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SWIMMING DYNAMICS OF THE MESOPELAGIC VERTICALLY MIGRATING PENAEID SHRIMP *SERGESTES SIMILIS*: MODES AND SPEEDS OF SWIMMING

David L. Cowles

ABSTRACT

The mesopelagic vertically migrating penaeid shrimp *Sergestes similis* was studied in situ in Monterey Bay, California, at depths ranging from 291–569 m using a remotely operated submarine equipped with a video camera. Instances both of routine swimming and of escape behavior were observed. In routine swimming, *S. similis* (mean total length 43.5 mm) swims at an average of 7.4 cm/s. Propulsion is provided exclusively by the pleopods, which beat in an adlocomotory metachronous wave at approximately 4 Hz. The pereiopods are generally held close to the underside of the thorax. The long second antennae (hereafter "antennae" unless first antennae are specified) are invariably deployed in a characteristic position, with the relatively inflexible proximal portion, over 1 body length long, directed anterolaterally and angling slightly ventrally, and the flexible distal portion, over 2 body lengths long, trailing posteriorly from a distinct articulation or "kink" at the end of the proximal portion. The antennae clearly respond to tactile stimuli, and perhaps have chemosensory function as well. *Sergestes similis* was never observed to stop swimming except for brief bouts of grooming or momentary reactions to tactile contacts on the antennae. Downward swimming was always active, and was not accomplished by passive sinking. The extremely long, setose antennae would be expected to produce substantial drag which must be overcome by metabolically generated thrust. Thrust of the pleopods is maximized during the propulsive stroke by extending and separating the pleopods and spreading the setae, while drag is minimized on the recovery stroke by retracting the pleopods and holding them in apposition to one another and by folding the setae. The escape reaction in this species is the typical decapod tail flip.

The midwater, vertically migrating shrimp *Sergestes similis* Hansen, 1903, ranges through the North Pacific Ocean from Japan to Alaska and down the west coast of North America to as far south as the Gulf of California (Butler, 1980). Classified as a subarctic species (Genthe, 1969), it is one of the most abundant midwater macrocrustaceans off California, Oregon, and British Columbia (Barham, 1956; Pearcy and Forss, 1969; Genthe, 1969; Omori, 1979), especially in waters of the continental slope and beyond. Though the species has been reported from the surface to depths of 1,200 m (Omori *et al.,* 1972), in the region off Oregon and California it is found most abundantly between 250–600 m during the day and 50–200 m at night (Pearcy and Forss, 1966; Omori and Gluck, 1979). It is negatively phototactic after protozoeal stage 2 (Omori, 1979), and is a diel vertical migrator. The vertically migrating population does not approach as near the surface as normal on a clear, moonlit night (Pearcy and Forss, 1966), as is consistent with its negative phototaxis. Barham (1956) and Clarke (1966) found that its diel vertical distribution correlated well with elements of deep scattering layers in the Santa Barbara Basin and in Monterey Bay off southern California; and Dietz (1962) reported seeing more *S. similis* than could be counted while at scattering-layer depth off southern California. Vertical migration is less evident in that part of the population living below 500-m depth (Pearcy and Forss, 1966).

Although the above-cited studies, based on net captures and sonic scattering, have clearly established that *S. similis* is a diel vertical migrator, little is known about the actual swimming dynamics of this species. It is not known, for example, whether *S. similis* swims constantly or is relatively quiescent at depth; how the pleopods, pereiopods, and the very long second antennae are deployed during swimming; at what typical speeds the species swims; whether it swims downward actively or sinks passively; or how the thorax and abdomen are positioned

Table 1. Swimming modes of the sergestid *Sergestes similis* in video sequences analyzed.

Swimming mode	Number of sequences
Steady horizontal swimming	3
Steady upward swimming	5
Steady downward swimming	18
Tail-flip "escape" reaction	3

during routine swimming. In addition, numerous hypotheses have been proposed to explain the adaptive value of vertical migration in midwater species such as *S. similis*. In situ observations of swimming in *S. similis* may help to evaluate the predictions of these hypotheses.

In this study, I report on in situ observations of *S. similis* from Monterey Bay, California, using the video capabilities of the Monterey Bay Aquarium Research Institute's remotely operated submarine *Ventana*. General characteristics of swimming in *S. similis*, as well as the pattern and sequence of propulsive pleopod beats during routine swimming, are discussed, based on video and depth data.

MATERIALS AND METHODS

Midwater sergestids were observed and filmed in situ from the Monterey Bay Aquarium Research Institute (MBARI)'s remotely operated submarine vehicle (ROV) *Ventana* during July of 1991. In addition, video sequences archived from previous dives were analyzed for sergestid swimming sequences. The ROV was tethered to the mother surface ship, and could dive to a maximum of 1,000 m. It was equipped with a Sony Betacam video camera with a zoom lens, having a live feed to the mother ship for real-time observations and control of the submarine. The video output was recorded on a Sony Betacam videocassette recorder. A simultaneous running record of ROV depth was recorded using a Paroscientific digiquartz pressure sensor 42K-023. All observations were made during daylight hours.

Video sequences of sergestids were subsequently analyzed using a Sony Betacam SP BVW-65 videocassette player. Modes of swimming in routine and escape modes; responses to the lights from the ROV; depth range, speed, and direction of swimming; position of the body, pereiopods, uropods, and antennae; and the pattern, position, and rate of propulsive strokes by the pleopods were noted. Slow-motion or stop-motion analyses were also made of many of the sequences for detailed analyses of the pattern of propulsive pleopod strokes. The frame rate of this system was 30 frames, or 60 fields, per s. Stop-frame analysis could thus distinguish events as little as 17 ms apart.

Photographic prints were made from 2 complete sequences of frames showing the full cycle of the pleopod propulsive strokes, from both a dorsal and a lateral view. These prints were scanned and digitized on an 80386 IBM compatible computer, and the position of each pleopod in each frame was noted, as well as that of the body and antennae.

Preserved *S. similis* were obtained from the museum collection at the Scripps Institute of Oceanography, and live and preserved specimens were obtained from J. J. Childress cruises off Point Conception, California. Body dimensions and pleopod lengths were measured in these samples for correlation with the video images.

There are 3 sizes of *S. similis* which may be commonly found in California waters at these depths in July, corresponding to first-, second-, and third-year cohorts (Omori and Gluck, 1979). Although the size ranges from some cohorts overlap during July (Barham, 1956), I was able to determine which instar was being viewed on the video if the video sequence included a sequence in which the sergestid was followed straight down through the water column, along with multiple notations of the submersible depth. The time it took the sergestid to swim a given distance down through the water column was used to calculate its swimming speed in cm/s.The sergestid's total length was then estimated by observing the time it took the sergestid to pass the essentially stationary particles of "marine snow" in the water while swimming at the known speed. Since this technique is susceptible to errors due to parallax in the camera view, only sequences in which both the sergestid and the particle were in sharp focus at the same time and close together, implying that they were equidistant from the camera, were used.

RESULTS

A total of 29 close-up video sequences of swimming sergestids, ranging in duration from several s to six min, were analyzed (Table 1). In most of the sequences in which the size of the subject could be determined, the subjects were second-year cohorts (average carapace length 11.7 mm, total length 43.5 mm) (Table 2), or third-year (average carapace length 14.1 mm, total length 49.2 mm). Most individuals studied were second-year, and the following discussion is based upon individuals of this size.

The in situ depths for the sequences ranged from 291–569 m. By far the most common swimming mode was steady downward swimming (Table 1). In several of the sequences in which the sergestid was initially encountered swimming horizontally or upward, the subject slowly turned and began steady downward swimming after a few s of observation within the ROV's spotlights, suggesting that the preponderance of observations of downward swimming may be due in part to a positive geotaxis elicited in response to light from the ROV. Subjects typically swam steadily throughout the observation period, with little evidence of

Table 2. Size measurements (in mm) of *Sergestes similis* based on live specimens captured off Point Conception, California, and on preserved specimens from the Scripps Institution of Oceanography planktonic invertebrates collection. Maximum lengths rather than mean lengths are given for the second antennal distal section because the distal part of the antennae were frequently broken during capture. SD = standard deviation.

	Carapace length mean (SD)	Total length mean (SD)	Antennal length Basal section mean (SD)	Antennal length Distal section maximum	Antennal length Total antenna length
Second year	11.7 (0.6)	43.5 (1.8)	56.2 (3.2)	102.8	159.0
Third year	14.1 (1.0)	49.2 (3.8)	59.2 (5.8)	125.2	184.4

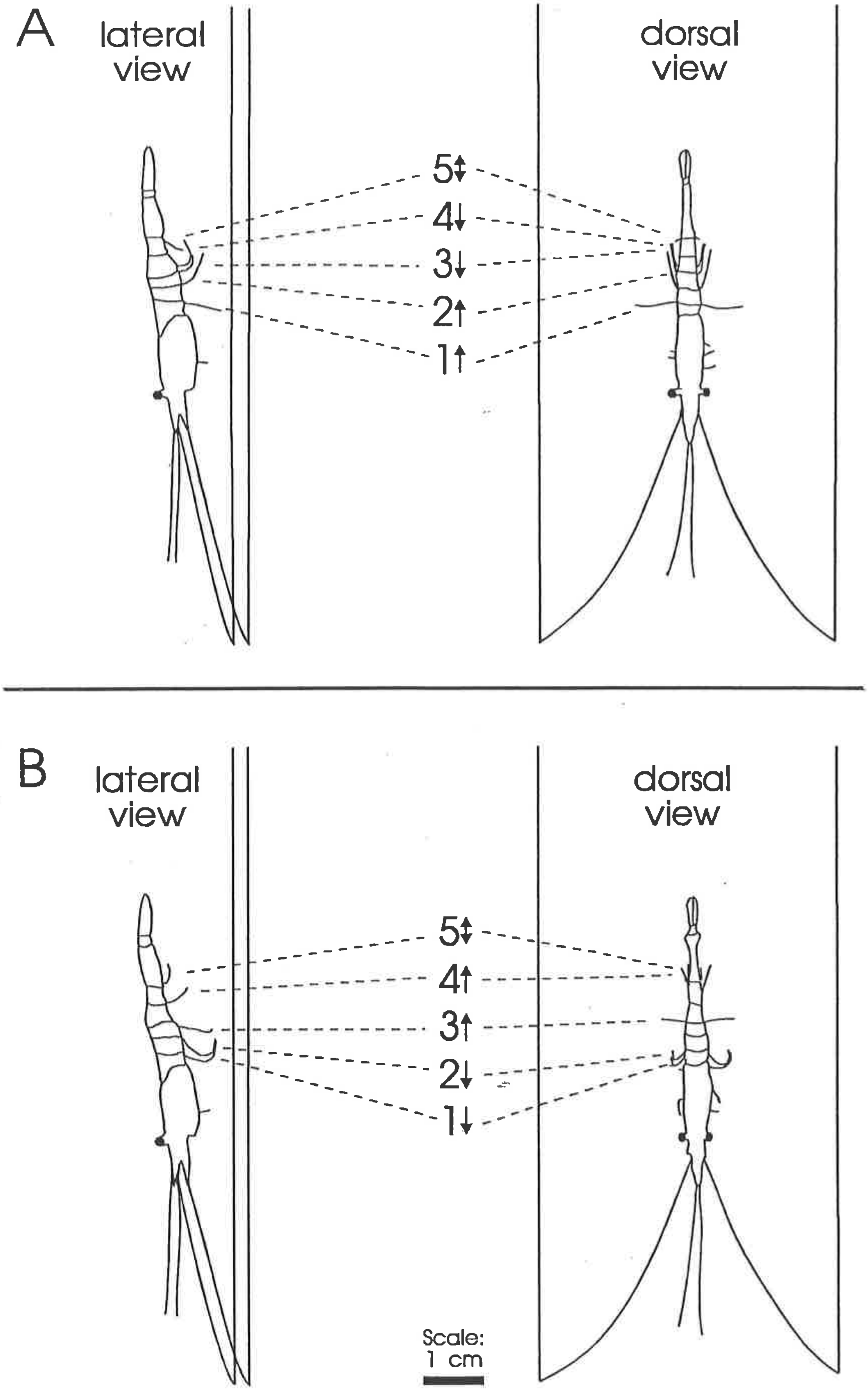
disturbance. Tail-flip "escape" reactions, however, were elicited when the sergestid contacted solid parts of the submarine or encountered turbulence from the ROV's propeller. These escape reactions were highly stereotyped and readily distinguishable from steady swimming. A detailed description of steady swimming and of the tail-flip reaction is given below.

Steady Swimming

Sergestes similis swims in a very characteristic manner, whether it is swimming upward, downward, or horizontally (Fig. 1). The following description will be based on downward swimming, since this is what most of the observed sequences consisted of. Behavior during upward and horizontal swimming, however, was virtually identical to that during downward swimming, with the exceptions noted. The thorax and abdomen were held rigid and in a nearly straight line, with the posterior end displaced at approximately a 5° angle dorsally from the direction of travel. Little flexing of the abdomen was observed except during a turn. The uropods were held slightly spread and parallel with the direction of travel, and appeared to be used for steering. The thoracic pereiopods were generally held tightly against the thorax and projecting forward, with only the tips (dactyls or propodus and dactyls) of a few protruding far enough out to visibly interrupt the streamlined profile of the thorax. On other occasions the posterior pereiopods were held in a partly extended position, resulting in slower swimming speeds due to the increased drag. Occasionally a subject fully extended the pereiopods momentarily, apparently to grasp at an object in the water or to groom some part of the body. Extension of these appendages resulted in a sharp increase in drag, as evidenced by an immediate near cessation of forward motion.

Forward thrust during steady swimming was provided entirely by the five pairs of abdominal pleopods, which beat in a metachronous wave proceeding from posterior to anterior (an adlocomotory wave; Sleigh and Barlow, 1980). Pleopod beat rate averaged 4.11 Hz for downward swimming (SD 0.36, $N = 18$) and 3.74 Hz while swimming upward (SD 0.46, $N = 7$). There was no significant difference between pleopod beat rate during upward-directed and downward-directed swimming (unpaired *t*-test, $t_s = 0.3628$, $P > 0.5$). Downward swimming speed averaged 7.4 cm/s (SD 2.7, $N = 7$), and was fairly steady unless interrupted by the extension of the pereiopods or by some other event; of 13 replicate uninterrupted speed measurements of the same individual swimming downward over a period of 4.5 min, mean speed was 8.7 cm/s and the standard deviation was 2.0 cm/s. The minimum speed measured for uninterrupted downward swimming was 4.0 cm/s, and the maximum was 13.1 cm/s over a short distance. Comparable measurements for upward-directed swimming were not available, since so few uninterrupted sequences of upward swimming in which a range of depths was recorded were observed. In the one timed sequence of upward swimming, swimming speed was 3.6 cm/s, but this may be atypically low, because the subject was swimming at the time with a posterior pair of pereiopods partially extended, which would have resulted in significantly reduced swimming speed due to increased drag. The pleopod beat rate during this sequence was also lower than the mean rate.

The first three pairs of pleopods were the longest, averaging 18.9 mm for a second-year individual. The fourth pair was shorter,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at 15.9 mm, and the fifth was shortest at an average 12.3 mm. The flagellum of each pleopod was armed with long setae, especially at the distal end. When spread, the cross section of these setae was much greater than that of the pleopod itself. During the propulsive stroke cycle each pleopod moved in synchrony with its contralaterally paired mate for the entire cycle. First, each pleopod pair was extended forward at an angle (12° forward of perpendicular for the first pair), and also ventrally and laterally. For an 18.9-mm first pleopod at maximum forward extension, the tip was 4 mm forward of the pleopod base, 14 mm ventral, and 12 mm lateral to it. After full anterior extension, the pleopods were swept posteriorly through the water and adducted toward the dorsoventral axis during the power stroke. Thrust was maximized on the power stroke by holding the pleopod in the fully extended position, by the spreading of setae on the pleopods, providing greater propulsive surface area, and by the fact that each pleopod pair was maximally separated from adjacent pleopods during the power stoke, providing the greatest undisturbed body of water for thrust generation. Each pleopod pair reached the end of its power stroke at an angle approximately 45° to the rear of perpendicular, and also nearer to the dorsoventral axis than at the beginning of the stroke. For an 18.9-mm pleopod, the tip was 9.5 mm behind the pleopod base, 8 mm ventral, and 5 mm lateral to it at the end of the power stroke. At this point the pleopod encountered the anterior surface of the next posteriormost pair of pleopods, which was already executing its return stroke. The pleopod pair then began its own return stroke, being held in a partially retracted position nearer the ventral surface of the abdomen and folding over the anterior surface of the next posteriormost pleopod pair. Drag on the return stroke was reduced in three ways. First, the pleopods were brought forward in a partially retracted position, closer to the ventral surface of the abdomen. Second, the setae on the distal ends of the pleopods, which had been spread during the power stroke, were now folded against the pleopod surface. Third, each pleopod pair was closely associated with the anterior surface of the pleopod pair posterior to it and with the posterior surface of the pleopod pair anterior to it during much of the return stroke. Consequently, the frontal areas of several pleopods on the return stroke were superimposed, making the total form drag of all the returning pleopod pairs little more than that experienced by only one returning pleopod pair. The returning pleopod pair was brought anteriorly near the abdominal midline until the next posteriormost pair reached full forward extension and began its power stroke. The pair was then brought synchronously to the fully extended position in the anterolateral direction and completed the cycle, ready for the next power stroke of its own.

The stroke cycle in the fifth, posteriormost pleopod pair was similar to that in the more anterior pairs except that at the end of the power stroke the fifth pair was angled 90° to the rear, and was parallel to and nearly touching the ventral surface of the abdomen. This pleopod pair was shorter than any of the others and probably generated only a small portion of the total forward thrust.

In the power-stroke/recovery cycle each pleopod pair was approximately 72° out of phase behind the nest posteriormost pair, so that each of the five pairs was at a different part of the cycle. There was only one wave of power-stroke/recovery cycles being performed at any one time within the set of five pleopod pairs, with 2 or 3 pairs being on the power stroke and 2 or 3 on the recovery stroke at all times. The anterior pleopod pair was 72° ahead of the posterior pair, but on the previous cycle. Each propulsive cycle was initiated by the fifth (posteriormost) pleopod pair, and proceeded anteriorly. In the video, each cycle was plainly visible as a distinct wave of motion moving

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Fig. 1. Lateral and dorsal views of a second-year *Sergestes similis* in two phases of the metachronous pleopod stroke cycle during steady downward swimming. A. Pleopod 1 is beginning its power stroke. B. Pleopod 1 is beginning its return stroke, 133 ms later. Numbers label pleopods 1–5. Arrows beside each number indicate the direction of movement of each pleopod.

anteriorly along the five pairs of pleopods, with the recovery part of each stroke being the most strikingly obvious because the pleopods were clustered together during the recovery stroke. Cessation of active pleopod beating was never observed beyond occasional momentary pauses, whether the swimming direction was upward, downward, or horizontal.

The second antennae, which are very long in *S. similis* compared to the body length (averaging 159 mm in a 43.5-mm individual), were always held in a characteristic position during steady swimming. In the basal section of the antennal flagellum, which is slightly longer than the animal's total body length, the segments articulate relatively inflexibly with each other. During steady swimming this section projects out in front of the body, at approximately 30° lateral to the body's longitudinal axis and angling slightly ventrally as well. The basal section of the antennae is terminated by an articulation, described in the literature as a "double kink" (Foxton, 1969; Ball and Cowan, 1977; Denton and Gray, 1985). The flexible distal section of the antennae, which is over twice as long as the total body length, trails directly posteriorly from the articulation, with the distal tip being well posterior to the uropods and telson when in normal swimming position. The exact position of the distal section is determined by the pattern of water flow past the body. Normally it trails directly posteriorly at about one-half body length to the side and slightly ventral to the body. During interruption or change of swimming direction, however, this section reflects the disruption of steady flow by a wave of flexure which passes along it until a new direction of steady swimming is reestablished. In addition, on several occasions it appeared that the distal flagellum encountered a particle in the water. On these occasions, steady swimming was momentarily halted and the sergestid flexed its body toward the side which had been disturbed. The basal section of the antennae was moved abruptly toward the longitudinal axis, causing the distal section to be drawn away from the particle much as pulling back on a fishing pole causes the fishing line to be drawn closer. The long distal portion of the antennal flagellum of *S. similis* is very flexible and, being heavily setose, readily adheres to objects. It was thus difficult to examine captured specimens with antennae intact and untangled. The antennal flagella of captured specimens stored together easily became tangled into a hopeless knot, whether the subjects were living or preserved. The second antennae, then, consist primarily of a long antennal flagellum slightly over three body lengths long. The flagellum has a less flexible basal section of more than one body length, corresponding to the "fishing pole" in the analogy above, directed anteriorly, to the side, and slightly ventrally during steady swimming; followed by a short articulation and a thin, flexible, heavily setose distal section of about two body lengths, corresponding to the "fishing line," trailing posteriorly. The first antennae, which were much shorter than the second antennae, were directed slightly laterally to directly anterior during steady swimming (Fig. 1).

Escape Reaction

The escape reaction, elicited when the sergestid encountered the ROV or turbulence from its propellers, was characteristic and readily distinguished from steady swimming. Contact elicited the standard crustacean tail-flip response (see Webb, 1979; Cooke and Macmillan, 1985; Krasne and Wine, 1988; Newland *et al.*, 1992) characterized by spreading of the uropods and several rapid, powerful ventral contractions of the abdomen, which accelerated the sergestid rapidly backward abdomen-first with its long antennae streaming behind in a straight line. After three or four tail-flip strokes, the sergestid resumed steady forward swimming unless it again encountered an obstacle.

DISCUSSION

The vertically oriented swimming of *Sergestes similis* makes it unusually well suited to study by the use of a submersible. The relatively long period of time it takes to swim from top to bottom of the field of view makes it possible to focus for some time on a single individual, and even to follow it down through the water column. Rapidly foraging horizontal swimmers, on the other hand, are more difficult to study, because they pass more quickly through the camera's relatively narrow plane of focus and out of view before the requisite adjustments can be made in camera focus and ROV trim to follow them through the water.

The swimming speeds observed are within the range expected for routine swimming in this species. Smith *et al.* (1989) reported that the deep scattering layer off Southern California, of which *S. similis* is a part, moved upward at a rate of 5–8 cm/s at dusk, and downward at 3–4 cm/s at dawn. Barham (1956) found that *S. similis* swam at 8 cm/s upon release into aquaria. A population of the related *Sergia lucens* (Hansen) migrated vertically at a maximum speed of 3 cm/s (Omori, 1974). The rate of movement of a population should be used as a minimum rate for individual movement, because of the possibility that individuals within the population may swim alternately upward and downward, resulting in a net population movement which is lower than the average swimming speed of individuals within the population. The nonmigrating *Gnathophausia ingens* Dohrn swam at 5–6 cm/s (Cowles and Childress, 1988), while *Euphausia pacifica* Hansen, a vertical migrator that does not have long antennae like *S. similis,* swam at up to 9.7 cm/s (Torres and Childress, 1983). The range of speeds of *S. similis* observed on video in this study is also similar to the range of routine speeds directly measured for this species in a swim tunnel (Cowles, unpublished data).

A variety of evidence indicates that the observed sequences are representative of routine activity, and not of an escape reaction in this species. Swimming was steady and generally in a straight line. No evasive maneuvers or tail flips were observed unless the subject encountered the ROV. Indeed, the steady swimming in these sequences was quite distinct and clearly distinguishable from the tail-flip "escape response." The brief pauses observed when the antennae encountered a particle, and even occasional stops for grooming, indicate that the subjects were swimming in a routine manner and not attempting to escape the ROV. The fact that subjects were most frequently observed swimming downward through the water column can be best explained by a positive geotaxis in response to elevated light levels. This could reasonably be expected to be a normal response in a diel vertical migrator such as *S. similis* and has been reported for this species (Omori, 1979; Pearcy and Forss, 1966). Such a response may not be elicited under all conditions, however. Other MBARI footage, taken from the submersible *Deep Rover* at shallower depths, shows *S. similis* swarming in all directions through the field of view, with no clear downward orientation. Tomohiko Kikuchi (personal communication) of Japan's Yokohama National University also reports that deeper-living, nonmigrating sergestid species observed from submersibles do not turn downward when exposed to the submersible's lights.

Although it has been suggested that vertical migrators such as *S. similis* may conserve energy by sinking passively through the water column on their downward migration (Rudjakov, 1970; Omori, 1974), this hypothesis is not supported by direct in situ observations in this species. The video records suggest that *S. similis* swims steadily at all times during its diel vertical migrations, whether it is swimming upward, downward, or horizontally, except for brief pauses for grooming or when its antennae encounter a particle in the water. There is no evidence that this species conserves energy at any time during downward migration by sinking passively through the water column. This conclusion is in accord with that of Roe (1974, 1984a), who, on the basis of net captures, determined that populations of several species of midwater oplophorids and sergestids must be migrating nearly constantly, and that of Roe (1984b), who determined that downward migration in copepods could not be accomplished by passive sinking. Both upward and downward migration in *S. similis* thus entail a real metabolic cost to the individual and must be accounted for when calculating the costs and benefits of vertical migration. Further, the constant deployment of the heavily setose second antennae in the fully extended position in this species must result in substantially increased drag, requiring even more metabolic power for swimming. Omori (1974) recognized this, though at the time he speculated that they may serve to retard the sinking rate through the water on a postulated passive descent. The effects of antennal drag can be readily seen in the lateral views of *S. similis* swimming (Fig. 1a, b). In these views, it can be seen that the distal antennal flagella are deployed slightly ventrally to the body. To compensate for antennal drag, which is strongest on the ventral side, the thorax and abdomen are angled slightly dorsally to the true direction of swimming, and the uropods, which act as a rudder, are flexed at an angle. Therefore, antennal deployment increases drag not only directly by antennal resistance to passage through the water, but also indirectly by forcing the sergestid to swim at a slightly oblique angle in order to balance thrust and drag forces.

The invariable deployment of the antennae in the extended position, in the face of such a clear metabolic cost due to the increased drag it entails, implies that there must be some clear benefit to their deployment in this manner. It would seem that the most likely explanation is that they are used for prey detection or capture, or for early detection of predators. Sergestids have been reported to prey mostly on small crustaceans, such as euphausiids and copepods, though coelenterates, "olive-colored debris," and a few other items make up smaller proportions of their diet (Renfro and Pearcy, 1966; Judkins and Fleminger, 1972; Flock and Hopkins, 1992). In turn, the sergestids are preyed upon by many species of pelagic and benthic fishes, squid, sharks, and whales (Pereyra *et al.*, 1969; Genthe, 1969; Omori, 1974). The antennae may function in several ways to enhance food capture. Foxton (1969) described sensilla on sergestid antennae to which he ascribed a chemosensory role on the basis of ultrastructure. Ball and Cowan (1977) also identified chemoreceptors on the antennae of *Acetes*, a related sergestid. Hamner and Hamner (1977) used behavioral studies to show that *Acetes* could readily track amino acid trails through the water at concentrations of at least as low as 10^{-4} M. Deployment of chemoreceptors on the widely spaced distal antennal flagella would clearly enhance the probability of detecting the chemical trails of prey while *S. similis* is swimming through the water. The flagella appear to have well-developed mechanoreceptors as well, as evidenced by the rapid response observed when the antennae encountered even a small particle in the water, and by the tail flips reported by Barham (1956) when the flagellar tips were stimulated. *Sergestes*, in common with several other penaeid genera, has a very distinctive pattern of setae on the distal antennal flagellum. The flagellum is subdivided into series of many articulated segments, most of which bear on the medial side a pair of long setae which arch out and nearly touch at the tip, forming a tube (Foxton, 1969; Ball and Cowan, 1977; Denton and Gray, 1985). Within this tube and partly occluding it, are setae of a second type, sensitive to longitudinal deflection. In all, the structure is very much like that of the teleost lateral line. Such a system should be able to detect the range and position of a vibrating object in the water from at least 20 cm (Denton and Gray, 1985). Omori (1971) reported that *Sergia lucens*, a related species with similar antennae, turns toward prey and proceeds to attack when it is about two body lengths away. The wide spacing of the trailing antennal flagella should improve sensitivity to the directionality and distance of the vibrating source, increase the range of detection, and decrease interference due to the sergestid's own propulsive movements. This gives the sergestid a capacity to detect near-field sound that compares favorably with that of fish (Denton and Gray, 1985). On the other hand, since this system gives less feedback regarding body position, it should be less effective at promoting schooling than is the fish system. At any rate, it would be effective in the relatively long-range detection of prey, and perhaps in the avoidance of some predators. In addition to the lateral-linelike system, sergestids and similar crustaceans have a number of other antennal receptors, which could be used for monitoring swimming speed, antennal angle at the articulation, waves of flexure as they pass along the antennae, touch, bending, and position (Laverack, 1964; Taylor, 1975; Ball and Cowan, 1977).

As useful as the widely spaced antennae may be for detecting prey, they may entail some risks beside increased drag. Because of their abundant setae, their surface is very rough and they attach readily to many surfaces, so much so that they often become hopelessly tangled together if a subject is kept in a container; and especially if two subjects occupy the same container. Once entangled, they adhere together so tenaciously that it is almost impossible to separate them again with antennae intact. Indeed, the antennae seem so "sticky" that

Hardy (1956) speculated that the antennal flagella may be used as "fishing rods" to snare prey. While I feel that this is unlikely, given the complex nature of the antennal setae, it is possible that in at least one predator-prey interaction the antennae are a distinct liability to the sergestid. Snipe eels (*Nemichthys* sp.), which inhabit similar depths and feed primarily on sergestids and other shrimp, have an unusually long curved "beak" covered with tiny teeth. This beak adheres very readily to the second antennae of sergestids, and it has been speculated that the eels may use their unusual beaks to snare their sergestid prey by the antennae. To test the feasibility of this mechanism of capture, the spacing of teeth was examined on several snipe eels, and compared to the spacing of antennal setae on *S. similis*. The snipe eel teeth were spaced at 2 per mm on the jaw and at 3 per mm on the vomerine plate, while the antennae of *S. similis* had six setae-bearing segments per mm. Another eel species, the dogface witch eel *Facciolella gilbertii* (Garman), has six teeth per mm on its somewhat shorter jaw and also feeds on small crustaceans. It thus appears that a good correspondence exists between the spacing of the teeth of these eels and setal spacing on sergestid antennae, with the teeth being used to adhere to the antennae in a lock-and-key fashion to snare the sergestid prey. If so, the adaptive advantage to having antennae that break free so readily is obvious. *Acetes sibogae* Hansen, a shallower-water sergestid with similar antennae, which has been observed in large numbers off Australia, seldom had both antennae intact (Ball and Cowan, 1977), suggesting that there may be frequent situations in which antennae are partially or wholly broken off. The question also may be asked whether the antennae ever become entangled during normal swimming, and if so, if the sergestid is able to untangle them. During a tail-flip escape response, for example, the antennae are held together and stream out in parallel for several body lengths in the turbulence behind the escaping sergestid. They would thus appear to have the potential for entanglement with each other. In sergestids confined to a container, once the antennae became entangled I did not observe them becoming untangled again, even over a period of a week or more. However, no sergestids swimming freely in midwater were observed with tangled second antennae.

While the widely spaced second antennae clearly increase drag during swimming, several aspects of the deployment of the pleopods and pereiopods serve to minimize drag from these appendages. The pereiopods could substantially increase drag if they were extended, because they are as long or longer than the pleopods and angle forward, so that they would immediately act as "bluff body" if extended. However, they are normally held quite close to the ventral surface of the thorax, minimizing form drag. Full extension of the pereiopods was generally brief and occurred only when an object was encountered or during grooming. However, in several sequences a sergestid was observed swimming with what appeared to be the posterior pair of pereiopods partially extended for several minutes. This pereiopod pair is covered with bands of long setae, which were clearly visible in the extended position as the sergestid swam through the water. Swimming in this position would substantially increase drag, and the adaptive value of swimming with this pair partially extended is not clear. It is possible that it represents an additional prey-capture mechanism, in that it would have tended to channel water toward the ventral side of the posterior thorax. It may be used to capture prey in the incoming water stream in a manner analogous to that of the thoracic basket of euphausiids. Barham (1956) reported observing *S. similis* in aquaria capturing particles of food in "a complex of long hairs on the thoracic appendages." Renfro and Pearcy (1966) speculated that the posterior pereiopods are used for capturing or holding prey. At any rate, though the abundant setae apparently led some earlier investigators (Barham, 1956; Genthe, 1969) to speculate that the posterior pereiopods were used for swimming along with the pleopods, I never observed them being used in a propulsive mode.

The pleopods increase their efficiency by maximizing thrust and minimizing form drag in several ways during their propulsive stroke cycle. The spreading of the long setae during the propulsive stroke greatly increases the effective surface area and maximizes thrust, while the folding of the setae on the return stroke minimizes drag. In addition, the fact that the pleopods are held in a fully extended position, perpendicular to the direction of movement and separated from the other pleopods during the propulsive stroke, maximizes thrust. Folding the pleopods, holding them closer to the body axis and in close apposition to each other on the return stroke, further reduces drag. The metachronous wave of pleopod beating provides steady forward propulsion through the water. It is not clear what relative benefit may accrue from the fact that the wave proceeds anteriorly (an adlocomotory wave) rather than posteriorly (a contralocomotory wave). Both patterns exist in nature, but the adlocomotory rhythm is most common in crustaceans, and the two members of each appendage pair generally beat in synchrony, as was observed in *Sergestes similis* (see Sleigh and Barlow, 1980).

The swimming stroke of *Sergestes similis* is in several respects similar to that of *Gnathophausia ingens*, another holoplanktonic macrocrustacean (Hessler, 1985; Cowles, personal observations). *Gnathophausia ingens* swims using thoracic exopodites and pleopods. The flagellum of the swimming appendages is armed with setae, as in *S. similis*. Thrust is maximized on the power stroke by full extension of the appendage and spreading of the setal fan, while drag is minimized on the return stroke by partial flexion of the limb and folding of the setal fan. On the other hand, *G. ingens* does not display a clear metachronous propulsive wave, as is seen in *S. similis*, and the contralateral appendages of each pair are 180° out of phase with each other. In *G. ingens*, the appendages are also not held in close apposition during the recovery stroke, as observed in *S. similis*, and thus probably experience more drag.

Implications for the Lifestyle of *Sergestes similis*

It appears likely that *Sergestes similis* is an active swimmer at all times, at all depths, and whether swimming upward or downward. In particular, it does not appear to sink passively during downward migration. The long antennae also appear to be invariably deployed in the characteristic extended position, except briefly during tail flips or after encountering a particle, which would tend to increase drag and the metabolic cost of active swimming. From the video observations, it would appear that most swimming is in the vertical mode, in which case diel vertical migrations may consist of a series of shorter round-trip vertical excursions trending in one direction. However, residence times at the surface or at depth would consist of similar short vertical excursions with no net directional trend. It is also possible, however, that the presence of the submersible lights biased observed swimming directions into the vertical mode, and that normal swimming while resident at a particular depth is oriented horizontally or in random directions.

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Address: Department of Natural Sciences, Loma Linda University, Loma Linda, California 92350, U.S.A.