

Long-distance horizontal migrations of zooplankton (Scyphomedusae: *Mastigias*)¹

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Abstract

Perennial swarms of sexually immature medusae of the genus *Mastigias* occur at high densities in three marine lakes in Palau, Western Caroline Islands. Numbers per lake are $1.76 \pm 0.10 \times 10^5$, $1.61 \pm 0.17 \times 10^6$, and $4.69 \pm 0.51 \times 10^6$. Local density within a swarm may exceed $1,000 \cdot \text{m}^{-2}$. Behaviorally generated swarms form in the early morning and late afternoon and are temporarily dispersed by directional horizontal migration of the entire swarm twice a day to opposite ends of the lake. Distance swum each day is up to 1 km, depending on the size of the lake. Compass direction of migration is different in each lake and appears to depend on both light and basin morphometry.

It is commonly believed that zooplankton are behaviorally rather passive and "... have little directed movement at horizontal scales above a few meters ..." (Steele 1978, p.9). This belief in behavioral passivity has been reinforced by collecting with horizontally towed plankton nets that provide only a single statistic—the mean—which in the absence of other measures of variance gives a deceptive semblance of uniformity, precisely the sort of spatial pattern one might expect for organisms preconceived to be passively drifting and behaviorally inert. We present here information on *Mastigias*, a rhizostome scyphomedusa, that swarms in large numbers in three marine lakes of Palau, Western Caroline Islands, and undertakes daily long-distance horizontal migrations in the absence of appreciable currents. The behavioral complexity shown by these neurologically simple animals suggests that future investigators should give more attention to the complex behavior of plankton populations.

Materials and methods

The southern archipelago in Palau is characterized by elevated limestone islands, with a karst topography exhibiting extensive carbonate erosion, caverns, subterranean passages, sharp ridges, and collapsed domes. The islands contain some 70 sea level marine lakes, separated from the sea by high ridges. The lakes communicate with the surrounding lagoon via tidal movement of seawater through tunnels and fissures in the limestone. The limestone islands do not support the freshwater lens that typically underlies sand or rubble substrate islands, and the seawater in the lakes is only modestly brackish. A more complete description of the lakes will be presented elsewhere (Hamner et al. in prep.). The two largest lakes on the island of Koror, Wet ra Edead Koror (Jellyfish Lake, Koror) and Wet ra Utoi (Goby Lake), and the most easterly lake on the island of Eil Malk, Wet ra Edead Eil Malk (Jellyfish Lake, Eil Malk) contain large populations of *Mastigias*. These lakes are all meromictic, highly stratified basins with limited horizontal water movement, oxygen depletion of the water column below 10–15 m, and high concentrations of H_2S below the chemocline (Hamner et al. in prep.). The lakes are similar to Lake Kaiike, Japan (Matsuyama and Shirouzu 1978), and to Lake Faro, Sicily (Genovese 1963; Sorokin and Donato 1975). *Mastigias* is restricted to the upper water

¹ W. Maech and L. Ilel provided field assistance. P. Hamner helped with the manuscript. I. Hauri and M. Kowalczyk prepared the figures. The work was supported by NSF OCE 77-27578 through the Marine Science Institute, University of California, Santa Barbara.

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column and during the day occurs within the top several meters of the surface. *Mastigias* harbors symbiotic zooxanthellae and apparently derives a major portion of its nutrition from these symbionts (L. Muscatine pers. comm.).

We sampled *Mastigias* in the lakes with vertical hauls from below the chemocline to the surface with 1–1.3-m-diam nets with 4-mm mesh, sampling in the early morning, at noon, in late afternoon, and at midnight. Jellyfish Lake, Eil Malk, was sampled at 32 separate stations for the four times of day noted above. Repeatability of movement was assessed by sampling through 48 h and thereafter sampling at noon for 4 days. In Jellyfish Lake, Koror, and in Goby Lake four sets of samples for the times noted above were taken at 20 and at 12 stations, for a total of 512 stations. Some 25,000 medusae were counted in all three lakes. Qualitative checks on the movement of medusae in these lakes were made by divers and by aircraft observation to confirm the regularity of migrations and aggregations. Data on distributions were plotted by hand from isopleth contours and confirmed by computer plots made by the Hawaii Coastal Zone Data Bank. The hand-drawn plots are visually more attractive and are presented here.

Total population numbers were obtained by measuring surface area within distribution isopleths, multiplying this by the average density per square meter, summing totals, and computing means and standard errors. To select a random sample for recording directional swimming during migrations, an observer would swim for 10 s with eyes closed, then upon opening his eyes would follow the nearest medusa for 30 s underwater with a compass. Orientational measurements were made at a point in the center of Jellyfish Lake, Eil Malk, for 53 jellyfish at 0730 and for 56 jellyfish at 1400, the times of peak migratory activity.

Results

Jellyfish Lake, Eil Malk, is 420 m long and the 1.61 ± 0.17 million *Mastigias* in the lake migrate about 400 m from west

to east in the morning and 400 m from east to west in the afternoon (Fig. 1). At midnight the medusae are located in the western basin. In the morning they swim east, aggregating in one dense shoal in the eastern basin by about 0930; the edge of the aggregation is abrupt and is 5–10 m from the edge of the lake. In the early afternoon the medusae reorient and swim west, arriving in the west basin by about 1530, where they aggregate into a large swarm at the far western end. On late sunny afternoons the setting sun casts shadows across the lake. The medusae move briefly east with the shadow line, but the shadows extend with increasing speed and the medusae cannot swim fast enough to keep in the sun. Nonetheless the center of distribution of the swarm shifts considerably eastward into the center of the west basin (Figs. 1, 2 right). On overcast days there are no distinct shadows, yet the medusae retain the ability to migrate directionally (Figs. 1, 2 left).

During periods of intense aggregation $>1,000$ individuals $\cdot \text{m}^{-2}$ are encountered. The bell diameter of the medusae averages 6.2 cm and at these densities the dramatically packed aggregations are clearly visible from an airplane at 1,000-m altitude. In the late morning, late afternoon, and night, when the aggregation as a whole is stationary, individuals are oriented randomly according to compass direction, but during migrations almost all individual medusae orient in the same compass direction (Fig. 2).

Mastigias also migrates horizontally in two lakes on the island of Koror. The larger lake (Jellyfish Lake, Koror) is roughly circular and the medusae migrate west in the morning and east in the afternoon (Fig. 3), exactly opposite to the migration pattern in Jellyfish Lake, Eil Malk. At night the medusae are relatively uniformly distributed, with a slight aggregation in the middle of the lake. This lake contains $4.69 \pm 0.51 \times 10^6$ medusae, three times the number in Jellyfish Lake, Eil Malk. Aggregations are less intense, however, and the largest number recorded at a given station was $457 \cdot \text{m}^{-2}$. The medusae are smaller and the aggregations not

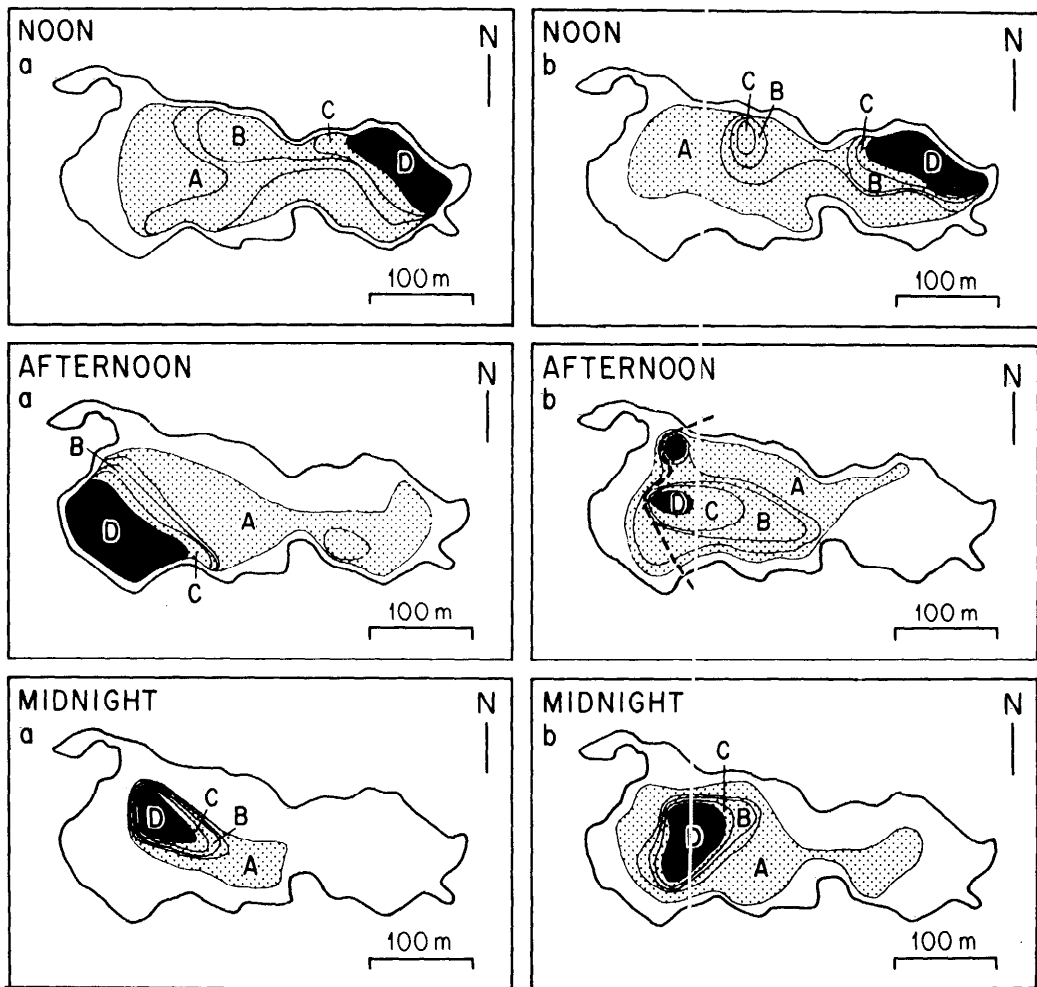


Fig. 1. Temporal and spatial changes in *Mastigias* swarms, Jellyfish Lake, Eil Malk. Series a—first day of sampling, sky overcast; series b—second day of sampling, full sun. Dashed line in b shows position of afternoon shadow at 1630. Isopleths ($\text{No.} \cdot \text{m}^{-2}$): A— $20 \cdot \text{m}^{-2}$; B— $40 \cdot \text{m}^{-2}$; C— $80 \cdot \text{m}^{-2}$; D— $>150 \cdot \text{m}^{-2}$.

so impressive visually. Migration distances are shorter because the E-W diameter of the lake is only about 250 m. Here the jellyfish swim about 500 m each day, whereas in Jellyfish Lake, Eil Malk, they swim almost 1 km during each diel round trip.

Goby Lake on the island of Koror is the smallest of these three lakes. Here the medusae migrate to the southwest in the morning and to the northeast in the afternoon (Fig. 4). The distance traveled each day is about 200 m, and the lake has $1.76 \pm 0.10 \times 10^5$ medusae, a tenth the population of Jellyfish Lake, Eil Malk.

The medusae are relatively large. The aggregation in the afternoon is small but intense.

Discussion

Dense aggregations of medusae have been observed by several investigators (Yasuda 1969; Russell 1970; Hamner and Jenssen 1974). Swarms of scyphozoans are usually related to spawning. Aggregations form in late summer or fall and consist of large, sexually mature individuals. Most scyphozoans are annual, the medusae dying after spawning. Planulae settle and metamorphose into scyphisto-

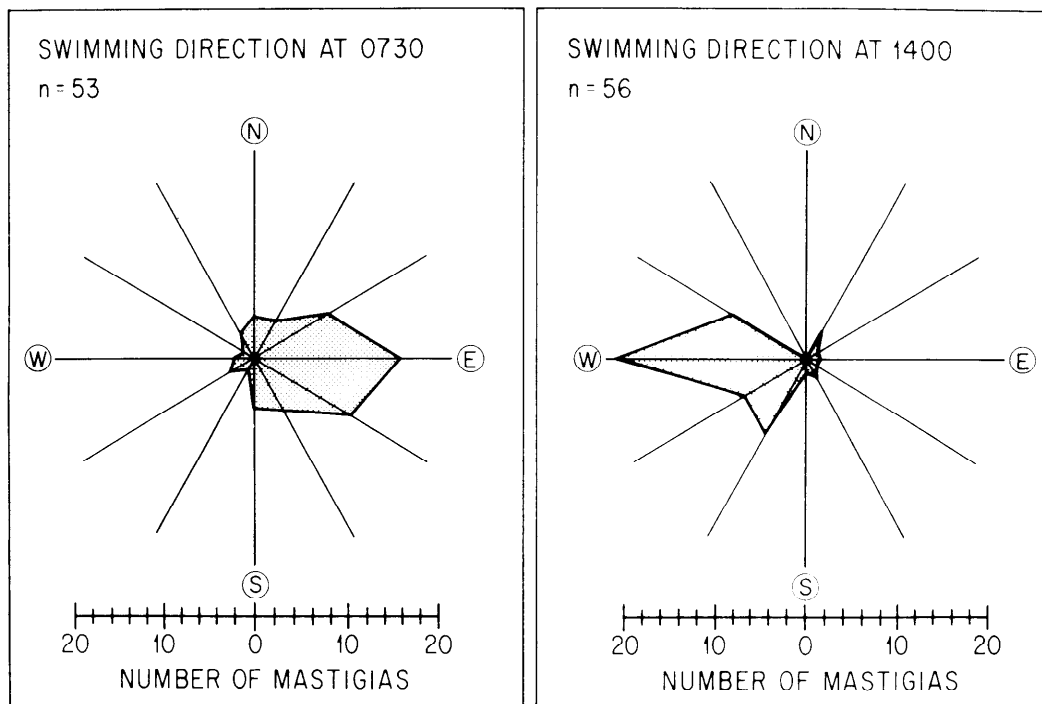


Fig. 2. Compass orientation of medusae in center of Jellyfish Lake, Eil Malk.

mae, which overwinter and strobilate in spring, producing the next crop of medusae. It has been supposed that reproductive aggregations, which generally occur in bays or estuaries, form when currents transport medusae to the head of the bay or estuary, and that the medusae maintain themselves in the aggregation through modest individual reorientation to chemical or physical gradients or peculiarities of water movement. Reproductive swarms of medusae thus are perceived to be generated primarily by the changing seasonality of the bay or estuary. The behavioral contribution of the medusae themselves has been given little attention.

In Palau, sexually immature *Mastigias* engage in daily, behaviorally mediated, long-distance horizontal migration and aggregation. Migration distances seem to be limited only by the size of the lake. In Jellyfish Lake, Eil Malk, medusae spend only 4–5 h of the day engaged in directional migration, yet during that time they manage to swim almost 1 km. The

migration pattern is unique to each lake and the direction of movement of medusae in each lake is distinctive. Clearly the medusae are adapted behaviorally to the lake in which they live. It is possible, therefore, that the formation of other aggregations of scyphozoans at sea or in bays and estuaries also results directly from behavioral migration and not simply from passive transport. Breeding aggregations may form in particular locations because these locations are favorable spawning sites, to which medusae actively migrate long distances horizontally once a year. Furthermore, as the movements of *Mastigias* in the marine lakes of Palau demonstrate, medusae with only modest neurological equipment can exhibit complex behavioral patterns adapted to a given suite of environmental factors. If medusae can migrate directionally, more complicated planktonic animals probably do also.

Medusae in the lakes of Palau do not migrate in order to spawn. Migrations in the marine lakes are diel migrations by

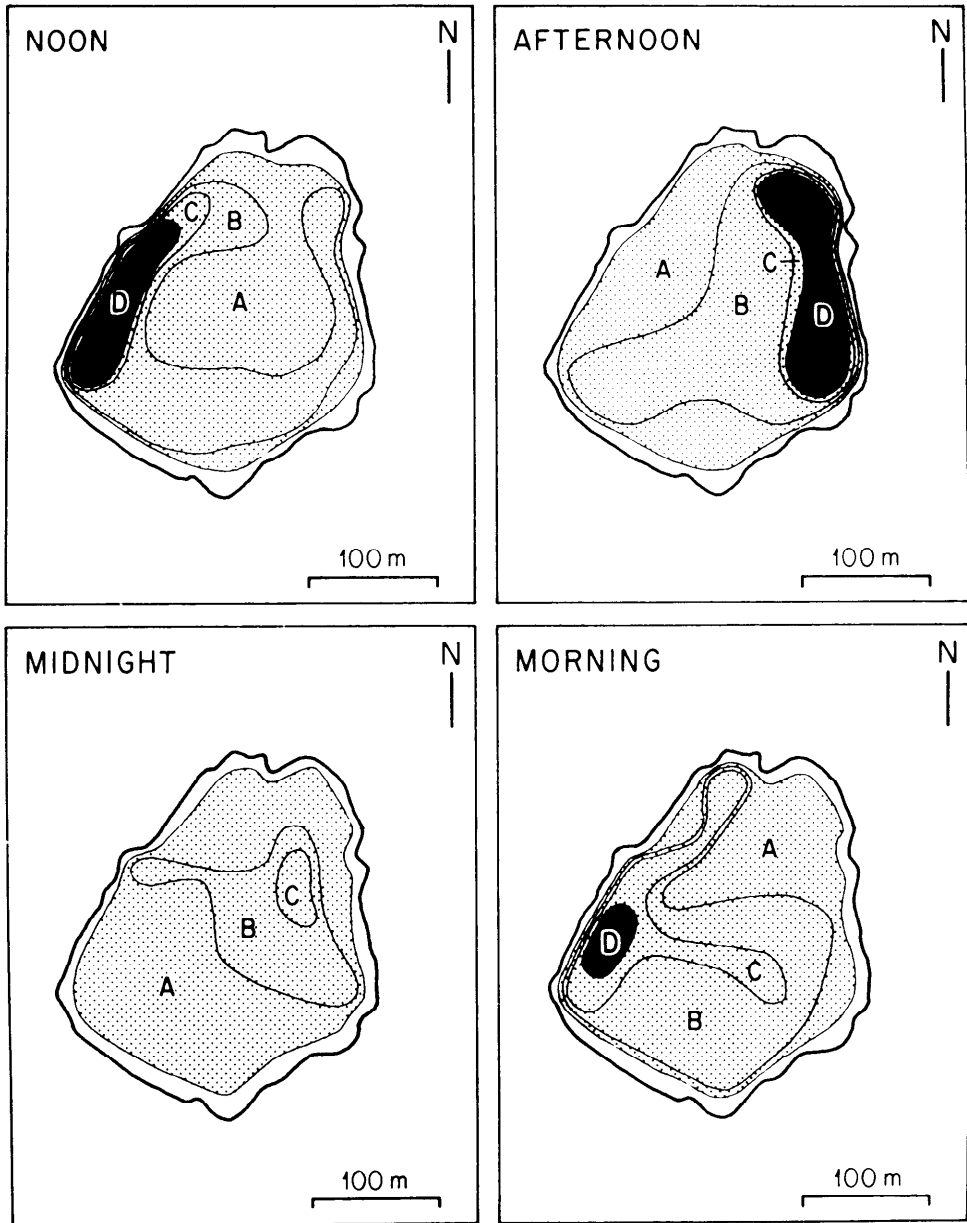


Fig. 3. As Fig. 1, but for Jellyfish Lake, Koror. A— $25 \cdot \text{m}^{-2}$; B— $140 \cdot \text{m}^{-2}$; C— $225 \cdot \text{m}^{-2}$; D— $>275 \cdot \text{m}^{-2}$.

medusae that are not sexually mature. In 2 years we never saw sexually mature medusae. Furthermore *Mastigias* are not annual in Palau. Each lake has a population with a full spectrum of sizes at all times of year (Hamner and Gilmer in prep.). Ephyrae are continuously present in the water and at least some of the scy-

phistomae collected from the lakes at any given time are strobilating. Populations seem to be replenished throughout the year by continuous asexual recruitment instead of by the normal pattern of sexual reproduction in fall and annual replenishment of one age class via strobilation in spring.

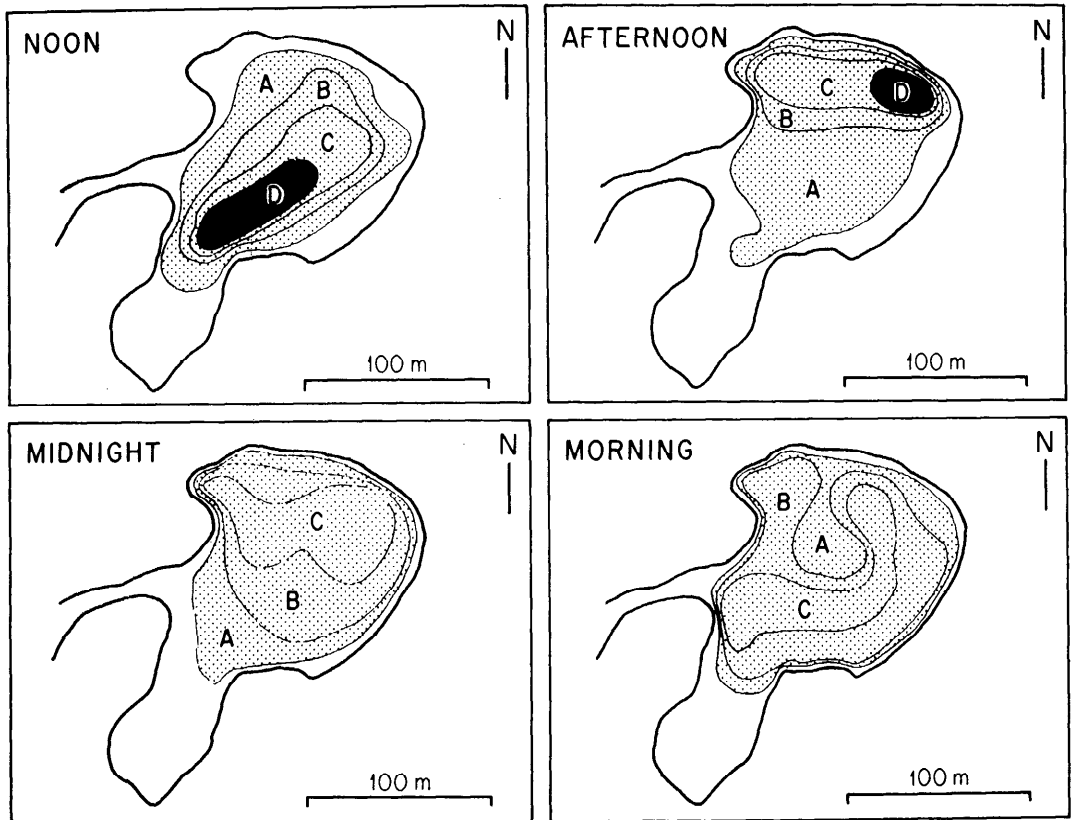


Fig. 4. As Fig. 1, but for Goby Lake, Koror. A— $5 \cdot \text{m}^{-2}$; B— $10 \cdot \text{m}^{-2}$; C— $20 \cdot \text{m}^{-2}$; D— $>50 \cdot \text{m}^{-2}$.

The migrations are not caused by tidal or wind-driven currents. The lakes are at sea level and modest changes in water level occur in phase with but lagging behind the tidal cycle in the lagoon. In all three lakes tidal heights are damped to an approximate 60-cm maximum spring rise, and flood and ebb are delayed 2–3 h. Seawater, diluted slightly by brackish groundwater from beneath the islands, enters the lakes from the lagoon through percolation channels scattered around the lake perimeter. The sizes of these channels vary considerably and the largest do generate modest surface currents immediately adjacent to the openings into the lake. During spring ebb-tides, the outward flow occasionally is strong enough to pull medusae toward the outlets, and one can then see local accumulations near the exits; however,

the medusae are then all oriented away from the exits and swim actively toward the center of the lake. The exits of these three lakes are all near the surface and at the edges of the lakes and are shadowed by mangrove trees. Since the medusae avoid shore via a shadow escape behavior, they invariably swim away from the exits during the day. Their swimming rates exceed the weak ebb-tide current even close to the exits and the medusae are almost never pulled out of the lake in daytime. As noted earlier, at night the medusae do not migrate, but congregate in the deep basins at some distance from the exits. Finally, tidal currents follow the tidal cycle, whereas the *Mastigias* migrations are precisely diurnal. It is reasonable to rule out tidally generated currents as causal to the directional movements of the medusae.

Wind-generated currents do not appreciably affect *Mastigias* either. The lakes are highly stratified by both temperature and salinity and do not mix below 2 m; often they are stratified completely to the surface. The lakes are surrounded by high hills and even on very windy days the winds at the lake surface are usually gentle. In October 1978, an 80-knot hurricane that deposited 50 cm of rain in 2.5 days had no mixing effect below 2.5 m in Goby Lake. Highly stratified water columns do not develop if currents are appreciable. Winds are also sporadic and irregular, whereas the migrations of *Mastigias* are directional and predictable. *Aurelia aurita* also lives in two of the lakes, but does not migrate horizontally and is randomly distributed. If water currents were responsible for the *Mastigias* distributions, one would expect similar patterns for *Aurelia*.

Mastigias in the Palau lakes shows a variety of behavioral adaptations to light. For example, it reacts quickly to changing light patterns. When shadows move across the lake, the medusae move immediately into the sun. When shaded by a swimmer or by a boat, they swim away. When illuminated by a light at night, they aggregate in the beam. In the lakes medusae exhibit an "avoidance of shore" (Siebeck 1968), presumably due to the dark background hue of jungle vegetation and the dark subtidal shoreline. Furthermore, migrations in each lake are responsive to light and are related to time of day, with movement in the morning to one particular site and with no additional migration until about an hour after the sun passes zenith; migration to the other side of the lake is then rapid and directional. The movements of medusae in Jellyfish Lake, Koror, seem to maximize daily exposure to sunlight. The ridges that surround this lake are high (± 80 m) and abrupt. By movement to the west side in the morning the medusae avoid morning shadows and by migration to the east side in the early afternoon they avoid afternoon shadows from the west. This consideration is also relevant for Goby Lake: in the afternoon the medusae ag-

gregate in the northeastern sector, where they are exposed to the last rays of light. Sunlight is clearly a proximate factor that aids immediate daily orientation, but it also may be an ultimate factor of evolutionary importance which has selected for different behavioral repertoires. Migrations in the lakes anticipate by many hours the distribution of shadows, particularly in the afternoon. The population moves to that portion of the lake where the effects of shadows are minimized, but the animals migrate long before the sun is low in the sky and they clearly anticipate dusk. Those that have not reoriented already—a modest but recognizable portion of the population—do react quickly if they are caught in afternoon shadows by swimming rapidly and directionally toward the sunny sector of the lake.

This simple and attractive hypothesis of light-directed migrations unfortunately does not apply so neatly to *Mastigias* in Jellyfish Lake, Eil Malk. Those medusae swim in the opposite direction—east in the morning and west in the afternoon. Some of the population usually is subjected to brief afternoon shadows and to slightly less sunlight per day than if they had remained in the east basin, but the differences of light due to shadows at each end of the lake are modest in comparison to those in the other two lakes. At Eil Malk the ridges that surround the lake are low and slope more gently away from the water. We must look for alternative explanations for the migrations here.

The medusae in Jellyfish Lake, Eil Malk, may migrate to reduce density-dependent mortality at night. The eastern basin is half the size of the western basin and 1.61×10^6 medusae crowd into this basin during the morning. Large numbers of animals are brought close to shore due to the intense aggregation and interference competition from swimming, but their light-mediated "avoidance of shore" reduces the chance of capture during the day by predators along the shore. Affixed to mangrove roots are large populations of a white anemone, *Aiptasia pulchella* Calgren (Faulkner

1974), which capture *Mastigias* with their tentacles. By gross extension of the coclntercon these anemones ingest and devour the largest *Mastigias*. In addition, two species of fishes in the lake, *Apogonis orbicularis* and an unidentified goby, leave the protection of shore for brief excursions to feed on the arms and bell margins of the medusae. At night the medusae do not migrate horizontally but instead aggregate in the center of the western basin and migrate vertically down to the chemocline (Hamner and Gilmer in prep.). The larger volume of the western basin and its proportionately shorter shoreline combine with the behavior of the medusae to reduce nocturnal mortality from predators. In the center of the basin there are no predators.

The migration pattern in Jellyfish Lake, Eil Malk, may also reduce the washout of medusae from the lake. The largest tidal entrance is at the southeast end, an area conspicuously free of medusae even during the morning when animals are most densely packed into the eastern basin. By spending the evening hours in the larger western basin, they eliminate entirely the chance of washout on the evening ebbtide. This does not, of course, explain why the medusae migrate into the eastern basin in the morning in the first place.

The medusae in Goby Lake on the island of Koror clearly reduce their mortality by migrating to the northeast in the afternoon. The principal tidal entrance into Goby Lake is from the west, via a quite shallow adjacent basin (not shown completely in Fig. 4). Aggregation at the northeast end of the lake during the afternoon minimizes washout at night. During the day there is a selective disadvantage to entering the shallow basin to the south. Oxygen (perhaps methane?) is released from the highly productive shallow muddy bottom of the southern basin and generates large-scale vertical motion of benthic algae and bacteria as bubbles lift thin layers of sediment to the surface. This phenomenon does not occur in the large, deeper northern basin, which goes anoxic at 13 m, and where almost none of

the medusae seen were damaged structurally. Relatively few medusae were found in the southern basin during the day, but 22.6% of them were damaged or had bacterial infections due to entanglement with decomposing materials vertically advected from the sediment by gas bubbles. We do not know the mortality rate from these infections, but medusae so infected were regularly found on the bottom, badly deformed and dying.

The horizontal migrations in Goby Lake and Jellyfish Lake, Koror, appear to serve useful adaptive functions. Our hypotheses for the adaptive value of horizontal migration in Jellyfish Lake, Eil Malk, are less satisfactory. Discontented with our initial explanations regarding *Mastigias* behavior in this lake (our initial study site), we sought enlightenment by examining the only two other lakes in Palau containing large populations of these medusae. Since in each of these two lakes the populations migrate in a different direction, our search for clarification by comparison added complexity rather than simplification. Perhaps additional investigation of the lakes will shed more light on these remarkable migrations. Elsewhere we will present a more complete description of the physical, chemical, and biological characteristics of Jellyfish Lake, Eil Malk (Hamner and Gilmer in prep.), and we will then further consider the migration pattern there.

Adaptive explanations aside, the migrations are interesting in themselves. They demonstrate behavioral complexity in plankton that had not previously been expected, and that is the principal message of this paper.

We attempted to test orientation patterns in large tanks at the mariculture center in Palau, but the medusae were suicidal and swam into the sides and bottom of the tanks, became deformed, and died. We also tested orientation in the field. On 20 February 1980, nine medusae from Jellyfish Lake, Koror, with a normal west-east afternoon migration, were taken to Jellyfish Lake, Eil Malk, where the resident *Mastigias* swim west in the afternoon. The jellyfish from Koror were

released in the center of the lake in the early afternoon. Seven of the nine medusae retained their normal afternoon swimming pattern and swam E-NE. One of the others swam straight down and disappeared and the second swam NW. Fourteen controls—resident medusae similarly handled—swam oppositely, to the W-SW, a statistically highly significant difference. The medusae in each lake thus seem to orient to incident light and to migrate in particular directions in ways related to their prior history.

Differences in migration patterns may be genetically determined. The medusae in the various lakes differ structurally at a level that might be considered of specific or subspecific importance. In Jellyfish Lake, Eil Malk, *Mastigias* do not have spots on the exumbrellar surface or clubs attached below the suctorial mouths. Medusae in Jellyfish Lake, Korr, have white spots on the exumbrellar surface but no pendant clubs, and those in Goby Lake have no spots but do have long clubs below the suctorial arms. Although systematists use these characters to differentiate species of *Mastigias* (Mayer 1910), we are reluctant at this stage to give these differences specific status. It is probable that all three lakes were originally infected by one particular species of *Mastigias* which entered from the lagoon, and the obvious morphological differences may be only of local significance. Further significant differences in size-frequency, numbers and, of course, behavior, characterize each population. These collective differences emphasize that the medusae are closely adapted to discrete habitats.

Other types of plankton, such as copepods in other Palauan lakes, also form complex aggregations and show long-distance horizontal migrations (Omori and Hamner in prep.). In the marine lakes of Palau horizontal migrations are as important as daily vertical migrations. In the open sea, however, horizontal migration may be less important on a daily basis than is vertical movement because of the absence of places of refuge and the lack

of gross horizontal pattern in the pelagic realm. Yet for long-lived planktonic species with complicated life cycles, horizontal migration may be extremely significant as animals shift seasonally between different water masses or return to particular coastlines before metamorphosis. Lobster larvae (Phillips 1975), sergestid shrimps (Omori 1969; Omori et al. 1973), and cubomedusae (Hamner pers. obs.) all exhibit great horizontal differences in seasonal distribution, and it is now certainly tenable to suppose that these patterns are generated behaviorally via directed horizontal migration rather than simply via transport by regularly recurring oceanic or coastal water movement.

Mastigias also migrates horizontally at sea. Off Townsville, Australia, 20 km from shore, we once recorded 29 of 31 sequential *Mastigias* swimming on a precise NS axis at the surface of the sea. There, of course, we did not know where they were going. In the lakes of Palau it seems that the medusae use a sun compass for orientation. This information is as available near the surface of the open sea as it is in the lake. Many planktonic animals show morphological adaptations that affect their horizontal distributions, the dextral and sinistral sails of chondrophorans being an obvious example. Behavioral adaptations are to be expected also.

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Submitted: 5 May 1980

Accepted: 10 October 1980