Development of micro-scale frequency distributions of plankton for inclusion in foraging models of larval fish, results from a Video Plankton Recorder

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A self-contained, analog Video Plankton Recorder (VPR) mounted on a 1-m² MOCNESS sampling system was used to obtain data on micro-scale (<10 m) distributions of zooplankton as prey for larval cod and haddock during May 1997 and May 1999 on Georges Bank. The negative binomial frequency distribution was selected to best describe the more abundant plankton categories in 10-second bins for 10-m depth intervals. Most of the strata had asymmetrical frequency distributions with low means and low k values indicating a clumped distribution. Water-column stratification was especially important in structuring micro-scale high-density layers of phytoplankton and copepods. The most symmetrical Poisson-like distributions with high means and high k values occurred in the upper 30 m above the base of the thermocline.

INTRODUCTION

In the marine environment, zooplankton patchiness exists on a continuum of spatial scales where physical driving forces dominate at large scales and biotic processes at small scales (Haury et al., 1978; Pinel-Alloul, 1995). Theoretical plankton modeling studies show that patch structure can greatly modify encounter rates of predators and prey (Davis et al., 1991). The microdistribution of plankton is known from field studies to vary from random to patchy (Cassie, 1963; Fasham, 1978; Owen, 1989). However, direct observations of micro-scale (<10 m) patchiness are limited so that the theoretical basis for modeling is not well developed. Technological advances in optics and acoustics now allow us to resolve the vertical structure of plankton on the spatial scale of centimeters. Significant patchiness has been found at small scales in addition to that previously observed on large scales (Cowles et al., 1998; Currie et al., 1998; Davis et al., 1992a,b; Dekshenieks et al., 2001; Donaghay et al., 1992; Gallager et al., 1996, 2004; Hanson and Donaghay, 1998; Jaffé et al., 1998; McManus et al., 2003; Tiselius, 1998; and others).

The fine-scale distribution of prey and their persistence is important for larval fish feeding, growth and survival. Foraging models of fish larvae specify searching and feeding behavior which is dependent on the patchiness of the prey (Davis et al., 1991; Beyer and Nielsen, 1996; Werner et al., 1996; Vlymen, 1977; Pitchford and Brindley, 2001; Pitchford et al., 2003; Lough et al., 2005). In larval fish feeding studies prey distributions have been modeled as various Poisson and negative binomial probability distributions (Winemiller and Rose, 1993; Beyer and Nielsen, 1996; Vlymen, 1977; Letcher and Rice, 1997; Pitchford and Brindley, 2001; Pitchford et al., 2003). Poisson or random process distributions are generally easier to use although models of patchy distributions are more realistic (Rothschild, 1991). Beyer and Nielsen (1996) modeled foraging in a patchy environment using
an interrupted Poisson process model, where predators encounter prey as a Poisson process only within a patch, but interrupted when traveling between patches. The negative binomial is a suitable model for exploring the underlying distributions when the variance is generally greater than the mean (Elliott, 1977; Owen, 1989). Data describing fine-scale distributions of prey are needed in order to provide a stochastic extension of the deterministic number of prey encountered (Werner et al., 1996).

Larval growth and recruitment are presumably higher in a food-limited environment as the variability increases (Pitchford et al., 2005). In this study, Video Plankton Recorders (VPR) were used to visualize a subset of the volume filtered by 1-m$^2$ MOCNESS profiles on the southern flank of Georges Bank. The fine-scale distribution of copepod prey for larval cod was characterized from VPR images to be used in a trophodynamic model as a stochastic element. We provide empirical data on the spatial structure of selected taxa, but not the underlying mechanisms for structuring patches.

**RESULTS AND DISCUSSION**

Field sampling was conducted within the context of the U.S. GLOBEC Georges Bank Program during 1995–99, focusing on the population dynamics of two copepods, *Calanus finmarchicus* and *Pseudocalanus* spp., and the early life of Atlantic cod and haddock (Wiebe et al., 2002). Sampling in this study was conducted near transsects of long-term current moorings in May 1997 and May 1999 (Fig. 1). At these sites a 1-m$^2$ MOCNESS with nine 333-μm mesh nets, a flow meter, CTD-profile, fluorescence, and light attenuation sensors, was used to sample larval fish and larger zooplankton at discrete depths between surface and within 5 m of the bottom (Lough and Potter, 1993). The tow profile was nominally 10-m strata from the surface to 60 m with 20-m strata used below 50 m for stations with depths greater than 60 m. Tow speed was 1.2 m s$^{-1}$ and the vertical retrieval rate was approximately 1 m 30 s$^{-1}$. Volume filtered for each net was calculated in 4 second increments by the MOCNESS software and accounted for tow speed and frame angle.

The Video Plankton Recorder was mounted above the net opening of the 1-m$^2$ MOCNESS and imaged an area 0.5 m in front of the net opening (Fig. 2). The VPR system used in 1997 was a single analog, high-magnification camera which imaged a field of view 6.0 mm in length, 4.5 mm in width and 21.0 mm in depth. In 1999, the VPR system had both low and high magnification cameras. Only the high magnification camera, which imaged an area 5.0 mm in length, 4.5 mm in width and 15.0 mm depth, was used in this study. Cameras in both VPRs were interfaced by software (Seascan, Inc., Falmouth, MA) to time code generators (Horita, Inc., Mission Viejo, CA), a strobe and video camcorders. Both systems were powered by a

![Fig. 1. Location of study sites on the southern flank of Georges Bank: Stations 180–183 sampled during 19–21 May 1997 and Stations 95, 100, 106 sampled during 13–19 May 1999.](https://academic.oup.com/plankt/article-abstract/29/1/7/2963062)
32 V-8amp battery pack. VPR images were recorded at 60 frames per second. VPR operation was independent of the MOCNESS. Recordings were later dubbed to S-VHS tape format together with a time code synchronized to the VCR. All in-focus images were identified by the technician to the lowest taxon possible. The high magnification cameras viewed the smaller phytoplankton and juvenile stages of zooplankton, especially copepod nauplii that are an essential component of the prey for larval fish. Taxonomic groups used in this study included: copepod nauplii, copepodites of *Calanus finmarchicus*, *Pseudocalanus* spp., *Oithona* spp., *Centropages* spp., *Temora* spp. and *Metridia* sp., an “Unidentified” category of copepodites most likely not *Calanus*, as well as *Obelia* spp. medusae, *Clytia* spp. hydranths, and *Limacina* sp. Avoidance of the gear by these groups was not likely since most imaged organisms did not appear to be in a disturbed state in this study or others reported by Davis *et al.* (2005).

Zooplankton data were initially standardized to number per m$^3$ then placed in 1-m depth bins and plotted with vertical profiles of physical parameters to examine meter-scale variability. In this case the VPR images were standardized using the volume sampled in 1 s$^{-1}$ (30 frames) times the number of seconds the gear resided within a 1-m depth level (Gallager *et al.*, 1996). Comparison of abundance estimates of selected taxa from the VPR and MOCNESS-net data were made in another study and were found to agree closely (Broughton and Lough, 2006).

Statistical measures such as mean ($\bar{x}$) and variance ($s^2$) were calculated for taxa within a depth bin. Since contagion ($s^2 > \bar{x}$) was typical for the plankton data, the negative binomial distribution was used to characterize the distribution of taxa within a depth stratum (Elliott, 1977). The minimum time and space scales to have sufficient data to generate a curve were the taxa counts within a 10-sec bin, and over a depth range of 5 m or 10 m, depending on the taxa abundance. This would allow us in future simulations to match a depth-specific prey distribution with a sample of cod larvae collected by the 1-m$^2$ MOCNESS. The probability mass function for the negative binomial is given by:

$$P(x) = \left(1 + \frac{\mu}{k}\right)^{-1} \frac{(k + x - 1)!}{x!(k - 1)!} \left(\frac{\mu}{\mu + k}\right)^x$$

where, $P(x)$ is the probability of $x$ individuals in a sampling unit. Expected frequency is therefore $n \cdot P(x)$, where $n$ is the number of sampling units in the sample. The parameters $\mu$ and $k$ were estimated from statistics $\bar{x}$ and $k$. The taxa mean and variance were calculated for each depth strata and negative binomial
$k$ values were approximated by the equation:

$$\hat{k} = \left( \frac{\bar{x}^2}{s^2 - \bar{x}} \right)$$

The more accurate method of maximum likelihood was not used given the sparseness of the data with little benefit to be gained by the small change in increased resolution. The approximation was still efficient for values of $k$ below 4 since most of the means also were less than 4. Curves were fitted to the predicted frequency distributions using the Marquardt-Levenberg algorithm (Systat Software, Inc.-SigmaPlot, Richmond, CA) to give the best fit between the equation and the data. The algorithm seeks to minimize the sum of the squared differences between the observed and predicted values. The goodness of fit of the expected and actual frequencies was tested by Chi-Square. As $k$ approaches 0, the series becomes logarithmic, and as $k$ becomes larger, it becomes more like a Poisson series ($s^2 = \bar{x}$). The negative binomial distribution is asymmetrical when $k$ is small, notably for a distribution with large number of zeros, but approaches normality when $k$ increases and the mean is reasonably large.

The speed of the VPR through the water was 120 cm s$^{-1}$ horizontally and 3.33 cm s$^{-1}$ vertically. Therefore, processing at 30 frames s$^{-1}$, the VPR has traveled 4 cm horizontally and 1.11 cm vertically for each 2.1 cm frame. Thus, the 10-sec bin counts used for the negative binomial distribution were at a sampling scale of 12 m horizontally and 33 cm vertically, with a total imaging volume of 170 mL. In May 1999, the high magnification camera had a depth of field of 1.5 cm resulting in a 10-sec imaging volume of 101.3 mL.
During May 1997, the environmental data showed a progression from mixed to stratified water (50–90 m bottom depth) for the four stations across the southwestern flank of Georges Bank (Fig. 3). At mixed Station 182, the temperature, salinity, and fluorescence values were uniformly about 7.7°C, 32.2 psu, and 0.7–0.8 volts. At the deeper stations, a thermocline had formed in the upper 20 m with colder (5–6°C), more saline water below. The increased temperature and salinity below 60 m at Station 183 was due to a shelf/slope-front intrusion. A relatively high fluorescence peak (1.2–1.4 v) was located at the stratified Stations 180 and 181 between 10–20 m depth. The deepest Station 183 had the lowest fluorescence values (<0.6 v). The VPR profiles indicated the fluorescence peak to be mostly due to the colonial diatom Chaetoceros socialis. This species had been previously observed by Sieracki et al. (1998) to reside within the pycnocline on the southern flank of Georges Bank in May/June. The copepodite stages of Calanus, Oithona, and Pseudocalanus were most abundant at the stratified stations in the upper part of the water column centered on the thermocline or peak fluorescence depth. Calanus and Oithona were mostly absent from the mixed water; however, Pseudocalanus was widespread. Calanus mostly occurred in the upper 20 m of the water column at stratified stations. The copepod densities were comparable to net-tow samples and peak values were in the range of 2,000–3,000 m$^{-3}$. There was considerable variability in numbers between adjacent meter bins, as much as an order of magnitude, especially in the upper part of the water column. The copepod nauplii were widespread but most abundant at the stratified stations in the surface 20 m with peak values of 2,000 – 3,000 m$^{-3}$.

The negative binomial fit to the number of nauplii and copepods in 10-second bins is shown for 10-m depth intervals in Figs. 4 & 5. The curves fit to the frequency distributions were generally reasonable but not necessarily highly significant in most cases due to the

![Image](https://academic.oup.com/plankt/article-abstract/29/1/7/2963062/148)
few data points and degrees of freedom. The negative binomial distributions are asymmetrical when \( k \) is small (<2.5) and the means are small. Low means can have a large number of zeros. The distribution of nauplii across transect generally varied from random to contagion. In a number of cases negative \( k \) values were estimated, indicative of a regular distribution (\( s^2 < \bar{x} \)) that may be more appropriately fit by a positive binomial. Most of the strata analyzed had low means and asymmetrical distributions regardless of the \( k \) values. The most symmetrical, Poisson-like distributions occurred with high means and high \( k \) values such as in the upper 30 m at the stratified Station 183 and surface 10 m at Station 181. To compare and contrast the copepodites, which have better swimming capability than the nauplii, the mixed Station 182 had similar asymmetrical distributions at all depths. However, there were more cases of symmetrical, Poisson-like copepod distributions at the stratified stations in the upper 20 m, particularly at high \( k \) and mean values.

During May 1999, the sampling stations were located within the excursion range of the tidal front (55–65 m bottom depth) so that the environmental parameters could change markedly at a station depending on the phase of the semi-diurnal tidal cycle. The three station profiles were characterized as Mixed (95), Frontal (100), and Stratified water column (106) based on the degree of stratification in the upper 20 m (Fig. 6). Mixed Station 95 had a uniform water-column of 7.8°C and 32.7 psu. Fluorescence was low at the surface (0.3 v), increased with depth to 0.5–0.6 v from 10 m to bottom. At Frontal Station 100, temperature was 10.5°C at the surface decreasing to 7°C at 10 m above bottom. Fluorescence had a peak value (0.42 v) at about 5 m and then decreased with depth to the bottom (0.22 v). At Stratified Station 106, the surface temperature was 10.8°C at the surface and decreased to 6.9°C at about 15 m. There was a slight freshening of the surface salinity above 15 m further sharpening the base of the pycnocline. A fluorescence peak (0.5 v) of a few meters
thickness was located just above the base of the thermocline at about 13 m. The VPR profiles indicated the fluorescence peak to be associated with the dinoflagellate *Ceratium* spp. *Calanus* were found mostly in the upper 20 m at the frontal and stratified stations, but with a pronounced low in the vicinity of the fluorescence peak. Abundance in adjacent meter-layers could range from 0–5,000 m$^{-3}$. The pronounced low in *Calanus* abundance where the peak abundance in the dinoflagellate *Ceratium* occurred at 13 m in May 1999 is probably
related to the fact that it rarely eats Ceratium based on gut contents (Esterly, 1916) and rearing experiments (Harvey, 1937). Abundance of Oithona and Pseudocalanus was <1,000 m⁻³ but these copepods were more wide spread through the water column. Nauplii were most abundant at Frontal Station 100 in the surface 20 m with values of 1,000–3,000 m⁻³. One depth, 12 m, had 10,000 nauplii m⁻³. Phytoplankton counts from the VPR followed the general pattern of fluorescence.

The negative binomial fit to the number of nauplii and copepods in 10-second bins is shown for 10-m depth intervals in Figs. 7 & 8. Most of the negative

Fig. 7. Frequency distributions of copepod nauplii from 10-sec bins by 10-m depth strata from three VPR profiles across the southeastern tidal front of Georges Bank, from mixed to stratified water during May 13–19, 1999. A predicted negative binomial curve is fit to each distribution and the $k$ and $\bar{x}$ values designated. Chi-Square goodness of fit is designated by a star (*) for $p < 0.05$. 

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Binomial distributions were asymmetrical for nauplii due to low means (<3.0) and low k values, indicating a contagious distribution for nauplii regardless of the water column structure. The most Poisson-like distributions of nauplii were at Frontal Station 100. The Copepods curve fits also were asymmetrical mostly due to the low means. Again, there were a number of negative k values without any apparent pattern. A further breakdown by 5-m depth intervals did not improve the negative binomial curve fits for these taxa.

For modeling purposes we would like to be able to specify the contagion parameter as a partial function of the local turbulence. However, the degree of water column mixing vs. stratification could not be estimated.

**Fig. 8.** Frequency distributions of copepodes (except Calanus) from 10-sec bins by 10-m depth strata from three VPR profiles across the southeastern tidal front of Georges Bank, from mixed to stratified water during May 13–19, 1999. A predicted negative binomial curve is fit to each distribution and the k and \( \bar{x} \) values designated. Chi-Square goodness of fit is designated by a star (*) for \( p < 0.05 \).
for the VPR profiles with such parameters as the specific turbulent dissipation rates, or the Richardson number used by Gallager et al. (2004), due to the lack of a specific shear flow measurement. Turbulence values are generally lowest near the pycnocline ($10^{-8}$ to $10^{-7}$ W kg$^{-1}$), higher near the surface due to wind mixing ($10^{-7}$ to $10^{-6}$ W kg$^{-1}$), and higher towards bottom due to tidal stirring ($10^{-5}$ to $10^{-4}$ W kg$^{-1}$) (Werner et al. 1996; Aretxabaleta et al., 2005; Lough et al., 2005). In the present study, the meter-scale vertical distributions of taxa suggest thin-layer aggregations of plankton varying by as much as an order of magnitude in abundance, especially in the thermoline region. Thin layers generally are on the order of 10’s of centimeters to several meters in thickness vertically and are closely associated with the depth and strength of the pycnocline (Dekshenieks et al., 2001; McManus et al., 2003; Gallager et al., 2004). Formation of specific plankton layers is a function of vertical structure of the water column and plankton behavior and swimming speed (Gallager et al., 2004; Genin et al., 2005).

An important finding in this study is that the most Poisson-like distributions of taxa occurred in the thermoline region where densities were highest. Below the thermoline and where plankton densities were low, their distributions were patchy. This evidence is consistent with the Optical Plankton Counter (OPC) transects of Currie et al. (1998), where zooplankton was patchy at the meter scale, but within patches distributions were random. The implications are that different patch models need to be used for different patchy environments, such as the point-process mixed-Poisson model and the random closed sets model suggested by Rothschild (1992). The perception distance for detecting prey is approximately one body length of a larval cod (Hunt von Herbing and Gallager, 2000), comparable to the single frame view of the high magnification cameras used in this study. It remains to be explored whether the VPR images can be used directly in a simple encounter rate binary model of Prey-No Prey.

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REFERENCES


