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Energetic cost of position-holding behavior in the planktonic mysid *Mysidium columbiae*

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ABSTRACT: *In situ* videotapes indicate that the planktonic mysid *Mysidium columbiae* exhibits positive rheotactic behavior and can use prop roots and other objects as visual cues to maintain position in currents of changing speed within the mangrove prop root environment. The ability of mysids to hold position in currents of different speed was measured in the laboratory in a flow-through chamber. The response of mysids to visual cues was tested with an optokinetic drum. When the drum rotates, the mysids swim at the same speed and in the same direction as the moving stripes. Swimming speed of the mysids was measured using video-computer motion analysis techniques. By varying the speed of currents in the flow-through chamber or by changing the rotational speed of the optokinetic drum, mysids can be 'forced' to swim at various speeds. By measuring the decrease in oxygen concentration within a sealed chamber, while simultaneously monitoring swimming speed with a video camera, the metabolic cost of increased swimming speeds was calculated. The respiration rates of *M. columbiae* more than double when swimming at sustained high speed (ca 25 mm s^{-1}). These mysids are preyed on by a wide range of planktivorous fish under laboratory conditions, and their survival may depend upon their ability to maintain their position within the safety of the prop root habitat during daylight hours in spite of currents and turbulence that would tend to disperse them into adjacent open water habitat.

KEY WORDS: Mysids · Aggregation Respiration · Rheotaxis Optokinetic response

INTRODUCTION

Zooplankton aggregations such as mysid swarms and schools, which occur on scales of centimeters to meters, affect population dynamics through changes in encounter rates between predator and prey, and by enhanced mating opportunities. The formation and maintenance of these aggregations must include a behavioral component, since they are usually composed of a single species of zooplankter where numerous species are found, and since turbulent diffusion would lead to dispersal of the aggregation in the absence of active behavior (Okubo 1980). Since there are energetic costs associated with maintaining these aggregations, both in terms of increased metabolic costs associated with swimming behavior to overcome turbulence and currents, and in terms of decreases in food availability within densely packed swarms and schools, it seems reasonable to assume that the zooplankters must accrue some adaptive advantage from these aggregative behaviors. The suggested adaptive values of swarming and schooling behavior in planktonic mysids include protection from predators (O'Brien & Ritz 1988, Ritz 1991), facilitation of mating (Clutter 1969), and maintaining position in the environment (Clutter 1969, O'Brien 1988, Ritz 1994).

Mysid schools have been extensively studied (e.g. Clutter 1967, 1969, Mauchline 1971, Wittman 1977, 1984, O'Brien 1988, 1989, Modlin 1990, 1993) but much remains to be learned about these active crustaceans with sophisticated sensory capabilities and complex social interactions. While many species of mysids are associated with the benthos during the day, *Mysidium* spp. are predominantly holoplanktonic (Emery 1968, Mauchline 1980). The mysid *Mysidium columbiae* is usually found in the shaded areas near mangroves (Steven 1961); it is also found in the vicinity of coral reefs, mainly in areas protected from strong currents (Emery 1968). It has well developed compound eyes

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that are thought to have limited visual acuity but highly developed movement perception (Waterman 1961, Buskey unpubl.). Holoplanktonic mysids like *M. columbiae* have been shown to use visual cues in the maintenance of shoals and schools (Steven 1961, Clutter 1969, O'Brien 1988) These mysids are fed on voraciously by a wide range of planktivorous fish in the laboratory (Buskey unpubl.) although predation is rarely observed in nature (Modlin 1990). Their survival may depend upon their ability to maintain schooling behavior and the school's position within the prop root habitat during daylight hours.

The mysid *Mysidium columbiae* appears to use visual cues in combination with a rheotactic response to currents to maintain the position of schools adjacent to the mangrove prop-root habitat in spite of currents and turbulence that would tend to disperse them. Evidence for the role of vision in schooling and position-holding behavior comes from the optomotor responses of mysids. Optomotor responses, in which movements of the body compensate for the displacement of images over the eye, are well known in higher crustaceans and fish (e.g. Fraenkel & Gunn 1940 for mysids, Pankhurst et al. 1993 for fish). One method of testing for optomotor responses is with an optokinetic drum. In this method, a vertically oriented drum with vertical black and white stripes is rotated around the outside of a clear cylinder containing the experimental animals. Animals with a strong optomotor response will swim in the same direction as the striped outside drum is moving. *M. columbiae* show a very strong response; they move in the same direction as the drum is rotated and at the same speed. They fall into lock-step with the drum movement almost immediately and reverse direction when the direction of drum movement is changed. This strong optokinetic response suggests that vision may play an important role in position-holding behavior in mysids, since mysids will swim continuously to prevent the movements of high contrast images through their visual field. These same types of visual stimuli would occur when mysids drift with currents in a visually complex environment such as the mangrove prop root habitat.

Both the rheotactic and optokinetic behaviors of *Mysidium columbiae* can be used to measure the energetic cost of position-holding behavior. Since mysids will hold position in currents of varying speeds or follow stripes in an optokinetic drum, they can be 'forced' to swim at known speeds for extended periods of time, and the relationship between swimming speeds and respiration rate determined. In this study I examine the position-holding behavior of *M. columbiae* in nature, examine its behavior responses to currents and optokinetic stimuli in the laboratory, and then use these behavioral responses to simultaneously measure swimming speed and respiration rate to examine the metabolic cost of position-holding behavior.

METHODS

Field studies were carried out at the Smithsonian Institution's field station on Carrie Bow Cay in Belize. Mysids for laboratory study were collected in Twin Bays and Lair Channel of Twin Cays, a pair of mangrove covered islands ca 2 km to the NW of the laboratory. Fresh mysids were captured each day between 08:00 and 10:00 h while snorkeling near the mangrove prop root environment using a 25 × 18 cm aquarium net. By sampling near the bottom of an aggregation, mainly adult mysids were captured (>90% adults; mean length 5.4 mm), since the shoals organize vertically by size (Modlin 1990). Mysids were immediately transferred to a large insulated cooler filled with seawater and taken back to the laboratory on Carrie Bow Cay. The mysids were then transferred to a 50 l glass aquarium with a continuous flow of fresh seawater. Inter-individual distances in shoals of *Mysidium columbiae* are reported to range between 0.5 and 5 cm in nature (Modlin 1990). The average density of mysids used in behavioral and respiration experiments was ca 300 mysids l^{-1}, which corresponds to an average inter-individual distance of 1.8 cm, assuming isohedral packing (Hamner & Carlton 1979).

In situ video recording of the copepod swarms was performed using a Cohu 3315 monochrome CCD video camera equipped with a macro lens (Micro-Nikkor 55 mm f2.8), placed within a waterproof housing (Video Vault). The camera and housing were mounted on an aluminum tripod. Images were recorded on a Sony FX-710 camcorder integrated into a field portable video system (Furhman Diversified Fieldcam WCMS) that remained in a small boat anchored nearby and was connected to the camera via a waterproof cable. Mysid swarms or schools were located by snorkeling along the edge of the mangroves. When a suitable mysid aggregation was located, the tripod was placed on the bottom and the camera was adjusted to allow the mysids to be videotaped. An area of ca 70 cm^2 was viewed in the vertical plane at a distance from the camera housing of ca 90 cm, allowing the aggregation to be recorded without being disturbed by the camera. Mysid schools generally swam parallel to the mangrove fringe; by orienting the camera perpendicular to the mangrove fringe, accurate measures of swimming speed could be obtained. After recording each aggregation, a metric ruler was filmed under water to calibrate the spatial scale.

Respiration rates of mysids swimming at different speeds were measured using a sealed, variable speed,

flow-through chamber (as in Buskey 1998) and in a sealed chamber within the optokinetic drum. The recirculating flow-through chamber was constructed of clear acrylic plastic, with overall outside dimensions of 17 × 8 × 8 cm; the respiration chamber had inside dimensions of 7 × 7 × 7 cm. The total volume of water contained within the flow-through system was 620 ml. Seawater collected at the end of the respiration chamber was pumped to the forward section of the chamber by a Rule 360 bilge pump. To make the flow more laminar, water passed through a plastic grate (3 mm square openings) and a bed of small pebbles (ca 1 cm diameter) before entering the center of the respiration chamber. A wall of 153 µm mesh screening on each end retained the mysids within the center portion of the respiration chamber. Water was pumped between sections through a stainless steel return pipe, which served as a heat exchanger to keep the water temperature constant. The chamber was placed in a flow-through water bath at 28°C. Pump speed was controlled by varying the electrical current to the pump. Temperature of the water within the flow-through chamber and in the water bath was monitored with bead type thermistors using a 2-channel Omega Model 747 digital thermometer. A vertical tube allowed for a small reservoir of extra water, so that small samples could be withdrawn from the chamber during the experiment; the tube was topped with a layer of mineral oil to retard any oxygen exchange between this reservoir and the atmosphere.

Before each experiment, the flow-through chamber was thoroughly flushed with fresh 20 µm mesh filtered seawater and rotated until all trapped air bubbles were removed. A group of ca 100 freshly collected *Mysidium columbiae* was then added to the chamber through a port in the top and sealed with a silicone rubber stopper. At 20 min intervals over the course of 1 h, small water samples (ca 1 to 2 ml) were withdrawn from the circulating chamber with a syringe through the silicone stopper on the top of the chamber and injected into the small volume (ca 70 µl) water-jacketed respiration chamber, held at the same temperature as the experimental chamber Oxygen concentrations were measured using a Cameron Instrument Company OM200 oxygen meter and an E101 oxygen electrode. The oxygen electrode and meter were calibrated using oxygen saturated seawater (100%) and a sodium sulfite solution (100 mg Na_2SO_3 in 5 ml 0.1 M sodium borate solution) to set the zero point before each measurement to correct for electrode drift. Oxygen concentrations were typically reduced to 60 to 80% of saturation by the end of the experiment. No changes in oxygen concentration were observed in either chamber over similar time intervals in the absence of mysids.

At the end of each experiment, all the mysids used in that experiment were collected on a 153 µm mesh sieve and preserved in 5% buffered formalin. The dry weight of each of these samples was determined 1 mo after they were collected. Samples were dried on pre-weighed glass fiber filters at 60°C, and weighed on a Sartorius AS200S analytical balance.

An optokinetic drum was also used to test the relationship between swimming speed and respiration rate of *Mysidium columbiae*. An optokinetic drum is used to move black and white vertical stripes past the fields of view of the mysids. The mysids (ca 200 individuals) are placed in a circular, clear acrylic plastic raceway, constructed of 2 concentric cylinders of plastic (0.5 cm thick) with a clear plastic top and bottom. Two holes (2 cm diameter) on opposite sides of the top surface were used for adding seawater and mysids to the raceway. During respiration measurements, the chambers were completely filled with seawater and the holes sealed with silicone stoppers. Water temperature within the chamber was monitored with a digital thermometer (Omega model 747) and remained between 27 and 29°C. Small samples of seawater were removed from the chamber at 20 min intervals during the 1 h experiments through one of the silicone stoppers using a 20 ml syringe. A reservoir of additional seawater was provided by a second syringe containing extra seawater which penetrated the other silicone stopper. This reservoir was sealed with mineral oil to retard gas exchange with the atmosphere. The inside diameter of the larger cylinder was 12.7 cm and the outside diameter of the smaller opaque cylinder was 6.3 cm. The area between these walls formed the circular raceway with a volume of 630 ml in which the mysids were free to swim. Black and white stripes 11 mm in width moved past the outer wall of this container at constant speeds. The drum consisted of a plastic cylinder just slightly larger than the diameter of the plastic raceway. The cylinder had a white inner surface; computer generated black stripes were photocopied on to clear plastic acetate sheets, and these sheets were taped to the inside surface of the drum. The drum was rotated by a low RPM, variable speed, reversible electric motor. Drum speed was regulated by varying the voltage to the motor with a potentiometer. Drum direction was reversed by reversing the polarity of the current to the motor

Preliminary experiments indicated a strong optokinetic response of mysids to stripes of 11 mm width. Visual observations indicated that the mysids were swimming in the same direction as the stripe rotation and at approximately the same speed. When the direction of drum rotation was reversed, the mysids would reverse their direction of swimming within a few seconds. Since *Mysidium columbiae* was reported to be

able to swim at speeds of up to 150 mm s^{-1} (Steven 1961), the effects of changing drum rotation speed on the swimming speed of the mysids were tested. Ten drum speeds were tested ranging from 4 to 47 mm s^{-1}. Although the drum was designed to rotate at speeds of up to 120 mm s^{-1}, it became clear that the mysids would not continue to swim with the stripes at higher speeds. Each speed was tested between 1 and 5 times; each test used a fresh group of mysids. Mysid swimming speeds within the test cylinder were recorded on videotape for later analysis.

Mysid swimming behavior was quantified using a video-computer system for motion analysis. Swimming behavior was recorded using a Cohu 3315 monochrome video camera equipped with a macro lens (Micro-Nikor 55 mm f2.8) and connected to a Sony FX-710 camcorder. Contrast of mysid images on videotape was enhanced using darkfield illumination, provided by a set of infrared light emitting diodes (peak wavelength 890 nm). Indirect ambient sunlight in the room was held between 15 and 25 µM photons m^{-2} s^{-1} (measured with a LICOR LI-250 light meter) by adjusting blinds on nearby windows. To improve the accuracy of swimming speed measurements, the video camera was oriented perpendicular to the swimming direction of the mysid schools. Mysids were viewed from the side (vertical plane) in a field of ca 20 cm^2 in the flow-through chamber and from above (horizontal plane) in a field of ca 10 cm^2 in the raceway of the optokinetic drum. Cultures of a large, non-motile dinoflagellate (*Pyrocystis noctiluca*) were added to the chamber with a fine pipette and used as tracers to estimate current speed in the flow-through chamber at different pumping speeds.

Calibration videotapes and tapes of mysid swimming behavior were quantified with an Expertvision Cell-Trak motion analysis system. Videotapes were digitized with a Motion Analysis VP-110 processor, and digital outlines of mysids or dinoflagellates were sent to a personal computer at a rate of 15 frames s^{-1}. These digitized images were processed to calculate the swimming speeds (mm s^{-1}) and the rate of change of direction (degrees s^{-1}) of the mysids' paths of travel (Buskey 1984) relative to the fixed position camera or the dinoflagellates' drift with the current (to calibrate flow). Swimming speeds of mysids in the flow-through chamber for the respiration experiments were calculated as described in Buskey et al. (1996), to calculate true swimming speeds of copepods swimming in a current, but observed from a fixed point. Each segment of a copepod's swimming path was treated as a vector defined by the animals' orientation with respect to the current (0° in the same direction as the current, 180° moving opposite to the current) and its swimming speed measured from the fixed reference point. The current speed vector was then added to each path segment and the magnitude of the resulting vector was used to estimate the true swimming speed for the copepod in the moving body of water.

RESULTS

Mysidium columbiae showed remarkable ability to hold position within the mangrove prop root environment in currents of up to 30 mm s^{-1}. *In situ* videotapes revealed that mysids tended mainly to form swarms in weak currents (< ca 5 mm s^{-1}). Individuals within these swarms had varying orientations, although they would occasionally orient into schools, with all individuals swimming in the same direction for a few seconds, usually in response to the approach of a fish or to another disturbance in the water. In stronger currents, *M. columbiae* exhibit positive rheotaxis and form schools oriented to face into the flow, and hold the position of the school in a fixed location within the mangrove prop root environment. Although individual mysids tend to surge forward into the current, and drift back for periods of a few tenths of a second, overall they do remarkably well at maintaining their position in the school. Individual mysids also appear to change their vertical position in the school frequently, while maintaining their horizontal position with respect to the current. When currents frequently change direction and intensity, as with wave surge into a shallow bay from offshore swells, the mysids rhythmically reverse direction with incoming and outgoing surges, always swimming into the current and maintaining their position near the prop roots.

In the laboratory, mysids exhibited slower swimming speeds than when observed *in situ* (Table 1). In the absence of water movement, mysids swam at a mean speed of 4.4 mm s^{-1} (<1 body length s^{-1}). In the flow-through chamber, mysids were exposed to constant speed flows of ca 5, 12 and 24 mm s^{-1}, and as current speed increased, swimming speed relative to the fixed position camera increased, from 5.4 to 9.9 mm s^{-1} (Table 1). Mysids easily maintained their position within the center of the flow-through chamber without contacting the mesh partitions at the front or back of the chamber. Their movements relative to the fixed position camera reflect vertical adjustments in position and occasional surges into the current or drifting back with the current. These movements are also reflected in the rate of change of direction (RCD) which increased with increasing current speed in laboratory experiments (Table 1). When their swimming behavior was recorded in nature, waters were never completely still; currents ranged from ca zero for a few seconds to up to 29 mm s^{-1}. Currents often reversed direction with

Table 1. Parameters describing movements of *Mysidium columbiae* relative to a fixed-position camera either *in situ* or swimming in a flow-through chamber in the laboratory. Mean speeds and rates of change of direction (RCD) are based on 3 min of video taped behavior with several mysids in view simultaneously, analyzed at a rate of 15 frames s^{-1} (ca 5000 to 10000 measures for each parameter). One standard deviation is given in parentheses

Location	Flow speed (mm s^{-1})	Speed (mm s^{-1})	RCD (degrees s^{-1})
Lab	0	4.4 (2.9)	222 (168)
Lab	5.5	5.4 (3.8)	279 (221)
Lab	11.9	6.9 (4.4)	304 (262)
Lab	24.3	9.9 (6.6)	324 (305)
In situ	0–3	12.2 (8.5)	261 (227)
In situ	0–5	11.7 (9.3)	224 (203)
In situ	3–10	15.2 (10.3)	226 (212)
In situ	0–22	18.9 (13.2)	245 (218)
In situ	0–26	21.4 (18.5)	214 (193)

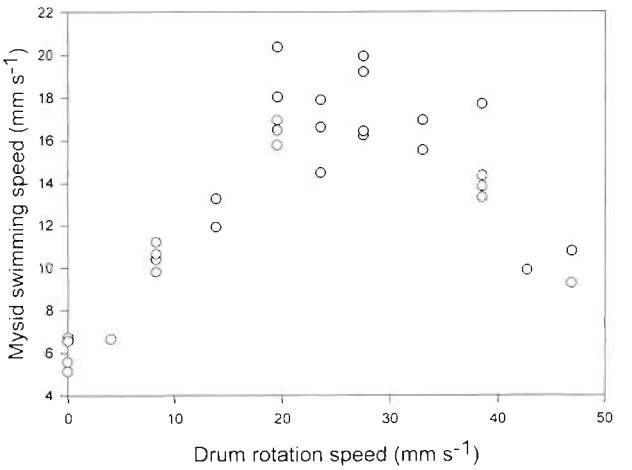

Fig. 1. Behavioral response of *Mysidium columbiae* within an optokinetic drum to changes in drum rotation speed

the surge and return flow of waves into the prop root habitat. Even under the calmest conditions, when the mysids tended to form swarms rather than schools, their swimming speeds were much faster in nature than those measured in the laboratory (range 11.7 to 21.4 mm s^{-1}, Table 1).

Mysidium columbiae shows a strong optokinetic response over a range of drum rotation speeds of ca 5 to 20 mm s^{-1} (Fig. 1). The average swimming speeds of the mysids increase proportionally to the increase in drum rotation speed. When exposed to drum rotation speeds ranging from 20 to 40 mm s^{-1}, the mysids show no further increase in swimming speed. At speeds above 40 mm s^{-1}, the mysids exhibited reduced swimming speed. At high drum rotation speeds, some mysids would follow the stripes for a period of time, but would then stop and press their heads against the opaque center drum and stop swimming. This behavior may have allowed them to ignore the moving stripes and block their optokinetic response while resting. Experiments examining the effects of swimming speed on respiration rate were all carried out at drum speeds between 5 and 20 mm s^{-1}, where swimming speeds corresponded to drum rotation speed.

Two different methods were used to examine the relationship between swimming speed and respiration rate in *Mysidium columbiae*. Using a flow-through chamber originally designed to be used with copepods swarms (Buskey 1998), 2 different flow speeds were tested, 5 and 20 mm s^{-1}. These 2 flow speeds yielded 2 ranges of average mysid swimming speeds, from ca 5 to 8 mm s^{-1} and from ca 21 to 26 mm s^{-1}. Since the higher speed was the maximum that could be obtained with the flow-through chamber, and the mysids appeared to have no difficulty maintaining position in this flow, it was hoped that the optokinetic drum could be used to sustain higher average swimming speeds. This turned out not to be the case. The maximum speed that mysids could be forced to maintain using the optokinetic drum was also ca 20 mm s^{-1} Measured respiration rates ranged from ca 4 to 16 µl O_2 mg_{dw}^{-1} h^{-1} at 28°C at various swimming speeds.

Three metabolic rates have been defined for the relationship between swimming activity and oxygen consumption, based on studies conducted with fish (e.g. Fry 1971, Brett & Groves 1979). Standard metabolic rate is the rate when there is no activity, and it can be estimated by the *y*-intercept of the relationship between swimming speed and respiration rate. Routine metabolic rate is the average rate associated with normal spontaneous swimming behavior. In this study routine metabolism is the rate measured when swimming speeds are similar to those measured in the absence of a current. The active rate is the metabolic rate at maximum sustained activity under conditions of forced swimming. Active metabolism was measured in this study at the maximum swimming speed at which mysid schools could be maintained for periods of up to 1 h. Based on the relationship between swimming speed and respiration rate (Fig. 2), and using a value of 5 mm s^{-1} (ca 1 body length s^{-1}) for normal spontaneous swimming speed in the laboratory and 25 mm s^{-1} (ca 5 body lengths s^{-1}) for maximum sustained swimming speed, metabolic rates of 2.75, 4.7 and 12.5 µl O_2 mg_{dw}^{-1} h^{-1} are calculated for standard, routine and active metabolic rates, respectively.

The net cost of transport for *Mysidium columbiae* is the amount of energy per unit body weight required to move a given distance through the water. For a mysid swimming at 5 or 25 mm s^{-1}, it requires 55.6 or 11.1 h, respectively, to swim 1 km. Given our measured values

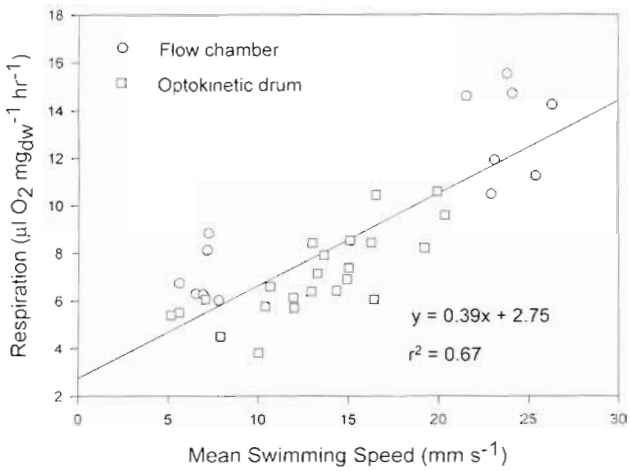

Fig. 2. Respiration rate of *Mysidium columbiae* as a function of its swimming speed in a sealed flow-through chamber or a sealed raceway within an optokinetic drum. Mysids were induced to swim at different speeds by varying current speed or by varying the rotational speed of the optokinetic drum

of respiration for *M. columbiae* swimming at these speeds, it requires 261.1 µl O_2 mg_{dw}^{-1} to swim 1 km at 5 mm s^{-1}, but only 138.9 µl O_2 mg_{dw}^{-1} to swim the same distance at 25 mm s^{-1}, respectively. If an average value of 4.86 kcal liberated per liter of O_2 respired is used (Winberg 1971), these values are equivalent to 1.27 and 0.67 kcal g_{dw}^{-1} km^{-1}.

DISCUSSION

Schools of *Mysidium columbiae* exhibit position-holding behavior in the face of currents in red mangrove prop root habitat. Other mysids have been shown to have strong affinity for particular locations (Hahn & Itzkovitz 1986) or particular substrate types (Wittman 1977). Roast et al. (1998) investigated the position-holding behavior of the hyperbenthic mysid *Neomysis integer* in response to current velocity, and found a decreasing proportion of mysids exhibiting positive rheotaxis as current speed increased over a range of current speeds from 30 to 150 mm s^{-1}. However, position maintenance increased with increasing current speed as these mysids sheltered themselves behind sand ripples or burrowed into the mud at high current speeds. Although position-holding behavior in the holoplanktonic mysid *M. columbiae* appears to involve rheotactic behavior, visual cues may also aid in position-holding behavior. Steven (1961) suggested that cohesion of *M. columbiae* schools is maintained by visual cues, and the role of vision in schooling behavior has been demonstrated for other mysid species (Clutter 1969, O'Brien 1988). The strong optokinetic response demonstrated for *M. columbiae* in this study also indicates a role for vision in position-holding and schooling behavior. The mysids will swim at sustained high speeds to avoid the perception of objects moving past their field of vision, as would be the case if they were drifting with currents or falling out of position with members of a school.

The metabolic cost of position-holding behavior can be large when current speeds are high. Active metabolism is 2.7 times greater than routine metabolism and routine metabolism is 1.7 times greater than standard metabolism for *Mysidium columbiae* at its normal environmental temperature of 28°C (Fig. 2). The total metabolic cost of position-holding behavior for these mysids in their natural environment is unknown, but will depend on the strength, duration and frequency of tidal currents and wave induced surges. Although direct measurements of current speed have not been made in the mangrove prop root environment for extended periods of time, it seems likely that the highest metabolic costs may be associated with periods when large offshore swells impact the mangrove cays, producing strong, frequently reversing currents for periods of up to several days.

Other studies with large plankton crustaceans, such as those of Torres & Childress (1983) with the euphausiid *Euphausia pacifica*, found somewhat higher results, with routine metabolism approximately 3 times greater than standard metabolism. However, Foulds & Roff (1975) found only a 1.2 times increase in active metabolism over routine metabolism in the mysid *Mysis relicta*. For the swarm-forming copepod *Dioithona oculata*, found in the same mangrove prop root environment as *Mysidium columbiae*, there appears to be a greater cost of position-holding behavior, with active metabolism 3.2 times greater than routine metabolism, and routine metabolism 2 times greater than standard metabolism (Buskey 1998). Swimming behavior of *M. columbiae* is more efficient than that of the copepod *D. oculata*. At speeds of 18 mm s^{-1}, the cost of transport for *D. oculata* is 3.5 kcal g_{dw}^{-1} km^{-1} (Buskey 1998) compared to only 0.67 kcal g_{dw}^{-1} km^{-1} for *M. columbiae* swimming at 25 mm s^{-1}. The relationship between swimming speed and oxygen consumption appears to be linear for *M. columbiae* (Fig. 2). Similar linear relationships between swimming speed and respiration have been found in other free swimming crustaceans including the amphipod *Gammarus oceanicus* (Halcrow & Boyd 1967), the euphausiid *E. pacifica* (Torres & Childress 1983), the mysid *Gnathophausia ingens* (Cowles & Childress 1988) and the copepod *D. oculata* (Buskey 1998).

The mysids generally seemed to do a better job of holding position under laboratory conditions than in nature (i.e. there was more movement relative to the

fixed position camera). This may be due to the more laminar flow in the laboratory flow-through chamber compared to the obvious turbulence observed *in situ*. The superior position-holding behavior may also be due to better visual cues in the flow-through chamber in the laboratory compared to visual cues in nature which were generally further away and themselves subject to motion (e.g. movements of seaweeds with the current).

The swimming behavior of *Mysidium columbiae* differed when recorded on videotape in the laboratory or in nature. Swimming speeds of mysids in small containers (flow-through chamber volume ca 350 ml; optokinetic raceway volume ca 630 ml) in the laboratory were ca one half of that measured in nature under conditions of similar flow (Table 1). However, light intensities in the laboratory (ca 15 to 25 µM photons m^{-2} s^{-1}) may have been lower than those in the field (up to 160 µM photons m^{-2} s^{-1} in midday mangrove shade; Ambler et al. 1991). Steven (1961) reported that swimming speed of *M. columbiae* was photokinetically controlled, with mysids swimming faster at higher light intensities. Clearly the factors affecting behavior of *M. columbiae* in the laboratory are complex, and may involve container effects, light intensity, visual cues and/or water movements. In a previous study of swarming behavior of the copepod *Dioithona oculata*, the presence of water movement under laboratory conditions produced swimming behavior in the laboratory that was similar to that recorded in nature (Buskey et al. 1996). Likewise, behavior of *M. columbiae* in the flow-through chamber was more similar to behavior in nature than that recorded in the laboratory without flow. The results of this study and previous studies investigating the effects of turbulence on copepod behavior (Costello et al. 1990, Saiz 1994, Kiørboe & Saiz 1995) emphasize the importance of biological-physical interactions in planktonic processes, and suggest that results from laboratory experiments conducted in the absence of water movements must sometimes be interpreted with caution when applied to field conditions.

A variety of juvenile fishes were observed to feed on *Mysidium columbiae* held in the laboratory in aquaria (e.g. juvenile *Abudefduf saxatilus*, juvenile *Haemulon* spp., juvenile *Stegaste* spp.). Predation on swarming or schooling individuals in nature was never observed in this study or by Modlin (1990) in the same location. Mysid schools are not completely immune from predation, however. McFarland & Kotchian (1982) found that postlarval french grunts occasionally fed on *M. columbiae* when they mingled into their shoals. Caridean shrimp that move from *Thalassia* beds into the mangrove prop root habitat after dark may also be important predators on mysids (Kneib 1988). Schooling behavior in mysids is thought to help protect them from predators, perhaps after schools have been located by visual predators, as with the confusion effect seen with fish schools (Godin 1986). Stragglers on the fringes of a swarm or school generally are thought to be more vulnerable to predation (Hobson 1968, Milinski 1977). There may be additional protection from predators by maintaining schools in the vicinity of the prop root habitat. Large schools of small planktivorous fish (*Anchoa, Harengula, Jenkinsia*) are found beyond the edge of the mangrove prop root habitat, but not where the *M. columbiae* swarms and schools form. Mysid schools may use rheotaxis and visual markers to maintain their position near the prop roots and prevent being washed out into the dense schools of planktivores. The planktivores may avoid the prop root habitat because of the piscivorous fish (mangrove snappers, barracudas) that are found in these areas. Additional studies are needed to determine the effects of schooling and position-holding behavior of mysids on predator-prey interactions.

There has always been considerable interest in trying to understand the factors regulating plankton patchiness in the sea; it has extremely important implications for understanding trophic interactions (Haury et al. 1978, Tanaka et al. 1987a, b). The relative importance of physical forces (water movements) and biological factors (behavior, growth, reproduction, predation) in determining planktonic patchiness have only been revealed in a few studies (e.g. Alldredge & Hamner 1980, Hamner 1988, Haury et al. 1990). Zooplankton aggregations such as mysid schools represent one end-member of a continuum between patchiness that is highly controlled by biology and those that are mainly controlled by physically concentrating mechanisms. By achieving a clear understanding of the factors influencing behaviorally controlled zooplankton aggregation, the range of possible contributions of behavior to other forms of patchiness will become clearer. Also, by understanding the adaptive value of swarming and schooling behavior in zooplankton, the overall role of patchiness in oceanic plankton dynamics may be revealed.

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