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Cephalic Appendage Motion during Swimming of a Calanoid Copepod, *Subeucalanus crassus* (Giesbrecht, 1888)

Erin WITTKE, Takashi ISHIMARU and Yuji TANAKA

Abstract: The swimming behavior of *Subeucalanus crassus* was observed by video equipment, with focus on 3-dimensional motions of the cephalic appendages. High-speed recordings showed that only the rotation of the 2nd antennae (A2) and the mandibular palp (MP) contributed to propulsion for typical swimming, jerky swimming, and hovering. During typical swimming, both appendages rotated at a frequency ranging 70–80 Hz with the maximum rotation angle of 90°. During hovering, the frequency of appendages ranged 60–70 Hz with the maximum rotation angle of 45°. Sinking was accomplished by horizontal spreading of the motionless 1st antennae, A2 and the MP, while being pulled posteriorly by gravity. Previous observations of *S. crassus* behaviors from Australian and off Georgia waters could not be confirmed by the present observation on *S. crassus* from Sagami Bay suggesting that the latter represents a different species or a behaviorally differentiated population.

Keywords: *Eucalanidae, hovering, swimming, sinking, cephalic appendages*

Introduction

Copepods are the most abundant metazoan plankton in the ocean and their behaviors are fundamentally important for their existence in the food chain and ecosystem interactions. JIAN *et al.* (2002) compiled an overview of copepod species behaviors and general propulsionary appendage usage. Species specific or taxon specific behaviors and methods for feeding and swimming are important for prey detection, predator avoidance, and mate recognition (JIAN *et al.*, 2002; LOWNDES, 1935; STRICKLER, 1982).

The family Eucalanidae have a world-wide distribution (BOLTOVSKOY, 1999; BRADFORD-GRIEVE, 1994; LANG, 1965) and were used for some of the first feeding studies (ESTERLY, 1916) and repeatedly used for optical recording studies (ALCARAZ *et al.*, 1980; PAFFENHÖFER and LEWIS, 1989; PAFFENHÖFER *et al.*, 1982; STRICKLER, 1982, 1985) taking advantage of their large and robust bodies. *Subeucalanus crassus* has exhibited the following basic behaviors in the laboratory, while unrestrained: swimming to the surface, then sinking to the bottom, jagged and backward swimming, and remains suspended in the water for prolonged periods of time (STRICKLER, 1982). Previous behavioral studies on tethered *S. crassus* have concentrated on feeding currents (JIANG *et al.*, 2002) and prey selection (ALCARAZ *et al.*, 1980; PAFFENHÖFER *et al.*, 1982; PRICE and PAFFENHÖFER, 1986). However, the role of appendages involved in achieving different propulsionary or feeding methods has not been well addressed.

LOWNDES (1935) observed the motions of the cephalic appendages of various calanoid copepods such as *Calanus finmarchicus* and *Diaptomus gracilis*. He took particular notice of the 2nd antennae (A2) and how it rotates from a vertical position to a horizontal position. Recent 3-dimensional analyses have focused on the appendages used during feeding, such as the 1st maxilla (M1), 2nd maxilla (M2) and maxilliped (MX) (STRICKLER, 1984), and

Department of Ocean Sciences, Tokyo University of Marine Science and Technology, 4–5–7 Konan, Minato-ku, Tokyo 108–8477, Japan
Fax : 03–5463–0494
Corresponding Author, Takashi Ishimaru
e-mail : Ishimaru@kaiyodai.ac.jp

the 3-dimensional flow field around a copepod have examined (FIELDS and YEN, 1993; JIANG *et al.*, 2002). However, despite the availability of advanced optical technology, recent studies have not examined 3-dimensional movements of the A2 and the MP, which are involved in prey capture, ingestion and locomotion by creating currents.

For better understanding of the feeding behavior of copepods, the present study aimed to re-examine the swimming behaviors of *S. crassus* with particular reference to the movements of the cephalic appendages as propulsionary or food collecting apparatuses, using a simple high-speed camera set up. In this paper, the precise movements of the cephalic appendages, particularly the A2 and the MP during swimming are re-described.

Methods

Collection and Culture

During cruises on the training and research vessel Seiyo Maru of Tokyo University of Marine Science and Technology, female *S. crassus* were collected year round at a fixed station (35° 00' N 139° 20' E) in Sagami Bay, Japan. Vertical tows from 300 m depth were conducted during the daytime with a NORPAC net (45 cm diameter with 330 μm mesh), and copepods were sorted live with pipettes and stored in 1 L or 125 mL containers filled with cooled surface seawater. The containers were kept in insulated coolers and maintained at approximately 10℃. On land, copepods were maintained at 15℃ and re-sorted into glass containers, 1 animal per 250 mL of filtered seawater (Whatman GF/F), and fed a mixed diet of flagellates, *Isochrysis galbana* and *Tetraselmis* sp. (both less than 5 μm in diameter) and diatoms, *Chaetoceros* sp. (approximately 10 μm in width per individual cell), *Coscinodiscus wailesii* (160–350 μm in diameter), *Eucampia zodiacus* (approximately 15 μm width per individual cell), and *Thalassiosira weissflogii* (approximately 13 μm in diameter per individual cell).

Non-tethered filming and calculations

Non-tethered copepods were placed in a 1 L rectangular acrylic container (20.5×12.5×4.5 cm), in a 15℃ room in filtered seawater, under room light conditions. Copepods were filmed with and without food against a white background with an ordinary video camera (NVGS500, Panasonic, Japan). Eye observations were made on a daily basis for newly caught animals for a period of 7 days. Filming and observations of free swimming animals were made with the lens axis parallel to the horizon. Prey items were gently pipetted into the experimental chamber and evenly distributed by gentle pipetting. Concentrations were not recorded, as our purpose was to observe the feeding behavior. Prey items were added singly and as various mixtures to encourage the copepods to alter their behavior. Copepod feeding and food selection observations will be published elsewhere. Swimming and sinking velocities were calculated by importing the video data into the Adobe Professional Video Collection software where a grid of 1 mm lines was superimposed on the image to measure the ani mals' velocities. Only clear images of copepods swimming or sinking for at least 1 s in a linear line were used. The time in seconds was provided from the date/time stamp of the original recording device.

Tethered filming and calculations

Adult female copepods were kept overnight in the experimental room, without food. Copepods were then tethered to a hair by fast acting adhesive (Aron alfa, TOA, Japan). Wild grizzly bear hair of approximately 1 cm in length was used after being washed and rinsed with deionized water, and then acetone. One end of the hair was glued to the dorsal side of the copepods carapace and the opposite end was glued to a piece of gold wire, with a diameter of 1 mm; which was connected to the rod of a micromanipulator (UB-K, Kanetec, Japan). The tether for *S. crassus* was similar to that as described by ALCARAZ *et al.* (1980), although the tether was only attached to the dorsal cephalosome.

Previous observations used dog hair as the tether (ALCARAZ *et al.*, 1980; BUNDY and PAFFENHÖFER, 1996; COWLES and STRICKLER, 1983; PAFFENHÖFER *et al.*, 1982). However pet hair was found to be inadequate for this study as it was too brittle and copepods quickly died,

probably from the release of a contaminant into the water. An assortment of wild Canadian animal hairs were tried with a variety of problems; hairs being too flexible or brittle, too narrow or thick. Canadian grizzly bear (Arctoidea; *Ursus arctos horribilis*) hair was found to be adequate for tethering. Grizzly hair, approximately 200 μm in diameter is strong, sturdy, and is flexible enough that the copepod could jump and was slowly returned back to the focal position with minimal stress.

A high-speed digital video camera (Fastcamnet from Photron, Japan) was mounted on top of a dissecting microscope (SZX12, Olympus, Japan) with light provided by a Cold Spot fiber optic (PCS-UMX250, NPI, Japan). Tethered copepods were kept in a 550 mL (14.5×9.0×6.0 cm) rectangular acrylic container of filtered seawater for a minimum of 1 hour before digital recording. All instruments used for filming were placed on a 1 - cm thick black-painted iron plate with stabilizing mat to reduce vibrations. Animals were rotated around the behavior of interest at approximately 5° increments by micromanipulator to allow repositioning of the copepods without jarring or shaking. The process was repeated for each new position observed, and the animal was rotated until the limit of the equipment had been reached. Digital images were examined using the Adobe Professional Video Collection and the Adobe Premium Creative Suite. The appendage rotation frequency (Hz) was calculated by analyzing 1 s of high-speed video recordings.

S. crassus general body schematic, appendage structure, tether construction, notational and directional terms used for figures and photos are shown in Fig. 1. All the appendages have hairs or spines (setae) on them, which have only been drawn on the A2 and MP. The setae are covered with even smaller, finer hairs (setules), only included on the A2 exopod for reference.

Taxonomic verification of *S. crassus* was based on the re-description of *Eucalanus crassus* by MORI (1937) and confirmed against the integumental pore signatures from the Atlantic (FLEMINGER, 1973) and New Zealand waters (BRADFORD-GRIEVE, 1994). The *S. crassus* from Sagami Bay was also covered with small spinules reported on those from New Zealand by BRADFORD-GRIEVE (1994).

Results

Non-tethered Swimming Modes

The copepods, during swimming, oriented vertically with the A1 spread outward, which is characteristic of calanoid copepods (LOWNDES, 1935). "Swimming" in the present paper is defined as the active movements of the copepod relative to the water. Swimming was further subdivided into the following four swimming modes. 1) Typical swimming: active and smooth propulsion through the water. 2) Hovering: extremely slow linear upward swimming. 3) Jerky swimming: active shift of location by the urosome movement. 4) Escape: active, sudden, short-lived, erratic propulsion. Sinking was excluded from swimming modes as it was the passive downward movement due to gravity, with no movements of body parts or appendages. Sinking was done by spreading the A1, A2 and MP out much like a parachute allowing gravity to pull the animal downwards. Once the appendages were spread, no appendages were observed to actively move and the urosome was positioned dorsally.

In filtered seawater without food, copepods showed repeated linear sinking and swimming, as well as random smooth looping patterns, which was also included in typical swimming. During linear swimming and sinking sessions of six individuals, swimming speeds of 0.43-0.90 cm s^{-1} and sinking speeds of 0.48-1.60 cm s^{-1} were observed. Typical swimming mode was used to swim to the surface, as was verified by eye and video recordings by use of the A2, and MP. Looping speeds were observed by eye to be quick, but could not be measured due to the a nimals' 3-dimensional motions and our methods. The urosome was positioned dorsally for both typical swimming and sinking, but its movements could only be observed by eye when the animal moved linearly. Any of the small diatom species (*Chaetoceros* sp., *E. zodiacus* and *T. weissflogii*) added to the chamber media resulted in the copepods swimming mode to change. There was no difference between the feeding modes of copepods fed single diatom species and those fed mixtures of more than

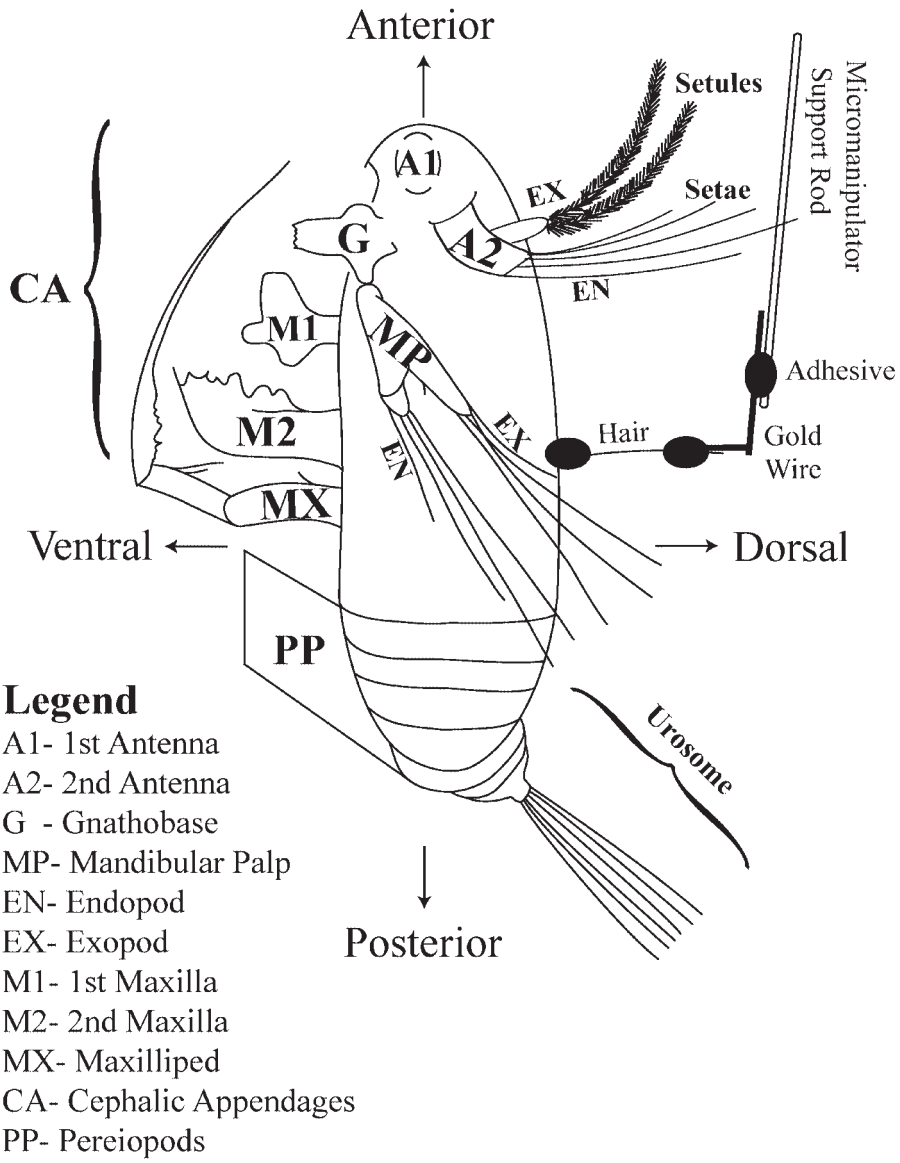

Fig. 1. The basic schematic of a female *Subeucalanus crassus* in a typical tethered position, with general appendage placement, tether construction, direction and notation legend. Diagram is not to scale.

one species. When the diatoms had been found by the copepod, the animals switched from typical swimming mode to the hovering mode and remained within the food area by maintaining a constant slow speed of 0.14 cm s^{-1}. Only when fed the large diatom *C. wailesii*, which sank when introduced, did the copepod swim to the surface in a jerky manner. The jerky swimming was attributed to the dorsal-ventral flicking of the urosome, which was easily observed by eye. The A2 and MP behaved in the same way as observed for typical swimming. The main propulsion for typical swimming, hovering and jerky swimming were observed to be created by the movement of the A2 and MP.

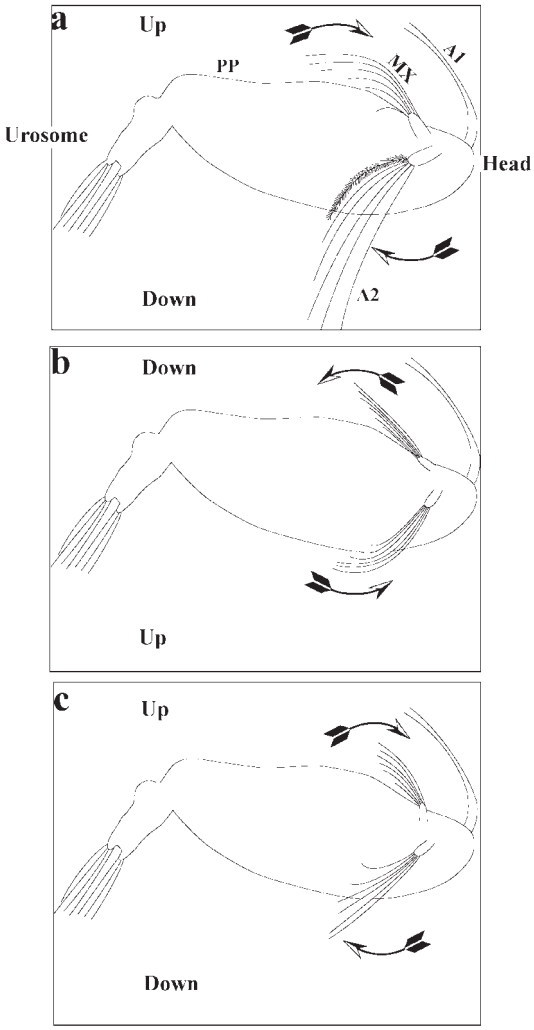

Fig. 2. Left side of a female *Subeucalanus crassus* typical swimming schematic sketches, when unfed. The animal is tethered horizontally, lying on its side with the filming lens axis at a 45° angle to the body. The arrows indicate the appendage stroke direction for the 2nd antennae (A2) and the mandibular palp (MP). See text for details.

Tethered Swimming Modes

High speed video images showed two distinct movements of the cephalic appendages, which corresponded to "typical swimming" and "hovering." At first there seemed to be no noticeable difference between typical swimming and hovering. The urosome was positioned dorsally during both of these swimming modes. The present description of the cephalic appendages is limited to the A2 and the MP, as the M1, M2 and MX were not observed to contribute to swimming modes, but become active during prey capture and ingestion, which will be published elsewhere. The left and right A2 and MP rotated in the same elliptical motion during typical swimming and hovering modes, and their endopods and exopods moved through the water much like oars on a row boat.

Typical Swimming Mode

Typical swimming was observed when the copepod was tethered and unfed with a stroke-frequency range of the A2 of 70-80 Hz, where only the A2 and MP were found to move. The animal was positioned with the left side of the cephalic appendages slanted 45° towards the lens axis while the body was parallel to the horizon. This position allowed the left side appendages to remain in focus. From sequential digital images recorded at 250 frames s^{-1} for a total duration of 0.032s, 3 photos were extracted every 0.016s to create schematic sketches demonstrating the change in appendage motions (Fig. 2). Fig. 2a shows the MP during the up-stroke with setae bending posteriorly and the A2 during the down-stroke with spread setae. The setae of the MP in Fig. 2b is almost straight, as it is about to change direction from an up-stroke to a down-stroke, while those of the A2 are bending posteriorly during the up-stroke. Both the MP and A2 are about to turn and change direction in Fig. 2c. As the A2 beats down, the MP is coming up and vice versa, creating a rotary pattern, which does not rotate in unison, giving a constant thrust.

A slight change in angle allowed the endopods and exopods motions of the MP position in the water column to be observed. The animal was tethered perpendicular to the horizon and the lens axis was mounted directly above. From sequential digital images recorded at 250 frames s^{-1} for a total duration of 0.044 s, 3 photos were extracted at intervals of 0.024 s and 0.020 s, demonstrating the change in appendage motions and accompanied by schematic sketches (Fig. 3). A relaxed appendage occurred when setae were evenly spaced with the tips pointing in the same direction, as illustrated by the A2 in Fig. 3a. The up-stroke is

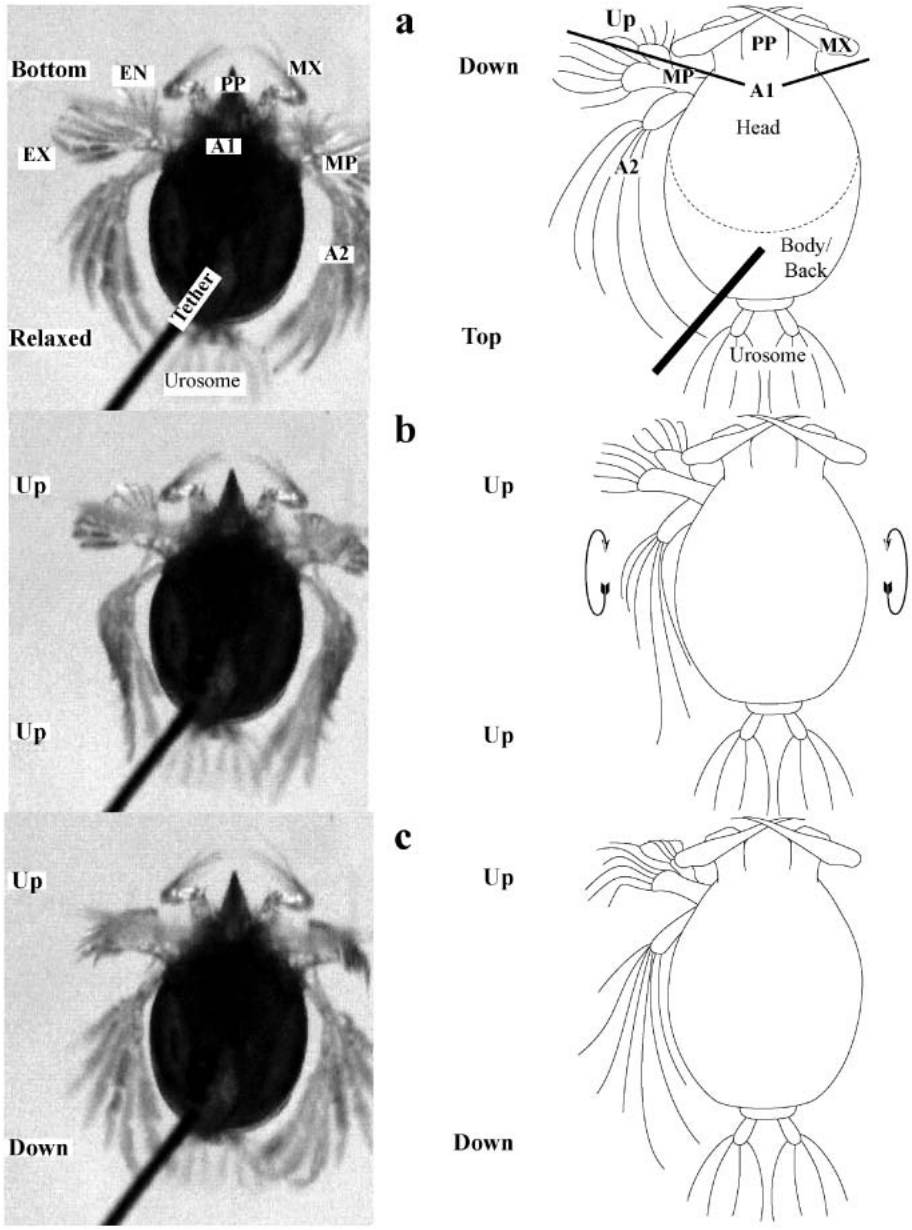

Fig. 3. Typical swimming photos and schematic sketches of a female *Subeucalanus crassus*, when unfed. The animal is vertically tethered with the lens axis located above the head. Circles with arrows represent the stroke direction of both the 2nd antenna (A2) and mandibular palp (MP) on each side of the animal in (b). See text for details.

where all the setae become pushed together; as the appendage is pulled through the water (refer to the A2 in Fig. 3b). The down-stroke is shown by the A2 in Fig. 3c, the setae are spread further apart and no longer point in the same direction as they are being pushed through the water.

The A2 and MP of the left side rotates as a mirror image of the right side (Fig. 3b: arrows). The MP endopods and exopods also exhibit a rotary motion. In Fig. 3a, the MP is almost at the bottom of its stroke as the

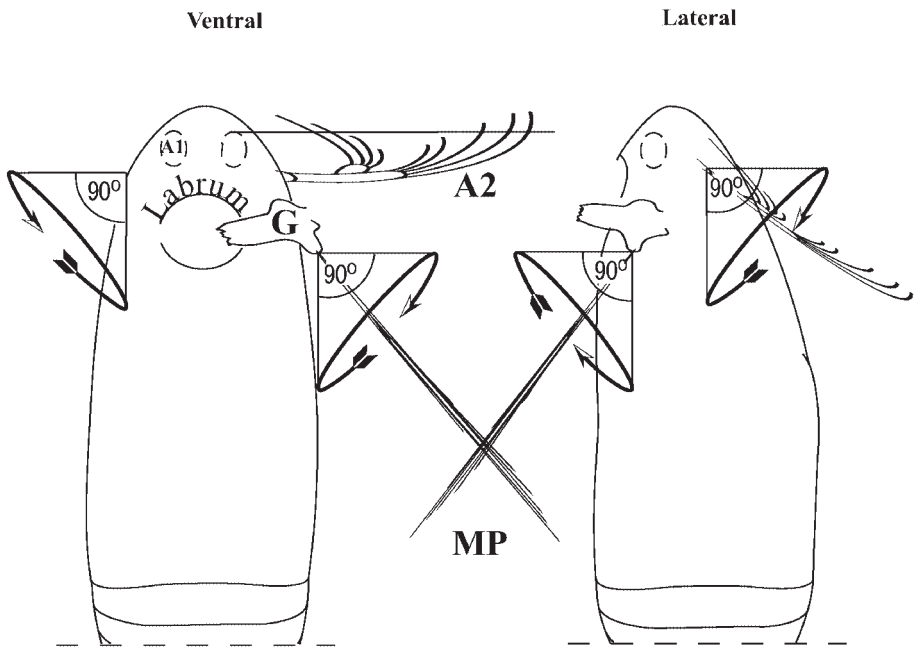

Fig. 4. Schematic ventral and lateral view of the left side of *Subeucalanus crassus* mandibular palp (MP) and 2nd antennae (A2) during typical swimming, unfed. The MP pivots around the gnathobase (G) joint within a 90° circular motion, as does the (A2), whose angle references is on the right side of the front view.

endopod is just turning and starting to come up to the anterior endopods of the stroke, while the exopod remains in the down-stroke. The same motion is also exhibited by the A2 and its associated endopods and exopods.

Both the A2 and MP are angled away from the body during typical swimming. Animals constantly adjust the stroke angle within a maximum appendage rotation of 90° as seen in Fig. 4. The setae lagged behind and trailed beyond the 90° maximum. When the copepod was tethered perpendicular to the horizon the angled stroke pattern of the A2 and MP appeared to give the animal lift as it pulled against the tether.

Hovering Mode

Hovering photos were taken when food was present and the animal was first positioned perpendicular to the horizon and then slanted 45° towards the right to allow the left side of the cephalic appendages to be observed. The copepod changed the A2 and MP stroke frequency to 60–70 Hz, and also changed the path of the appendage rotation. From sequential digital images recorded at 250 frames s^{-1} for a total duration of 0.044 s, 3 photos were extracted at intervals of 0.024 s and 0.020 s demonstrating the change in appendage motions (Fig. 5). The A2 (left panel) and a magnified view of the same A2 motion (right panel) are shown. The endopod of the A2 was rotating in the ventral direction on the ventral side of the A1, while the exopod is rotating dorsally on the dorsal side of the A1. Both follow horizontal elliptical paths which remain in the focal plane most of the time (Fig. 5a). Fig. 5a also shows the A2 endopod to be completing its up-stroke, with the exopod beginning its down-stroke. The down-stroke of the exopod can be seen in Fig. 5b, while the endopod is being pulled upward. Both the endopod and the exopod are reaching a turning point in Fig. 5c. The setae of the endopods aligned perpendicular to the horizon and the exopod has reached its lowest point, with the setae trailing behind. The magnified photos of the A2 exopod (Fig. 5c) show the left and right motions relative to the animals' body as well as the exopods turning to the side with the setae aligning parallel to the body for a directional change. Fig. 6 shows generalized

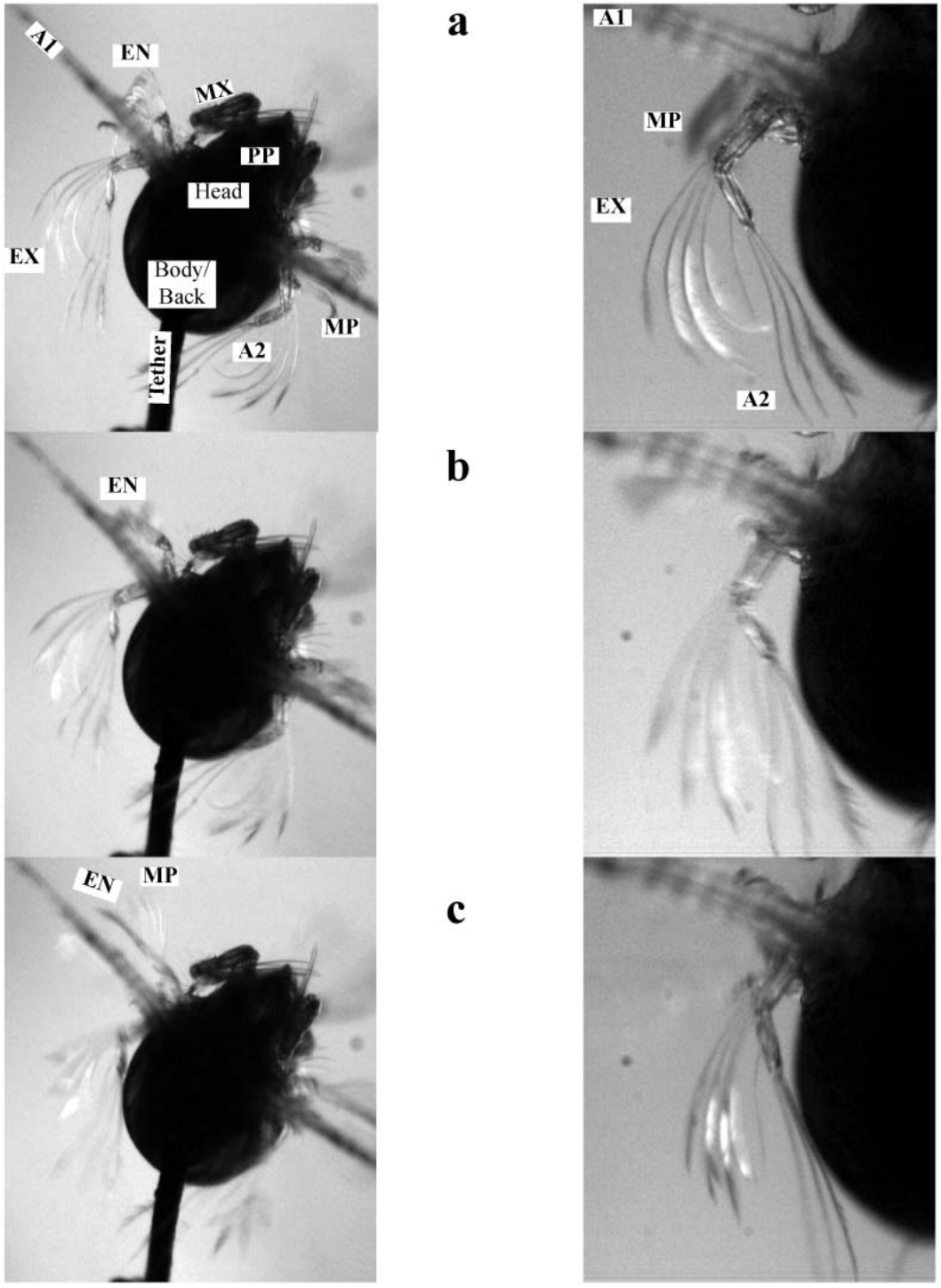

Fig. 5. Photos of the hovering behavior of the 2nd antennae (A2) and mandibular palp (MP) of a female *Subeucalanus crassus*, fed. The copepod is tethered vertically and tilted horizontally 45° angle to the right, with the lens axis located above the head. See text for details.

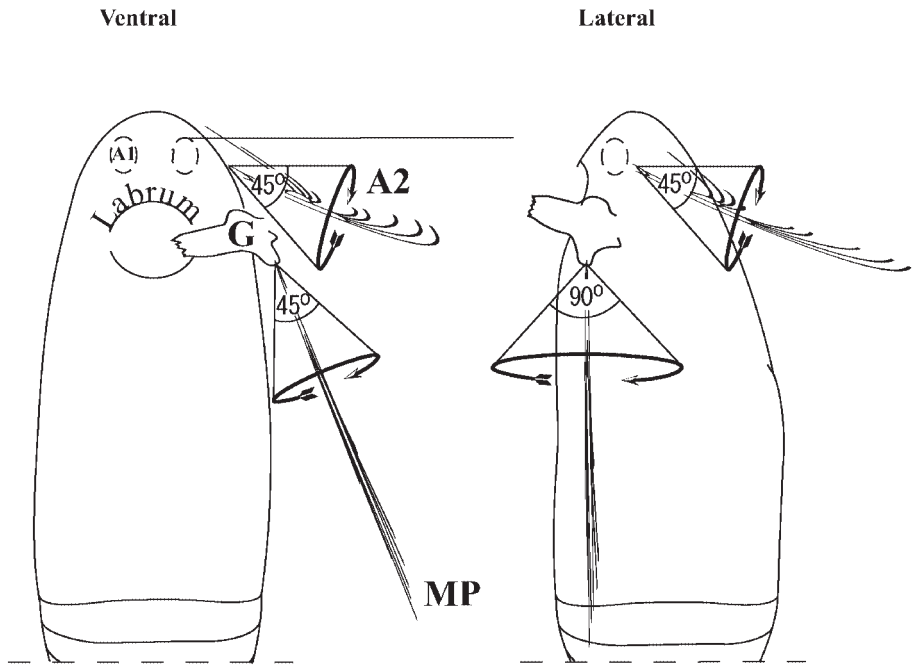

Fig. 6. Schematic ventral and lateral view of the left side of *Subeucalanus crassus* mandibular palp (MP) and 2nd antennae (A2) while hovering, fed. The MP pivots around the gnathobase (G) joint within a 45° elliptical motion and the A2 pivots around the joint at a 90° circular motion.

ventral and lateral sketches of this behavior mode, in which both the A2 and MP still contain a rotary action, but the MP stroke shifted posteriorly and gave the copepod a vertical thrust. The A2 endopod rotated horizontally in the dorsal direction with the exopod being raised anteriorly above the endopod. When tethered perpendicular to the horizon, the animal appeared to be balanced as it did not pull away from the tether and the urosome remained in the dorsal position.

Escape Mode

While tethered, this escape mode was very erratic and usually resulted in death or escape from the tether. During tether acclimation, the copepod would flick the urosome and the A1 although it was unclear if this mode was due to unusual disturbances or foraging attempts. Once the animal acclimated to the tether, the urosome jerking was rarely observed on 20 animals of 23 filmed. However, 3 of the animals constantly flicked the urosome and exhibited escape mode, resulting in quick exhaustion and death, as also observed by STRICKLER (1982) on *S. crassus*. Once adjusted to the tether, escape mode was only observed in response to external disturbances, such as large vibrations or jarring caused by adjusting nearby equipment. The A2 and MP held close and parallel to the body; the A1 was pulled into the center of the body and were held in place with the MX, while the pereiopod (PP) moved rapidly. The actual stroke beat of the PP involved in this mode could not be observed and no cephalic appendages were observed to contribute to the copepods thrust, as it is beyond the scope of our equipment.

Discussion

Three dimensional movements of the cephalic appendages have been historically difficult to study, but accepted as a means for propulsion through the viscous ocean environment (HUTCHINSON, 1967; JIANG *et al.*, 2002; STRICKLER, 1984). CANNON (1928) originally studied a copepod in a drop of water, as a restraint was needed to observe the fine movements of the animal. LOWNDES (1935) employed

various techniques in an attempt to observe the 3-dimensional movements of the appendages, as well as inferences from larger visible unrelated crustacean analogs *Chirocephalus* (fairy shrimp). An overview of a single animal requires the assembling of several papers utilizing different study methods and techniques (JIANG *et al.*, 2002). Recent optical technology has not been used for the observations of 3-dimensional movements of cephalic appendages on a single species.

Precise high-speed recordings of *S. crassus* appendage motions showed 3-dimensional stroke angles during typical swimming and hovering. Typical swimming copepods were found to have an elliptical rotation of 90° for both the A2 and MP in Fig. 2, creating the downward force that propels the copepod through the water. During hovering, the right and left MP rotated much like a set of egg beaters (two beaters on electric hand mixers). The A2 rotated dorsally at 45° and the MP at a 45° posterior orientation resulting in a reduced posterior elliptical angle (Fig. 6). The mechanisms for the creation of differing behavior modes were attributed to the reorientation of the appendage rotational angles and changing of stroke frequencies.

Typical swimming behaviors were exhibited by our non-tethered and tethered animals. Only the A1, A2, MP, PP and the urosome movements were observed on non-tethered animals. When *C. wailesii* was introduced, the copepod would use the jerky swimming mode to ascend to the surface. When cells were encountered, the animal would hover, assumably taking time to ingest the item. The animal would also swim in a jerky line to the surface to capture closely spaced cells, as also noted by STRICKLER (1982), and the behavior was attributed to flicking of the urosome. Jerky swimming was a modified version of typical swimming, as the only difference was the use of the urosome for steering. Non-tethered animals used a combination of typical swimming, hovering and sinking behaviors to search for prey. Tethered *S. crassus* with small phytoplankton in the media behaved as though the animal were actively remaining in areas of food.

The A2 and MP were the main active propulsionary appendage for typical swimming, jerky swimming and hovering, and were used passively as parachutes during sinking. The combined rotary action of the A2 and MP appendages allowed for constant propulsion or negated each others' thrust, suspending the copepod when hovering. The A1 remained stretched out for all swimming modes except for escape. During escape behaviors, the A1 were pulled into the body by the MX and held as the PP and the urosome moved erratically. Other cephalic appendages such as the M1, M2 as well as the MX were not observed to be used for creating swimming currents.

Different swimming modes or combination of swimming modes were used to feed on prey of different sizes. *S. crassus* has relatively large A2 and MP. By changing the frequency, position and angle of rotation of these appendages the copepod is able to alter its orientation in the water. Copepods were able to ascend and descend to search for prey and hover in areas of small diatom prey. In the presence of large *C. wailesii* cells the copepod would swim directly towards the cells, in a jerky manner. A size-dependent change in foraging behavior was supported by the 3-dimensional movements of the cephalic appendages.

The basic behavior of *S. crassus* from Sagami Bay was observed to differ from previous studies. STRICKLER (1982, 1984) examined *S. crassus* from Great Barrier Reef, Australia and off Georgia, USA; the sampling locations were unreported, but confirmed by personal communication. The natural body orientation of *S. crassus* was observed to be vertical for those from Sagami Bay, Australian and off Georgia waters, although the achieved position was different. The *S. crassus* from Sagami Bay maintained its vertical orientation with no aid from the urosome. *S. crassus* from Australian and off Georgia waters vibrates the urosome to maintain its natural orientation (STRICKLER's personal communication). The typical swimming mode was created by the rotary action of the A2 and MP for the *S. crassus* from Sagami Bay. Non-tethered and tethered recordings of *S. crassus* from Sagami Bay, typical swimming, hovering and its natural orientation in

the water showed the urosome to be positioned dorsally. On the contrary, the tethered or non-tethered, photos and sketches of *S. crassus* from Australian and the off Georgia waters, while swimming and in the natural position have the urosome pointing along the body axis (Fig. 1b in STRICKLER, 1982) or with a ventral orientation (Fig. 1b and Fig. 2 in STRICKLER, 1982). The urosome placement would change how the copepod moves through the water. STRICKLER (1982) observed backwards swimming in *S. crassus* from Australian and off Georgia waters. This could only physically be achieved if the urosome is positioned ventrally. Combined with movements of the M1 and M2, the copepod would gain a backward thrust.

Behavioral differences may have been caused by different experimental conditions, such as food, light, and container size, etc. However, it was most likely caused by species differences, as fundamental behaviors differed. Recently, DNA research by GOETZE (2003) has found genetic differences among Eucalanidae copepods. *S. crassus* from the South Korean Strait was found to be a cryptic species, diverging from the original *S. crassus* line in the North Atlantic and the South Western Pacific (GOETZE, 2003). Behavioral observations suggest that *S. crassus* from Sagami Bay is not the same as the *S. crassus* from Australian and off Georgia waters. The proximity between Japan and Korea may indicate that the *S. crassus* from both waters are more closely related if not the same species.

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