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E. J. Buskey

Energetic costs of swarming behavior for the copepod *Dioithona oculata*

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Abstract The cyclopoid copepod *Dioithona oculata* forms dense swarms within shafts of sunlight that penetrate the mangrove prop-root habitat of islands off the coast of Belize. Previous studies, based on in situ video recordings and laboratory studies, have shown that *D. oculata* is capable of maintaining fixed-position swarms in spite of currents of up to 2 cm s^{-1}. The purpose of this study was to examine the energetic costs of maintaining these swarms, in terms of increased metabolic costs of maintaining position in currents and in terms of reduced feeding rates in densely packed swarms during the day. Using a sealed, variable-speed flow-through chamber, the respiration rates of *D. oculata* were measured while swarms maintained position in different current speeds. The results indicate that active metabolism (swimming at maximum speed to maintain the swarm in a current) is approximately three times greater than routine metabolism (normal swimming speeds in the absence of currents), indicating a significant metabolic cost of maintaining swarms in the presence of currents. In addition, gut-pigment analysis indicated that feeding rates of these copepods were often reduced in swarms during the day compared to when the copepods were dispersed at night. Given the high "cost" of swarming, the adaptive value of swarming in terms of reduced predation, increased opportunities for mating, and reduced dispersal, must be substantial.

Introduction

Swarming behavior of zooplankton has been observed in both marine and freshwater environments (Emery 1968; Byron et al. 1983; Ueda et al. 1983). The cyclopoid copepod *Dioithona oculata* (Farran) is a swarm-forming copepod commonly found in tropical marine environments near coral reefs and mangrove cays (Hamner and Carlton 1979; Ambler et al. 1991; McKinnon 1991). Previous studies have shown that *D. oculata* forms swarms during the day near prop roots of the red mangrove and that the swarms disperse at night (Ambler et al. 1991). These swarms, composed mainly of adults and late-stage copepodites, form primarily in shafts of light that penetrate through the mangrove canopy, and light seems to be the primary cue used in swarm formation (Buskey et al. 1995). *D. oculata* swarms can maintain a fixed position in currents of up to 2 cm s^{-1} in nature (Buskey et al. 1996) which is equivalent to swimming at 25 body lengths s^{-1} for extended periods of time. It seems likely that the energetic costs of this behavior are high. In situ observations have shown that these swarms reach high density (mean 34.5 copepods ml^{-1}) in nature (Buskey et al. 1996). The high densities within swarms should make competition for food very intense. The proposed adaptive value of this swarming behavior includes reduced dispersion by currents, protection from predators, and enhanced opportunities for mating (Hamner and Carlton 1979; Ambler et al. 1996; Buskey et al. 1996). These selective pressures must be great given the apparent costs of swarming behavior in terms of reduced feeding opportunities and the metabolic costs of swarm maintenance.

The few previous studies which examined the relationship between activity and respiration rates in zooplankton were done mainly on larger zooplankters such as euphausiids and mysids for direct measurements of the relationship between respiration and swimming behavior (Foulds and Roff 1976; Torres and Childress 1983; Cowles and Childress 1988). Because of the technical difficulties associated with measuring changes in respiration rate with activity for small organisms, studies of copepods have relied on hydromechanical models (Vlymen 1970; Klyashtorin and Yarzhombek 1973; Svetlichnyi et al. 1977; Morris et al. 1985, 1990). The relationship between activity and respiration for zoo-

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E.J. Buskey
Marine Science Institute, University of Texas at Austin,
Port Aransas, Texas 78373, USA

plankton is of interest because it will provide insight into the metabolic costs of behavioral activities such as vertical migration and aggregative behavior.

Several characteristics of the swarm-forming copepod *Dioithona oculata* make it ideally suited for study of the relationship between activity and respiration. Large numbers of *D. oculata* can easily be collected in the field by enclosing swarms within clear plastic bags (Ambler et al. 1991); the swarms are composed of a single species, are mainly adults, and are in excellent condition for laboratory study. Recent studies have shown that *D. oculata* readily forms a swarm in the laboratory within a collimated shaft of light (Buskey et al. 1995), and copepods maintain swarms under laboratory conditions within unidirectional currents for extended periods of time (Buskey et al. 1996). As current speed increases, copepod swimming speed increases proportionally, to maintain the fixed position of the swarm within the light shaft (Buskey et al. 1996). Therefore, by building a sealed, variable speed flow-through chamber in which copepod swarms could form within a shaft of light, copepods can be forced to swim at different, known speeds, and their respiration rates measured during this time. Furthermore, these copepods are normally found at high density within swarms in nature (up to 90 copepods ml^{-1}, Buskey et al. 1996), so high densities of copepods can realistically be used in respiration experiments without concern for their effects on behavior.

The quantity of photosynthetic pigments (chlorophyll *a*, phaeopigments) found in the guts of copepods has been used to examine diel variations in feeding activities of copepods (Mackas and Bohrer 1976) and to calculate natural ingestion rates of copepods collected in the field (Dagg and Wyman 1983). The gut-pigment method was used in the present study to compare the feeding activities of *Dioithona oculata* on phytoplankton when they were swarming at high densities during the day to their feeding activities when they were dispersed at night.

Materials and methods

These studies were carried out at the National Museum of Natural History's field station at Carrie Bow Cay off the coast of Belize (~16°50′N; 88°05′W). Copepod swarms used in the respiration studies were collected in mid-morning (9:00 to 10:00 hrs) during May 1996 along the mangrove shorelines of Twin Cays (~2 km NW of Carrie Bow Cay) by enclosing a swarm of *Dioithona oculata* in a plastic bag with a 153 μm-mesh sieve attached to the bottom of the bag. This allowed a large volume of water from the swarm to be gently concentrated into the plastic bag. Copepods were then rinsed into a large insulated cooler and transported back to Carrie Bow Cay. Respiration experiments were all carried out between 11:00 and 16:00 hrs.

A series of preliminary experiments was performed to determine if the final percent oxygen saturation had any effect on measured respiration rates over a short (15 min) interval. This was done by placing ~150 copepods in a 40 ml plastic syringe with ~35 ml of filtered seawater. Experiments were initiated after varying time intervals so that the final percent saturation level of the water would vary at the end of experiments. Oxygen concentrations were measured at 15 min intervals using the procedure outlined below. Copepods were preserved in 5% buffered formalin at the end of each experiment for determination of dry weight.

Respiration rates of copepods swimming at different speeds were measured using a sealed, variable speed, flow-through chamber. The chamber was constructed of clear acrylic plastic, with overall outside dimensions of $17 \times 8 \times 8$ cm; the respiration chamber had inside dimensions of $7 \times 7 \times 7$ 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 (~1 cm diam) before entering the center of the respiration chamber. A wall of 153 μm mesh-screening on each end retained the copepods 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 bilge pump. Temperature of the water within the flow-through chamber and in the water bath were monitored with bead-type thermistors using a two-channel Omega Model 747 digital thermistor 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 ~2000 to 3000 freshly collected *Dioithona oculata* was then added to the chamber through a port in the top and sealed with a silicone rubber stopper. This produced a 5 to 10 ml^{-1} concentration of copepods within the respiration chamber, which is slightly lower than the mean density of copepods within swarms in situ (Buskey et al. 1996). A fiber-optic illuminator with a focusing lens was used to produce a vertical column of light within the respiration chamber to induce swarming behavior in *D. oculata* (Buskey et al. 1995). At regular time intervals through the course of an experiment, small water samples (~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 (~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 meter and oxygen electrode were calibrated using oxygen-saturated seawater (100%) and a 0.1 *M* sodium borate solution to set the zero point before each measurement to correct for electrode drift.

At the end of each experiment, all the copepods used in that experiment were collected on a 80 μm-mesh sieve and preserved in 5% buffered formalin. The dry weight of each of these samples was determined one month after they were collected. Samples were dried on pre-weighed glass-fiber filters at 60 °C, and weighed on a Sartorius AS200S analytical balance. Live adult *Dioithona oculata* were brought back to the laboratory in Texas to estimate the weight loss of the preserved samples. Samples of 100 adult female *D. oculata* from fresh and preserved samples were weighed on a Sartorius XM100P microbalance.

Copepod swimming behavior at different current speeds and the flow rate of water through the flow-through chamber were measured using a video-computer system for motion analysis. Copepod swimming behavior within the respiration chamber 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. Cultures of large dinoflagellates (*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 voltage settings to the pump. Calibration videotapes and tapes of copepod 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 dinoflagellates or copepods were sent to a personal computer at a rate of 15 frames s^{-1}. Swimming speeds of copepods and flow rates in the flow-through chamber were then calculated as described by 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 copepod's 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.

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 and 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 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 flow rate at which swarms could be maintained for periods of up to one hour.

Copepods used for gut-pigment analysis were collected in April 1995 during the day (mornings between 08:30 and 10:00 hrs, early afternoon between 13:00 and 14:30 hrs, and late afternoon between 16:00 and 17:30 hrs) from swarms, using plastic bags with a 153 μm-mesh sieve fitted in the bottom. These copepods were immediately rinsed into 250 ml plastic bottles with ~50 ml filtered seawater containing 2 g l^{-1} of MS-222 anesthetic (Finquel, Argent Laboratories). A seawater sample was also collected near the swarm for chlorophyll analysis. After sunset (19:00 to 20:00 hrs) and before dawn (05:00 to 06:00 hrs), when the swarms were dispersed (Ambler et al. 1991), copepods were collected by towing a 30 cm diam, 153 μm-mesh net along the periphery of the mangrove prop root habitat for ~5 min. The contents of the cod-end were then rinsed into a plastic bottle containing MS-222. A seawater sample was also collected for chlorophyll analysis.

Samples were refrigerated and held in darkness until sorted (usually < 1 h). A small aliquot of sample was then placed in a plastic petri-dish, and copepods were sorted using a dissecting microscope. Individual adult female *Dioithona oculata* were grasped with fine-pointed forceps, rinsed in filtered seawater, and then placed on a damp 25-mm diam glass-fiber filter. When 50 adult female copepods had been selected, the filter was folded, wrapped in aluminum foil, and placed in a freezer. When at least three replicates had been sorted from each swarm or plankton tow, the filters and copepods were ground in a tissue grinder with 10 ml of acetone. The grinding tube was held in a beaker with ice to avoid heating the sample during grinding. The sample was then centrifuged before chlorophyll analysis. For seawater chlorophyll analysis, 100 ml of seawater was filtered onto a GF/F glass-fiber filter. These filters were then placed in a scintillation vial with 10 ml of acetone, wrapped in aluminum foil, and placed in a refrigerator to extract over 24 h. Chlorophyll *a* and phaeopigment concentrations were determined using a Turner Designs Model 10 fluorometer and the equations for in vitro fluorometry (Strickland and Parsons 1968).

Results

The mean dry weight of egg-bearing adult female *Dioithona oculata* was estimated to be 32.2 ± 7.5 μg copepod^{-1} for fresh copepods and 25.1 ± 4.5 μg copepod^{-1} for copepods preserved for 1 mo, based on 12 measures of dry weight with 100 copepods per sample for each treatment. Dry weights of preserved samples from respiration experiments were corrected for the estimated 22% weight loss resulting from preservation for one month.

Initial measurements of routine metabolism of *Dioithona oculata* showed no significant dependence of metabolic rate on the percent oxygen saturation at the end of the experiment (Fig. 1). Respiration rates varied between 10 and 20 μl O_2 mg^{-1} dry wt h^{-1} at a temperature of 28 °C ± 1 C°. Despite the apparent lack of effect of percent oxygen saturation on respiration rates, it was decided to conclude all future experiments when oxygen concentration fell below 50% saturation.

Respiration measurements in the flow-through chamber were made at three current speeds (<1, 7.7 and 17.2 mm s^{-1}) that resulted in three estimated swimming speeds as these copepods held swarm position in currents: 3.5, 8.6 and 18.1 mm s^{-1}. The mean respiration rate measured in a very slow current (< 1 mm s^{-1}; just enough to keep the water mixed), with copepods swimming at ~3.5 mm s^{-1}, was 13.94 ± 3.20 μl O_2 mg^{-1} dry wt h^{-1} (mean ± 1 SD, $n = 10$). At an intermediate swimming speed of ~8.6 mm s^{-1}, the mean respiration rate was 27.09 ± 3.98 μl O_2 mg^{-1} dry wt h^{-1} (mean ± 1 SD, $n = 12$). At the highest swimming speed the copepods could sustain for extended periods of time, 18.1 mm s^{-1}, the mean respiration rate was 45.41 ± 3.63 μl O_2 mg^{-1} dry wt h^{-1} (mean ± 1 SD, $n = 8$). This respiration rate should represent active metabolism. A regression of respiration rate against swimming speed (Fig. 2) shows a high coefficient of determination ($r^2 = 0.92$) for this relationship. The *y*-intercept of this line can be used as an estimate of standard metabolism, the respiration rate expected in the absence of all activity (7.5 μl O_2 mg^{-1} dry wt h^{-1}).

The net cost of transport for *Dioithona oculata* is the amount of energy per unit body weight required to move a given distance through the water. For a copepod

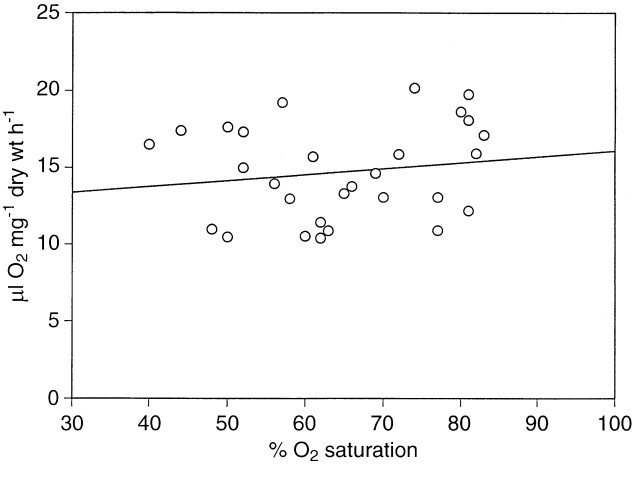

Fig. 1 *Dioithona oculata.* Respiration rate as a function of % oxygen saturation at end of 15 min experiment. Separate group of copepods was used for each experiment

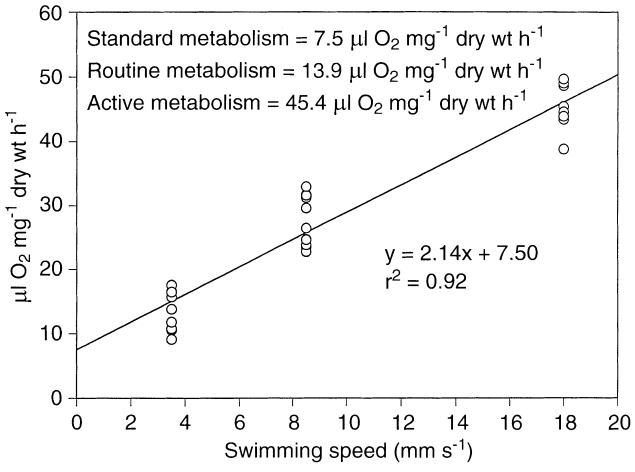

Fig. 2 *Dioithona oculata.* Respiration rate as a function of swimming speed in sealed flow-through chamber. Copepods were induced to swim at different speeds by varying current speed

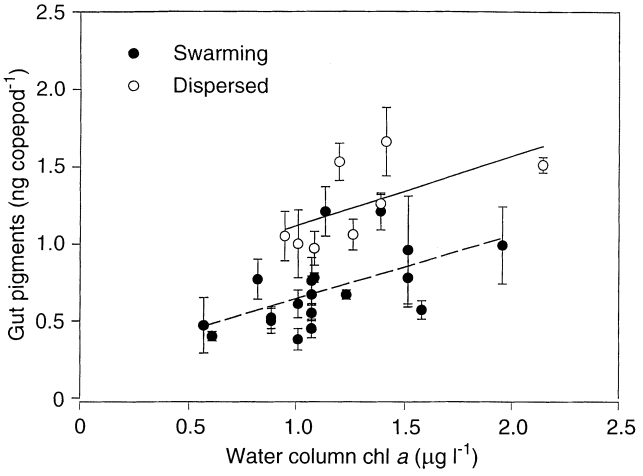

Fig. 4 *Dioithona oculata.* Gut-pigment concentration of adult females as a function of water-column chlorophyll *a* concentration at time and location where copepods were collected. Water-column chlorophyll *a* values are mean of two measurements of single sample

swimming at 3.5, 8.6 or 18.1 mm s^{-1}, it requires 79.4, 32.3 or 15.3 h, respectively, to swim 1 km. Given our measured values of respiration for *D. oculata* swimming at these speeds, it requires 1106.8 µl O_2 mg^{-1} dry wt to swim 1 km at 3.5 mm s^{-1}, but only 875 or 694.8 µl O_2 mg^{-1} dry wt to swim the same distance at 8.6 or 18.1 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 5.17, 4.25 and 3.38 kcal g^{-1} dry wt km^{-1}.

Mean gut-pigment concentrations (chlorophyll *a* plus phaeophytin *a*) in *Dioithona oculata* appeared to vary over a diel cycle (Fig. 3). For dispersed copepods collected before dawn (and before swarms form) the mean concentrations were 1.30 ± 0.34 ng chlorophyll per copepod (mean ± 1 SD, $n = 4$). Gut pigments declined for copepods collected within swarms during the day to 0.56 ± 0.13 ng chlorophyll per copepod ($n = 6$) and 0.54 ± 0.14 ng chlorophyll per copepod ($n = 6$) for copepods collected between 08:30 and 10:00 hrs or between 13:00 and 14:30 hrs, respectively. However, for swarming copepods collected shortly before dusk (between 16:00 and 17:30 hrs), mean gut pigments increased to 0.95 ± 0.23 ng chlorophyll per copepod ($n = 7$), which was only slightly lower than for non-swarming copepods collected after dusk, 1.21 ± 0.24 ng chlorophyll per copepod ($n = 4$). Water-column chlorophyll *a* concentrations near the swarms during the day had a mean value of 1.13 ± 0.34 µg chlorophyll *a* l^{-1} ($n = 19$), compared to 1.31 ± 0.36 µg chlorophyll *a* l^{-1} ($n = 8$) for water samples collected at night when the copepods had dispersed. Gut-pigment concentrations in adult females were positively correlated with chlorophyll *a* concentration in the water from which they were collected (Fig. 4), both for swarming copepods collected during the day ($r = 0.56$) and dispersed copepods collected at night ($r = 0.62$).

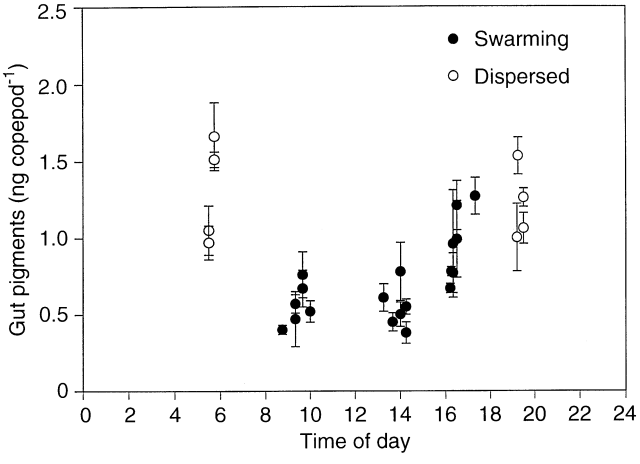

Fig. 3 *Dioithona oculata.* Gut-pigment contents (chlorophyll *a* plus phaeophytin *a*) of adult females collected either while swarming during day or while dispersed at night. Each estimate of gut-pigment concentration is mean (±1 SD) of 3 subsamples of 50 copepods from each collection

Discussion

This study represents the first direct measurement of changes in copepod respiration rate with activity, and the results show that routine metabolism is approximately twice as large as standard metabolism for *Dioithona oculata*, and that active metabolism is three times greater than routine metabolism and six times greater than standard metabolism. Although these values have not been empirically determined for copepods before, they have been measured for other swimming crustaceans, and a variety of results have been found. Some studies, such as those of Torres and Childress (1983) with the euphausiid *Euphausia pacifica*, reached similar results, with routine metabolism approximately three times greater than standard metabolism. Other studies,

such as that of Foulds and Roff (1976) found only a 1.2 time increase in active metabolism over routine metabolism in the mysid *Mysis relicta*. For *D. oculata* there appeared to be a linear relationship between copepod swimming speed and oxygen consumption, although the ability to resolve the shape of this relationship is limited by having tested only three swimming speeds. Similar linear relationships between swimming speed and respiration have been found in other free-swimming crustaceans including the amphipod *Gammarus oceanicus* (Halcrow and Boyd 1967), the euphausiid *E. pacifica* (Torres and Childress 1983) and the mysids *Gnathophausia ingens* (Cowles and Childress 1988) and *Mysidium columbiae* (Buskey unpublished data).

The lack of experimental data on the relationship between copepod swimming speeds and respiration rates is due to the fact that most copepod species cannot be induced to swim at specific rates of speed in response to environmental variables such as light and currents. In previous studies, the cost of locomotion has been estimated using principles of fluid dynamics, and the increase in metabolism with maximal activity was thought to be negligible (Vlymen 1970) or at most 1.25 times the standard metabolic rate (Klyashtorin and Yarzhombek 1973; Svetlichnyi et al. 1977), while other theoretical studies have predicted that the metabolic cost of swimming could be three to five times higher than the standard metabolic rate (Minkina and Pavlova 1981; Petipa and Ostravskaya 1984). Morris et al. (1985) used a hydromechanical model to predict the metabolic costs associated with swimming in the large calanoid copepod *Pleuromamma xiphias*. This model predicted maximum swimming speeds of 30 mm s^{-1} for the 6 mm-long copepod (five body lengths per second) and that the metabolic costs of this active metabolism would be about three times larger than routine metabolism. The maximum sustained swimming speed for *Dioithona oculata* was $\sim$18 mm s^{-1}, which corresponds to >20 body lengths per second, and a ratio of active:standard metabolism of $\simeq 3$ was also measured.

In the Morris et al. (1985) model, the net cost of transport, the amount of energy per unit of biomass required for an organism to swim a set distance, increased with higher swimming speeds. In the present study, the net cost of transport decreased for *Dioithona oculata* with increasing swimming speed. This is similar to the results of Cowles and Childress (1988), who found that cost of transport decreased with increasing swimming speed for the bathypelagic mysid *Gnathophausia ingens*. In order to compare the net cost of transportation in *D. oculata* to that measured for other aquatic organisms (e.g. by Schmidt-Nielson 1972; Beamish 1978), it is useful to calculate cost of transports as 75% of maximum sustained swimming speed based on the wet weight of the organism. Assuming that dry weight is 15% of wet weight for *D. oculata*, and 75% of the maximum speed is 13.5 mm s^{-1}, the net cost of transport of *D. oculata* is estimated to be 25 kcal g^{-1} km^{-1}. For the larger copepod *Pleuromamma xiphias*, Morris et al. (1985) estimated the cost of transport to be between 7.6 and 10 kcal g^{-1} km^{-1}, based on their model of copepod swimming, whereas for the smaller cyclopoid copepod *Acanthocyclops robustus*, Morris et al. (1990) estimated the cost of transport to be between 40 and 62 kcal g^{-1} km^{-1}. Although there are no other direct measures for cost of transportation in copepods, the values measured for *D. oculata* are consistent with the calculated values of Morris et al. (1985, 1990) and the trend of increasing cost of transport with decreasing body size for aquatic organisms (Schmidt-Nielson 1972; Beamish 1978).

The respiration rates of copepods vary primarily with temperature, body size and nutritional state, with a trend of increasing respiration rates with increasing temperature and body size (Ikeda 1970, 1974). Weight-specific respiration rates tend to increase with decreasing body size, however. For tropical copepods, respiration rates at temperatures between 28 and 30 °C varied between 7.5 and 95.4 µl O_2 mg^{-1} dry wt h^{-1} (Ikeda 1970), although all of the species tested were larger than *Dioithona oculata* and only one of the species tested was a cyclopoid copepod. Part of the reason for the high respiration rates of *D. oculata* (given its small size) may be related to its active behavior; *D. oculata*'s spontaneous swimming speed is >4 body lengths per second (Buskey et al. 1996). Some copepods spend a large proportion of their time motionless in the water column, and as a result have low metabolic rates. For example, the cyclopoid copepod *Oithona nana* has a routine metabolic rate of $\simeq 3$ µl O_2 mg^{-1} dry wt h^{-1} (Lampitt and Gamble 1982), compared to nearly 14 µl O_2 mg^{-1} dry wt h^{-1} for *D. oculata*.

There is an apparent diel cycle in the amount of chlorophyll and phaeopigments in the gut of *Dioithona oculata*. One interpretation of this pattern is that there is more competition for food within the dense swarms during the day, and this reduces the amount of chlorophyll in their gut compared to when they are dispersed at lower densities at night. However, many other species of copepods that do not form swarms also exhibit clear diel patterns of gut pigmentation (e.g. Mackas and Bohrer 1976; Baars and Oosterhuis 1984). Until it is determined whether or not *D. oculata* exhibits a diel pattern of gut pigments in the absence of swarming behavior, it will not be possible to determine if reduced feeding in swarms can be considered a metabolic cost associated with this behavior. It should also be noted that in the presence of currents, these fixed-position swarms are continually supplied with fresh seawater and the food it contains. Therefore, food limitation in these swarms is not as severe as it would be if the swarms drifted with the currents. Furthermore, although *D. oculata* has been raised through several generations in the laboratory on a mixed phytoplankton diet (Buskey unpublished data), there is no reason to suspect that microzooplankton do not play a role in the nutrition of this copepod. Many copepods are known to consume both phytoplankton and protozoans (Stoecker and Capuzzo 1990; Pierce and Turner

1992). Gut-pigment analysis, therefore, may reveal only a fraction of the feeding pattern of these probably omnivorous copepods.

The adaptive value of swarming behavior in *Dioithona oculata* is thought to accrue primarily from allowing the copepods to remain within a habitat that is largely free from predators during the day. Large schools of small planktivorous fish (species of *Anchoa*, *Harengula*, *Jenkensia*) continually patrol the edges of the prop-root habitat, but they do not swim between the prop roots where *D. oculata* swarms form. These schooling planktivores probably avoid the areas between the prop roots because numerous piscivorous fish (snappers, groupers, barracudas) spend their days beneath the fringe of the prop-root habitat. By forming swarms in shafts of sunlight within the prop-root habitat, these copepods can maintain positions away from the majority of their predators during daylight hours when visual predation is most effective. At night the swarms disperse, and the copepods drift into channels and bays adjacent to the mangrove prop-root habitat. These copepods are probably incapable of vision in terms of image formation, but use their abilities for phototaxis and photokinetic behavior to hold their position within this safe habitat during the day (Buskey et al. 1995, 1996).

There is a considerable cost associated with this swarming behavior, when swarms are exposed to strong currents for extended periods of time, since respiration rates triple at maximum swimming speeds. However, there are advantages to at least a moderate degree of flow to the swarms, since this brings fresh oxygen-rich, food-laden water into the swarm continuously. Measurements of small-scale circulation patterns within the mangrove environment over a daily cycle during different tidal phases and weather conditions will provide a better understanding of the overall energetic costs of swarm maintenance to these copepods.

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