Note

Estimating the in-situ orientation of *Calanus finmarchicus* on Georges Bank using the Video Plankton Recorder

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Fine-scale plankton patches are frequently a manifestation of the behaviors of individual animals in response to a variety of physical and biological stimuli (Haury et al. 1978). Quantification of the behavior of individuals is therefore an important step in understanding the behavioral basis of patchiness (Hamner 1985). Ten years ago, Hamner (1988) noted that such measurements were largely lacking for pelagic zooplankton and with few exceptions, his criticism remains valid today.

The impediments to ethological studies on zooplankton have primarily been technological. Small, highly motile organisms such as copepods are particularly difficult to observe in their natural milieu. For this reason, most direct observations have been performed on swarms rather than on individuals by SCUBA divers in relatively shallow water (e.g. Emery 1968; Omori & Hamner 1982; Ambler et al. 1991; Buskey et al. 1996). Larger organisms such as ctenophores have been observed in open ocean waters by divers (Hamner et al. 1975) while the behavior and orientations of animals beyond the depth limits of human divers have been quantified with the aid of remotely operated vehicles or manned submersibles (Kaartvedt et al. 1994). Even with such vehicles, the movements and orientations of small and/or active organisms such as copepods are difficult to track and resolve. The advent of optical samplers has made it practical to collect undisturbed images of even small zooplanktors and these images are beginning to provide insights into the natural orientations of individual organisms as small as copepods in the open ocean.

Measurements of orientation alone cannot define behaviors but they are an important first step because orientations can yield insights into activities associated with vertical migration, mate-finding, predator avoidance, or prey detection and feeding. Orientation can also have important implications for acoustical detection of plankton patches because the angle of incidence of non-spherical organisms with respect to a sonar beam can alter the echo energy returned to the transducer, and

thus can change the apparent target strength and volume backscattering, a factor that can have important implications for bioacoustical surveys.

In late May 1992, a small region of Georges Bank was the subject of an intense, joint-ship investigation designed to survey the distributions of zooplankton in relation to hydrography during the onset of vernal stratification. The survey, conducted at a weakly stratified site on the southern flank of Georges Bank (40.68°N, 68.21°W) on 24 May 1992 between approximately 1200–1600 h (local time), involved two ships: the R/V *Albatross IV* and the R/V *Endeavor*. Details of the survey are provided in Benfield et al. (1996). The R/V Endeavor deployed a Video Plankton Recorder (VPR) that was towed in a continuous saw-tooth trajectory between the surface and near bottom (75 m) at a horizontal velocity of approximately 2.9 kt. The cruise was part of the U.S. Global Ocean Ecosystem Dynamics Program (GLOBEC). *Calanus finmarchicus* is one of the GLOBEC target species and the data collected by the VPR provided an opportunity to assess the in-situ orientations of this species.

The VPR (Fig. 1) used in the 1992 study was a high-speed tow body that incorporated four video cameras and environmental sensors (Davis et al. 1992; Benfield et al. 1996). Each camera recorded video data using the National Television System Committee standard of 640 vertical lines by 480 horizontal lines. Data from the high-magnification camera that imaged a volume of approximately 0.6 ml (6 mm horizontal×4.5 mm vertical×23 mm depth of field) were used in this study. This provided images with an approximate resolution of 1067 pixels cm^{-1}. Video images were illuminated by an 80 W collimated, red-filtered xenon strobe that provided a 1 s light pulse that was synchronized, and directed at an oblique angle relative to the cameras in order to provide dark-field illumination. Environmental sensors monitored temperature, conductivity, fluorescence, transmittance, pitch and pressure. Both video and environmental data were telemetered to the surface via fiber optic cable and archived to videotape for subsequent analysis.

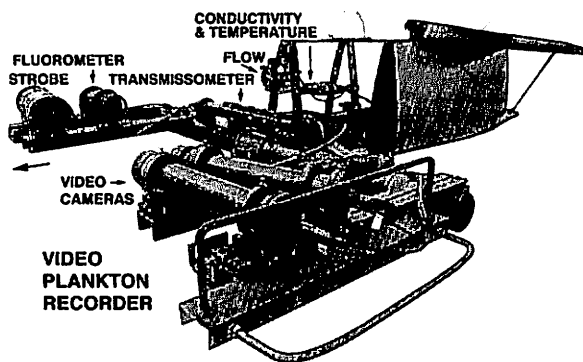Corresponding author: Mark C. Benfield; e-mail, mbenfie@lsu.edu

Fig. 1. A Video Plankton Recorder configured similarly to the vehicle used in this study. The front of the VPR is on the left with the arrow indicating the direction of travel.

Video tapes were analyzed semi-automatically using an image processing system that examined each video field in real-time, identified all in-focus targets above a user-defined size threshold, and then wrote those regions of interest (ROIs) to disk for subsequent identification and enumeration (Fig. 2). The system is described in more detail in Davis et al. (1996). A subsection of video collected between 1317 and 1352 h (local time) was examined to estimate the vertical orientations of *C. finmarchicus*. This section encompassed 10 saw-tooth trajectories of the VPR between 10- and 70-m depth. All *C. finmarchicus* in the extracted ROIs were identified and enumerated manually. It is important to note that every copepod imaged by the VPR is free to rotate in three dimensions. The orientations of animals that are tilted away from, or towards the viewing plane cannot be reliably estimated. A total of 152 copepods (primarily stage 5 copepodites and adults based on examination of images from the high magnification camera) that did not appear to be tilted towards or away from the plane of the camera were selected for analysis.

We used a MATLAB (The Mathworks Inc.) routine to measure the orientation of individual copepods. As each ROI was presented, the taxonomic identity of the constituent animal was selected from a pull-down menu and the length of the animal was measured by selecting two points at either end of the prosome. These two measurement were at opposite ends of the long axis of the body and the angle of the line that connected both points provided an estimate of its vertical orientation. Although the VPR was towed horizontally; the vehicle did pitch upward and downward. Downward (negative) pitch angles would cause the observed copepod angle to increase while upward (positive) pitch would have the opposite effect. The time-code of each ROI was matched to the pitch angle data file and the observed copepod angle was corrected for VPR deviations from horizontal.

The distribution of orientations of individual *C. finmarchicus* appeared to be non-random (Fig. 3). The majority of individuals were oriented with the long axis of their prosome towards the surface (Figs. 2, 3). A minor peak of individuals in a head down orientation was also evident. Assuming that an orientation of 0°–30° represented vertically oriented animals,
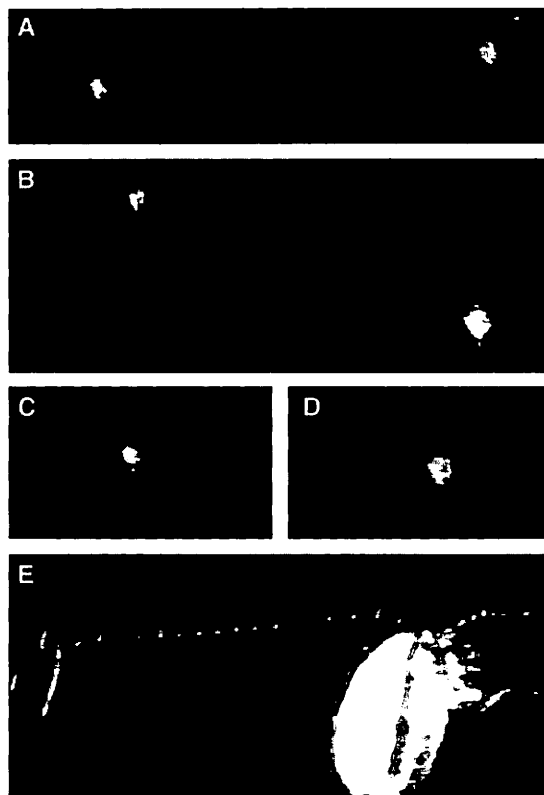

Fig. 2. Example regions of interest (ROIs) containing *Calanus finmarchicus*. During the process of transferring these images from video tape to hard copy, the quality of these images has been considerably degraded and details that were visible on the video and computer monitors such as antennules and antennule setae are difficult to distinguish in this figure. A, B. Pairs of individuals from camera 2 in vertical orientation. C, D. Single copepods in vertical orientation from camera 2. E. A single individual from the high magnification (camera 4) illustrating the high resolution and the degree of detail that can be obtained from the VPR. Note that this study utilized data collected with camera 2.

60.5% of individuals were oriented towards the surface.

While the behaviors underlying this orientation pattern are not clear, we speculate that they may lie in a predator avoidance strategy related to orientation towards incident light, maintenance of position within the water column, a requisite posture for effective feeding, or possibly the reproductive behavior of *Calanus*. The vertical orientation we observed may be a fairly common posture for *C. finmarchicus*. Recent work by C. B. Miller (personnal communication) at Oregon State University suggests that the oil sac of *C. finmarchicus* is capable of collecting incident downwelling light. These rays pass down through the oil sac via internal reflection and emerge as an intense, somewhat collimated bundle of light that would appear as a bright point of light emitted from the posterior end of the prosome. Such a bright source might render the copepod more conspicuous to predators located beneath it unless it possessed an adaptation to prevent this phenomenon. *Calanus finmarchicus* possesses a red pigment mass that is located at the
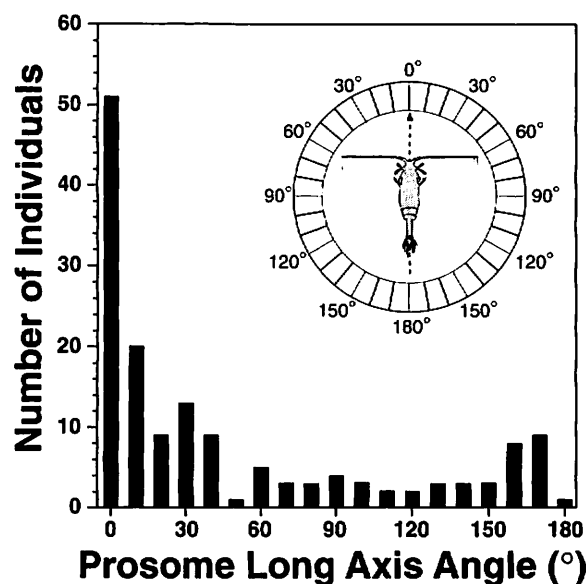
Fig. 3. The orientations of 152 *Calanus finmarchicus* measured from VPR images. The compass inset indicates a copepod in a prosome-up orientation at 0°.

posterior base of the oil sac and Miller speculates that this pigment may block the exit of light focused via the oil sac. Such a phenomenon would cause the copepods to blend into the downwelling light field rather than stand out against it and would act as a form of countershading in a manner analogous to adaptations of many marine fishes. However, in this case, the pigment would serve to reduce, rather than increase, the brightness of *Calanus* when viewed from below. If this hypothesis is correct, it suggests that *Calanus* is frequently oriented towards the surface. Hamner (1995) lists four categories of predator avoidance adaptations in pelagic zooplankton: very small size; invisibility due to tissue transparency; diurnal vertical migration; and exploitation of the sea surface. To this we might add, orientative behaviors that reduce conspicuousness when viewed from above or below.

Calanoid copepods are negatively buoyant (Strickler 1982). The vertical orientation with outstretched antennules would also function as a mechanism to reduce their sinking rate (Strickler 1982; Mauchline 1998) due to the combined drag of the antennules with their setae and aesthetasc sensillae.

Strickler (1982) examined the orientation of several species of calanoid copepods under laboratory conditions designed to reduce artifacts caused by small study volumes. Vertical posture was a common orientation for both *Paracalanus parvus* and *Eucalanus crassus*. Depending upon the species, vertical orientation may be the only posture that permits the flow field generated by feeding appendages to interact effectively with mechanoreceptors and chemoreceptors (Strickler 1982).

It is possible that vertical orientation is related to reproductive behavior. We tender this hypothesis with some caution because the assemblage we observed appeared to contain many stage 5 copepodites that were not reproductive. However, reproductively-capable female *C. marshallae* tend to move verti-

cally in the water column. Their hop and sink behavior described by Tsuda & Miller (1998) is manifested by vertical hops and slow sinking that may introduce a vertical pheromone trail in the water. Male *C. marshallae* frequently engage in horizontal search swimming although other more complex swimming behaviors were also observed by Tsuda & Miller (1998). Such horizontal swimming would likely enhance the probability of intercepting a female pheromone plume. If *C. finmarchicus* engage in similar swimming behavior, then some proportion of the vertically oriented animals that we observed may have been reproductively capable females. Our study occurred during a period when *C. finmarchicus* is known to be reproducing on the Bank (Davis 1982; Lynch et al. 1998). However, we recognize that the extremely restricted observational period makes it difficult to determine whether our animals were in fact engaged in reproductive behavior.

The orientations we observed have clear implications for bioacoustical surveys. Our data suggest that the majority of individuals (75%) were within ±30° of a prosome-up or prosome-down orientation. Such individuals would present a greatly reduced cross-sectional area to an echo-sounder's transducer with a correspondingly diminished target strength. Recent simulations of the influence of orientation of a calanoid copepod with respect to an incident sonar beam on acoustic target strength at 420 kHz (Stanton & Chu 2000), revealed a reduction of approximately 12 dB when a 3-mm copepod (modeled as a high-resolution approximation of the animal profile) shifted its aspect from head-on to broadside.

Mapping the distributions and abundances of diapausing *C. finmarchicus* in the deep basins of the Gulf of Maine is part of an ongoing GLOBEC investigation. The vehicle used in that study is a towed, multi-frequency acoustical platform equipped with a single-camera VPR and environmental sensors, called BIOMAPER II (Wiebe et al. 1997). Diapausing aggregations of *C. finmarchicus* are pre-reproductive and seldom feed. If the orientations we observed in 1992 are a consequence of reproductive behaviors or responses to light, then the diapausing copepodites in the deep basins will likely display a very different distribution of orientations.

Acknowledgments

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