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Video Plankton Recorder estimates of copepod, pteropod and larvacean distributions from a stratified region of Georges Bank with comparative measurements from a MOCNESS sampler

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Abstract—A two-vessel exercise was conducted over the southern flank of Georges Bank during the onset of vernal stratification in May 1992. The Video Plankton Recorder (VPR), a towed video system, was used to map out the fine-scale distributions of zooplankton to a depth of 70 m along a trackline which described a regular grid (3.5 × 4.5 km) in Lagrangian space. A second vessel following a parallel course conducted Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) sampling during the last section of the grid, which provided an opportunity to compare data from the two systems. Both the VPR and the MOCNESS provided similar data on the taxonomic composition of the plankton which was numerically dominated by copepods (*Calanus*, *Pseudocalanus*, *Oithona*), pteropods (*Limacina*) and larvaceans (*Oikopleura*). The absence of rare ($<43.1\ m^{-3}$) species from the VPR dataset was a consequence of the small volume sampled ($0.0694\ m^3$) by the high magnification camera, while fragile gelatinous taxa were undersampled by the MOCNESS. Estimates of copepod and pteropod concentrations were comparable for the two gear types. While the species composition of the plankton did not change statistically along the grid, abundances of the dominant taxa varied along the transect and each taxon demonstrated pronounced fine-scale vertical patterns that appeared to be related to hydrographic features. The VPR represents a powerful tool for rapid surveys of the micro- to fine-scale structure of zooplankton assemblages either alone, or in conjunction with other sampling techniques. Copyright © 1996 Elsevier Science Ltd

INTRODUCTION

The patch structure of pelagic macrozooplankton populations reflects heterogeneity in their physical, chemical, and biological environments on scales ranging from millimeters to hundreds of meters (Mackas *et al.*, 1985; Davis *et al.*, 1992a; Donaghay *et al.*, 1992). High-resolution samplers have demonstrated that physico-chemical parameters exhibit substantial fine-scale (1–1000 m, Haury *et al.*, 1978) variability which is correlated with the distributions of planktonic larvae (Donaghay *et al.*, 1992). Many authors (e.g. GLOBEC, 1979; Marine Zooplankton Colloquium 1, 1989; Davis *et al.*, 1992b; Donaghay *et al.*, 1992; Kils, 1992; Schulze *et al.*, 1992) have pointed out the need for direct measurement of physical, chemical, and biological distributions on ecologically meaningful scales. However, limitations of conventional samplers (e.g. nets, pumps) have

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precluded sampling at resolutions finer than 10 m horizontally or 5 m vertically (Davis *et al.*, 1992a). Multiple net systems such as MOCNESS (Wiebe *et al.*, 1976, 1985), BIONESS (Sameoto *et al.*, 1980) and the Bé "multi-net" (Weikert and John, 1981), and the discrete sampling LHPR (Longhurst *et al.*, 1966; Longhurst and Williams, 1976) are an improvement over conventional nets because they permit relatively short discrete tows, but these systems may still obscure fine-scale structure. Recent developments in video imaging systems (Froese *et al.*, 1990; Gorsky *et al.*, 1992; Schulze *et al.*, 1992) provide the potential to continuously record zooplankton distributions over small spatial scales. For example, the Video Plankton Recorder (VPR) is a towed system capable of recording high-resolution video images of zooplankton on scales ranging from micrometers to kilometers (Davis *et al.*, 1992a). This system has been used to quantify microscale zooplankton patch structure in shelf and Slope Water near Georges Bank (Davis *et al.*, 1992b). It is not always possible to identify organisms imaged with video to the species level. During missions that require corroborative species data or physical samples of plankton, the VPR is optimally employed in conjunction with systems such as the MOCNESS, which capture a sample of the zooplankton assemblage for subsequent "ground-truthing".

The objectives of this study were: (i) to obtain data on the distribution of zooplankton in relation to hydrography during the onset of spring stratification, and (ii) to intercalibrate measurements of zooplankton distributions in relation to hydrography obtained using the newly developed VPR with data from the established MOCNESS sampling system. A two-vessel sampling exercise, conducted during the onset of vernal stratification over Georges Bank, provided an opportunity to deploy both the VPR and MOCNESS. This paper examines the horizontal and vertical distributions and species composition data generated by the VPR and contrasts data generated by the two methods for a subsection of the transect where the MOCNESS was concurrently deployed.

METHODS

Samples were collected during the pilot GLOBEC cruises of R.V. *Endeavor* 237 and R.V. *Albatross* IV 92–05. Fine-scale sampling of an approximately 15.75 km^2 area was undertaken during daytime(12:50–16:30 h) operations on 24 May in a stratified region of Georges Bank (Fig. 1). R.V. *Albatross IV* steamed along six 1.85 km tracklines separated by 370 m while R.V. *Endeavor* simultaneously ran parallel tracklines offset by 180 m. In order to compensate for advection of the parcel of water by the strong tidal currents (often $> 0.5\ m\ s^{-1}$), all the geographic tracklines of both vessels were taken in relation to a free-drifting drogue (highflyer with radar reflector and light connected to a 15 m long holey sock drogue tethered at 15 m depth) so that their Lagrangian track approximated a regular grid (Fig. 1). The VPR was towed from the *Endeavor* while a 1 m^2 MOCNESS was deployed from the *Albatross IV* (Fig. 1) which was also towing a downlooking 420 kHz acoustic transducer on a V-fin body (see Wiebe *et al.*, 1996).

The VPR was similar to the system described in Davis *et al.* (1992a) and equipped with four CCD cameras that imaged volumes ranging from 147 ml to less than 1 ml (Fig. 2). Our data were obtained using the highest magnification (camera 4), which imaged a volume of 0.62 ml (6.0 mm wide × 4.5 mm high × 23 mm deep). The high magnification camera is designed for quantifying distributions of small ≤2 mm, abundant ($> 500\ m^3$) organisms, while the low magnification cameras are designed for larger, rarer taxa (Davis *et al.*, 1992b). The environmental sensor package mounted on the VPR provided data on

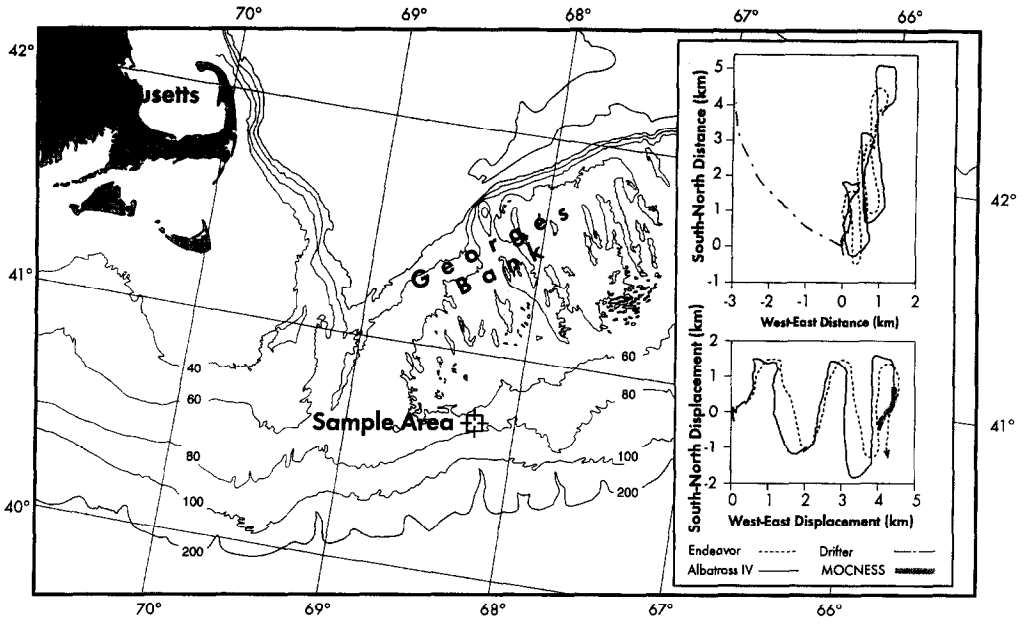

Fig. 1. Location of the sampling area on the southern flank of Georges Bank. The upper overlay panel illustrates the geographic tracklines of R.V. *Endeavor* and R.V. *Albatross IV* in relation to a drifter which was released at the onset of the grid. Each ship steamed a six leg grid from west to east in relation to the drifter. When the advection of the drifter was subtracted from the displacement of each ship, the Lagrangian displacement of the vessels describes a more regular grid (lower panel). The location of MOCNESS haul 990 is superimposed over the trackline of R.V. *Albatross IV*.

temperature, conductivity, pressure, fluorescence, light transmittance, and flow past the VPR (Fig. 2).

The vertical path of the system in the water described a series of saw-teeth (tow-yos) between the surface and near-bottom strata (Fig. 3). VPR images were recorded on SONY BETACAM-SP videotape and subsequently examined field-by-field with a SONY BVW-75 editing system. A video overlay card was used in conjunction with a MATLAB (The Mathworks Inc) routine developed to measure the widths of the video targets in frames of interest. This routine recorded the taxonomic identities, sizes, comments, and video timecode for each target on a data file. We determined the precise position of any organism along the transect by synchronizing the video timecode with the time and depth data recorded by the VPR. A custom MATLAB binning routine placed individual targets into temporally sequential 1 m depth bins. The number of individuals of dominant taxa recorded by the VPR were averaged across 1 m depth bins for each leg of the transect to evaluate changes in horizontal and vertical distributions within the water parcel. Size-frequencies based on animal width were calculated for dominant taxa during leg 6 of the grid. Width was used rather than length because the former parameter was least influenced by animal orientation in three-dimensional space. Salinity, temperature, and fluorescence data were gridded and contoured (Surfer for Windows, Golden Software) using a kriging algorithm with an anisotropy ratio that accounted for the strong vertical structure in this stratified region of the bank.

The MOCNESS (Wiebe *et al.*, 1985) was equipped with nine 1-m^2 335 μm nets, which on

tow 990 during leg 6 of the transect were triggered at 10 m intervals from 70 m to the surface (Fig. 3). This study uses data from the samples collected from nets 3–7 that obliquely sampled 10 m intervals from 50 m to the surface. Environmental sensors on the MOCNESS recorded conductivity and temperature. Samples were preserved in buffered 5% formalin and silhouette photographs (Ortner *et al.*, 1979, 1981) were taken of subsamples from Folsom plankton splits (net 3: 1/16, net 4–5: 1/32, net 6–7: 1/64). Taxonomic identities and size-frequency data were measured directly from the photographic negatives (Davis and Wiebe, 1985), and abundances were estimated from subsample data.

All comparisons among the video and net sampling systems were based on the leg 6 VPR tow-yos that coincided with the MOCNESS tow (27 down to 32 up, Fig. 3). Comparisons among the MOCNESS and VPR required modifications to both datasets. For example, the taxonomic categories used for analysis of the MOCNESS data did not distinguish among copepod taxa and a comparative VPR taxonomic category was created by pooling copepod genera to match the MOCNESS classifications. Unidentified organisms were excluded from comparisons of taxonomic composition.

The VPR size-frequency data were converted from widths to lengths in order to generate data that were directly comparable with the MOCNESS samples. Both lengths (L) and widths (W) digitized from a section of VPR tape were used to estimate the relationships between these two parameters for *Calanus* ($L=2.1869W^{0.7993}$), *Pseudocalanus* ($L=0.9931W^{0.3464}$), *Centropages* ($L=1.6567W^{0.6454}$) and *Oithona* ($L=0.3256W^{0.3971}$). Unidentified copepods that were smaller than the upper 95% confidence interval on mean *Oithona* width (0.231 mm) in leg 6 were assumed to be *Oithona*. The lengths of the remaining unidentified copepods were estimated by applying a function derived from the pooled data from *Calanus*, *Pseudocalanus* and *Centropages* ($L=2.0791W+0.1597$). Direct size comparisons of the generally spherical *Limacina* pteropods were possible because the VPR usually imaged these organisms in orientations which permitted measurement of their maximum diameter. Comparisons of the sizes of *Oikopleura*-type larvaceans were not possible because of fundamental differences in the way they were measured in the two systems. Measurements of larvaceans from silhouette photographs of MOCNESS samples encompassed total length (tail with or without the head). The heads of most preserved specimens had been detached during collection by the MOCNESS or during subsequent sample processing. Larvaceans were counted in VPR frames when the head was visible. However, the entire tail was seldom contained within a frame and its shape was usually too convoluted to estimate tail length.

RESULTS

Hydrographic conditions

A prominent thermocline in the upper 10 m of the water column (Fig. 4A) was indicative of vernal stratification. A general cooling trend extended from west to east which was manifested by an upward displacement of the thermocline and a shoaling in the depth of the 4.5°C and warmer isotherms. The deeper portion of the water column was occupied by more saline Georges Bank water, which was overlain by less saline (< 32.1‰) surface water (Fig. 4B). The latter may have been remnants of an intrusion by Scotian Shelf water during winter and early spring (Bisagni *et al.*, 1996). An eastward increase in the salinity of the upper 20 m zone was apparent (Fig. 4B).

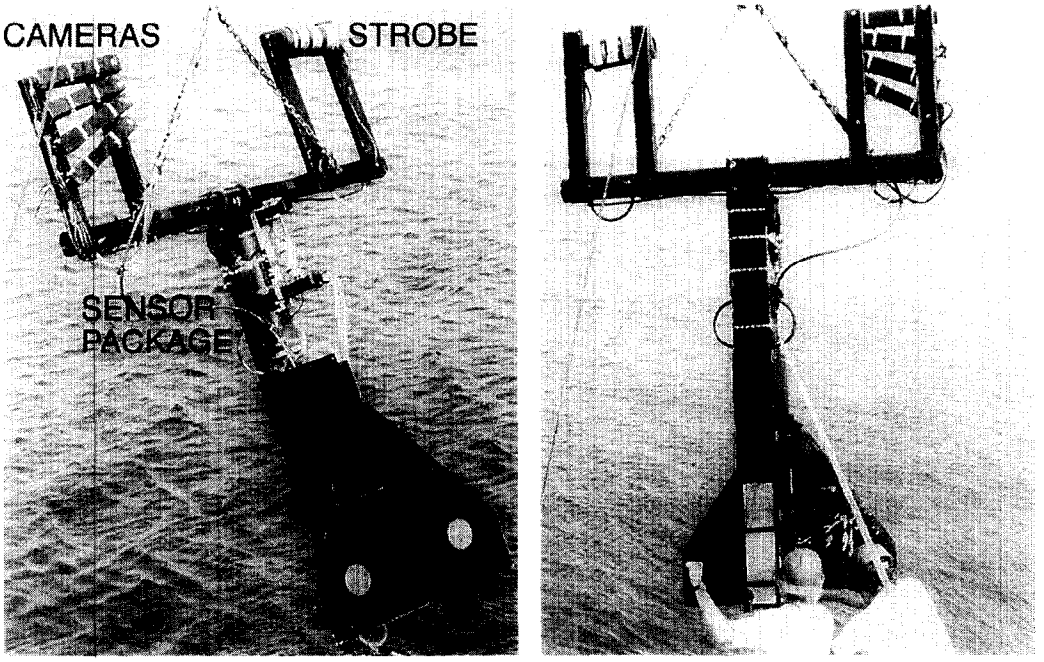

Fig. 2. Dorsal (left) and ventral (right) views of the Video Plankton Recorder prior to deployment. The system is configured similarly to that used in the present study and illustrates the four different focal length cameras imaging volumes from 0.6 to 147 ml, strobe, and sensor package consisting of a CTD, transmissometer, fluorometer and flowmeter.

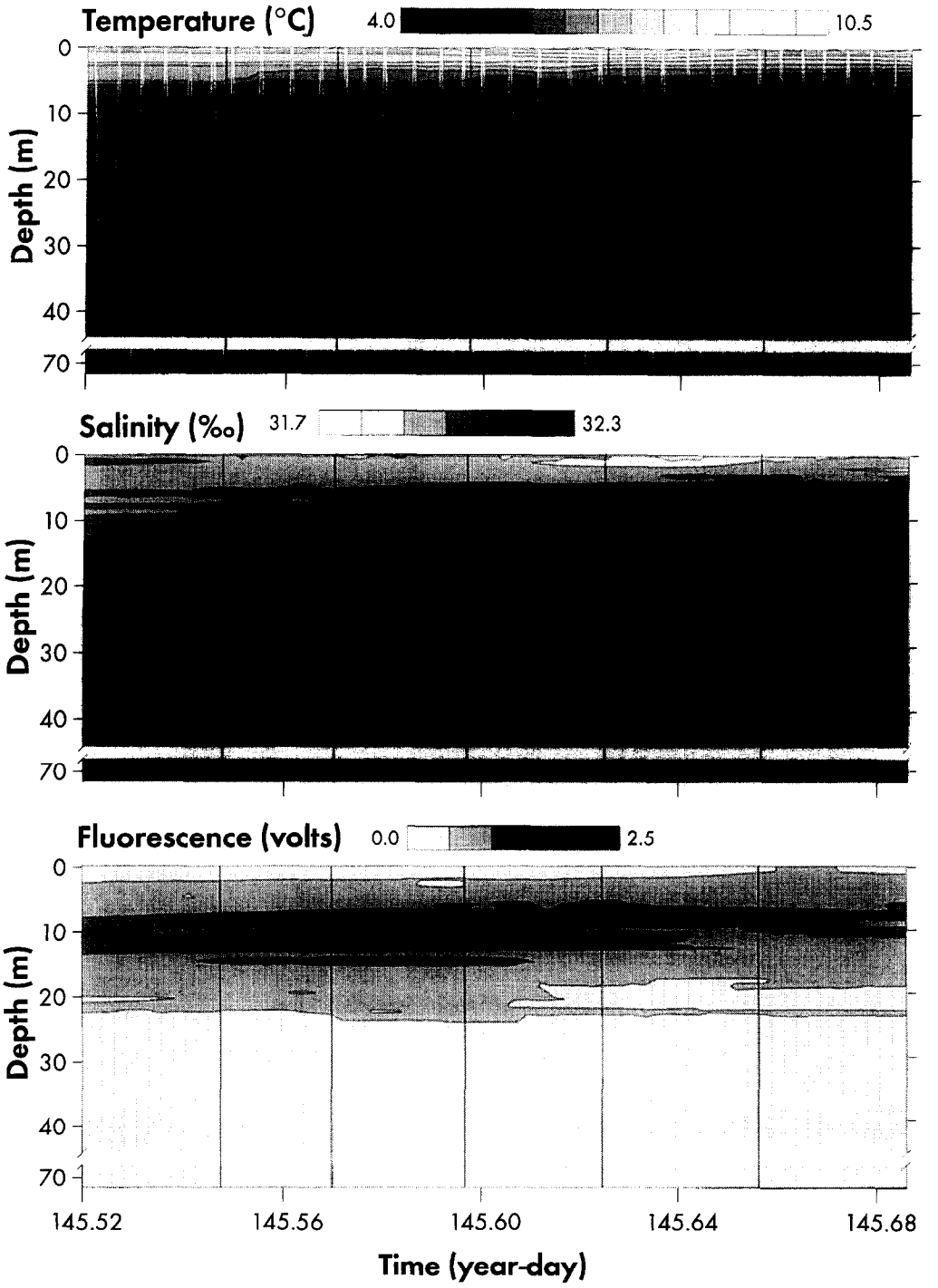

Fig. 4. Vertical temperature, salinity and fluorescence section obtained by contouring the data from on-board VPR sensors using an anisotropic kriging algorithm. Vertical lines delineate the six legs of the grid and the tow-yo path has been superimposed over the temperature plot. The depth axis has been broken below 45 m.

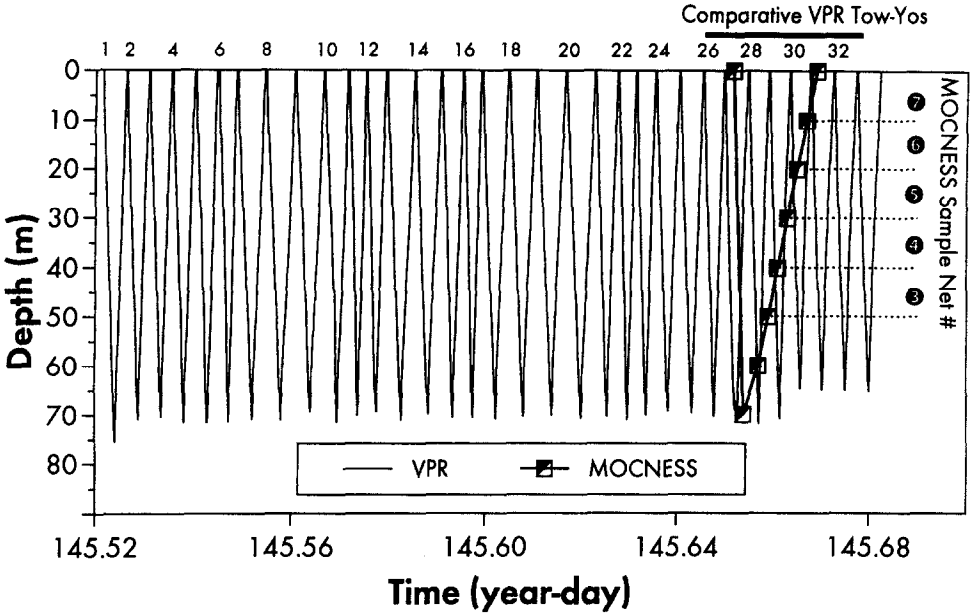

Fig. 3. Vertical tow-yo profile of the VPR in relation to the MOCNESS. Each tow-yo was sequentially numbered. The year-day time axis corresponds to a local time of 145.5 = 12:00 h.

Biological structure

A total of 5391 organisms were detected in the total volume of water sampled (549 l) with the VPR along the tow-yo trackline. This figure is exclusive of 522 copepod nauplii that were counted for some sections of the grid including the region coincident with the MOCNESS tow. Unidentified organisms comprised 4.5% of the total. Copepods, pteropods, and larvaceans numerically dominated (92.33%) the zooplankton assemblage (Table 1). Copepods alone comprised 74.33% of the targets, which were primarily *Oithona* spp., *Pseudocalanus* spp., and *Calanus* spp., with scattered *Centropages* spp., *Metridia* spp., *Temora* spp. and other unidentified copepoda. *Oithona* spp. that was probably *O. similis* (Davis, 1987), was most abundant followed by *Pseudocalanus* spp. (probably *P. newmani* and *P. moultoni*), and *Calanus* spp. (primarily *C. finmarchicus*). A larvacean that resembled *Oikopleura dioica* comprised 9.56% of sampled targets. Pteropods made up 8.44% of the targets and appeared to be *Limacina retroversa*, a thecosomate species that is a year-round inhabitant of the Bank (Redfield, 1939). It was not surprising that delicate gelatinous and soft-bodied organisms susceptible to shredding in nets (larvaceans, medusae, ctenophores and echinoderm larvae) were evident throughout the VPR dataset. The species composition of the six cruise legs appeared similar, and this was reflected in the high percentage similarities (> 80%) in all but one comparison (77%). A heterogeneity *G*-test (Sokal and Rohlf, 1981) was performed to evaluate the null hypothesis that the proportions of taxa in each leg were drawn from the same population. Numbers of animals from each taxonomic category in each leg were converted to percentages of the leg totals after adding 0.00001 to each category because the *G*-test employs natural logarithms and cannot handle zero values. The outcome of the test indicated that the relative proportions of taxa did not change significantly among the six grid legs ($G_n = 31.7264$, 75 degrees of freedom, $p > 0.995$).

Table 1. *Numbers of individuals imaged during each leg of the grid by the VPR. Parenthetical numbers indicate the percentage contribution by each taxon to leg total*

Taxonomic Group	Leg 1	Leg 2	Leg 3	Leg 4	Leg 5	Leg 6	Total
Oithona spp.	274 (19.99)	142 (18.88)	269 (21.76)	200 (23.09)	212 (27.57)	118 (29.72)	1215 (22.54)
Pseudocalanus spp.	285 (20.79)	140 (18.62)	307 (24.84)	173 (19.98)	160 (20.81)	91 (22.92)	1156 (21.50)
Calanus spp.	242 (17.65)	147 (19.55)	210 (16.99)	95 (10.97)	95 (12.35)	42 (10.58)	831 (15.41)
Unidentified copepods	156 (11.38)	116 (15.43)	152 (12.30)	131 (15.13)	90 (11.70)	26 (6.55)	671 (12.45)
Larvaceans (*Oikopleura* spp.)	113 (8.24)	77 (10.24)	127 (10.28)	94 (10.85)	73 (9.49)	28 (7.05)	512 (9.56)
Pteropods (*Limacina* spp.)	131 (9.56)	61 (8.11)	89 (7.20)	75 (8.66)	46 (5.98)	50 (12.59)	452 (8.44)
Unidentified	74 (5.40)	33 (4.39)	49 (3.96)	48 (5.54)	26 (3.38)	13 (3.27)	243 (4.51)
Other calanoid copepods	39 (2.84)	14 (1.86)	15 (1.21)	21 (2.42)	33 (4.29)	8 (2.02)	130 (2.43)
Echinoderm larvae	24 (1.75)	13 (1.73)	6 (0.49)	12 (1.39)	8 (1.04)	10 (2.52)	73 (1.36)
Ctenophores	18 (1.31)	5 (0.66)	5 (0.40)	5 (0.58)	15 (1.95)	6 (1.51)	54 (1.01)
Medusae	6 (0.44)	1 (0.13)	4 (0.32)	5 (0.58)	3 (0.39)	3 (0.76)	22 (0.41)
Polychaetes	7 (0.51)	1 (0.13)	0 (0.00)	2 (0.23)	4 (0.52)	0 (0.00)	14 (0.26)
Amphipods	1 (0.07)	1 (0.13)	3 (0.24)	0 (0.00)	0 (0.00)	2 (0.50)	7 (0.13)
Euphausiids	0 (0.00)	0 (0.00)	0 (0.00)	3 (0.35)	2 (0.26)	0 (0.00)	5 (0.09)
Hydrozoan polyps	0 (0.00)	0 (0.00)	0 (0.00)	2 (0.23)	2 (0.26)	0 (0.00)	4 (0.07)
Phoronid larvae	1 (0.07)	1 (0.13)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	2 (0.04)
	1371	752	1236	866	769	397	5391

The abundances of major taxa appeared to vary among legs. Collectively, copepod concentrations appeared to be highest in legs 1 and 3, intermediate in legs 2, 4, and 5, and lowest in leg 6 (Table 1, Fig. 5A). Copepods occupied all strata sampled; however, the highest concentrations (75% of all individuals) occurred in the upper 38 m of the water column with maxima between 2 and 5 m (Fig. 5A). The pooled "copepod" distributions masked pronounced differences in the vertical and horizontal distributions of the individual copepod taxa represented in the VPR dataset. *Calanus* were most abundant in the western half of the grid (legs 1–3) between 1 and 15 m, with vertical maxima occurring at approximately 7–9 m and sporadically distributed individuals from 15 m to the lower limits of the tow-yos (Fig. 5B). The abundance of *Pseudocalanus* was highest in legs 1 and 3 (Fig. 5C) and displayed a vertical distribution in which numbers were greatest in the surface waters. However, the zone of maximum *Pseudocalanus* abundance differed from that of *Calanus* in that it was broader and less well defined, extending from 1–25 m with bimodal local maxima at approximately 1–3 m and 10–15 m (Fig. 5C). These were distinct from the maximal concentration of *Calanus*. These copepods were also more abundant than *Calanus* below 25 m. The biomodality appeared to be due, in part, to the predominance of egg-bearing individuals between 5 and 18 m and non-egg-bearing *Pseudocalanus* in the upper 5 m of the water column. The distributions of both genera were coincident with a subsurface region of high fluorescence (Fig. 4C). The distribution of the most abundant copepod, *Oithona*, was similar among legs (Fig. 5D). *Oithona* also exhibited the most uniform vertical distribution, with some evidence of maximal concentrations between 15 and 35 m and a distinct minimum between 4 and 8 m (Fig. 5D). This minimum was evident in the distributions of both egg-bearing and non-egg-bearing individuals. *Oithona*'s vertical distribution was not obviously correlated with salinity, temperature, or the subsurface fluorescence maximum. Copepod nauplii were consistently noted during the last four legs (Fig. 6A), with maximal concentrations between 10 and 20 m. Their greatest abundance was coincident with the lower portion of the pycnocline and lower region of the subsurface fluorescence feature (Fig. 4).

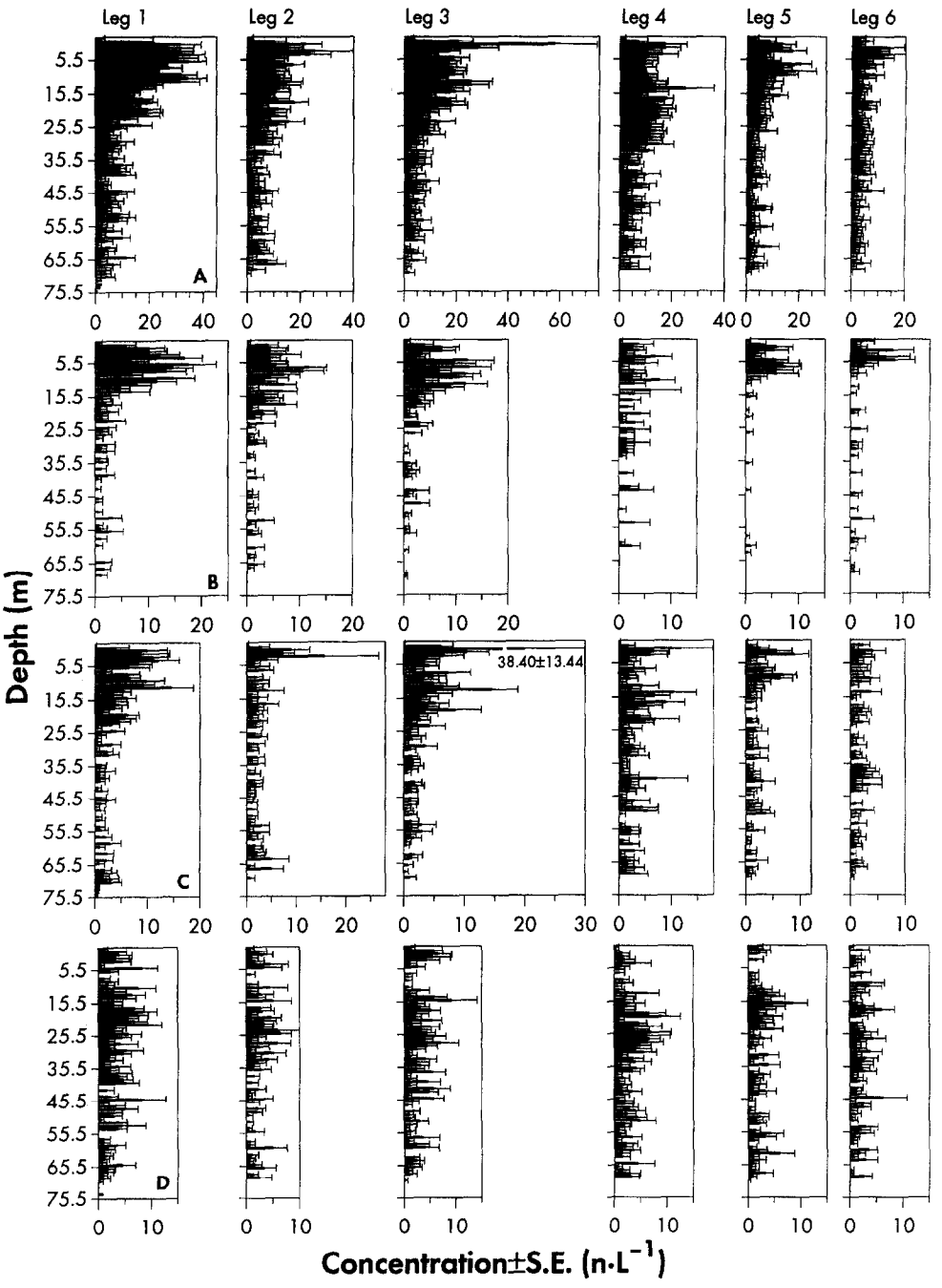

Fig. 5. Fine-scale vertical distributions of zooplankton measured by the VPR: (A) all copepods; (B) *Calanus*; (C) *Pseudocalanus*; and (D) *Oithona* for each leg of the grid. Mean distributions ± S.E. averaged from binned concentration estimates at each depth from all up and down tow-yos within each leg.

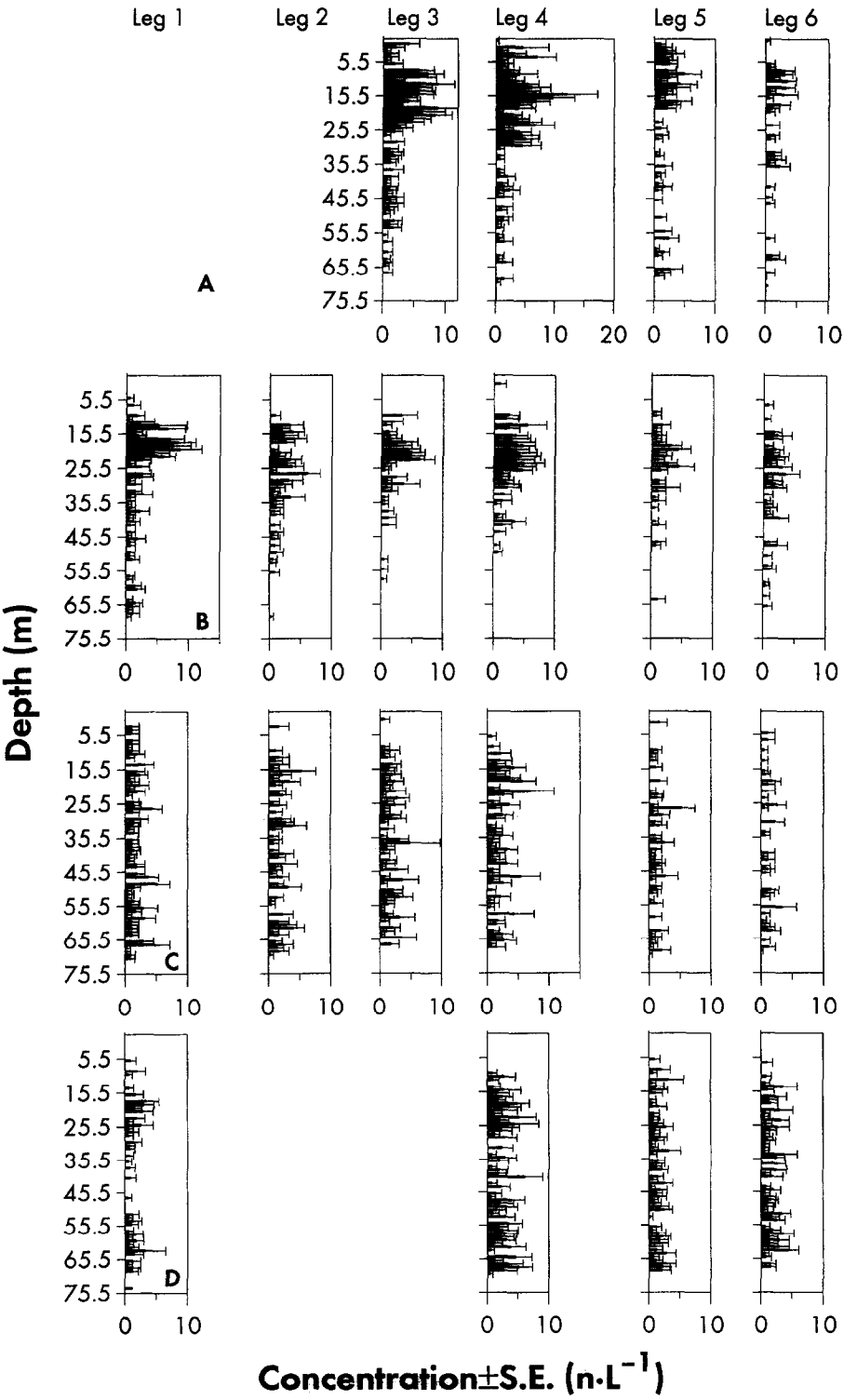
Leg 1
Leg 2
Leg 3
Leg 4
Leg 5
Leg 6
A
B
C
D
Depth (m)
5.5
15.5
25.5
35.5
45.5
55.5
65.5
75.5
0
10
20
Concentration±S.E. (n·L⁻¹)

Fig. 6.

Pteropod abundances peaked in legs 1 and 4 and were generally lowest in the two most easterly legs (Fig. 6B). *Limacina* occupied a distinct depth zone between 10 and 25 m (Fig. 6B) and were largely absent above the thermocline and below the 4°C isotherm. The pteropod distribution appeared to be associated with, but slightly below, a chlorophyll maximum that occurred from approximately 8–15 m (Fig. 4C). The highest fluorescence recorded over the entire grid coincided with elevated pteropod concentrations in leg 4 (Fig. 4C and 6B).

Larvaceans were most abundant in the first four legs (Fig. 6C). While generally absent above the thermocline, their distribution below 10 m was fairly uniform (Fig. 6C). Almost all larvaceans were observed within well-defined house structures, which exhibited varying degrees of clogging. The vertical distributions of abandoned houses generally corresponded to the distribution of live larvaceans (Fig. 6D), although data on abandoned houses were not consistently collected for abandoned houses in legs 2 and 3.

While the detailed comparison of the VPR and acoustic data will be examined in a subsequent paper, the volume backscatter (S_v) data collected along the transect indicated that most reverberation was being produced by targets between 10 and 40 m (refer to Wiebe *et al.*, 1996). Several patches of intense volume backscatter (> -58 S_v) were present within the 15–35 m isopleths. The volume backscatter appeared to decline slightly from west to east, supporting our VPR observation that abundance appeared to decline in the same direction.

VPR–MOCNESS comparisons

Both the VPR and MOCNESS provided similar data on zooplankton taxonomic composition. The vertically integrated data for leg 6 of the VPR and MOCNESS 990 were similar (Table 2). A heterogeneity *G*-test failed to reject the null hypothesis that the distributions were drawn from the same population ($G_n = 10.38$, 14 degrees of freedom, $0.5 < p < 0.9$). Nine groups of animals (crustacean larvae, chaetognaths, bryozoan cyphonautes larvae, decapods, euphausiids, fish, fish eggs, ostracods, and polychaetes) were represented in the MOCNESS tow, but were not detected by the VPR in leg 6 using camera 4. All of these groups were uncommon, collectively comprising only 0.32% of the MOCNESS numerical catch. Conversely, delicate and/or small species such as larvaceans, medusae, ctenophores, copepod nauplii and echinoderm larvae were absent or sparsely represented in the net samples.

Some taxa were clearly present in the leg 6 region, yet were not detected by the VPR (Table 2). These differences appear to be a consequence of the considerably larger volume of water sampled by the MOCNESS (mean = 149 m^3 per net) relative to the VPR (0.0694 m^3). The probability of not detecting a taxon known to be present can be estimated using the first term of a Poisson series: $p(n=0) = e^{-\lambda v}$, where λ is the concentration of the taxon and v is the volume sampled by the VPR. Both v and $p(n=0)$ can be specified allowing a solution for λ. By setting the probability for non-detection at a low value ($p = 0.05$), the corresponding

Fig. 6. Fine-scale vertical distributions of zooplankton measured by the VPR: (A) copepod nauplii; (B) *Limacina*-type pteropods; (C) *Oikopleura*-type larvaceans; and (D) abandoned larvacean houses. Gaps for the copepod nauplii and abandoned houses indicate legs where distributions were not consistently documented. Mean distributions ± S.E. from binned concentration estimates at each depth averaged across all up and down tow-yos within each leg.

Table 2. Comparative concentrations of zooplankton ($n\,m^{-3}$) estimated from VPR and MOCNESS samples at 10 m intervals during leg 6. The adjusted concentrations for copepods reflect the elimination of small copepods which were not retained by the MOCNESS from the VPR dataset

Depth interval	50–40 m		40–30 m		30–20 m		20–10 m		10–0 m		50–0 m	
Taxonomic category	MOC	VPR	MOC	VPR	MOC	VPR	MOC	VPR	MOC	VPR	MOC	VPR
Copepods	718.49	3576.33	1126.11	4898.95	1250.87	4324.25	3851.37	4883.61	1901.68	7713.63	1769.70	5079.36
Pteropods	302.31	596.34	543.34	857.24	292.30	1826.29	59.76	670.88	13.28	67.76	242.20	803.70
Larvaceans	50.61	540.43	44.22	372.71	26.27	596.34	9.07	428.62	0.44	203.30	26.12	428.28
Amphipods	14.95	0.00	4.87	0.00	13.46	0.00	16.48	74.57	14.61	0.00	12.87	14.91
Euphausiids	5.54	0.00	8.85	0.00	4.78	0.00	2.47	0.00	0.00	0.00	4.33	0.00
Decapod larvae	0.84	0.00	1.55	0.00	2.82	0.00	0.00	0.00	0.00	0.00	1.04	0.00
Chaetognaths	0.73	0.00	1.33	0.00	1.95	0.00	0.00	0.00	0.00	0.00	0.80	0.00
Echinoderm larvae	1.57	74.54	0.66	0.00	0.00	167.72	0.00	454.71	0.00	0.00	0.45	139.40
Cyphonautes	0.00	0.00	0.22	0.00	0.22	0.00	0.41	0.00	0.41	0.00	0.25	0.00
Medusae	0.00	0.00	0.00	0.00	0.43	0.00	0.00	55.91	0.00	101.65	0.09	31.51
Decapods	0.10	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00
Fish eggs	0.00	0.00	0.03	0.00	0.04	0.00	0.13	0.00	0.13	0.00	0.07	0.00
Ostracods	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00
Polychaetes	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00
Fish	0.06	0.00	0.06	0.00	0.05	0.00	0.02	0.00	0.00	0.00	0.04	0.00
Copepod nauplii	0.00	204.99	0.00	782.69	0.00	391.35	0.00	1528.13	0.00	715.78	0.00	724.59
VPR adjusted copepods	718.49	835.38	1126.11	1822.99	1250.87	1670.50	3851.37	1950.86	1901.68	4394.44	1769.70	2135.23

threshold concentration for detection is 43.1 organisms m^{-3} (Fig. 7). Organisms present at concentrations lower than 43.1 m^{-3} would have a higher probability of remaining undetected by the VPR (Fig. 7) even though the MOCNESS confirmed their presence. The taxa detected only by the MOCNESS occurred at concentrations that were considerably lower than the estimated detection threshold of 43.1 m^{-3} (Table 2, Fig. 7). The amphipod concentration estimate for the VPR was based on the presence of two individuals and is probably not reliable. Two groups (echinoderm larvae and medusae) were present in the MOCNESS samples at concentrations below the hypothetical threshold and were detected by the VPR, suggesting underestimation by the MOCNESS, which was probably due to shredding within the nets.

While both samplers provide similar estimates of the proportional contribution by taxa to total numerical catch in each depth zone (Fig. 8), the concentrations of dominant taxa estimated from the VPR consistently exceeded those of the MOCNESS (Table 2). The greatest discrepancies occurred among estimates for delicate organisms: echinoderm larvae (310×) and medusae (360×) and to a lesser degree, larvaceans (16.4×) (Table 2). Differences for these groups are most readily reconciled on the basis of their fragility. Few gelatinous taxa were retained in recognizable condition after passage through the plankton net and subsequent sample processing. The majority of larvaceans observed in silhouette photographs were mutilated specimens that generally were missing their head section and without mucous houses. Given their narrow cross-section, the net probably retained only a fraction of the larvaceans entrained in the net.

The vertically averaged (0–50 m) copepod concentration estimated by the VPR exceeded that of the MOCNESS by a factor of 2.9. Size frequency data suggest that the concentration discrepancy is due to a large proportion of small (< 300 μm prosome-length) individuals in

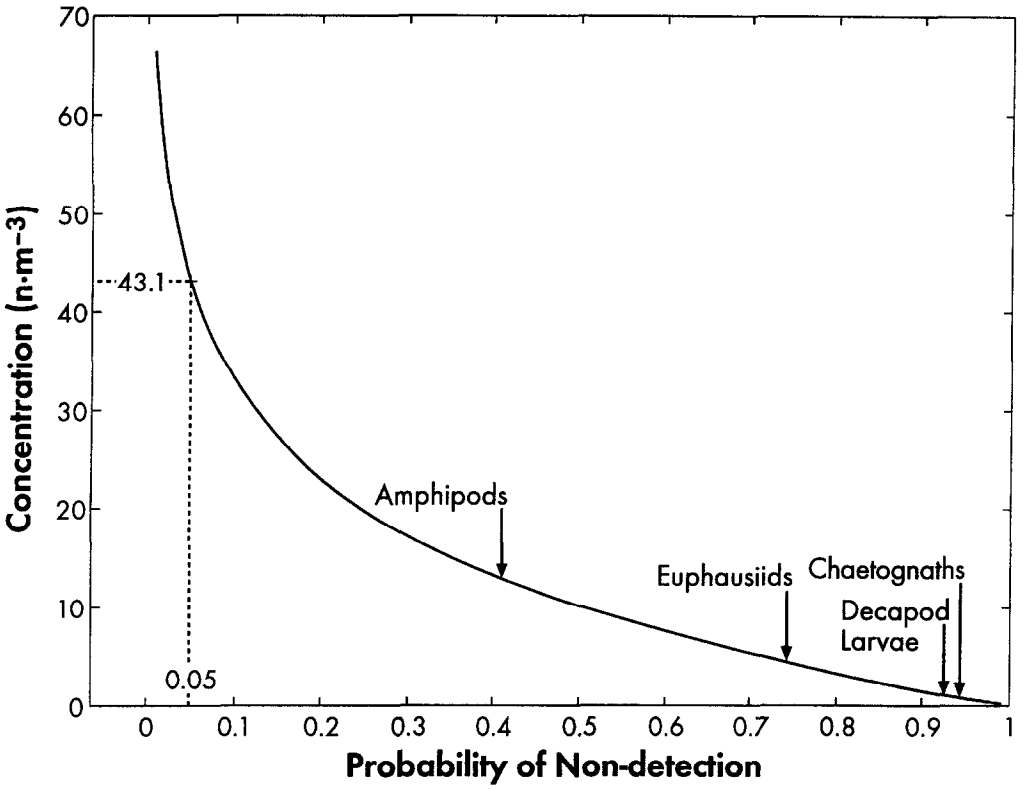

Fig. 7. The relationship between probability of non-detection and zooplankton concentration given the volume imaged by the VPR during leg 6. Taxa present at 43.1 m^{-3} have a 5% probability of non-detection. Amphipods were present in the MOCNESS but only 2 were detected by the VPR in leg 6, while euphausiids, decapod larvae, chaetognaths and other taxa present in the MOCNESS samples were absent from the VPR images. The arrows below these taxa indicate the probabilities of detection in the VPR based on their concentrations in the MOCNESS (see Table 2).

the VPR sample (Fig. 9A) that likely passed through the 335 μm mesh of the MOCNESS. When these small copepods, that were likely *Oithona*, were omitted from the VPR dataset, the vertically-averaged concentration estimates for copepods differed by only 1.2 (Table 2).

Pteropod concentrations were 3.3 × higher in the VPR dataset relative to the MOCNESS (Table 2). These differences could not be resolved in the same manner as the copepods. The size-frequency ranges measured by the two systems were comparable (Fig. 9B); however, the relative contributions by the three smallest size classes were lower in the MOCNESS. This may indicate that some of the smaller pteropods were forced through the net, but this is not a sufficiently large difference to account for the concentration differences among the two samplers. Differences among the concentration estimates from the two samplers for amphipods cannot be considered reliable owing to the presence of only two individuals in the VPR dataset.

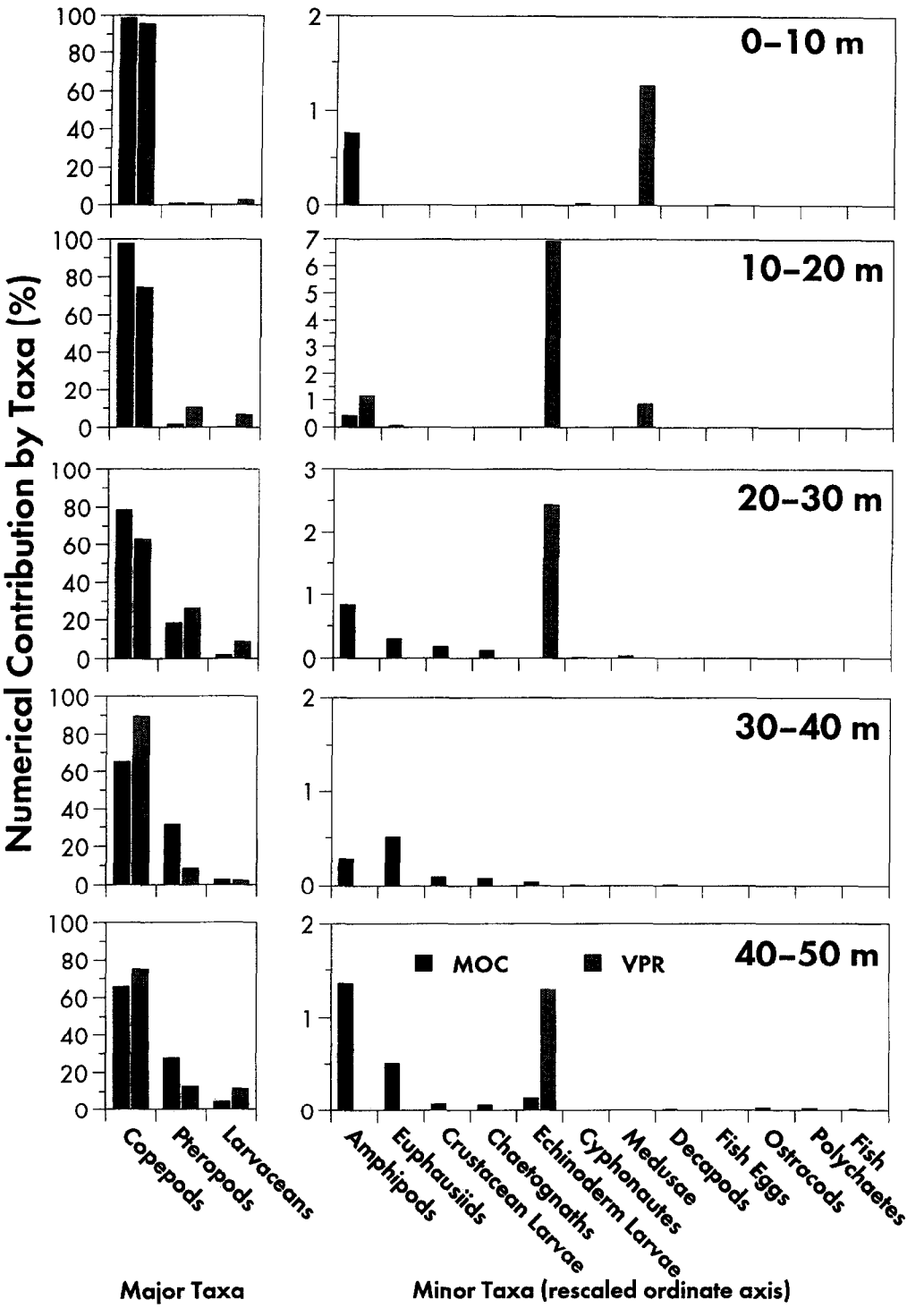
Numerical Contribution by Taxa (%)
0–10 m
10–20 m
20–30 m
30–40 m
40–50 m
MOC
VPR
Copepods
Pteropods
Larvaceans
Amphipods
Euphausiids
Crustacean Larvae
Chaetognaths
Echinoderm Larvae
Cyphonautes
Medusae
Decapods
Fish Eggs
Ostracods
Polychaetes
Fish
Major Taxa
Minor Taxa (rescaled ordinate axis)

Fig. 8.

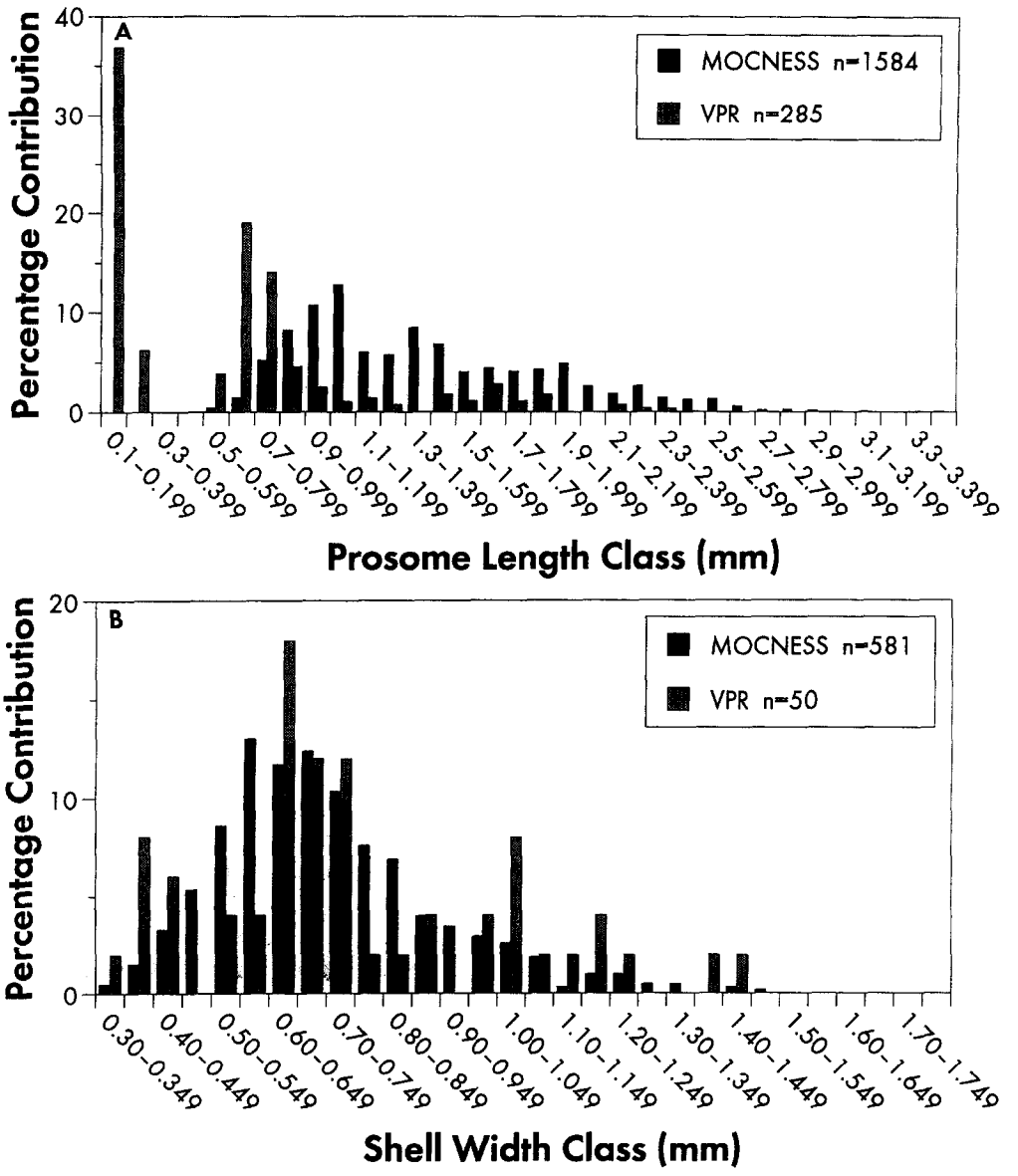

Fig. 9. Size–frequency data for zooplankton measured with the VPR: (A) copepods; and (B) pteropods, sampled by MOCNESS and VPR systems during leg 6. VPR estimates have been calculated from regression equations describing length and width.

Fig. 8. Species composition data expressed as a percentage contribution to total estimated for 10 m intervals from the MOCNESS and VPR during tows in leg 6. The ordinate axes have been rescaled to illustrate patterns for minor taxa.

DISCUSSION

Both the VPR and MOCNESS provide a picture of a zooplankton assemblage characterized by low species richness and dominated by copepods and pteropods. What is remarkable about the two datasets is their degree of congruence given the enormous disparity in their dynamic ranges. For example, camera 4 of the VPR sampled only 0.0694 m^3 during leg 6 while the five MOCNESS nets sampled an average $\pm$ S.E. of 149.2 $\pm$ 2.3 m^3 each. In spite of the substantial differences in volume sampled, both systems provided comparable estimates of the taxonomic composition of the plankton and the concentrations of copepods and pteropods. The VPR dataset reveals that fine-scale vertical distribution can be obtained from a very small sample volume; however, larger sample volumes are essential when data on rare or evasive taxa are required.

It is appropriate to evaluate the degree of correspondence between the two samplers in the context of the variation normally associated with replicate tows of a single net system. Substantial data on among-tow variance for a variety of taxa including copepods, euphausiids, larvaceans, and other taxa, summarized in Wiebe and Holland (1968) suggests that replicate casts frequently differ by 50–200% or more. More recent comparisons of the among-replicate variation in copepod and euphausiid concentrations for four different net types and a pump during eight replicate samples taken relative to a drogue (Pillar, 1984) indicated 95% confidences on the coefficient of variation of approximately 30–330. The degree of correspondence obtained by our two systems for copepods and pteropods is remarkable given the typical level of variation among replicate net tows. The overall 1:1.2 correspondence obtained for vertically integrated copepod concentrations after adjusting for size differentials is fortuitous, and probably due in part to chance, given that the samples collected by the two methods were not precisely spatially coincident (range for individual depth bins = 1:0.5–1:2.31). It is important to note that the VPR did not consistently yield higher copepod concentration estimates at each depth interval, which argues against the presence of some systematic bias in the video system. We also recognize that our comparisons are based on one set of VPR-MOCNESS tows which limits both our scope of inference and the statistical power of our tests.

Pteropods were a group for which the VPR estimated higher concentrations than the MOCNESS in all five depth comparisons, and these differences could not be reconciled on the basis of differential size distributions, as was the case for copepods. It is important to recognize that the tracklines of the two vessels were separated horizontally by approximately 180 m so that the two samplers did not sample precisely the same water mass. The VPR was located to the west of the MOCNESS in leg 6, and there is some indication that the abundance of pteropods increased westward towards the center of the grid (Fig. 6). This may explain why the VPR encountered consistently higher pteropod concentrations than the MOCNESS. Further replicate comparisons among the two systems are needed to evaluate the performance of the two systems; however, we emphasize that the magnitude of the differences noted for pteropods among the VPR and MOCNESS are well within the range expected for replicate tow variability at a single station.

Video systems are a recent development and have been used to quantify the feeding behavior of fish (Kils, 1992) and small zooplanktors (Schulze *et al.*, 1992), distribution of macrobenthos (Christiansen, 1993), and densities of zooplankton collected within nets (Welsch *et al.*, 1991; Lenz *et al.*, 1995). Towed video systems such as the VPR are only now being developed, and their novelty limits the number of comparisons with other video and

net systems. We are not aware of any comparisons of independently deployed nets and video systems. Welsch *et al.* (1991) describe a video system that images zooplankton and ichthyoplankton within the cod end of a high-speed Gulf III net. Although comparative concentration estimates from the net and video were not presented, their vertical profiles of copepod distributions from a stratified region of the central Baltic are very similar to the pattern noted in our study. Their highest abundances occurred in the upper 3–15 m of the water column above the thermocline, with substantially lower concentrations between 15 and 25 m and low number down to their maximum depth of 40 m. No data were presented by Welsch *et al.* (1991) on the species composition of the zooplankton assemblage sampled. A more recent evaluation of this system, termed the Ichthyoplankton Recorder (Lenz *et al.*, 1995), suggests that it provides concentration data for larval herring and chaetognaths that are comparable to estimates from conventional nets deployed at close time intervals to the video system. Olney and Houde (1993) describe a broadly similar configuration modeled after Ortner *et al.* (1981) that employed a 35 mm still camera within the cod end of one of a pair of 335 μm plankton nets. Their comparisons contain several findings which parallel our own study. Comparatively, their camera imaged only a small proportion of the total volume filtered by the net (5%) yet the camera and preserved samples provided similar data on the taxonomic composition of the plankton. Rare taxa that were generally present at concentrations of $\leq 1\ m^{-3}$ tended to be under-sampled or missed by the camera system relative to the net samples, while gelatinous taxa detected by the camera-net system were either absent, too damaged or dissolved to enumerate in the preserved plankton samples. In contrast to our results, gastropods, a category including pteropods and larval forms, were significantly underestimated by the camera system relative to the net. Results from an earlier deployment (Houde *et al.*, 1989) support the contention that camera/video systems are prone to undersampling of infrequent taxa.

Comparative studies that deployed both optical plankton counters (OPC) and nets (Herman *et al.*, 1993; Sameoto *et al.*, 1993) provide some results germane to our investigation. OPC systems provide size–frequency data from which taxonomic composition may be inferred from comparisons with measured samples collected with nets. In a situation where an optical plankton counter was mounted on a BIONESS multiple net system (Sameoto *et al.*, 1993), the vertical distribution patterns of euphausiids provided by both samplers were similar. Like the VPR, the OPC yielded finer vertical resolution than the BIONESS; however, the OPC numerical estimates of euphausiid concentration frequently exceeded those of the BIONESS.

The species composition observed in this study was typical of Georges Bank, which is usually dominated by six species of copepods, including *Calanus finmarchicus*, *Pseudocalanus* spp., and *Oithona similis*, that may comprise approximately 80% of the zooplankton concentration (Davis, 1987). An interesting feature of the VPR dataset is the apparent vertical homogeneity of the zooplankton taxonomic composition throughout the six legs of the grid. While the absolute numbers of organisms changed along the transects, the relative contributions by each taxon were not statistically different. The phenomenon of patchiness reflecting changes in the local abundances of taxa within an assemblage with little alteration in species composition has been noted in other studies (e.g. Greenblatt, 1982; Mackas and Anderson, 1986); however, we recognize that it is not always the case, particularly in regions of strong physical gradients. For example, Wiebe *et al.* (1992) noted decreasing similarity in species composition for copepods and euphausiids along transects through the edge of a warm-core ring.

The implications of the homogeneity in species composition are important to the interpretation of acoustic survey data. Recent at-sea measurements of the acoustical scattering properties of a variety of taxa from the Slope Water and Georges Bank (Stanton *et al.*, 1994) demonstrated that the echo energy/biomass relationships vary substantially among taxa depending upon their anatomical properties. These differences pose serious challenges for investigators attempting to estimate biological parameters (such as biomass) from acoustic data. A knowledge of the species composition and size–frequency distribution of the zooplankton coupled with an estimate of points where their taxonomic composition changes are essential to addressing this inverse problem (Wiebe *et al.*, 1996). In more heterogeneous regions, such as the Great South Channel, this assumption may not hold since species composition can vary greatly along a single transect (Gallager *et al.*, 1996).

Shipboard studies of the acoustic properties of a variety of Georges Bank and Slope Water zooplankton suggest that relative backscattered acoustic energy from *L. retroversa* per unit animal is disproportionately high in relation to other species (Stanton *et al.*, 1994). For example, the relative mean echo energy per unit biomass from pteropods such as *Limacina* is approximately 19 000 × greater than fluid-like taxa such as salps. Given the high backscatter of this taxon, it would not require very high concentrations of pteropods to generate substantial acoustic patches. We are currently analyzing the three-dimensional distribution of taxa in relation to the acoustic dataset in order to correlate the distributions of taxa with acoustic features in the water column.

We speculate that the subsurface fluorescence maximum may reflect the presence of a nutrient depleted surface layer similar to that observed over the Scotian Shelf in spring by Herman *et al.* (1991), possibly coupled with surficial depletion of phytoplankton due to heavy grazing by copepods above the thermocline. Maximum copepod grazing pressure should have occurred in the upper 10 m where densities were high, although many copepods were clearly positioned to forage directly in the fluorescence feature. Grazing by pteropods and copepod nauplii, which were prominent below the isopleths containing the highest fluorescence, may have governed the shape of the lower boundary of the fluorescence feature. The degree of vertical separation among the copepods and pteropods was quite striking and suggests some degree of resource partitioning. The more fragile larvaceans were clearly positioned below the thermocline, which, given their fragile architecture, should have reduced their exposure to shear in the turbulent surface waters. The high degree of correspondence between the distributions of larvaceans and their abandoned houses is indicative of the high turnover rates of these latter structures.

The dense belt of copepod nauplii detected along the lower edge of the pycnocline and the fluorescence feature appears to be a widespread phenomenon along the southern flank of Georges Bank. Pump samples collected by Incze *et al.* (1996) over the 3 days prior to, and on the same day as, our samples indicated that copepod nauplii also were concentrated along the lower edge of the pycnocline and fluorescence maximum in stratified regions of the Bank at concentrations comparable to estimates from the VPR. Copepod nauplii comprise one of the major prey groups for early larval stages of cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*. Gut contents of both species collected from the well-mixed region of Georges Bank revealed that copepod nauplii were the numerically dominant prey items (Lough and Mountain, 1996). Insufficient larvae were collected from the stratified region to categorize reliably the diet. Both Incze *et al.*'s and our results suggest that the pycnocline in the stratified region of the Bank's southern flank is a potentially important foraging zone for larval cod and haddock. Larval fish surveys were also a component of the

joint ship operations (Lough *et al.*, 1996), and their data from the stratified region generally indicate that both cod and haddock larvae were positioned to exploit the nauplii along the lower edge of the pycnocline. Larval fish were not present at sufficiently high concentrations to be detected by camera 4 of the VPR.

This study compares distributional data for zooplankton collected by a standard survey sampler—the MOCNESS, and a new video sampler—the VPR. The VPR provides the capability to rapidly survey and map out the fine-scale structure of zooplankton populations at previously unattainable resolutions. One of the major drawbacks of the VPR—the long time required to interpret manually the data stored on videotape—has recently been overcome through the development of a real-time focus-detection algorithm that identifies and digitally captures fields containing in-focus targets. This feature now provides the capability to census zooplankton in near real-time at sea (Davis *et al.*, 1996) while eliminating the human tendency to include prominent targets which are out of focus. Not all targets could be identified on video, and until higher resolution systems (e.g. HDTV, digital still cameras) become available, comparative sampling with nets such as MOCNESS will remain important. This limitation means that if quantification of major taxa to genus or species level is required, video/camera systems are best deployed in regions where diversity is low (Olney and Houde, 1993) or where many taxa possess identification characteristics that can be seen with video over a range of body orientations. Our study only examined data from the highest magnification camera, which, given its small image volume, undersampled or missed rare taxa. The other three focal length cameras onboard provide the capacity to quantify less abundant taxa provided that they are sufficiently large to identify (e.g. euphausiids, decapods, fish). The VPR shows great potential for deployment in conjunction with high-frequency acoustic systems. The large dataset collected with the VPR during the 1992 study is currently being examined in relation to the 420 kHz acoustic data collected onboard R.V. *Albatross IV*. The VPR appears to be the only operational sampler with the capability to provide fine-scale taxonomic composition and concentration data to ground-truth acoustic features.

CONCLUSIONS

1. A VPR survey of a 15.75 km^2 parcel of water revealed an assemblage dominated by the copepods: *Calanus*, *Pseudocalanus* and *Oithona*, and the thecosomate pteropod: *Limacina*, which all displayed pronounced vertical structure that appeared to correspond to strong vertical heterogeneity in temperature, salinity and fluorescence.

2. While the VPR provided higher vertical resolution than the 1 m MOCNESS, both systems produced similar mean estimates of the concentrations of copepods and pteropods.

3. Both systems yielded comparable information on the species composition of the assemblage. The VPR undersampled less abundant taxa due to its relatively small imaged volume, while small, delicate, and gelatinous taxa were under-represented or absent in the MOCNESS due to damage and loss.

4. The vertically-integrated taxonomic composition of the plankton, as measured with the VPR, appeared similar for each leg of the grid.

5. Given recent advances in the data processing capabilities of the VPR, the system provides a useful new tool for rapid surveys of the fine-scale vertical and horizontal distributions of zooplankton and provides a unique capability to ground-truth data from acoustic surveys.

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