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An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertical migrator

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Synopsis

A 4.9 m TL megamouth shark, only the sixth specimen known to science, was tracked continuously for 50.5 h, during which it exhibited distinct vertical migrations at the dawn and dusk transitions. The male shark was captured on 21 October 1990 in a drift gill net off Dana Point, California, restrained overnight in a harbor, and released at sea the next afternoon. Horizontally, the shark moved slowly southward, covering 62 km on a relatively straight path with no significant diel changes. For the major part of the tracking, its rate of movement was 1.15 km h^{-1}, as determined from positions at 15 min intervals. Considering a probable head current of 10–25 cm sec^{-1}, its estimated through-the-water swimming speed was more likely 1.5–2.1 km h^{-1} ($\bar{X}$ = 1.8, representing 0.1 body lengths sec^{-1}). Vertically, the shark stayed shallow at night (12–25 m depth range, $\bar{X}$ = 17) and deep during the days (120–166 m, $\bar{X}$ = 149) but still well above the bottom at 700–850 m. The four twilight depth-change events were very distinct and always spanned the times of sunset or sunrise. The ascent and descent profiles are a reasonble match to isolumes on the order of 0.4 lux for an extinction coefficient (0.07) calculated from water transparency measurements. Furthermore, the steepest parts of the shark's profiles correspond closely to the times of maximum rate-of-change of illumination. These findings suggest that, except during nights, the shark's chosen depth was to a large degree determined by light level.

Introduction

A rare scientific opportunity occurred in October 1990 when a megamouth shark was captured alive and made available for in situ observational study and subsequent telemetry tracking. This shark, a male of 4.9 m TL, was the sixth specimen of *Megachasma pelagios* Taylor, Compagno & Struhsaker 1983 known to science and the only one from which significant behavioral information was obtained. A general account of the capture and study of Megamouth 6 is provided by Lavenberg (1991). Herein we present the findings of the acoustic tracking of this shark.

Megamouth 1, the first known specimen and from which the species was described, was obtained in 1976 off Hawaii after becoming entangled in a U.S. Navy parachute sea anchor. Megamouth 2 was captured in a drift gill net off Santa Catalina Island, California in 1984. Although still alive when first seen in the net, the shark was landed and placed on exhibit at

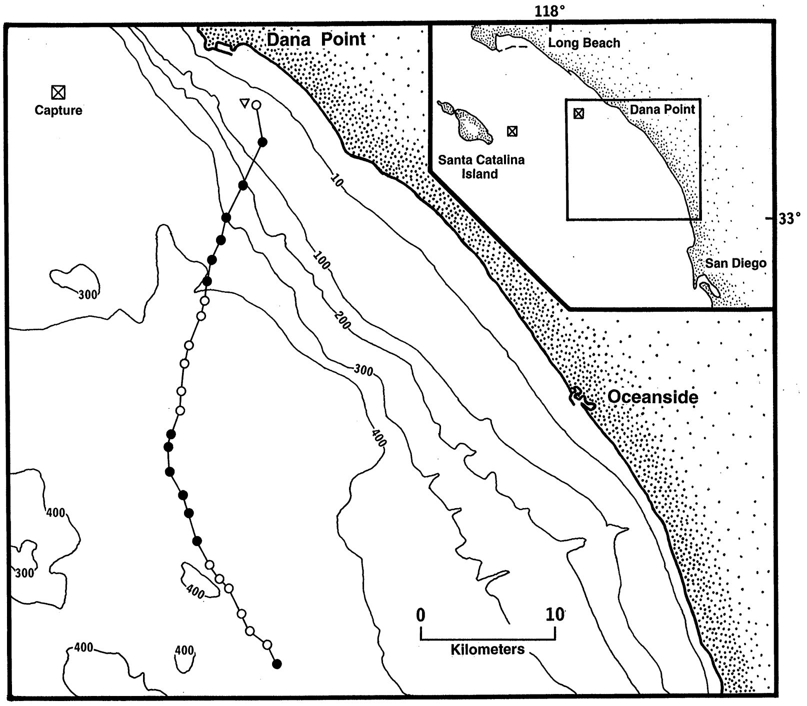

Figure 1. Horizontal movement of a megamouth shark tracked off southern California for 50.5 h. Total track length was 62 km. Position points are shown at 2 h intervals (starting at 18:00 h on 22 October). Triangle is the site of release at 17:30 h. Light points are day positions (after sunrise, prior to sunset). Dark points are night positions. X is the site of capture. Depth contours are in fathoms. Inset shows proximity of site of capture of tracked shark (Megamouth 6) to site where Megamouth 2 was caught six years earlier.

the Natural History Museum of Los Angeles County (Lavenberg & Seigel 1985). Megamouth 3 was stranded in 1988 south of Perth, Western Australia. Also alive when first found, it soon died and was preserved (Berra & Hutchins 1990, 1991). Megamouth 4, from Japan, was confirmed from photos of a dead specimen stranded in 1989, but which washed back to sea and was lost (Nakaya 1989). Megamouth 5, also identified from photos, was netted in Suruga Bay, Japan in 1989, but was not retained (Miya et al. 1992). Subsequent to the present study, Megamouth 7, the first known female, was found stranded in 1994 in Hakata Bay, Japan and later dissected by a team of scientists (Clark & Castro 1995). These seven sharks were all at least 4 m in total length.

In 1995, two much smaller specimens were reported captured by fishermen in the Atlantic. B. Seret (personal communication)[1] described a 1.8 m TL male from Senegal (specimen lost), and A. Amorim (personal communication)[1] reported a 1.9 m TL male from Brazil (specimen retained).

The discovery of *Megachasma* generated great interest and available specimens were studied in detail. Stomach contents showed it to be a planktivorous filter feeder. From anatomical and other evidences, speculations were made on its habitat, swimming speed, exact mode of feeding, and possible vertical migrations (Taylor et al. 1983, Lavenberg & Seigel 1985, Compagno 1990). The tracking data presented herein from Megamouth 6 allow these ideas to be examined in the light of actual behavioral measurements.

Methods

Megamouth 6 was captured in the early morning of 21 October 1990 in a drift gill net set by the vessel 'Moonshiner' for swordfish and pelagic sharks. It

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1 [1] Communicated on Elasmo-L, an Internet list server operated by the American Elasmobranch Society.

was first sighted in the net at about 2:30 h. The capture site was approximately 12 km west of Dana Point, California, a location only 33 km from where Megamouth 2 was caught six years earlier (Figure 1). Recognizing the still-living catch as unusual and probably valuable, fisherman Otto Elliot secured a rope around the shark's caudal peduncle and slowly towed it back to Dana Point Harbor, a 5.5 h journey. At the dock, the shark was left in the water, tied to the boat by a relatively short tail rope.

At the request of the first of us on site (Lavenberg), the fisherman agreed to try to keep the shark alive until underwater observations, measurements, and film/video records could be made. It was further decided that, if the shark were to remain alive long enough, it would be released and a telemetry tracking initiated. To everyone's surprise, and with increasing spectator and media attention, the shark did survive more than a day of restraint in the shallow, murky harbor. On the afternoon of 22 October the shark was towed back out to open water for underwater filming, attachment of acoustic transmitters, and release. The total duration of restraint for Megamouth 6 – from time of capture to time of release – was at least 39 hours.

The shark appeared to be in relatively good condition at release. Although it had deteriorated some during its long restraint in the harbor, it improved during the slow tow back to sea and during a subsequent period when it was allowed on a much longer tail rope while being filmed by divers. It was pump ventilating regularly and maintaining swimming motions and, when the tail rope was removed, it accelerated downward and away, outdistancing the divers. This escape speed was estimated to be several times faster than the sustained cruising speeds measured during the tracking that followed.

Two acoustic transmitters were dart-applied by a diver to the shark's mid-dorsal region just prior to its release at 17:30 h. A 32.77 kHz Vemco V4P-4HI unit telemetered depth data, while a 40.00 kHz 'Ultrasonic Telemetry Systems' pinger provided tracking redundancy. The primary tracking operation was conducted from the 15 m R/V 'Discovery', using a 'Vemco' VR-60 depth-decoding ultrasonic receiver and a staff-mounted directional hydrophone. During tracking, the vessel was slowly maneuvered to stay relatively near the shark, often directly over it when it was deep. Positions were determined at 15 min intervals using loran and radar ranges to landmarks. Bottom depths were determined from fathometer readings or from NOAA navigation charts. The shark's telemetered depths were recorded at 15 min intervals (also at 5 min or 1 min intervals during crepuscular depth changes).

While optimal instrumentation to measure light, temperature, currents, etc. could not be obtained on short notice, some environmental features were noted or measured using available equipment. Secchi-disc measurements indicated a vertical visibility of about 21 m. Two mechanical bathythermograph casts on 24 October showed the top of the thermocline to be at about 20 m and 18 °C with the temperature dropping to 8 °C at 90 m. Water currents in the tracking area were estimated from previous oceanographic data and were used to estimate the shark's through-the-water swimming speeds.

To examine hypotheses regarding the shark's depth changes, a family of isolumes was constructed to be compared to the shark's twilight depth profiles. These isolumes were calculated from the twilight illumination profile of Nielsen (1963) adjusted for depth using an estimated seawater light-extinction coefficient. Our estimate of the extinction coefficient (0.07) was based on the Secchi-disc readings ($\bar{X}$ = 21 m) taken during the tracking. The formula used (Brown et al. 1989) was K = 1.5/Zs, where K is the extinction coefficient (diffuse attenuation coefficient), Zs is the Secchi depth, and 1.5 is a constant derived empirically.

The twilight light-change profile was for a crepuscular unit or 'crep' (length of civil twilight) value of 25 min (Beck 1980), appropriate for the date and latitude of the tracking. Although Nielsen's profile was derived from measurements in air and thus did not involve the losses at the air/water interface at decreasing solar altitudes, his profile did not differ markedly from that measured underwater at a constant depth (Stearns & Forward 1984) at a similar season and latitude. The sunset/sunrise surface illumination used was 398 lux as given by Nielsen (1963). The extinction coefficient was kept constant with depth, and was not adjusted for the selective absorption of wavelengths occurring in the first few 10s of

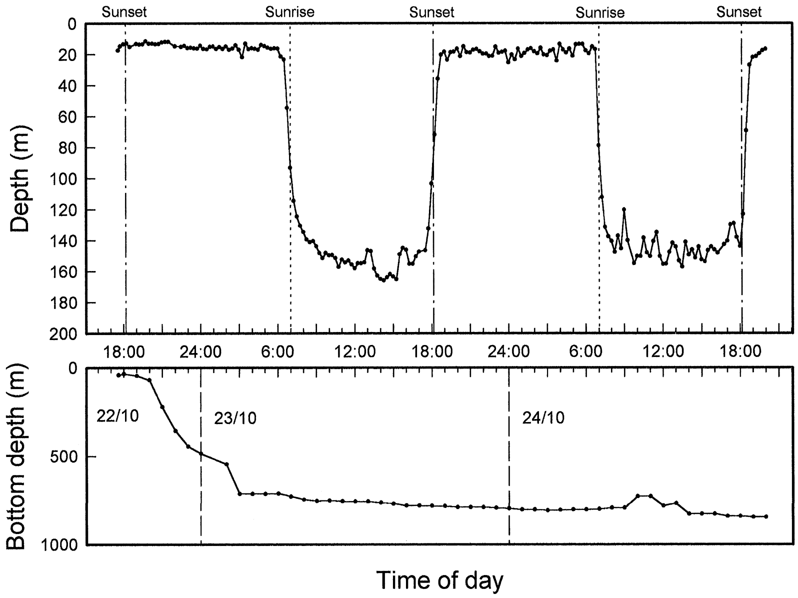

Figure 2. Vertical movement of a megamouth shark tracked off southern California for 50.5 h, showing close association of major depth-change events to times of sunrise and sunset. Telemetered shark depths are plotted at 15 min intervals. Lower curve shows ocean bottom depths, which were much deeper than the shark except near the start of the tracking.

meters. This was considered to have a negligible effect on the shapes of the calculated isolumes over the shark's depth range as, at those depths, the light was essentially monochromatic blue-green.

Results

We tracked Megamouth 6 continuously for 50.5 h, during which it passed through two complete diel cycles, i.e., four twilight transitions (not including the first dusk shortly after the shark was released). Details of the horizontal and vertical movements are shown in Figures 1, 2 and 3, with the most notable result being the very distinct crepuscular vertical migrations, apparently in response to changing light level.

Horizontal movement

Overall, the shark moved slowly on a relatively straight path as it travelled generally southward from its release site towards deeper water. Figure 1 displays the track path, showing positions at 2 h intervals for clarity. Based on the positions taken at 15 min intervals, the tracking covered 62 km with an overall mean point-to-point rate of movement (RM) of 1.22 km h^{-1}. The RM for the first few hours of the track (until the first midnight) was significantly higher (1.76 km h^{-1}) than for the rest of the track, possibly a post-release artifact or perhaps because it had not yet encountered a head current. During the major part of the track (beyond the first midnight, all over deep water), the RM was relatively consistent at a mean of 1.15 km h^{-1} (SD = ± 0.31). For the 4.9 m shark, this represents 0.065 total body lengths per sec (bl sec^{-1}), surprisingly slow for a shark that appeared to be moving steadily in one direction. The shark showed no significant difference in RM between phases of the diel cycle. The mean RM for the daytime was 1.16 km h^{-1}, for nighttime, 1.12 km h^{-1}, and during twilights, 1.25 km h^{-1}.

The above rates of movement were measured from the 15 min positions of the tracking boat, which approximated the positions of the shark. Through-the-water swimming speeds were estimated after considering the possibility of ocean currents and other factors (see Discussion). From this, adjusting for a probable head current, our estimate of the true

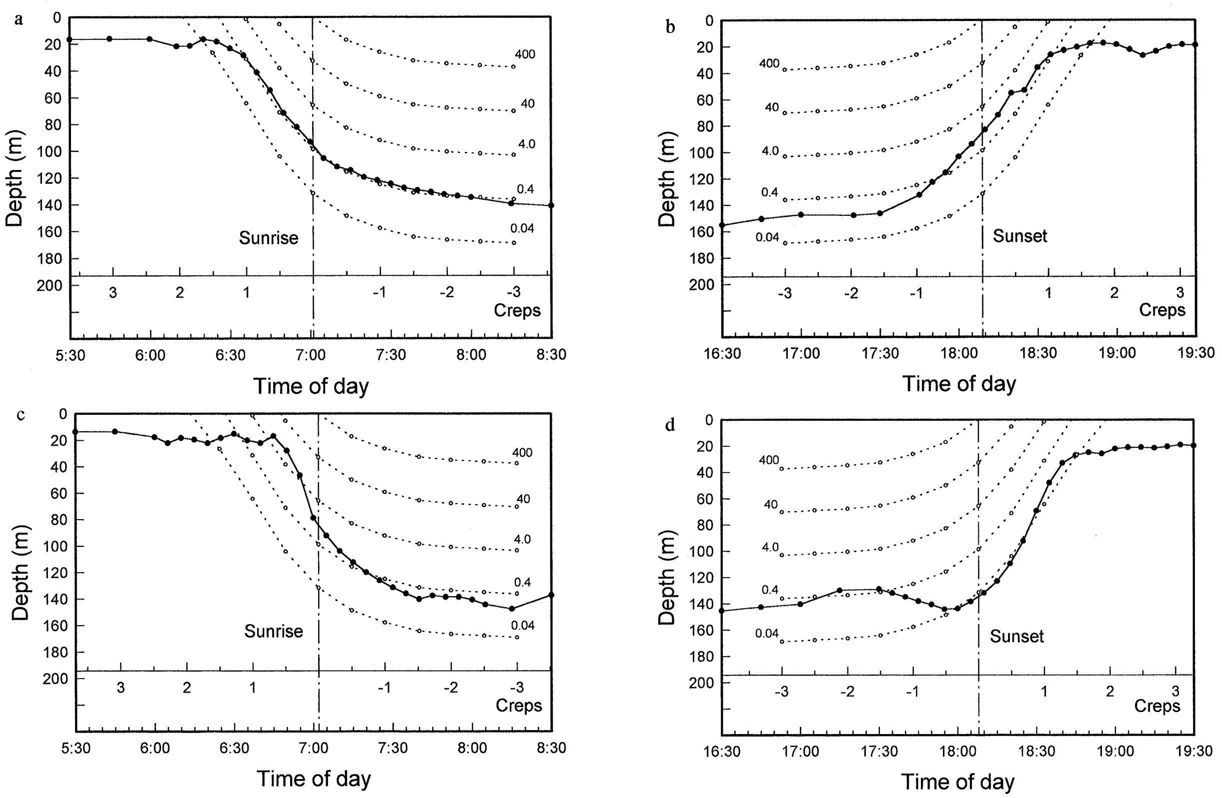

Figure 3. Details of a megamouth shark's vertical movements during four twilight transitions. a – dawn descent, 23 October. b – dusk ascent, 23 October. c – dawn descent, 24 October. d – dusk ascent, 24 October. Shark depths are plotted at 5 min intervals. Other curves (dotted lines) are calculated isolumes for five different illumination levels in lux (see text). One crep (crepuscular unit) is 25 min for the time and place of the tracking.

swimming speed of megamouth during the major part of the tracking was between 1.5 and 2.1 km h^{-1} ($\bar{X}$ = 1.8 km h^{-1}, which represents 0.10 bl sec^{-1}).

Vertical movement

Although the shark remained in the epipelagic zone, it showed a very distinct diel migratory pattern of swimming shallow at night and deep during the day (Figure 2). The major crepuscular depth changes occurred as single, smooth events closely associated with the times of sunrise and sunset. The shark's full diel pattern can thus be described in four parts: the deep day phase, the shallow night phase, and the two crepuscular depth-change events (the dawn descent and dusk ascent).

The night phase was characterized by a relatively constant shallow depth with numerous minor fluctuations (range = 12–25 m, $\bar{X}$ = 17, SD = ± 2.9). The day phase had similar fluctuations (120–166 m, $\bar{X}$ = 149, SD = ± 8.1), but the shark moved noticeably deeper in the middle part of the day (23 Oct, maximum depth of 166 m at 14:15 h; 24 Oct, 157 m at 13:30 h; peak sun altitude at 12:35 h). For these calculations, the day phase was considered to be from 1 h after sunrise until 1 h before sunset; the night phase from 1 h after sunset until 1 h before sunrise.

The crepuscular depth-change events, once in progress, were unmistakable and always spanned the times of sunrise or sunset. Their onsets were more abrupt at the night end than at the day end where the depth profile graded more gradually into the day phase (Figure 3). The depth-change events were approximately 1–2 h in duration (more precise measures would be arbitrary, depending on how the beginning and ending points are defined). During the morning-twilight dives, the maximum rates of descent were 3.4 and 6.4 m min^{-1} and occurred at depths of 64 and 63 m respectively, and at times 13 and 4 min prior to sunrise. For the evening-twilight ascents, the maximum rates of climb were 3.4 and 4.6 m min^{-1}, at depths of 45 and 81 m, and at 19 and 20 min after sunset. If one assumes straight line swimming with a horizontal component of 1.8 km h^{-1}, these rates represent slope angles of between 7 and 12 degrees.

As shown in Figure 3, the shark's depth-change profiles match reasonably well to the shapes of the isolumes during the major portions of its ascents and descents. The best match is for isolumes in the region of 0.4 lux. Although not visible in Figure 3, this relatively close coincidence continues throughout the day, with a midday level of 0.4 lux being at 140 m (about 0.2 lux at 150 m). However, the shark did not (indeed, could not) follow this isolume much beyond its dusk ascent as, even at the surface, illumination soon drops below this, reaching 0.0009 lux at midnight. At the shark's nighttime depths, the level was about 0.0002 lux (for 20 m at midnight). This depth was also the approximate top of the thermocline (bottom of the mixed layer) and this may have been the reason the shark rose no further.

Discussion

The tracking of Megamouth 6 was a serendipitous event, initiated on very short notice, and without the instruments to measure directly parameters such current and subsurface light. More trackings of this species are obviously desired, but the probability of another oppurtunity in the near future is small. We therefore discuss the results of this tracking now using the environmental data we have or can reasonably estimate.

Horizontal movement

The point-to-point rate of movement (RM) we measured (1.15 km h^{-1}, 32 cm sec^{-1}) was unexpectedly low for a shark the size of Megamouth 6. However, for this and most other tracking studies, the rate of movement does not necessarily represent through-the-water swimming speed. This relationship can be affected by both ocean currents and the shark's deviations from straight-line swimming. For the megamouth tracking, we estimated current drift from published reports, unpublished data, and observations of fishermen familiar with the area.

The major part of the tracking occurred in the general vicinity of the Southern California Countercurrent, a poleward (upcoast) movement or eddy off the more offshore, downcoast California Current. In addition, when the shark was deep during the day, it may have been under the influence of the California Undercurrent, an upcoast flow of maximum strength at 100–300 m depth. Speeds and directions of these currents vary with location, depth, tide, and season as well as other less predictable factors. A review by Bakus (1989) reports the Countercurrent as flowing northward thru the Channel Islands at 5–10 cm sec^{-1}, with deeper waters upcoast at up to 25 cm sec^{-1}. Hickey (1992), who examined offshore currents over the Santa Monica-San Pedro Basin, gives a mean upcoast offshore flow of 10–25 cm sec^{-1} with considerable seasonal and other fluctuations. Fisherman Otto Elliot reported that his drift gill net, when set in the general area of the megamouth tracking, usually moved northwestward (upcoast), at estimated speeds of up to half a knot (25 cm sec^{-1}) and rarely, if ever, moved downcoast.

Taken together, this evidence suggests that megamouth was probably swimming against an upcoast current. If this current averaged 10 cm sec^{-1} directly against the shark, it would raise the estimate of the shark's through-the-water speed from the RM of 1.15 km h^{-1} to 1.51 km h^{-1}. A 25 cm sec^{-1} head current would raise the estimate to 2.05 km h^{-1}. Taking the average of these ocean-current values, we estimate the shark's through-the-water swimming speed to have been about 1.78 km h^{-1} (50 cm sec^{-1}) or 0.10 bl sec^{-1}. It is interesting that this speed is close to the 1.76 km h^{-1} RM for the early tracking hours prior to the first midnight. One possible reason for this is that the shark, while closer inshore, had not yet encountered the offshore head current and was really swimming at the same speed as later in the track.

Independent of the effect of current, the point-to-point RM measurements would have underestimated swimming speed if the shark, between recorded positions, made deviations from horizontal, straight-line swimming. This has been seen in trackings where swimming speeds telemetered from a sensor on the shark were compared to point-to-point RMs. For a lemon shark, *Negaprion brevirostris*, a shallow water, home-ranging species, telemetered swimming speeds were up to two times greater than the corresponding rates of movement obtained from points taken at 15 min intervals (Gruber et al. 1988). For pelagic species in open water, however, evidence suggests that the sharks typically maintain relatively straight, oriented paths over long periods of time. Carey & Scharold (1990) reported a 19 h tracking segment for a blue shark in which telemetered swimming speeds closely matched the RM determined from the tracking positions. Klimley (1993) tracked scalloped hammerhead sharks, *Sphyrna lewini*, using transmitters with swimming-direction sensors. These sharks showed prolonged periods of very consistent directional headings during their long nightly forays away from and back to their daytime refuging sites.

Another consideration involves the accuracy of the plotted position points, i.e., how closely did the tracking boat's position represent the shark's position? Every 15 min, we maneuvered the boat relatively close to the shark to obtain a position, but varying inaccuracies undoubtedly resulted. Thus, if the shark had been swimming a perfectly straight line for several 15 min periods, the plotted positions would not lie in a straight line and the resulting RM would overestimate the swimming speed. This effect is opposite to that caused by zigzags by the shark between the 15 min points – which results in the RM underestimating swimming speed. For this tracking, we could not estimate these apparently small errors, nor the degree to which one canceled the other. Therefore our estimated swimming speed of 1.8 km h^{-1} (50 cm sec^{-1}) was based on the rate-of-movement measurements corrected only for the effect of probable current. Except for the few trackings involving speed sensors on the animal, most published references to swimming 'speed' are based on rate-of-movement data similar to ours, and comparisons between species are made on that basis.

For aquatic animals in general, two major factors that correlate to swimming speeds are lifestyle (e.g., how food is obtained) and body size (scale effects).

Using a theoretical approach, Weihs (1977) calculated optimum sustained swimming speeds as a function of body length, using data from trout as a baseline. Considering drag and other factors, his 'optimum speed' (which varies with body form) is that resulting in 'minimum energy required per unit distance crossed'. This is presumably the speed preferred by a fish during migrations or routine daily travels, but not while actively chasing prey or fleeing from predators. Optimum speed in absolute terms increases with body length, but decreases with body length when expressed in terms of body lengths per second (bl sec^{-1}). This scale effect is important and should be taken into account when deciding whether a species is 'slow swimming' or 'fast swimming'.

The optimum speed is what one would expect as the typical speed of a tracked shark after it recovers from the stress of capture or transmitter attachment. Indeed, the sensor-telemetered swimming speed of a 2.1 m lemon shark matched the prediction of Weihs' formula very closely (Gruber et al. 1988). Weihs' optimum swimming speed for a 4.9 m fish (e.g., Megamouth 6) is 100 cm sec^{-1}, with a 'range of uncertainty' of from 80 to 125 cm sec^{-1} (0.16–0.26 bl sec^{-1}). Our megamouth RM of 32 cm sec^{-1} is very much below this, but even when adjusted for estimated current, the resulting speed of 50 cm sec^{-1} (0.10 bl sec^{-1}) is still well below it.

The adjusted megamouth speed is also well below that reported for some active, predatory species of approximately similar body size. Carey et al. (1982) tracked a 4.6 m white shark, *Carcharodon carcharias*, for 3.5 days at an average speed of 3.2 km h^{-1} (89 cm sec^{-1}) which is 0.19 bl sec^{-1}. Several large white sharks tracked by Strong et al. (1992) also yielded an average rate of movement of 3.2 km h^{-1} (0.21–0.25 bl sec^{-1}) over a total of 36 h of tracking. A 4 m tiger shark, *Galeocerdo cuvier*, tracked for 48 h by Tricas et al. (1981) averaged 3.6 km h^{-1} (100 cm sec^{-1}) or 0.25 bl sec^{-1}. It is clear that these predatory species are 'faster' swimmers than megamouth, as expected considering their lifestyle, and their speeds are well within the optimum range of Weihs.

Eighteen blue sharks, *Prionace glauca*, ($\bar{X}$ = 2.0 m TL) tracked by Landesman (1984) yielded a mean

RM of 1.5 km h^{-1} or 0.21 bl sec^{-1}. Carey & Scharold (1990) also reported 1.5 km h^{-1} for acoustically tracked blue sharks averaging about 2.3 m. This speed is somewhat below Weihs' range and suggests that, considering scale, blue sharks swim relatively slowly, but still faster than the megamouth.

In comparison to the other two large planktivorous sharks, megamouth appears to be slower, at least from the available tracking data. A 7.0 m basking shark, *Cetorhinus maximus*, tracked by satellite was estimated to swim at 74 cm sec^{-1} (0.11 bl sec^{-1}) between successive position fixes (Priede 1984). A 9.5 m basking shark tracked by a shipboard scanning sonar moved at 94 cm sec^{-1} (0.1 bl sec^{-1}) (Harden Jones 1973). A 3 m whale shark, *Rhincodon typus*, tracked by satellite, showed an average rate of movment of 1.74 km h^{-1} (48.4 cm sec^{-1}, 0.16 bl sec^{-1}) for a 14 day period of daily contacts (Scott Eckert personal communication). From these data, both species appear below Weihs' optimum range, but not as far below as megamouth.

Some non-planktivorous sharks also appear to have lifestyles compatible with low cruising speeds. For example, fast swimming is unnecessary and probably inefficient for odor-locating and scavenging dead-animal falls in the deep sea. Two sixgill sharks, *Hexanchus griseus*, of 3.3 and 3.8 m TL, tracked by Carey & Clark (1995) in depths of 600–1500 m showed movement rates of 14 to 28 cm sec^{-1} (0.04–0.08 bl sec^{-1}). These rates are very low, but may be underestimates of swimming speeds because of probable 'side-to-side searching movements'. Also reported were swimming speeds measured from various video scenes, some with bait present. Sharks between 2.1 and 4.0 m TL averaged 37 cm sec^{-1} (about 0.1 bl sec^{-1}), making them as 'slow' or slower than megamouth in relation to Weihs' range. Interestingly, the megamouth shark has propulsive morphology (strongly heterocercal tail, lack of keel) more similar to the sixgill than to either the basking shark or the whale shark.

Our data indicate that megamouth has a very slow sustained swimming speed, slower than the other large planktivores. This finding supports the suggestion of Taylor et al. (1983), based on anatomy, that the species is a 'slow, weak swimmer'. It can, of course, move much faster at times, as was seen just after the shark was released. It also remains possible that our swimming-speed estimate may be low due to undetected deviations from continuous linear movement, e.g., the shark holding position while suction-gulp feeding on clumps of plankton, as suggested by Compagno (1990) from its jaw mechanics. That megamouth survived by pump ventilation during more than a day of restraint shows that it does not have to swim continuously to ram ventilate as other pelagic sharks apparently must do.

Vertical movement

In regard to depth, Megamouth 6 performed one of the most clearly defined diel patterns ever obtained from a telemetered shark, confirming the suggestion of Lavenberg & Seigel (1985) that the species is a vertical migrator. Like Megamouth 6, Megamouth 2 was also caught at night in a gill net set relatively shallow, the lowest part no deeper than 38 m. In contrast, Megamouth 1 was entangled during the day in a parachute sea anchor set at 165 m. The stomachs of these two sharks contained vertically migrating plankton (crustaceans and sea jellies) typical of the deep scattering layer.

The megamouth pattern of remaining shallow at night and deep during the day is different from other sharks tracked in the open ocean – except for one night shark, *Carcharhinus signatus*, tracked by S. Gruber (unpublished data) in the Gulf Stream off Florida. Blue sharks show a distinct diel component in the repetitive vertical excursions they make between the near-surface and deeper waters, their day dives being to greater depths than those at night (Carey & Scharold, 1990). Unlike the megamouth, however, blue sharks did not remain at depth all day, but repeatedly returned to surface waters. In contrast, the two sixgill sharks tracked by Carey & Clark (1995) stayed deep (600–1500 m) both day and night, without a discernable diel pattern. These sharks appeared bottom oriented and may have been too deep to detect the diel light cycle.

The hammerhead trackings of Klimley (1993) included direct measurement of isolumes as well as measurement of light levels at the shark (using photocells on the transmitters). The depth profile illustrated (for his shark E) shows strong repetitive vertical excursions both day and night, but without the decreased maximum depths at night shown by the blue sharks tracked by Carey & Scharold (1990). During the dusk transition the hammerhead maintained its vertical excursions and did not follow the upward-sweeping isolumes as did the megamouth.

The megamouth pattern does somewhat resemble those of the swordfish tracked by Carey & Robison (1981) and the tuna tracked by Holland et al. (1990). These fish swam shallow by night (although some with moderate vertical excursions) and deeper by day. One tracked swordfish showed a diel profile quite similar to that of megamouth – dramatic depth changes at dawn and dusk, remaining deep during the day and attaining maximum depth at midday. This pattern was suggested to be in response to light, probably an effort to follow an isolume.

For Megamouth 6, we compared the shark's twilight depth-change profiles with the light levels estimated to have occurred at the depths of the shark. This was done to determine the illumination level (or rate of change of illumination) which may have triggered the depth-change events and also to examine the hypothesis that the shark was following an isolume during its ascents and descents.

As shown in Figure 3, the shark's crepuscular profiles, in shape and position, most resemble the isolume for a light level of 0.4 lux – indeed, the match is very close for the dawn of 23 October. The isolumes shown were constructed using a clear-sky twilight profile (Nielsen 1963). However an unusual situation occurred at dawn on 24 October – heavy fog was present until past sunrise. Therefore, the actual light levels during that twilight were undoubtedly lower than indicated by the isolumes of Figure 3c. The shark behaved in a way consistent with this reduced illumination – delaying the onset of descent, then (as the fog dissipated) diving steeper than usual, probably in an effort to catch up with the preferred isolume.

The dusk ascent on 24 October was also noteworthy. After the shark appeared to be starting upwards along the 0.4 lux isolume, it then reversed itself by moving deeper until starting its final ascent along the 0.04 lux isolume. A possible explanation for this reversal is that the shark encountered an increase in illumination due to entering a patch of clearer water. If so, then the light level during its ascent may have been brighter than the 0.04 lux value indicated in Figure 3d.

It is impossible to know how relatively bright or dim 0.4 lux appears to the megamouth since we have no information on its visual thresholds (presumably most sensitive in the blue-green). Would the shape of a shark's spectral sensitivity curve affect its depth profile if it is following what it perceives to be an isolume? Not if the light is monochromatic, which was essentially the case for the depths over which the megamouth's ascents and descents occurred. The effect of differing spectral curves would be in how bright or dim the animal perceives a given level of light, which could somewhat affect the profile's vertical placement, but not its shape.

The effect of light on vertically migrating zooplankton has been studied experimentally, and may be relevant to the megamouth case since it feeds on such organisms. Forward (1987) reviews two competing hypotheses on how light controls, initiates, and orients this behavior. The preferendum hypothesis states that the organism attempts to remain in one preferred light intensity, i.e., it follows an isolume. A consideration here is that an animal's perception of a given intensity varies with its state of dark or light adaptation. The rate-of-change hypothesis suggests that vertical movement is initiated by a certain relative rate-of-change of illumination. Laboratory studies have primarily supported the latter hypothesis, or a mechanism involving aspects of both applied during different phases of the migration (Forward 1987, Stearns & Forward 1984).

What do our data suggest about how light controls the shark's ascents and descents in regard to the preferendum and rate-of-change hypotheses? Data accuracy, of course, must be considered. The shark's telemetered depth measurements appear reliable. The transmitter manufacturer's calibration was used, and the depth reading was zeroed at the surface prior to transmitter attachment. The readings increased as expected as the shark swam down and away and never exceeded (or even neared) the bottom depths which were as shallow as 33 m early in the tracking. The light-level estimates are based on published twilight data and an extinction coefficient calculated from our Secchi-disc measurements in the upper 21 meters. For this discussion, we make the assumption that these light estimates were reasonably valid at the depths of the shark.

The shark's depth profiles support the preferendum hypothesis in that they reasonably match the isolumes through the twilight and daytime phases (another factor, besides light, influenced depth at night). In regard to the question of isolume following, the absolute light values at the surface are less important than the extinction coefficient of the water. The absolute values could vary considerably without substantially affecting the similarity between the shapes of the isolumes and the shark's profiles. While the shark's path approximated the slope of the isolumes for K = 0.07, adjoining families of isolumes differ markedly in shape, e.g., isolumes for K = 0.05 are much steeper, while those at K = 0.1 are much less steep. Megamouth's behavior, therefore, was consistent with isolume following since its curves best matched the isolumes we calculated using the Secchi-disc measurements.

The rate-of-change hypothesis proposes that the depth-change events are 'triggered' by a specific rate of change of illumination and that the remainder of the event is controlled by other factors or by an innate preferred rate of ascent or descent. This would imply swimming slopes independent of the slopes of the isolumes (which vary with K). Our data provide no support for this. On the contrary, the shape of the 24 October dawn profile (Figure 3c) suggests a response to the unusual light levels that occurred that day due to early morning fog.

There is also an inherent problem with the rate-of-change hypothesis, unless one postulates that the dusk and dawn events are triggered by different rates-of-change. During twilight, the maximum rate of change occurs at crep 0.75, which for the time and location of the tracking is at 19 min before sunrise and 19 min after sunset. But the shark initiated its dusk event before sunset (when it is deep and light is changing slowly) and its dawn event before sunrise (when it is shallow and light is changing rapidly). It is also noteworthy that both dawn descents started out steeper than did the dusk ascents and that there is a close correspondence between the times of maximum rate-of-change of light and the times of maximum rate-of-change of the shark's depth. The dusk ascent maxima of 19 and 20 min after sunset were essentially at the light-change maxima (19 min). The descent maximum on the first dawn (13 min prior to sunrise) was close to the light-change maximum at 19 min. The shark's last dawn descent maximum at 4 min before sunrise was undoubtedly delayed by the foggy (then clearing) condition that morning. This evidence further supports the preferendum hypothesis, with the shark continuously responding to a changing light level rather than using rate-of-change as only a trigger.

Other factors, besides illumination, might have been involved in controlling the shark's depth, but our tracking data provides no information on this. As mentioned above, something besides light (possibly temperature) limited the shark's nighttime depth to no shallower than 12–25 m ($\bar{X}$ = 17). It is possible an endogenous circadian component might have interacted with light in timing the depth-change events, especially if conditions were unusually dark or light at the normal times of these events. This effect has been shown in laboratory experiments on activity onsets in horn sharks, *Heterodontus francisci* (Finstad & Nelson 1975). Finally, the shark may have been following vertically migrating food organisms that themselves were responding to light cues. We note that there is a correlation in diel depth distributions between megamouth and a vertically migrating krill, *Euphausia pacifica*, that is common in southern California waters. The primary nighttime concentration of adults and juveniles was reported as between the surface and 40 m, with a deeper and wider daytime distribution peaking for adults at 200 m (Brinton 1962). During our tracking we did not detect a scattering layer on the vessel's 50 kHz sounder and we are not certain such a layer would be detectable with this device. However, plankton following is not necessary to explain the shark's vertical pattern, which would be an adaptive searching style whether or not planktonic food is actually being detected during the depth-change events. The shark needs to know only when and where the food organisms are most likely to be encountered.

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