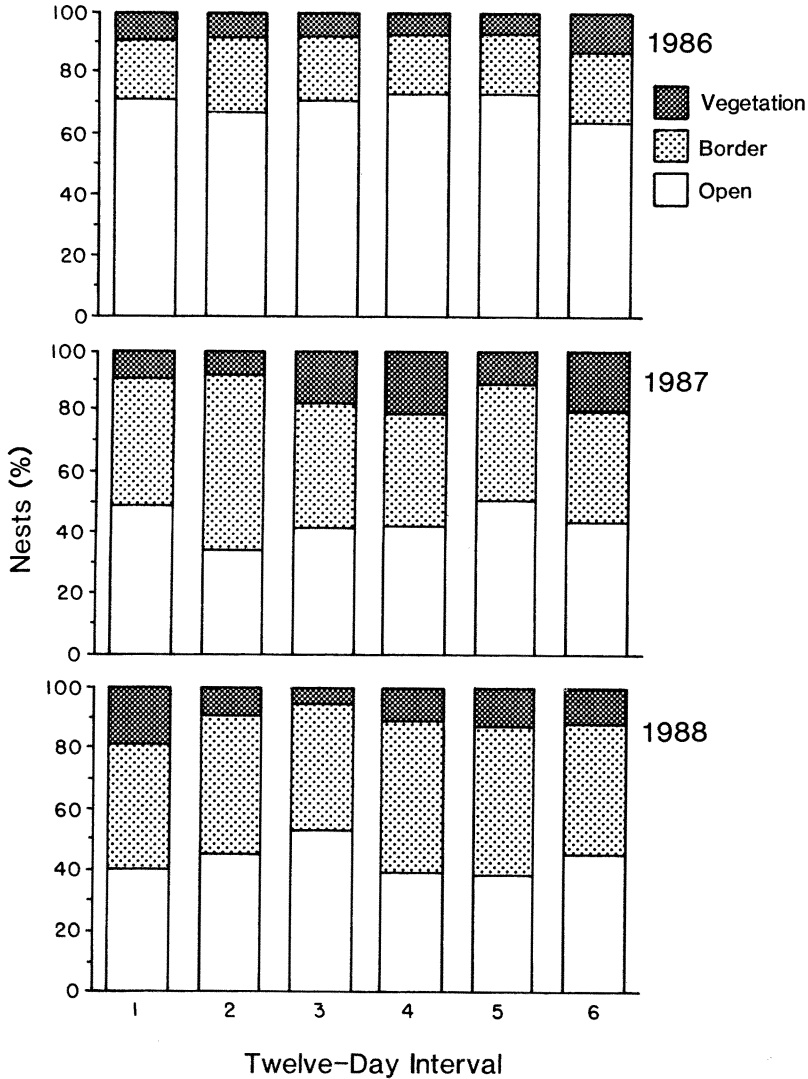


Fig. 2. Distribution of green turtle nests among three beach zones in each of six, sequential, 12-day intervals in 1986, 1987, and 1988 at Tortuguero, Costa Rica.

The turtle that nested seven times nested in more than one zone.

To determine whether consistent nesters varied among years in the zone most often used, we compared distribution of nests in each year by three- and four-time consistent nesters. We only examined three- and four-time nesters because two-time nesters had not nested a sufficient number of times to establish a strong consistent pattern, and sample size was too small for five- and six-time nesters. The vegetation zone had the fewest nests laid by consistent nesters. Only one multiple nester, a three-time nest-

er in 1988, consistently placed clutches in the vegetation zone. Of the turtles that nested consistently within one zone, a greater proportion nested in the open zone in 1986 than in 1987 or in 1988 for both three-time and four-time nesters (two-sample chi-square or Fisher exact probability test when expected value less than five, $df = 1$, $P < 10^{-6}$). Proportions of turtles nesting consistently in the open zone or border zone in 1987 were not significantly different from those in 1988 for both three- and four-time nesters (two-sample chi-square).

To further elucidate the patterns of clutch

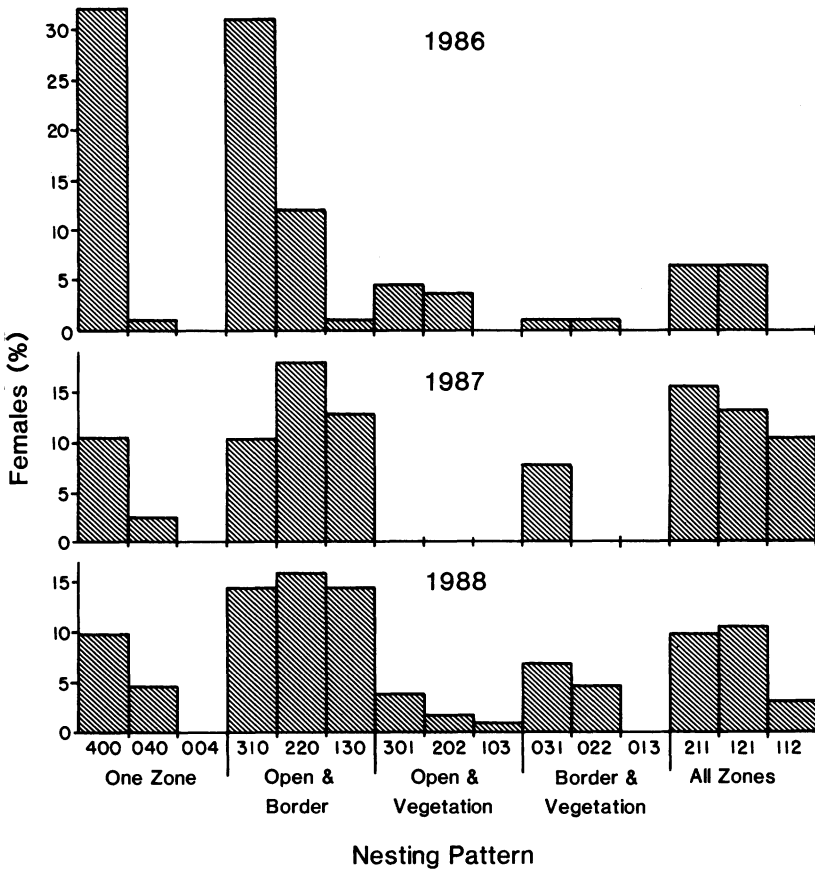


Fig. 3. Patterns of nest distribution by green turtles nesting four times in 1986 (n = 109), 1987 (n = 39), and 1988 (n = 132) at Tortuguero, Costa Rica. The code below each bar indicates the number of nests in the open zone, border zone, and vegetation zone successively. For example, "130" represents one nest in the open zone, three nests in the border zone, and no nest in the vegetation zone. These nesting patterns are grouped into five "strategies" (see Fig. 4).

distribution of individual females, we plotted distribution of nests for four-time nesters in each year (Fig. 3). We chose four-time nesters because, for many of these females, we have recorded all clutches and the sample size is large (280 for the three years combined). Because of the small sample sizes in some of the categories, categories were combined for statistical analysis into five "strategies" of clutch placement. Females can place all clutches in one zone, clutches in all three zones, or clutches in only two zones (three separate strategies): open and border, border and vegetation, and open and vegetation. The distribution of these five strategies, each of which have three possible zone combinations for four-time nesters (Fig. 3), differs significantly among years (Fig. 4, three-sample chi-square, $df = 8, P < 0.0001$).

To assess whether individual green turtles maintain similar nesting patterns between successive breeding years, we compared nest distribution for those green turtles for which we had data in two nesting years. In 1988, we recorded nest placement for 350 turtles for which we also had data in 1986 (=interyear turtles). For the 58 turtles for which we recorded three or more clutches in both 1986 and 1988, there is no significant difference between the number of turtles that used the same zones in different years and those that shift in their zone use between years (two-sample chi-square, $df = 1$). For those turtles that used the same zones in both years, seven nested only in the open zone, 12 nested in both the open and border zones in both years, and four nested in all three zones in both years.

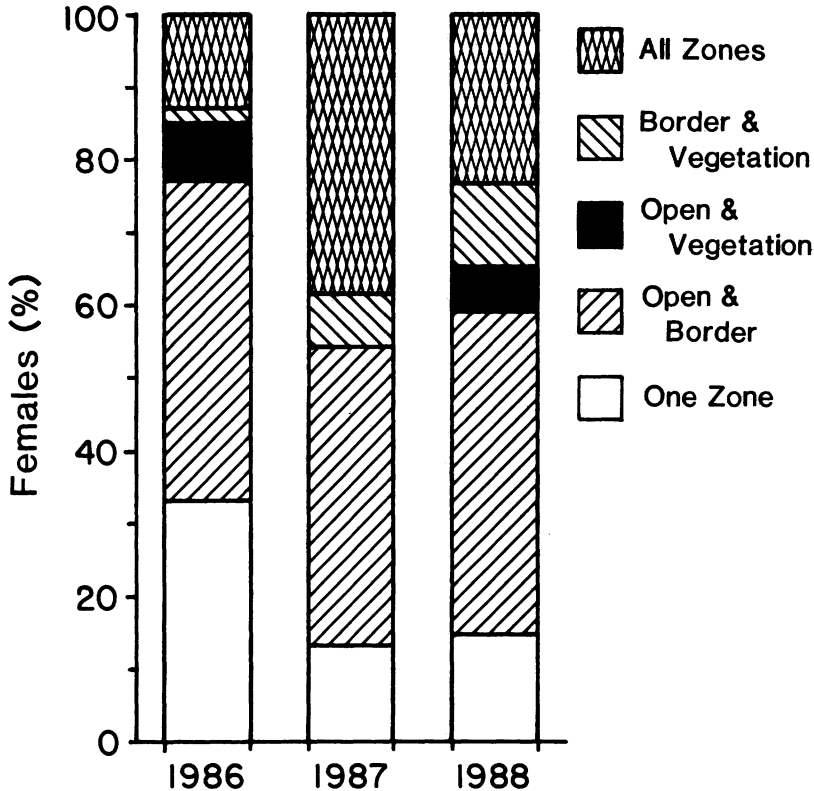


Fig. 4. Distribution of green turtles nesting four times in 1986, 1987, and 1988 among five nesting strategies at Tortuguero, Costa Rica. A female can either place her clutches in all three zones, in any two zones (three possible strategies) or in only one zone.

To determine whether inherent individual nesting patterns or annual factors had greater influence on nest placement, we evaluated whether interyear turtles maintained their individual patterns between years or exhibited patterns consistent with the population for that year. The 350 interyear turtles exhibited significantly different patterns of nest distribution between 1986 and 1988 (two-sample chi-square, $df = 2$, $P < 10^{-6}$). Patterns of nest distribution were not significantly different between 1986 interyear turtles and all turtles in 1986 (two-sample chi-square, $df = 2$, $P = 0.679$) or between 1988 interyear turtles and all turtles in 1988 (two-sample chi-square, $df = 2$, $P = 0.463$). Thus, annual factors had a greater effect on nest placement than did inherent individual nesting patterns.

A small population of hawksbills, *Eretmochelys imbricata*, nests at Tortuguero (Bjorndal et al., 1985). Because of the small sample size for

hawksbills, we combined the border and vegetation zones into one "shade-affected" zone. We recorded nest placement for three nests (two open, one shade) in 1986, eight nests (five open, three shade) in 1987, 11 nests (three open, eight shade) in 1988, and six nests (three open, three shade) in 1989. We compared the relative nest distribution in these two zones by hawksbills and green turtles. There was no significant difference between nest placement in hawksbills and green turtles in 1987 (Fisher exact probability test, $P = 0.24$) or in 1988 (Fisher exact probability test, $P = 0.23$). We did not test distributions in 1986 because of small sample size.

DISCUSSION

Nest distribution among zones.—Our primary objective in analyzing these data was to determine whether green turtles nesting at Tortuguero are consistent in their pattern of nest distribu-

tion among zones. We found that pattern of nest distribution is not consistent, either at the population level (Fig. 1) or at the individual level. The 350 females for which we had clutch placement data in both 1986 and 1988 varied significantly in their nest distribution between years and did not differ significantly from the population's pattern in each respective year. Thus, environmental factors (e.g., rainfall) apparently have a greater effect on nest placement for an individual green turtle than any individual pattern of choice.

Distribution of nests among the three zones varies among years. In 1986, a higher proportion of nests were placed in the open zone than in 1987 or 1988 (Fig. 1). The 1986 nesting season (July, Aug. and Sept.) had greater rainfall (2178 mm) than either 1987 (1518 mm) or 1988 (1086 mm) (K. Horikoshi, unpubl.). In 1988, the driest of the three years, some females made a number of attempts to dig nest chambers in the open zone without success because the dry sand would continually collapse the sides of the nest chamber. They would continue to walk and make nesting attempts until they reached the border or vegetation zone where, because of greater sand moisture near the vegetation, they were able to construct a nest chamber successfully (C. Lagueux, pers. comm.). Mortimer (1990) reported that green turtles at Ascension Island also must make repeated nesting attempts in dry sand. Therefore, sand moisture levels may be partially responsible for the greater relative numbers of nests in the border and vegetation zones in 1987 and 1988 relative to 1986 when the open zone may have been more acceptable as nesting habitat because of higher rainfall.

Patterns of clutch placement for individuals within a year (Fig. 3) reflect the population's pattern each year. In 1986, within each of the five strategies, those combinations that had high representation of the open zone tended to be more common (Fig. 3). In 1987 and 1988, combinations of open and border zones tended to be more common, as were combinations of all three zones (Fig. 3).

Nest distribution and predictability of nest success.—A female has only a limited ability to assess the current nesting environment when selecting a nest site, and changes in the nesting environment over the 60-day incubation period are unpredictable. This environmental uncertainty and

the inability of the female to assess the habitat in terms of ultimate hatching success may be responsible for the lack of any consistent patterns in nest distribution at Tortuguero.

In a long-lived species that cannot accurately assess the nesting environment, it may be better to select a nest site on the basis of the survivorship of the adult female rather than on the survivorship of the egg clutch. For example, at Ascension Island, green turtles nest on a series of small, cove-head beaches that vary greatly in mean hatching success. Nesting density on these different beaches was negatively correlated with hatching success and most strongly correlated with offshore approach (Mortimer, 1982). Those beaches with clear, unobstructed approaches were used to the greatest extent. Females are sometimes killed by becoming entrapped in or smashed against rocky approaches (Mortimer, 1982).

Nest placement in olive ridleys, *Lepidochelys olivacea*, is also not correlated with nest success. Nest distribution among beach zones by olive ridleys nesting at Ostional, Costa Rica, does not appear to be affected by differential hatching success (Acuña M., 1983).

Distribution of nests has received greatest attention in leatherbacks, *Dermochelys coriacea*, probably because large proportions of leatherback clutches are often lost to erosion and tidal inundation (Schulz, 1975; Mrosovsky, 1983; Eckert, 1987). From 2.5–40% of clutches in different leatherback populations are placed below high tide line and suffer almost complete mortality (Mrosovsky, 1983). Leatherbacks commonly nest on extremely unstable beaches. Perhaps in response to this environmental unpredictability, leatherbacks exhibit wide nest dispersal or a "scatter nesting" strategy both at the population level (Mrosovsky, 1983) and at the level of the individual turtle (Eckert, 1987).

Differential nest distribution by species.—In a study of green turtles and leatherbacks in Suriname, Whitmore and Dutton (1985) found that the distribution of green turtle clutches varied between the two years of the study and that green turtles nested higher on the beach than did leatherbacks. They hypothesized that green turtles avoided the area used by leatherbacks because the shallower nests of the green turtles would have a greater chance of being destroyed by nesting leatherbacks that dig much deeper nests.

At Tortuguero, the leatherback nesting season precedes that of the green turtle, but the nesting season of a small hawksbill population overlaps with that of the green turtle. The distribution of nests between open and "shade-affected" beach zones does not differ between green turtles and hawksbills. Although hawksbills dig more shallow nests than do green turtles, hawksbills apparently do not avoid the areas most used by green turtles. The tendency of hawksbills to nest in the open zone as often as in the shade-affected zone at Tortuguero contrasts with nest distribution at other nesting beaches, where hawksbills tend to nest under dense vegetation (Mortimer, 1982; Witzell, 1983).

Conclusions.—There is no consistent pattern of green turtle nest distribution among zones at Tortuguero. This lack of consistency may result from environmental uncertainty and low predictability of nest success. Annual or environmental factors apparently have a greater effect on nest placement than do individual nesting patterns. At Tortuguero, the sex ratio of hatchlings in a nest is affected by the zone in which the clutch is deposited (Spotila et al., 1987). However, the primary sex ratio at Tortuguero cannot be predicted by only measuring temperatures in the zones. Because patterns of nest distribution are not consistent among years, nest distribution among zones must also be determined each year. Also, we would predict that neither individuals nor the population will produce hatchlings with consistent sex ratios from year to year.

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Reproductive Ecology of the Inland Silverside, *Menidia beryllina*, (Pisces: Atherinidae) from Blackwater Bay, Florida

DOUGLAS P. MIDDAUGH AND MICHAEL J. HEMMER

The reproductive ecology of the inland silverside, *Menidia beryllina*, was studied during Feb. 1988–March 1989 at Robinson Point, Blackwater Bay, Florida. Environmental variables including pH, rainfall, salinity, water temperature, and dissolved oxygen were measured weekly or biweekly. Fish were sampled weekly with a seine designed to catch adult, juvenile, and young-of-the-year (YOY) individuals. Most reproductive activity occurred during Feb.–April 1988. The maximum mean weekly female gonadosomatic index (GSI) of 12.5 occurred in April. Fecundity ranged from 63 to 419 hydrated eggs/female. The maximum mean weekly male GSI of 6.1 occurred in early March. Catches of YOY individuals 7.6–37.5 mm SL were greatest in May. Some of these YOY individuals matured in July–Sept. and spawned. This reproductive activity resulted in recruitment of a second group of YOY fish into the population during Aug.–Oct. Growth rates of YOY in May–July, calculated by regression methods from weekly frequency distributions of standard length, was 0.34 mm/day for females and 0.31 mm/day for males.

The reproductive pattern of *M. beryllina* from Blackwater Bay, Florida indicates that qualitatively it is an r-strategist with rapid growth of YOY, sexual maturation at an early age, relatively high fecundity, and multiple spawnings within the first reproductive period for YOY fish in July–Sept. and again as 1- to 1-plus-year-old individuals.

THE inland silverside, *Menidia beryllina*, occurs in estuaries, coastal rivers, and lakes from Massachusetts to Vera Cruz, Mexico, and is also found in the Mississippi River Basin (Gosline, 1948; Rubinoff and Shaw, 1960; Johnson, 1975). It was introduced to Clear Lake, California, in 1967 (Cook and Moore, 1970) and has since moved to the Sacramento–San Joaquin River system and into San Francisco Bay (Moyle et al., 1974; Wang, 1981).

The reproductive season varies according to latitude and, apparently, water temperature. Sexually mature *M. beryllina* are found in Rhode Island for several weeks in June and July (Bengt-

son, 1984). In New Jersey, *M. beryllina* spawns from May through July (Coorey et al., 1985), in North Carolina from March to Sept. (Hildebrand, 1922), and in Tampa Bay, Florida, in all months except Aug. and Jan. (Springer and Woodburn, 1960). In coastal Texas, Gunter (1945) reported sexually mature females from Feb. through Aug. with spawning peaks during spring and late summer. Springer and Woodburn (1960) also reported two apparent spawning peaks (April and again in Sept.–Oct.) but were puzzled by intense breeding only during two comparatively brief periods as ripe females were taken throughout the year in Tampa Bay.