Gaps and patches in the ocean: a one-dimensional analysis of planktonic distributions

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ABSTRACT: The Optical Plankton Counter (OPC) was used to count individual animals *in situ*, and to produce a one-dimensional spatial-series from which gap relationships could be quantified at the millimeter scale and above, using a Distance to Next Encounter (DNE) technique. Both DNE and one-dimensional neighbor analyses indicated that zooplankton distributions in all transects were significantly ($p < 0.0001$) aggregated into patches. Within patches, zooplankton were effectively ($r^2 \approx 0.94$) randomly distributed, resulting in important implications for some of the newer foraging models concerning zooplankton. The DNE frequency distributions all exhibited a distinct pattern that would not be expected from single Poisson distribution, indicating patchiness at the meter scale. This allowed calculation of various statistics used to describe *in situ* patchiness such as: relative percentage of a transect occupied by patches (79 to 89%) and gaps, estimates of patch size (~2 m diameter), and patch densities (7000 to 14 000 organisms m^{-3}).

KEY WORDS: Plankton · Zooplankton Patchiness · Gaps Transect

INTRODUCTION

There can now be little surprise at the mention of the patchiness of planktonic organisms in the oceans. However, the study of these spatial relationships has focused almost entirely on scales which are large relative to the size of these animals. At the macro- and mesoscales (tens to thousands of meters), a variety of mechanisms or processes have been implicated as determining the distributions of organisms. These include tidal fronts (Franks 1992) internal waves (Shanks 1983, Lazier & Mann 1989, Davis et al. 1991, Haury et al. 1992), stratification, diel vertical migration (Riley 1976, Hill 1991), and Langmuir circulation (Ledbetter 1979, Schneider & Bajdik 1992).

Within this context of physical-biological interactions, little attention has been paid to the investigation of micro-scale patchiness (<1 m), the very smallest scales approaching the distances between individuals. The

interactions of physical and biological processes at these scales, and their extent and influence in the physically dominated pelagic environment is not yet understood. This deficiency is due to the requirement for a simultaneous knowledge of both the physical processes and the concomitant biological distributions. Although models of the interactions between individuals in aquatic communities have been created for feeding and encounter rates (Rothschild & Osborn 1988, Yamazaki et al. 1991, Hwang et al. 1994, Kiørboe & Saiz 1995), they have been developed without the support of empirical knowledge of spatial relationships of organisms at the appropriate scale. While some theoretical work has been accomplished on the micro-distribution of organisms within plankton patches (Osborn et al. 1990, Rothschild 1992, Yamazaki & Haury 1993), the investigations that were carried out have taken place in enclosures under laboratory conditions (Price 1989, Cuddington & McCauley 1994, Leising & Yen 1997).

In contrast, within terrestrial and benthic communities, the use of *in situ* transect sampling and the mea-

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surement and analysis of neighbor distances as a tool to describe and interpret spatial relationships among individuals is now well established due to the work of plant ecologists (Greig-Smith 1964, Pielou 1969, Southwood 1978). Such spatial relationships among individual organisms in pelagic aquatic communities are virtually unknown due to the inherent problems visualizing distributions in the open water. Conventional methods of sampling (e.g. plankton nets, traps, or pumps) integrate their collections either vertically or horizontally over relatively large scales; as a result they lack the resolution to gather single individuals, and their collection requires tremendous time and effort to analyze (Davis et al. 1992, Pinel-Alloul 1995).

The development of the *in situ* Optical Plankton Counter (OPC) allows us to count individual animals and, through a simple modification, to develop time/spatial-series from which neighbor relationships can be quickly and easily quantified. This methodology allows a relatively unobtrusive determination of zooplankton spatial distributions from the km scale down to that of millimeters. Due to the three-dimensional nature of the sampling device and the one-dimensional nature of the output, the true *nearest* neighbor measures cannot be calculated; however the *next* value is known within the one-dimensional series. In recent years, this application of neighbor analysis from one-dimensional series has become well established (Selkirk & Neave 1984, Shiyomi & Yamamura 1993, Weingart & Selvin 1995). In this paper we present a method of analyzing patch dynamics in planktonic systems using a one-dimensional Distance to Next Encounter (DNE) technique, from a spatial data series collected by the OPC.

METHODS AND ANALYSIS

OPC operation. The Focal Technologies Inc. OPC quantifies plankton abundance by measuring the optical surface area of individual zooplankters encountered along a transect in the water (Herman et al. 1992). As the OPC is towed in the water, plankton pass into a flow-through tunnel where they cross a thin rectangular light beam that measures the profile area of each individual target. The OPC thus provides *in situ* measurements of targets, ranging in size from 250 µm to 20 mm in equivalent spherical diameter, at rates up to 200 counts per second. The electronic size of each particle was converted into Equivalent Spherical Diameter (ESD) using the manufacturer's OPC Lab-Windows® Data Acquisition Software. Particle counts at the towing speed (approx. 1.3 m s^{-1}) ranged from 20 to 70 counts s^{-1} and never exceeded 80 s^{-1}; this is well below the level at which coincidence counts would become significant (>200 s^{-1}) (Herman et al. 1992).

At our request, the manufacturer modified the micro-controller of an OPC to add a time stamp with a $\frac{1}{1000}$ s resolution to the data file, for each recorded particle. As a result, the data file contained the absolute time of encounter for each particle in addition to the existing data on particle size, index of light attenuation and *in situ* velocity from the device's onboard OMEGA FP-5200 velocity meter. The OPC was coupled with a SeaBird-25 CTD profiler which stored synchronously collected information on temperature, salinity, light transmission, and oxygen concentration, and a Seatech fluorometer which collected *in situ* fluorescence.

The sampling devices were towed laterally at various fixed depths from 2 to 8 m in the near-shore region (bound by the 4 m and 35 m isobaths) of the St. Lawrence Estuary near Mont-Joli, Quebec, Canada (48° 40' N, 68° 10' W), at various points of the tidal cycle during July and August of 1995. Transects were typically 1024 s in length (4096 sampling points for the CTD at 4 Hz), or approximately 1700 m at 1.3 m s^{-1}. A 250 µm mesh plankton net was affixed to the outflow of the OPC for these samples to collect all particles passing through the device for counting calibration and taxonomic identification.

DNE calculation. DNE measures were calculated using a velocity value averaged over 10 s. DNE is a simple statistic calculated from:

$$DNE = V(T_i - T_{i-1})$$

where T_i is the time of encounter for the ith particle and V is the towing velocity. This value was calculated using all size categories of particles within the data sets. The one-dimensional neighbor technique of Selkirk & Neave (1984) was also used to test the degree of patchiness of particle distributions as a whole. Briefly, this technique compares nearest-neighbor (N-N) distances along a line transect to those expected due to a random distribution and requires no distributional assumptions. A N-N statistic greater than 0.5 indicates a tendency towards regular spacing, values below 0.5 represent a tendency towards aggregation in the distribution. In addition, we assessed the frequency distributions of the DNE values themselves. Given no bias in particle position when it enters the OPC, if the particles are randomly distributed along the space-time axis of the OPC, then the distance (time) between 2 successive particles should follow an exponential distribution; this would appear as a straight line on a log-frequency versus distance to next-encounter plot.

Various descriptive patch statistics were generated using an extension of Rothschild (1992), and a variety of other useful descriptors were also calculated to illustrate the nature of patchiness at the scale of the individual (Table 1).

Table 1. Calculations for the various patch statistics listed in Table 2 of the Distance to Next Encounter technique for 11 transects using an Optical Plankton Counter (OPC)

A_{opc}	OPC sampling surface area = 0.22×0.02 [m]
D	Total distance of transect [m]
V_s	Total volume sampled [m^3] = $D \times A_{opc}$
N	Total particles within patches = Σ all particles
n_t	Number of patches in the transect = Σ particles within the 'second distribution' + 1
n_p	Number of patches per 100 m
n_{pp}	Number of particles per patch = N/n_t
d_{max}	DNE value for limit of the 'first distribution' (within patch). (Refer to Fig. 2)
D_p	Total transect distance taken up by patches [m] = $\Sigma_0^{d_{max}}$ (DNE) for within patch
$P_{\%}$	Percent of transect occupied by patches = D_p/D
$G_{\%}$	Percent of transect forming gaps = $1 - D_p/D$
ϕ_p	Estimated average linear patch size [m] = D_p/n_t
V_p	Mean volume per patch assuming isotropic sphere [m^3] = $\frac{4}{3} \pi (\phi_p/2)^3$
ρ_l	Linear density [organisms m^{-1}] = n_{pp}/ϕ_p
V_{sp}	Mean patch volume sampled [m^3] = $\phi_p \times A_{opc}$
ρ_s	Within patch density [organisms m^{-3}] = n_{pp}/V_{sp}
ρ_p	Overall average patch density [organisms m^{-3}] = N/V_s

The one-dimensional neighbor distance statistic (Selkirk & Neave 1984) indicated that individual particle distributions in all the transects were significantly non-random (p < 0.0001, Table 2). The individual N-N values were significantly <0.5, ranging between 0.3667 and 0.4143, indicating that particles in all 11 transects showed a tendency towards spatial clustering, i.e. patch formation. Histogram plots of log abundance versus DNE were then constructed for each transect, combining all size classes of particles encountered (Fig. 2).

A random distribution of particles along a transect should produce a single exponential distribution of DNE values (Fig. 2), forming a linear frequency distribution on a log-linear scale (Sokal & Rohlf 1981). However, the observed DNE frequency distribution plots (Fig. 3) all exhibited 2 distinct regions which would not be expected and which cannot be expressed as a single, simple Poisson distribution. The example plot (Fig. 2) illustrates that the 'first region' of the distribution (at distances between organisms <0.2 m) corresponds rather well to an exponential decrease (r^2 = 0.89 to 0.97); however, a second distribution is also

RESULTS

Approximately 200 transects were carried out with the OPC during the 1995 field season. Of these, 11 examples—which were analyzed in detail and in which taxonomic collections were made for calibrating the OPC—are presented here to illustrate the DNE methodology. Taxonomic composition varied somewhat from transect to transect, but 3 basic categories of size distributions can be seen (Fig. 1): predominantly small particles only, <1000 µm ESD (e.g. Fig. 1g, i); small particles with a tail of larger particles, up to 1500 µm ESD (e.g. Fig. 1b, c); a mixed size distribution with a greater proportion of large particles up to 2000 µm ESD and larger (e.g. Fig. 1a, h). The smallest size category consisted of sea urchin larvae, cladocerans (mainly *Evadne* sp.), nauplii of calanoid copepods, barnacle nauplius and cypris larvae, and fish eggs. The intermediate size category contained larger nauplii, copepodites of *Acartia* and *Eurytemora*, and fish larvae. The largest size category included late stage copepodites, adult copepods, fish larvae, and euphausiid juveniles.
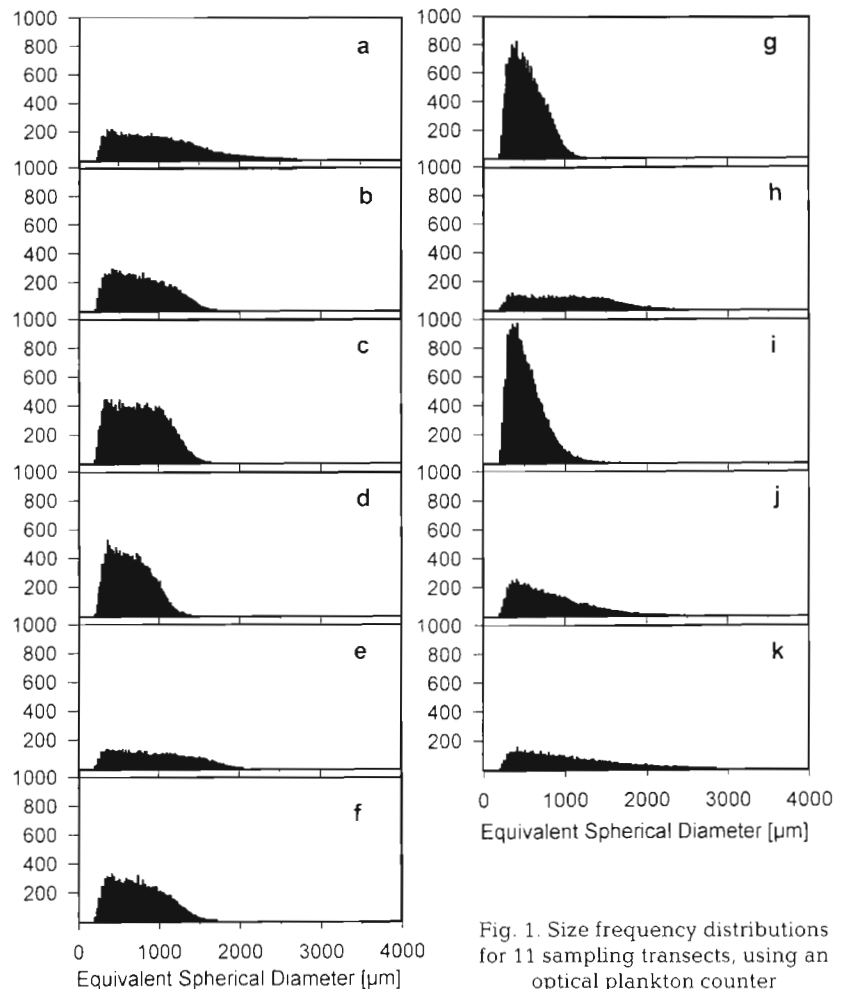

Fig. 1. Size frequency distributions for 11 sampling transects, using an optical plankton counter

Table 2. Patch statistics calculated using the Distance to Next Encounter technique for 11 transects in 1995 using an Optical Plankton Counter (OPC). The Neighbor statistic (Selkirk & Neave 1989) for individual zooplankters indicates that all of the transects suggest significant non-randomness (p < 0.0001) and clumping, while the distribution of patches indicate non-randomness with a tendency towards regular spacing (p < 0.0001)

Patch statistic	16 Jul (a)	18 Jul (b)	18 Jul (c)	25 Jul (d)	27 Jul (e)	27 Jul (f)	1 Aug (g)	2 Aug (h)	3 Aug (i)	3 Aug (j)	3 Aug (k)
Total no. of particles, N	31285	28776	45647	32251	18921	29187	34733	17443	36563	22084	18603
Total no. of patches, n_t	487	303	483	344	218	261	318	375	352	231	222
No. of patches per 100 m, n_p	4.04	2.76	5.49	4.55	4.18	4.56	4.49	6.65	5.53	4.63	4.60
Total transect distance, D [m]	1205.0	1098.5	879.4	756.7	521.0	572.5	709.0	564.1	636.9	498.7	482.8
Total sample volume, V_u [m³]	5.30	4.83	3.87	3.33	2.29	2.52	3.12	2.48	2.80	2.19	2.12
Within patch limit, d_{max} [m]	0.295	0.320	0.165	0.190	0.215	0.175	0.175	0.250	0.150	0.180	0.215
Distance occupied by patches, D_p [m]	1009.6	918.4	787.3	626.4	450.5	449.2	599.1	492.4	528.4	434.1	426.2
No. of particles per patch, n_{pp}	64.2	95.0	94.5	93.8	86.8	111.8	109.2	46.5	103.9	95.6	83.8
% transect occupied by patch, $P_\%$	83.8	83.6	89.5	82.8	86.5	78.5	84.5	87.3	82.9	87.0	88.3
% gap space, $G_\%$	16.2	16.4	10.5	17.2	13.5	21.5	15.5	12.7	17.1	13.0	11.7
Mean patch size, ϕ_p [m]	2.07	3.03	1.63	1.82	2.07	1.72	1.88	1.31	1.50	1.88	1.92
Mean spherical patch volume, V_p [m³]	4.67	14.58	2.27	3.16	4.62	2.67	3.50	1.19	1.77	3.48	3.71
Density of patch (linear), ρ_l [m]	31.0	31.3	58.0	51.5	42.0	65.0	58.0	35.4	69.2	50.9	43.6
Patch sampled volume, V_{sp} [m³]	0.00912	0.0133	0.00717	0.00801	0.00909	0.00757	0.00829	0.00578	0.00660	0.00827	0.00845
Within patch density per m³, ρ_p	7040	7120	13180	11700	9550	14770	13180	8050	15730	11560	9919
Overall mean density per m³, ρ_t	5900	5950	11800	9690	8250	11590	11130	7030	13050	10060	8760
Neighbor statistic (individuals)	0.3855	0.3667	0.4143	0.3782	0.3884	0.3799	0.3946	0.4079	0.3696	0.3733	0.3773
Neighbor statistic (patches)	0.6290	0.6481	0.6441	0.7180	0.6538	0.6724	0.6887	0.6202	0.7243	0.6475	0.6065

apparent at scales >0.2 m. This second distribution, indicating large distances between successive particles, clearly departs from a simple, single exponential distribution. The tail of greater distances, at scales >0.2 m, indicates that greater DNE values were observed 10^2 to 10^5 times more frequently than expected if due to a random distribution. Thus, within our transects, the greatest probability is that of having the next particle very close, with an exponential decrease in probability of having the next encounter further away. In other words, gap distances follow this exponential distribution. However, at a certain distance threshold there is an unexpected increase in the probability of having this size of gap, far greater than can be explained from a single Poisson distribution (Fig. 3).

If we assume that plankton abundance is patchy, then it follows that the first part of the distribution must reflect the distribution of gaps between particles
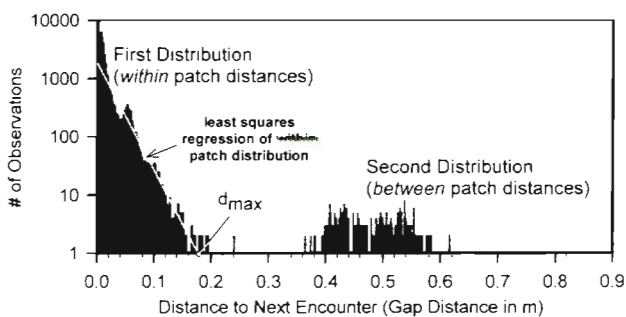

Fig. 2. Illustration of the parts of the log-normal histograms of abundance vs Distance to Next Encounter (DNE)

within patches and the second distribution (indicating large inter-particle gaps) corresponds to the distribution of gaps between particles which belong to different patches (the edge of one patch to the beginning edge of the next). The Selkirk & Neave (1984) neighbor distance statistic, on the distribution of the patches themselves, indicated that the patches were arranged significantly non-randomly (p < 0.0001) with a tendency toward non-aggregated (regular) spacing.

The calculation of various descriptors of patchiness now becomes possible. Knowing the surface area of the sampling beam, the length of the profile (sum of the distances between particles) and the number of distributions allows calculation of the percentage of the transect occupied by patches ($P_\%$) or gaps ($G_\%$), an estimate of patch size (ϕ_p) and patch densities (ρ_l, ρ_p, ρ_t) as summarized in Table 2.

The limit of the first distribution (within patch) d_{max}, given by the intercept of the line of best fit, varies from 0.17 to 0.34 m (0.216 ± 0.019 SE) within these 11 transects. The distance to next patch value of DNE varied from 0.22 to 0.59 m, and the estimated patch size ranged from 1.3 to 3.0 m (1.9 ± 0.13 SE) in diameter. We could not clearly find any relationship between the size spectrum of the transects (Fig. 1) and any of the calculated patch statistics such as d_{max}.

Note that the majority of distance along a transect is considered to be within a patch, ranging from 78.4 to 89.5% (85.0 ± 0.95). In terms of density estimation, it can be seen that as the percentage of space occupied by patches decreases, the overall average density

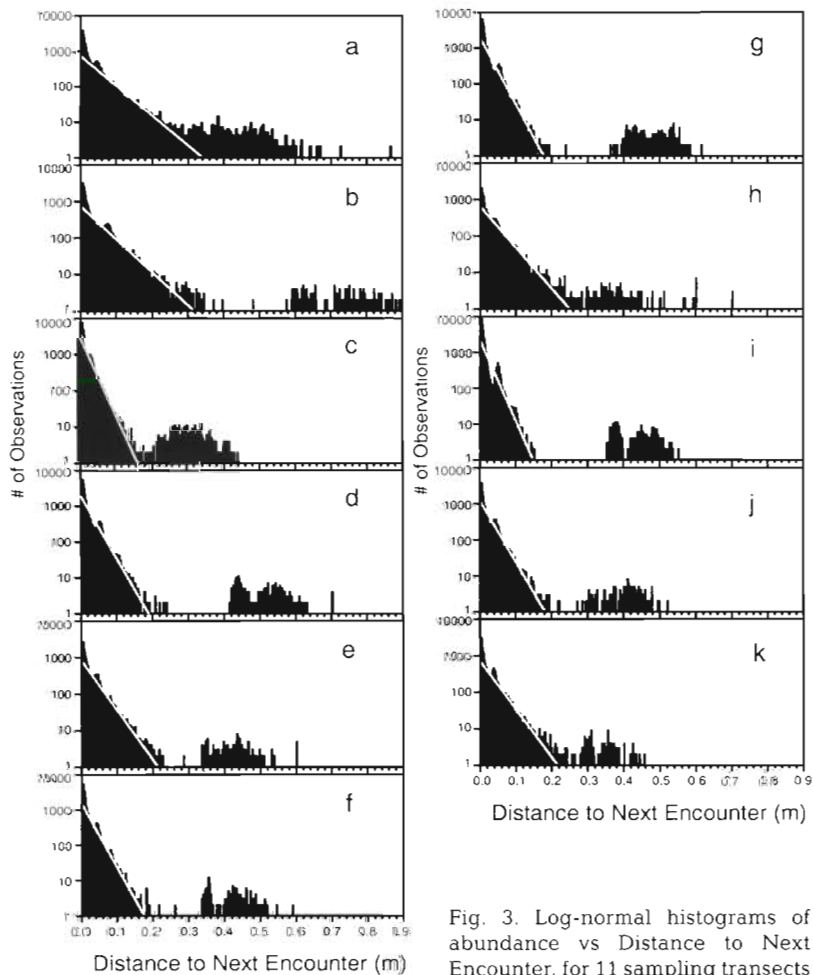Fig. 3. Log-normal histograms of abundance vs Distance to Next Encounter, for 11 sampling transects

munities over a century ago (Haeckel 1891). However if a distribution is patchy, then conventional statistical methods become less useful as analytical tools due to violations in assumptions such as randomness. The neighbor method of Selkirk & Neave (1984) and our DNE analysis both describe strong patchiness at the meter scale. This extends the existing hierarchy of patchiness in coastal zooplankton populations, which is well documented by conventional techniques at larger scales (Pinel-Alloul 1995), to the meter and centimeter scales.

The 2 sections of the DNE histograms most likely point to different processes. The first pattern (within-patch: see Fig. 2), characterized by DNE below approximately 0.2 m, is well described by an exponential distribution of gaps; thus, within the patches, the zooplankton are randomly distributed ($r^2 \approx 0.94$). The second section (between-patch) is the existence of another region in the DNE, at gaps greater than 0.3 m, where the probability of encountering these large gaps is on the order of 10^2 to 10^5 times greater than would be expected given a simple exponential distribution. These 2 patterns thus define both the gaps between zooplankton within patches at the micro-scale, and the gaps of rarefied abundances between the patches themselves.

Elongation or iteration of the 'second' distribution, at scales above 1 m, might be expected on the DNE histograms given a large enough sample size. These would represent iterations of the patchy distributions that may or may not be fractal. However, given our high zooplankton densities, the probability of encountering a gap greater than 1 m (no particles encountered) becomes infinitesimally small. In very long transects which record approximately 1 million particles, only rarely do we see many gaps greater than 1.5 m.

For the present, the structure of the gaps can be well described, but the structure of the patches themselves requires additional exploration with alternative techniques. Our technique produces an estimate of patch size, but uses an assumption of a regular distribution of patches. This assumption is in fact reasonable, based on the evidence from the neighbor statistic of the patches themselves, which suggested a tendency toward non-aggregated (regular) spacing (Table 2). This

diminishes proportionally and becomes less accurate as an estimate of within-patch density (see Table 2). For instance, for transect (a), the overall density is 5900.8 organisms m^{-3}, but the within patch density is 7042 m^{-3} when $P_\%$ is 84%. If $P\%$ was 100% then the entire transect would be considered within a patch, so the overall density would equal the within-patch density. Also, a low value of d_{max} can lead to very high within-patch densities due to the large slope of the line of best fit. In addition, the wide variation among transects for the estimated densities of organisms within patches (ρ_p) and in the other descriptive statistics allows for quick comparisons between transects. For instance, transects (b) and (f) have a very similar size structure (Fig. 1), yet transect (f) has more than twice the within-patch density (ρ_p) of transect (b).

DISCUSSION

The recognition of patchiness is hardly new to plankton ecology; it was described within zooplankton com-

is then perhaps a good first approximation of patch density, but it is obvious that it is not sufficient description of the patch pattern. A preliminary analysis of the distribution of biomass within and between patches is in progress, and suggests that the combined influence of particle numbers and particle size leads to a fractal pattern of biomass.

Neither the mechanism favoring generation of gaps and patches within the zooplankton, nor the processes underlying their apparent random distribution within patches, are yet clear. Some coupling of swimming behavior of the animals with micro-scale turbulence of water motion seems implicated. In our environment, this coupling may represent the lower scale limit of turbulent effects on zooplankton distributions, and is currently under investigation.

Our evidence of the existence of zooplankton patches, but random distributions within the patches themselves, has implications for some of the newer foraging models concerning zooplankton. These models tend to generate and use aggregations of zooplankton which may be considerably more influenced by turbulence than those observed within our data (Rothschild & Osborn 1988, MacKenzie & Leggett 1991, Yamazaki et al. 1991, Kiørboe & Saiz 1995, Landry et al. 1995). This will also change the nature of the food signal these models represent. Planktonic animals have been shown to remain within patches when feeding (Price 1989), or exhibit more fine-scale movements in areas of higher food concentration (Bundy et al. 1993, Cuddington & McCauley 1994). Thus encounter rates might actually be best described using a simple model of random encounter when feeding within patches (intensive search), yet they could be considerably different during the search for new patches (extensive search) as has been described in the foraging behavior of beetles (Ferran & Dixon 1993). Foraging models will likely have to incorporate switching between feeding and searching behaviors as scaled to the organism size, in order to effectively simulate these complex physical-biological relationships (Noda et al. 1992).

There now exist a variety of instruments for quantification of zooplankton abundances at high resolution, some of which allow organism identification (e.g. Hardy continuous plankton recorder, Video Plankton Recorders) (Dickey 1988, Weibe et al. 1992). Given the application history of size spectra in the pelagic ocean (Sheldon et al. 1972), the lack of taxonomic information collected by the OPC is more than compensated for by the high spatial resolution (2 mm), ease of deployment, cost in terms of both physical and labor dollars, and the large number of transects that can be rapidly sampled and processed.

The OPC is steadily increasing in use, but it is still generally used only as a size-distribution probe.

Higher quality information can be gathered from this instrument, permitting generation of high resolution *in situ* data on spatial distribution of zooplankton. The OPC is one of the few oceanographic instruments that can collect biological information on large scale distributions without compromising high resolution data at the small spatial scales. This is important because investigating a phenomenon at extremely small scales often hampers our understanding of larger scale patterns, due to physical data storage limitations, the complex analysis of large data sets, and mere statistics.

Patchy distributions, even at scales well below the sampling resolution of most devices (nets, plankton recorder, etc.) indicate the need for adaptive sampling strategies. The OPC is accommodating in this sense because processing of the data can be done at almost any (or all) scales; this allows the use of statistical methods of analysis (e.g. on biomass estimates) when investigating larger scales of distribution. Comparison of zooplankton distribution data to the synchronously gathered physical oceanographic measurements from the CTD or ADCP is also possible, and will hopefully shed light on the mechanisms underlying zooplankton patchiness over a range of scales. Unfortunately at this time, the sampling resolution of the CTD (4 to 24 Hz in recent models) and ADCP is still coarser than the OPC. This puts biological oceanographers in the unfamiliar position of having the capability to gather information at a higher resolution than their physical oceanographer colleagues.

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