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ORIENTATION TO OCEANIC WAVES BY GREEN TURTLE HATCHLINGS

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Summary

Minutes after emerging from underground nests, hatchling green turtles (*Chelonia mydas* L.) enter the sea and begin a migration towards the open ocean. To test the hypothesis that migrating hatchlings use wave cues to maintain their seaward headings, we released turtles offshore during unusual weather conditions when waves moved in atypical directions. Hatchlings swam into approaching waves in all experiments, even when doing so resulted in orientation back towards land. These data suggest that green turtle hatchlings normally maintain seaward headings early in the offshore migration by using wave propagation direction as an orientation cue. Because waves and swells reliably move towards shore in shallow coastal areas, swimming into waves usually results in movement towards the open sea.

The physiological mechanisms that underlie wave detection by sea turtle hatchlings are not known. Calculations indicate that, at the depth at which hatchlings swim, accelerations produced beneath typical waves and swells along the Florida coast are sufficient to be detected by the vertebrate inner ear. We therefore hypothesize that hatchlings determine wave direction while under water by monitoring the sequence of horizontal and vertical accelerations that occur as waves pass above.

Introduction

Sea turtle hatchlings emerge from underground nests on oceanic beaches, scramble into the sea, and swim towards the open ocean in a migration lasting several days. Hatchlings establish an offshore course a few minutes after entering the sea, then maintain the seaward heading even after swimming beyond sight of land (Frick, 1976; Ireland *et al.* 1978).

Recent experiments have demonstrated that loggerhead sea turtle hatchlings (*Caretta caretta* L.) can orient using the magnetic field of the earth (Lohmann, 1991). Initial experiments in the field, however, have suggested that neither loggerhead (Salmon and Lohmann, 1989) nor green turtle hatchlings (Lohmann

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et al. 1990) rely on magnetic cues during the initial phase of the offshore migration. Instead, hatchlings tethered offshore in floating orientation arenas consistently swam towards the direction of wave approach (Salmon and Lohmann, 1989; Lohmann *et al.* 1990). Wave tank experiments have confirmed that tethered hatchlings will readily orient to waves in the laboratory (Lohmann *et al.* 1990; Wyneken *et al.* 1990).

Although these experiments clearly demonstrated that hatchlings can use waves as an orientation cue, the restraint of the tethering system used in earlier field experiments (Salmon and Lohmann, 1989; Lohmann *et al.* 1990) might conceivably have altered the normal orientation behavior of the turtles or precluded use of other, as yet unidentified, cues. To determine whether green turtle hatchlings also use wave cues to maintain seaward orientation when unrestrained, we released hatchlings offshore during unusual weather conditions when waves moved away from shore or in other uncommon directions. Hatchlings swam into the approaching waves regardless of wave propagation direction. These results are consistent with the hypothesis that wave direction is indeed the primary orientation cue employed by hatchlings in the initial stages of the offshore migration (Salmon and Lohmann, 1989). Because waves move in reliable and predictable patterns over large areas of the ocean surface (Bascom, 1980), they could also represent an important open-sea orientation cue for sea turtles and other long-distance ocean migrants such as fish and cetaceans.

Materials and methods

Animals

Hatchling green turtles (*Chelonia mydas* L.) were obtained from nests deposited on beaches in the vicinity of Fort Pierce or Boca Raton, Florida, USA. Each morning during the nesting season, a beach patrol identified green turtle nests deposited the night before, marked each nest site, and noted the date of deposition. Nests were then checked daily as the time of expected emergence neared. When a depression formed in the sand above the eggs (indicating that the eggs had hatched and that emergence would probably occur that evening), we gently dug into the sand by hand and extracted 12–24 hatchlings. The turtles were placed into styrofoam coolers and transported within 1 h to a laboratory at the Harbor Branch Oceanographic Institution (in Fort Pierce) or to Florida Atlantic University (in Boca Raton). All turtles were tested and released within 48 h of capture.

Transport of hatchlings offshore

All experiments were conducted between 10:00 h and 17:00 h at distances of 7.4–11.1 km offshore near Fort Pierce or 4.6–5.6 km offshore near Boca Raton. The sun and at least some blue sky were visible during all experiments. Hatchlings were placed in styrofoam coolers lined with damp paper towels and transported offshore by motorboat. The lids of the coolers were left ajar to ensure adequate ventilation, but the coolers were kept beneath the canopy of the boat where hatchlings could not see the sky.

Assessment of wave direction and weather conditions

Immediately before and after each experiment, detailed notes were made of wind, wave and weather conditions. At each offshore position, latitude, longitude and distance from shore were recorded using a Loran C recorder system accurate to within 6 m. Wind speed was measured using a mechanical wind gauge (Davis Turbometer). Wind direction was determined by mounting a length of yarn on a pole and sighting along the yarn using a handheld digital compass (Autohelm). Wave direction was measured by sighting down the axis of wave propagation with the digital compass (Lohmann *et al.* 1990). When more than one wave type could be discerned, we calculated the mean wave direction using the procedures of Lohmann *et al.* (1990).

Treatment of hatchlings before experiments

In all but two releases (see below), hatchlings were placed into a plastic bucket filled with sea water at least 15 min prior to release. This step was taken because (1) hatchlings released into a floating orientation cage in previous experiments (Lohmann *et al.* 1990) usually dove or circled for their first several minutes in the water before establishing a course, and (2) preliminary experiments indicated that dry hatchlings placed directly into the ocean often dove and disappeared from view before their orientation could be assessed, whereas hatchlings that had been in water for several minutes before release usually swam within 0.5 m of the surface (as hatchlings normally do while migrating offshore).

In two releases, we compared the orientation of hatchlings placed in water beforehand with that of nestmates kept dry until release. In each case hatchlings were obtained from a single nest; half were placed into a bucket of sea water at least 15 min before the trial (as before), while the other half remained in a styrofoam cooler lined with damp paper towels. Hatchlings from the two groups were then released into the ocean alternately (i.e. first a turtle from the wet group, then one from the dry group, then a wet hatchling, and so on).

Assessment of orientation

Hatchlings were dropped over the side of the boat so that they entered the water approximately 1.5 m away. Swimming sea turtle hatchlings reportedly ignore nearby boats and swimmers and do not change course to avoid them (Frick, 1976; Salmon and Wyneken, 1987; Salmon and Lohmann, 1989). Nevertheless, we released turtles alternately to the north and south of the boat to reduce possible directional biases that could result if hatchlings consistently sought to avoid the boat. Evidence of such biases was not found (see Results).

After each hatchling had been released, two observers began independently recording its directional heading. Each observer was equipped with an Autohelm handheld digital compass which recorded the bearing of the turtle each time a button was pressed. Readings were recorded approximately once per second until the turtle disappeared from view. The last bearing obtained by each observer was recorded; a vanishing bearing for each turtle was then calculated as the mean of these two measurements. Vanishing bearings for each group were analyzed using the Rayleigh test (Batschelet, 1981) to determine whether the turtles were significantly oriented as a group.

Calculations of water mass accelerations beneath waves

The accelerative forces a swimming green turtle hatchling might experience when a wave passes overhead were calculated using the procedures of Cook (1984). The equations for calculating the horizontal component (**U′**) and vertical component (**W′**) of acceleration experienced by a swimming turtle are:

$$\mathbf{U}' = Kagk\cdot\frac{\cosh k(h+z)}{\cosh kh}\cdot\cos(K\sigma t)$$

and

$$\mathbf{W}' = Kagk\cdot\frac{\sinh k(h+z)}{\cosh kh}\cdot\sin(K\sigma t)\,,$$

where $K=(F\sin\theta)/C-1$, F is swimming speed, θ is angle to the wave crest, C is wave celerity, a is wave amplitude, $\mathbf{g}$ is acceleration due to gravity, k is wave number, h is depth of water, z is depth of turtle below surface, σ is wave frequency and t is time.

The calculations assumed typical wave parameters near the east coast of Florida during August, the first month of the green turtle hatching season; these include wave heights of 0.5–1 m and a wave period of 5 s (Hogben and Lumb, 1967). We also assumed an average hatchling swimming depth of 20 cm (Frick, 1976), an average swimming speed of 43.6 cm s^{-1} (Frick, 1976) and a swimming course in the same direction that the waves moved (so that the calculated accelerations represent the minimum a turtle would encounter).

Results

Swimming behavior after release

Upon release into the ocean, hatchlings usually submerged for 5–30 s. During this time most turtles (approximately 90 %) remained within 1 m of the surface and were easily visible from the boat. A few turtles (5–10 %) dove to greater depths and were immediately lost from view; no data were obtained for these hatchlings.

After resurfacing from their initial dive, hatchlings usually paddled with their heads above water for about 5–20 s before beginning to swim rapidly just below the surface. Some hatchlings then immediately established courses into the waves and did not deviate from them during our observations. Others started on initial courses that did not lead into the waves (but were nearly always within ±70° to the direction of wave approach); in these cases, hatchlings typically changed course once or twice during the next minute before establishing a course that they maintained consistently until vanishing from sight. Adoption of the 'final' course was often associated with a marked increase in swimming speed. Between 45 and 150 s typically elapsed between the time a hatchling was released and the time it swam out of sight (at a distance of about 30–50 m from the boat).

Orientation

In 10 of 11 sets of releases, there was no significant difference (Watson test, using $P<0.05$ as criterion) between the orientation of hatchlings released north and south of the boat. These data suggest that the position of release with respect to the boat had little or no effect on the orientation of hatchlings under the experimental conditions. Data from turtles released to the north and south each day under otherwise identical conditions were therefore combined.

Results of three different releases conducted on days when waves moved in a typical onshore direction are shown in Fig. 1. In each experiment hatchlings oriented in a seaward direction and towards the approaching waves; mean angles of orientation for the three groups of hatchlings ranged from 65° to 92°, similar to the range of directions for wave approach (74–104°).

Results of four releases conducted when waves moved in directions other than directly towards land are shown in Fig. 2. In each case, the mean angle of orientation was within 21° of the direction of wave approach. In one experiment in which waves moved almost directly away from land and towards the open sea, hatchlings swam back towards land (Fig. 2C).

In two different releases, the orientation of hatchlings kept dry prior to release was compared to that of nestmates previously placed in sea water. In both cases, the 'wet' group was significantly oriented (Rayleigh test, $P<0.001$) and swam towards approaching waves (Fig. 3A,C), whereas the orientation of the 'dry' turtles was statistically indistinguishable from random (Fig. 3B,D). The vanishing bearings of the dry hatchlings were significantly more dispersed ($P<0.001$ in the first experiment, $P<0.025$ in the second) than those of the wet hatchlings (Wallraff's modified Wilcoxon–Mann–Whitney U-test; Batschelet, 1981).

The mean angles of orientation for all releases (excluding the hatchlings kept dry prior to release) are plotted as a function of the direction of wave approach in Fig. 4. Circle–circle correlation analysis (Batschelet, 1981) indicated that wave direction and hatchling orientation were significantly related ($P<0.001$).

Calculation of accelerations beneath waves

The vertical and horizontal accelerations that a migrating green turtle hatchling presumably encounters while swimming beneath typical Florida waves are plotted in Fig. 5. For waves 1 m in height, the peak accelerations of approximately 72 cm s^{-2} (Fig. 5) easily exceed the minimum linear acceleration of 5 cm s^{-2} that can be detected by the vertebrate inner ear (Lewis *et al.* 1985). Even smaller waves of 0.5 m would produce accelerations that exceed this threshold (Fig. 5).

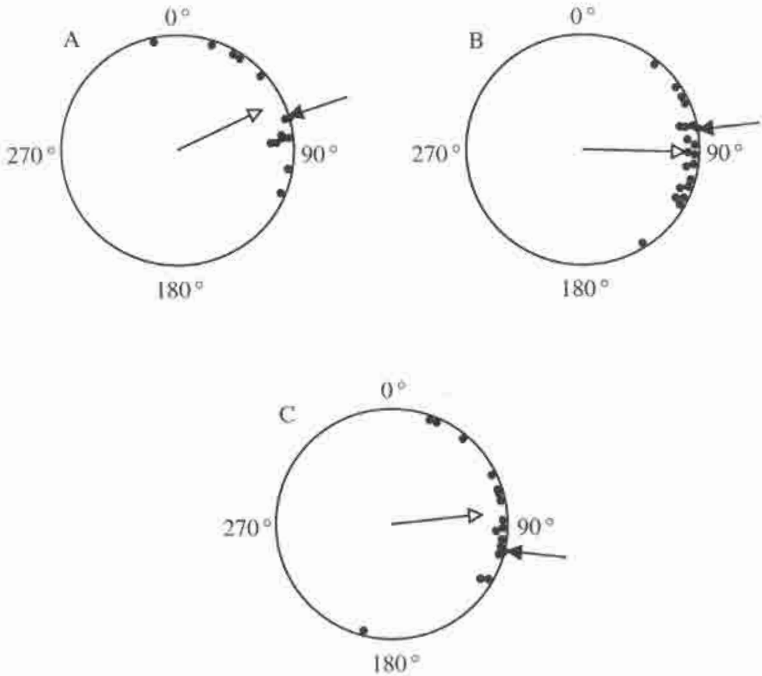

Fig. 1. Results from releases of green turtle hatchlings when waves approached from the east. Filled circles indicate the mean vanishing bearing of each turtle. Open-headed arrows indicate the mean orientation angle of each group; the length of each arrow is proportional to the r-value (mean vector length). Filled arrows indicate the direction of wave approach (mean wave angle) during each set of releases. (A) The direction of wave approach was 74°. The turtles were significantly oriented as a group with a mean orientation angle of 65° (r=0.82, z=8.74, P<0.001, Rayleigh test). (B) The direction of wave approach was 80°. The turtles were significantly oriented as a group with a mean angle of 92° (r=0.90, z=16.20, P<0.001). (C) The direction of wave approach was 104°. The turtles were significantly oriented as a group with a mean angle of 85° (r=0.78, z=9.73, P<0.001).

Discussion

Orientation to waves

The results provide strong evidence that unrestrained hatchlings orient by swimming into approaching waves when released offshore. The mean angle of orientation for turtles in each experiment was strongly correlated with wave direction (Figs 1, 2, 3A,C, 4). Hatchlings swam into waves even when doing so resulted in orientation back towards land instead of out to sea (Fig. 2C).

These results are consistent with data obtained using tethered green turtle (Lohmann *et al.* 1990), leatherback (Lohmann *et al.* 1990) and loggerhead (Salmon and Lohmann, 1989) hatchlings restrained inside a floating cage. The present results suggest that the behavior of tethered hatchlings accurately reflects

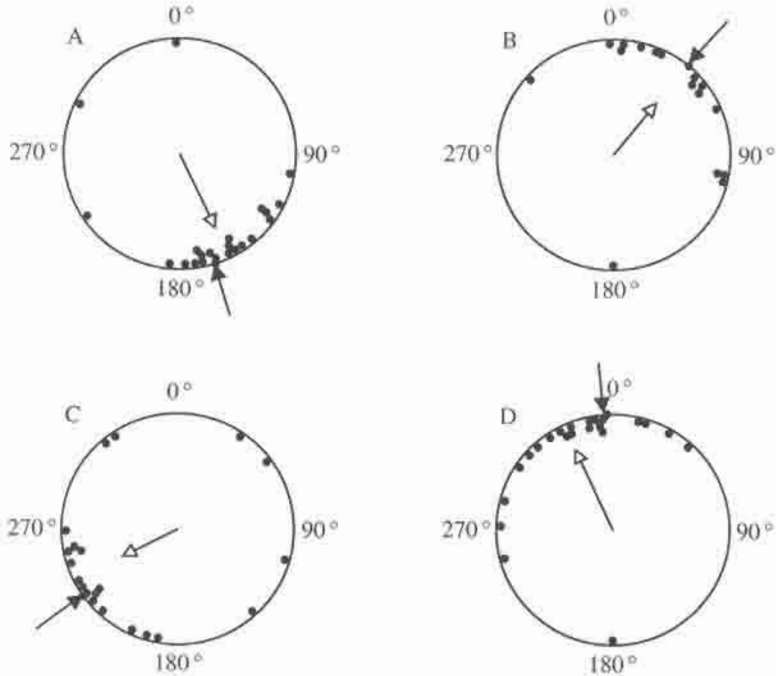

Fig. 2. Results from releases of green turtle hatchlings when waves moved in unusual directions. Conventions as in Fig. 1. (A) The direction of wave approach was 162°. The turtles were significantly oriented as a group with a mean orientation angle of 154° (r=0.72, z=11.40, P<0.001). (B) The direction of wave approach was 40°. The turtles were significantly oriented as a group with a mean orientation angle of 41° (r=0.58, z=5.38, P=0.003). (C) The direction of wave approach was 234°. The turtles were significantly oriented as a group with a mean orientation angle of 241° (r=0.54, z=6.12, P=0.002). (D) The direction of wave approach was 357°. The turtles were significantly oriented as a group with a mean orientation angle of 336° (r=0.74, z=12.05, P<0.001).

the behavior of free-swimming turtles; hatchlings tested under both conditions oriented towards waves.

As waves enter shallow water and approach shore, the propagation direction is refracted until it is nearly perpendicular to the beach (Denny, 1988). Thus, for hatchlings entering the ocean under natural conditions, swimming into waves reliably results in offshore movement. Several marine crustaceans (Walton and Herrnkind, 1977; Nishimoto and Herrnkind, 1978) and molluscs (Hamilton and Russell, 1982; Gendron, 1977) are also known to use waves or wave surge (the horizontal oscillation of water near the sea floor) as an orientation cue in shallow water.

In deeper water far from shore, wave and swell direction often still provide a consistent directional cue for orientation. Because swells originate in the open ocean and move great distances before reaching shore, swell direction is

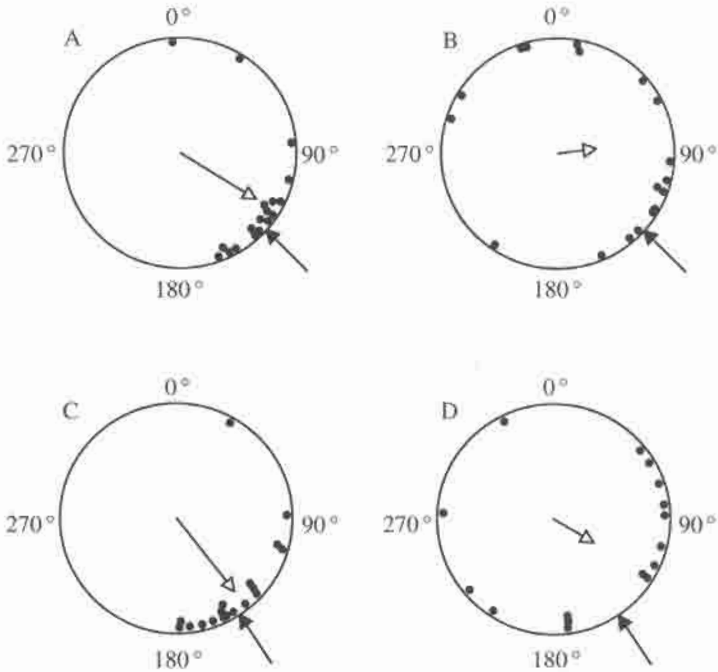

Fig. 3. Comparison of results from two methods of handling turtles prior to release. Turtles were kept either in sea water for at least 15 min before release ('wet' turtles) or in a styrofoam cooler without water ('dry' turtles) and then released alternately during the same trial. Conventions as in Fig. 1. (A) Results from 'wet' turtles released when the direction of wave approach was 132°. These turtles were significantly oriented as a group with a mean orientation angle of 123° (r=0.79, z=11.23, P<0.001). (B) Results from 'dry' turtles released alternately during the same trial as the turtles in A. These turtles were not significantly oriented (r=0.35, z=2.20, P>0.10). Walraff's modified Mann–Whitney U-test (Batschelet, 1981) indicated that the orientation angles of dry hatchlings were significantly (P<0.001) more dispersed than those of the wet turtles. (C) Results from 'wet' turtles released when the direction of wave approach was 147°. These turtles were significantly oriented as a group with a mean orientation angle of 142° (r=0.83, z=12.40, P<0.001). (D) Results from 'dry' turtles released during the same trial as the turtles in C. These turtles were not significantly oriented (r=0.42, z=2.82, 0.10>P>0.05). As in the previous experiment, the orientation angles of the 'dry' hatchlings were significantly more dispersed (P<0.025, Wallraff's modified Mann–Whitney U-test) than those of their wet siblings.

established far out at sea and is largely independent of local weather patterns occurring near land. The seasonal constancy of swell direction has long been recognized; Polynesian navigators, for example, used swell propagation direction as a cue in long-distance voyages (Lewis, 1978). Swell direction could hypothetically be used in open-ocean orientation by hatchling and adult sea turtles, fish (Cook, 1984), cetaceans and perhaps even flying migrants (birds and insects) able to perceive swell patterns from the air.

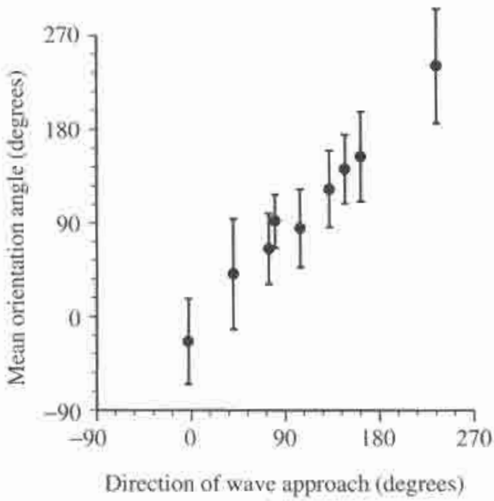

Fig. 4. The mean orientation angles (in degrees) of all groups of turtles (except the two 'dry' groups) plotted with respect to the direction of wave approach (in degrees). Error bars indicate angular deviation. Circle–circle correlation analysis (Batschelet, 1981) indicates that orientation angle and direction of wave approach are significantly related ($P<0.001$).

Whether sea turtle hatchlings continue to use wave direction as a cue after entering deep water is not known. Recent efforts to track loggerhead hatchlings leaving the east coast of Florida suggest that turtles may normally swim into waves for only a relatively short time after entering the sea (Witherington, 1992). After distancing themselves from shore, hatchlings may subsequently maintain their directional bearings using the geomagnetic field (Lohmann, 1991) or other, as yet unidentified, cues.

Effects of handling and the role of the beach crawl in ocean orientation

When hatchlings emerge naturally from their underground nests, they must crawl across the beach before entering the sea. In a previous study of hatchling green turtle orientation in the ocean, hatchlings deprived of a beach crawl and released offshore dove repeatedly and swam in erratic circles, apparently unable to establish a seaward course (Frick, 1976). This result led to the hypothesis that a beach crawl is essential for subsequent orientation at sea (Frick, 1976; Mrosovsky, 1983).

In the present experiments, however, none of the hatchlings crawled across a beach before they were released offshore, but all groups placed in water prior to release were significantly oriented (Figs 1, 2, 3A,C). Moreover, other recent experiments have failed to provide evidence that beach crawl experience modifies

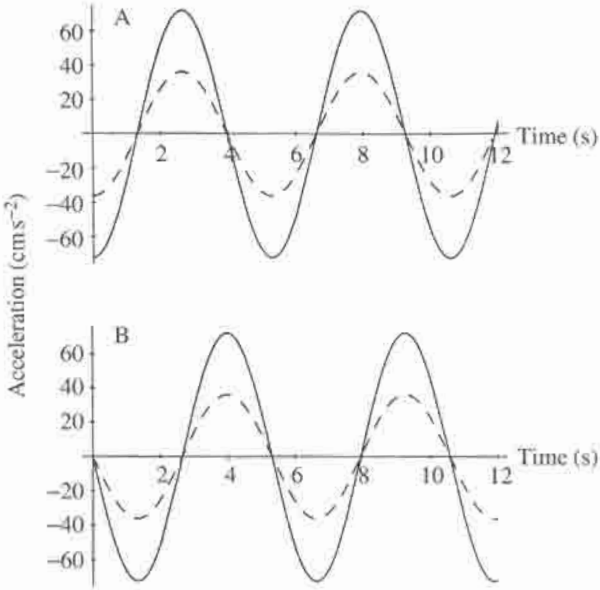

Fig. 5. Accelerations theoretically experienced by a green turtle hatchling swimming at typical depth (20 cm) and velocity (43.6 cm s^{-1}) beneath a wave 0.5 m high (dashed line) or 1 m high (solid line) with a period of 5 s. Because the turtle and wave are moving in the same direction, these graphs indicate the minimum accelerations the turtle would experience. (A) Horizontal component of acceleration. (B) Vertical component of acceleration.

the way in which hatchlings respond to waves early in the offshore migration (Salmon and Lohmann, 1989; Lohmann *et al.* 1990).

The difference between the present results and those of Frick (1976) may be attributable to differences in treatment of hatchlings immediately prior to release into the sea. In experiments comparing two different handling methods, some hatchlings were placed into a bucket of sea water at least 15 min before release, while others were kept dry (see Materials and methods). Turtles from the wet group reliably oriented towards waves (Fig. 3A,C), whereas dry hatchlings were not significantly oriented as a group (Fig. 3B,D).

Hatchlings may therefore require several minutes in water before they attain the behavioral or physiological state in which they reliably orient to waves. This time could represent a brief transition period during which (1) hatchlings are attentive to cues other than waves, (2) hatchlings become acclimated to the water and the change from a motor program for crawling to one for swimming, and/or (3) the motivational state of the hatchlings changes, perhaps as a consequence of the slightly lower temperature of water or sensory cues associated with submergence. We speculate that the hatchlings released offshore by Frick (1976) appeared disoriented because they were released while dry and thus disappeared from the view of observers before they began to orient to waves.

Physiological mechanisms underlying wave detection

The mechanism underlying wave detection by sea turtle hatchlings is not known. In principle, however, hatchlings could use one of at least three different mechanisms to determine wave propagation direction. First, turtles could detect wave direction visually by looking at approaching waves while at or just below the surface. Second, hatchlings could indirectly determine wave direction by detecting the frequency of waves encountered while swimming in different directions (a Doppler shift). Finally, a swimming hatchling might determine wave direction by detecting the sequence of horizontal and vertical accelerations caused by a wave passing above.

Wave tank experiments have indicated that green turtle hatchlings can orient to waves even in the absence of visible light (Lohmann *et al.* 1990). Thus, hatchlings do not need to see waves in order to determine wave propagation direction.

A Doppler shift could also be used to determine wave propagation direction. Relative to a stationary hatchling, a turtle swimming towards approaching waves will experience an increase in wave frequency, whereas a turtle swimming in the direction of wave movement will experience a decrease. The number of waves encountered per unit time could be determined by monitoring the frequency of accelerations due to the passing waves (see below). Whether hatchlings can detect differences in wave frequency with sufficient resolution to discriminate different directions is, however, not known. Moreover, tethered hatchlings oriented to waves while essentially stationary (Salmon and Lohmann, 1989; Wyneken *et al.* 1990; Lohmann *et al.* 1990), and unrestrained hatchlings often established courses towards waves almost immediately after release into the ocean (see Results). Because a hatchling would presumably need to contrast the Doppler shifts encountered while swimming in different directions to determine the direction of wave approach, this mechanism appears unlikely.

Cook (1984) hypothesized that salmon might orient using wave cues and might determine wave propagation direction by monitoring the phase relationship between the horizontal and vertical components of acceleration occurring in water beneath oceanic swells. Calculations revealed that the accelerative forces produced beneath typical swells are probably detectable by migrating fish down to depths of about 30 m.

We repeated the calculations of Cook (1984) using parameters appropriate for sea turtle hatchlings swimming beneath waves off the Florida coast. The results (Fig. 5) indicate that accelerations encountered by migrating sea turtle hatchlings exceed by an order of magnitude the minimal $5\,\mathrm{cm\,s^{-2}}$ threshold linear acceleration known to be detectable by a vertebrate inner ear (Lewis *et al.* 1985).

Given that the horizontal and vertical accelerations are theoretically detectable by a turtle, the sequence of accelerations could be used to determine orientation relative to wave direction. The phase relationship between horizontal and vertical accelerations can be seen quantitatively in Fig. 5 for a turtle swimming with waves and qualitatively in Fig. 6 for a turtle swimming either with or against waves. In qualitative terms, a hatchling swimming towards approaching waves would

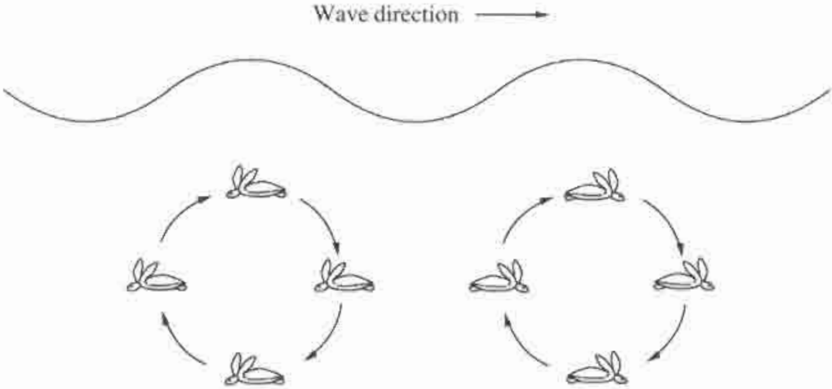

Fig. 6. The motion of a hatchling turtle swimming with and against the direction of wave propagation. For a hatchling oriented into the waves (left), the sequence of accelerations during each wave cycle, beginning on the left, is upward, backward, downward and forward. A turtle swimming with the waves (right) is accelerated upward, forward, downward and backward.

experience a sequence of upward, backward, downward and forward accelerations with each wave cycle (Fig. 6). In contrast, a hatchling swimming in the same direction as the waves moved would encounter a sequence of upward, forward, downward and backward accelerations (Fig. 6). The nervous system of the turtle would need only to distinguish between these sequences (perhaps by simply determining whether a backward or forward acceleration followed the initial upward movement) to differentiate orientation against and with wave propagation direction.

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