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EFFECTS OF TEMPERATURE ON SWIMMING SPEED OF THE DINOFLAGELLATE *GYMNODINIUM SPLENDENS*

Dinoflagellate blooms or red tides frequently occur in a stratified water column having low nutrients near the surface (Huntsman et al. 1981). Under these conditions dinoflagellates have a competitive advantage over other phytoplankton due to their motility and diel vertical migration pattern. In the absence of turbulence, active swimming allows them to overcome sinking and thereby, remain close to the surface. The normal diel vertical migration consists of an ascent to some minimum depth during the day and descent to a maximum depth at the night (reviewed by Forward 1976). Through this pattern they have access to nutrients over the area covered by migration and they can migrate to the surface during the day to obtain more light for photosynthesis (Ryther 1955; Margalef 1978; Huntsman et al. 1981).

The success of dinoflagellates depends to a great extent upon their swimming capability. There have been few measurements of actual swimming speeds of individual dinoflagellates (e.g., Hand et al. 1965) or estimates of speeds from population movements during migration (Eppley et al. 1968; Kamykowski and Zentara 1977). This is unfortunate because such measurements are necessary to estimate the depth of the water column available to dinoflagellates for nutrients during migration.

The most pronounced and widespread dinoflagellate blooms off the coast of Peru are caused by *Gymnodinium splendens* Lebour. Blooms occur most frequently during the summer and are usually associated with the phenomenon of El Niño (Rojas de Mendiola 1979). At the beginning of the 1976 El Niño, there was a major bloom of *G. splendens*. Blasco's (1979) surface measurements during this bloom indicated the dinoflagellate vertically migrated with the suggested pattern involving an ascent in the early morning and maintenance of a deeper distribution at night. This pattern was similar to that observed by Kiefer and Lasker (1975) for this species in the Gulf of California. Vertical chlorophyll a profiles indicated the cells rose in the morning and descended in the evening. The present study was undertaken to measure swimming speeds of *G. splendens* under different temperature conditions. The observed speeds vary with temperature and are similar to those calculated from field studies.

Materials and Methods

The dinoflagellate *Gymnodinium splendens* Lebour was cultured as described previously (Forward 1974) in a Sherer[1] environmental chamber (Model CEL-44) on a 14:10 LD cycle at a salinity of about 34 ppt. All experiments were performed in the middle 4 h of the light phase with cultures having densities of about 2,000 cells/mL. This cell density was used because it was similar to that used in past studies (Forward 1974, 1977) and thus past results can be applied to the present study. Swimming speed during phototaxis was only measured during a specific time interval because there is a circadian rhythm in phototaxis (Forward 1974). *Gymnodinium splendens* shows about average levels of phototaxis during the middle 4 h of the light phase. It is not known whether there is a similar rhythm in swimming.

Subcultures were exposed to two sets of temperature conditions to test for the effects of 1) temperature acclimation and 2) acute temperature changes upon swimming speed. In the first tests cells were acclimated to selected temperatures from 13° to 25°C for at least 5 d prior to swimming speed measurements. These temperatures were used because they encompass the range in which the cells grow at reasonable rates (Thomas et al. 1973). For the second tests, cultures were acclimated to 19°C for at least 5 d. At the time of testing cultures were exposed to an acute temperature change by placing the flasks in a water bath set at selected temperatures for 0.5 h, after which time swimming speed was measured. Room lights were on during this 0.5-h period. The temperature of the room in which swimming was measured was regulated to approximately each test temperature. Each test was performed on four separate subscultures.

To measure swimming speeds, a sample of cells was removed from a subculture and placed in a clear

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

cuvette. The cells were viewed by the closed circuit video system described by Forward (1974). During random swimming the cells can move in any direction and are not necessarily moving in the plane of view of the video camera. Thus measurements of swimming speeds during random swimming tend to underestimate true speed. To prevent this problem, cells were stimulated horizontally with light and speed measured during oriented swimming toward the light (positive phototaxis). Room lights were off during light stimulation.

The light stimulus was a tungsten light source filtered with a 4-96 Corning filter. The spectral composition of the light was similar to the spectral sensitivity of phototaxis of *G. splendens* (Forward 1974). A constant light intensity of 4.79×10^2 Wm^{-2}, as measured with an EG and G radiometer (Model 550) and calculated at 465 nm, was used for all tests because maximum positive phototaxis occurs in this intensity range, and it was necessary to measure swimming speed during phototaxis. Swimming was recorded on video tape and speed analyzed using previous techniques (Forward 1974).

Results

Swimming speed varied greatly with temperature (Fig. 1) as mean speeds approximately double upon acclimation to temperatures between 13° and 25°C (0.56 h^{-1} to 1.16 mh^{-1}). The dinoflagellate seems capable of limited temperature acclimation. If the cells were acclimated to 19°C and suddenly exposed to other temperatures, there was always a significant difference (Student's t test; $P < 0.001$) between these mean speeds and those upon acclimation. At a lower temperature of 13°C the acclimation speed was higher; while at temperatures above 19°C, the acclimation speeds were lower. This trend is expected with acclimation.

The effects of temperature can be further assessed by calculating the temperature coefficients upon acclimation and exposure to acute temperature changes (Table 1). The Q_{10} values for acute changes are always higher than those upon acclimation, which is expected if swimming rates are adjusted through acclimation. When acclimated to temperatures between 13° and 19°C, the cells showed total compensation (Q_{10} = 0.98). In contrast, they were less able to adjust their rates upon acclimation to higher temperatures between 19° and 25°C (Q_{10} = 3.42). Partial acclimation occurred over this temperature

TABLE 1.—Temperature coefficient values for the dinoflagellate *Gymnodinium splendens* upon temperature acclimation and exposure to acute changes in temperature.

Temperature range	Acute Q_{10}	Acclimation Q_{10}
13°-19°C	1.47	0.98
19°-25°C	4.68	3.42

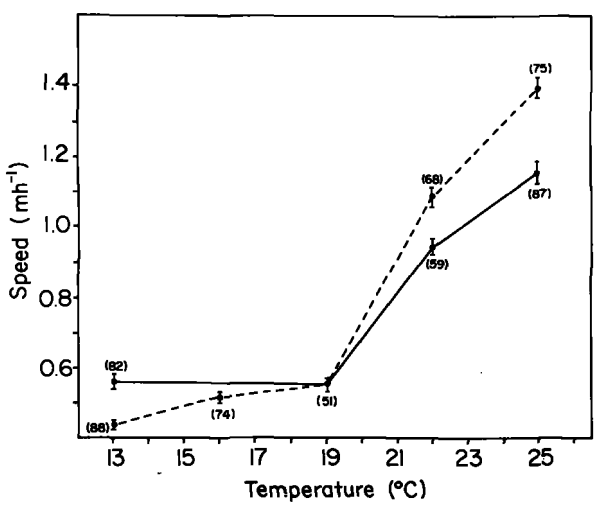

FIGURE 1.—Swimming speeds of the dinoflagellate *Gymnodinium splendens* upon acclimation to various temperatures (solid line). The effect of acute temperature change was measured by acclimating the animals to 19°C and measuring speeds upon exposure to other temperatures (dashed line). The number beside the points are the sample sizes and the vertical bars are standard errors.

range since the acclimation Q_{10} is lower than the acute Q_{10} (Table 1).

Discussion

Blooms of *G. splendens* occur off the coast of Peru in temperatures ranging from 17° to 23°C with optimum being 18°-21°C (Rojas de Mendiola 1979). The lower temperature agrees with laboratory measurements of vertical migration, as Kamykowski (1981) found migration in the laboratory occurred at temperatures above 16°C. In the laboratory, this dinoflagellate can survive and divide at temperatures from 12° to 29°C. The most rapid growth rates (0.4 divisions/d), however, occur at 20°-27°C (Thomas et al. 1973). Within the optimum temperature range suggested from these studies (18°-26°C), swimming speed of *G. splendens* approximately doubles (Fig. 1). These speeds and their change with temperature are similar to those reported for other dinoflagellate species (Hand et al. 1965).

The speeds of movement calculated from field studies of vertical migration of *G. splendens* agree with the speeds found in the present study. Blasco (1979) calculated that a speed of 1 m/h was sufficient to account for the migration off Peru during the 1976 El Niño. In the Gulf of California, *G. splendens* migrated over a depth of about 9 m and had a calculated descent velocity at sunset of 1.7 m/h (Kiefer and Lasker 1975). The present study predicted this speed would occur at temperatures above 25°C. Unfortunately Kiefer and Lasker (1975) did not state the water temperature at the time of migration.

An objective of the present study was to use the measured swimming speeds to determine the distance over which *G. splendens* should be capable of migrating. A conservative estimate of distance can be calculated from the speeds upon acclimation to optimum temperatures (19°-25°C) and assuming the dinoflagellate 1) swims continuously in either the upward or downward direction for half of the migration cycle (12 h) and 2) does not have a diel rhythm in swimming speed. At 19°, 22°, and 25°C the calculated distances are 6.6, 11.3, and 13.9 m respectively. These distances would increase slightly if a temperature gradient existed because speed is approximately constant at 19°C and lower temperatures, and acute exposure to higher temperatures, which would occur high in the water column, would elevate speeds above those upon acclimation (Fig. 1). In addition, these values would probably vary if *G. splendens* is exposed to different environmental conditions, since salinity, light intensity, and nutrient levels can affect migration patterns (Kamykowski 1981).

Acknowledgments

This work was supported by an International Oceanographic Commission travel grant to BRM and a National Science Foundation Grant No. OCE-8110702.

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MORPHOLOGY AND POSSIBLE SWIMMING MODE OF A YELLOWFIN TUNA, *THUNNUS ALBACARES*, LACKING ONE PECTORAL FIN

In September of 1982, the Mexican bait boat, *Paesa*, fishing off Baja California, captured a 36.5 cm fork length (861.2 g wet weight) yellowfin tuna, *Thunnus albacares*, that lacked a left pectoral fin (Fig. 1). The fish was frozen and was brought to the Inter-American Tropical Tuna Commission, La Jolla, CA, for study by W. H. Bayliff.

Pectoral fins provide virtually all hydrodynamic lift in scombrids and are essential for stable and efficient swimming at sustained speeds (Magnuson 1973, 1978). A specimen with only one pectoral fin raises questions on what ways the fish might have compensated for an asymmetrical decrease in hydrodynamic lift and how the presence of only one pectoral fin might have affected its locomotion. We examined the fish to determine what may have caused fin loss and whether morphology was noticeably altered in a manner suggesting some compensation.

Skin in the area where the left pectoral fin should have been was thin, smooth, and silvery in appearance (Fig. 1). There was neither a trace of pectoral fin remnants nor a skin groove for it, suggesting the fin had never formed. On the other hand, the appearance of the skin and the presence of variably sized scales in the area around the normal fin position is compatible with a healed wound, and we thus could not rule out the possibility that the fin had been bitten off cleanly.

Methods

The specimen was X-rayed and maximum body height and width measured. We measured and traced its median fins, caudal keel, pectoral fin, and both pelvic fins, and estimated their surface areas with a planimeter. The same body and fin measurements were made on similarly sized, preserved yellowfin tuna in the Scripps Institution of Oceanography Fish Collection (SIO). Morphometric data were compared with values derived from the literature (Gibbs and Collette 1967; Fierstine and Walters 1968; Magnuson 1973, 1978; Magnuson and Weininger 1978, app. II). Although some of the specimen's caudal rays were bent (Fig. 1), all rays were present, and the fin was extended to a more natural position before its span was measured and area (which was well defined) traced. Also, to avoid measurement errors noted by Fierstine and Walters (1968) and Magnuson (1978), care was taken not to overextend caudal fins during span measurement.

Density of the thawed fish was determined by water displacement (density = wet weight/displacement volume). The right and left pectoral girdles were then removed and the gas bladder was inspected. Transverse sections were cut (see Graham et al. 1983), concentric myotomal rings on the right and left sides were counted, and red and white muscle were weighed for each section.

Results

The abundance of comparative morphometric and anatomical data for the yellowfin tuna permits a nearly complete assessment of the morphologic and hydrodynamic status of the one-finned specimen. The length (L; 36.5 cm)/weight (861.2 g) relationship and the density (1.080 $g \cdot mL^{-1}$) agree with values published for yellowfin tuna by Magnuson (1973, tables 1, 4). Also, the maximum thickness value (i.e., max. height + max. width/2 = 21.6% L) is within the range (20.5-23.0% L) measured for four SIO specimens (L from 28.5 to 42.5 cm) and near the value given by Magnuson (1973, table 7, 22.3% L). Finally, the point of maximum body thickness in the study fish (39.7% L) and that of SIO fish (36-40% L) are near Magnuson's value of 41.2% L (for fish from 28 to 45 cm L).

The dorsal fin of this fish is normal in shape, with 13 spinous rays, a maximum height of 3.5 cm and a surface area of 9.5 cm^2. The second dorsal fin is