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Spatial heterogeneity as a multiscale characteristic of zooplankton community

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Abstract

Zooplankton spatial heterogeneity has profound effects on understanding and modelling of zooplankton population dynamics and interactions with other planktonic compartments, and consequently, on the structure and function of planktonic ecosystems. On the one hand, zooplankton heterogeneity at spatial and temporal scales of ecological interest is an important focus of aquatic ecology research because of its implications in models of productivity, herbivory, nutrient cycling and trophic interactions in planktonic ecosystems. On the other hand, estimating zooplankton spatial variation at the scale of an ecosystem, is a powerful tool to achieve accurate sampling design. This review concentrates on the spatial heterogeneity of marine and freshwater zooplankton with respect to scale. First to be examined are the concept of spatial heterogeneity, the sampling and statistical methods used to estimate zooplankton heterogeneity, and the scales at which marine and freshwater zooplankton heterogeneity occurs. Then, the most important abiotic and biotic processes driving zooplankton heterogeneity over a range of spatial scales are presented and illustrated by studies conducted over large and fine scales in both oceans and lakes. Coupling between abiotic and biotic processes is finally discussed in the context of the 'multiple driving forces hypothesis'.

Studies of zooplankton spatial heterogeneity refer both to the quantification of the degree of heterogeneity ('measured heterogeneity') and to the estimation of the heterogeneity resulting from the interactions between the organisms and their environment ('functional heterogeneity') (Kolasa & Rollo, 1991). To resolve the problem of measuring zooplankton patchiness on a wide range of spatial scales, advanced technologies (acoustic devices, the Optical Plankton Counter (OPC), and video systems) have been developed and tested in marine and freshwater ecosystems. A comparison of their potential applications and limitations is presented. Furthermore, many statistical tools have been developed to estimate the degree of 'measured heterogeneity'; the three types most commonly used are indices of spatial aggregation, variance: mean ratio, and spatial analysis methods. The variance partitioning method proposed by Borcard *et al.* (1992) is presented as a promising tool to assess zooplankton 'functional heterogeneity'.

Nested patchiness is a common feature of zooplankton communities and spatial heterogeneity occurs on a hierarchical continuum of scales in both marine and freshwater environments. Zooplankton patchiness is the product of many physical processes interacting with many biological processes. In marine systems, patterns of zooplankton patchiness at mega- to macro-scales are mostly linked to large advective vectorial processes whereas at coarse-, fine- and micro-scales, physical turbulence and migratory, reproductive and swarm behaviors act together to structure zooplankton distribution patterns. In freshwater environments, physical advective forces related to currents of various energy levels, and vertical stratification of lake interact with biological processes, especially with vertical migration, to structure zooplankton community over large to fine- and micro-scales. Henceforth, the zooplankton community must be perceived as a spatially well-structured and dynamic system that requires a combination of both abiotic and biotic explanatory factors for a better comprehension and more realistic and reliable predictions of its ecology.

Introduction

Among the earliest and most persistent concepts in ecology were homogeneity and its antonym heterogeneity (McIntosh, 1991). The great tradition of balance of nature imputed homogeneity, constancy and equilibrium to natural systems and abhorred thoughts of extinction, chaos and randomness. The development of plankton ecology in the late nineteenth century took its roots within this context of homogeneity. The etymological derivation of the term 'plankton' (noun of πλαγκτ οζ = wandering, drifting) and its early use by Hensen (1884) implied that zooplankton were randomly distributed and assumed a 'uniform' (regular or equidistant) distribution in space (Lussenhop, 1974). Since its statement, this assumption of homogeneous distribution of plankton has been vigorously attacked (Haeckel, 1891). Most of the earlier limnologists, A. J. Forel in Lake Geneva and E. A. Birge and C. Juday in Wisconsin lakes, confronted the problem of heterogeneity in the physical structure of lakes and recognized significant spatial variation in plankton distribution in both vertical and horizontal dimensions. However, the subjective ideal of uniformity and homogeneity in plankton distribution persisted during the early decades of the twentieth century, and the importance of spatial heterogeneity in plankton ecology became apparent only during the 1940s and 1950s. First, Hutchinson (1953) developed the concept of pattern in ecology and adopted the terms 'superdispersion' for aggregated distributions and 'infradispersion' for regular distributions. Then, since the sixties, zooplankton patchiness and its measurement have been well documented both in marine and freshwater ecosystems (Cassie, 1962, 1963; Frontier 1973; Riley, 1976; Fasham, 1978; Malone & McQueen, 1983).

It is now clearly recognized that most zooplankton organisms are distributed in clumps, swarms or aggregates; this spatial heterogeneity has profound effects for the understanding and modelling of species population dynamics and their interactions with other planktonic compartments, and consequently, it has important implications for the structure and function of planktonic ecosystems. On the one hand, zooplankton heterogeneity at spatial and temporal scales of ecological interest is an important focus of aquatic ecology research because of its importance for models of productivity, herbivory, nutrient cycling and trophic interactions in planktonic ecosystems. On the other hand, within-lake zooplankton spatial heterogeneity, reflected by the variation between samples, must be known to achieve accurate sampling design (Downing, 1991). During the last three decades, most investigations have focused on the spatial and temporal scales of greater heterogeneity (Dumont, 1967; Wiebe, 1970; Haury *et al.*, 1978; De Nie *et al.*, 1980; Pont, 1986; Pinel-Alloul *et al.*, 1988) and estimation of patch size (Colebrook, 1960a; Cushing & Tungate, 1963; Klemetsen, 1970; Johnson & Chua, 1973; Tessier, 1983; Byron *et al.*, 1983; Pinel-Alloul & Pont, 1991). It is only since the 1980s that the study of the forcing processes responsible for zooplankton heterogeneity over a range of spatial scales has become central to the development of ecological theory in limnology and oceanography (Downing *et al.*, 1987; Pinel-Alloul *et al.*, 1988; Simard & Mackas, 1989; Kolasa & Pickett, 1991; Simard *et al.*, 1992; Dutilleul & Legendre, 1993).

This review concentrates on the spatial heterogeneity of marine and freshwater zooplankton with respect to scale. Scale is emerging as one of the critical problems that must be considered in community ecology (Allen & Hoekstra, 1991), landscape ecology (Milne, 1991) and hierarchy theory (O'Neill *et al.*, 1991). In zooplankton ecology, scale dependence arises from the numerical and functional responses of species to environmental factors operating at different scales. Thus, the degree of zooplankton spatial heterogeneity and the importance of different generative processes vary among sampling scales. First to be examined in this review are the concept of spatial heterogeneity, the sampling and statistical methods used to estimate zooplankton heterogeneity, and the scales at which marine and freshwater zooplankton heterogeneity occurs. Then, the most important abiotic and biotic processes driving zooplankton heterogeneity over a range of spatial scales will be presented and illustrated by studies conducted over large and fine scales in both oceans and lakes. Coupling between abiotic and biotic processes will finally be discussed in the context of the 'multiple driving forces hypothesis'.

Zooplankton spatial heterogeneity: concept and ecological significance

Smith (1972) defined heterogeneity in the spatial sense and considered a variable or a process to be heterogeneous when it varied over space in relation to structural variations of the environment. Smith's definition refers to the concept of 'functional heterogeneity' which arises from the ecological interactions at scales relevant to the ecological entities and to their environment. Thus, the 'functional heterogeneity' depends on spatial scales at which individuals, populations or communities operate. Ecological entities can be either populations, communities or ecosystems, and the degree of 'functional heterogeneity' will increase with habitat complexity and extent (Kolasa & Rollo, 1991). This concept opposes that of 'measured heterogeneity' which concentrates on the estimation of the magnitude of heterogeneity without *a priori* consideration of generative processes, and the development of indices of spatial heterogeneity. This duality of the spatial heterogeneity paradigm has recently been discussed in detail by Dutilleul & Legendre (1993). They concluded that the 'measured heterogeneity' is a product of the observer's perspective whereas the 'functional heterogeneity' provides the perspective of the ecological entities. The distinction between these two concepts depends on the resolution of the study. If the scale, extent, and resolution of the study address relevant aspects of habitat heterogeneity for the ecological entities, then the 'measured' and 'functional' heterogeneities tend to converge.

Past studies of zooplankton spatial heterogeneity refer to both concepts of 'measured' and 'functional' heterogeneity. Most earlier works deal with the estimation of 'measured heterogeneity' (see references in Tables 3 and 4, and Frontier, 1973; Fasham, 1978; Downing *et al.*, 1987; Pinel-Alloul *et al.*, 1988, Pace *et al.*, 1991; Downing, 1991). The model developed by Downing *et al.* (1987) which predicts the variance in replicate zooplankton samples as a function of the mean abundance and sample volume, has been applied to a variety of aquatic systems and levels of taxonomic organization (Anderson *et al.*, 1982; Morin, 1985; Pace *et al.*, 1991; Morin & Cattaneo, 1992). Mean-variance relationships (Fig. 1) provide a powerful tool for valid comparative analyses of zooplankton aggregation at different spatial sampling scales, and across ecosystems (Pinel-Alloul *et al.*, 1988; Downing, 1991; Pinel-Alloul & Pont, 1991); they also allow *a priori* decisions about the number of samples necessary to achieve a given level of precision in the estimation of zooplankton mean estimates (Downing *et al.*, 1987; Pace *et al.*, 1991). However, this approach lacks biological relevance since it reveals little of how zooplankters are organized in space, and gives no information about patch pattern and size in relation to their generative processes. More recently, spatial analysis based on correlograms, variograms and mapping have fulfilled this complementary need (Mackas, 1984; Pinel-Alloul & Pont, 1991; Simard *et al.*, 1992; Crawford *et al.*, 1992; Dutilleul & Legendre, 1993). The alternative concept of 'functional heterogeneity' has been less explored, even though it offered more biological relevance by relating the observed patterns of distribution to environmental processes operating over different scales. Such zooplankton 'functional heterogeneity' has been investigated in recent studies (Simard & Mackas, 1989; Price, 1989; Pinel-Alloul *et al.*, 1990; Johannsson *et al.*, 1991; Sameoto & Herman, 1992; Mackas, 1992; Patalas & Salki, 1992; Pace *et al.*, 1992), using mapping, spatial analysis, and canonical correspondence analysis.

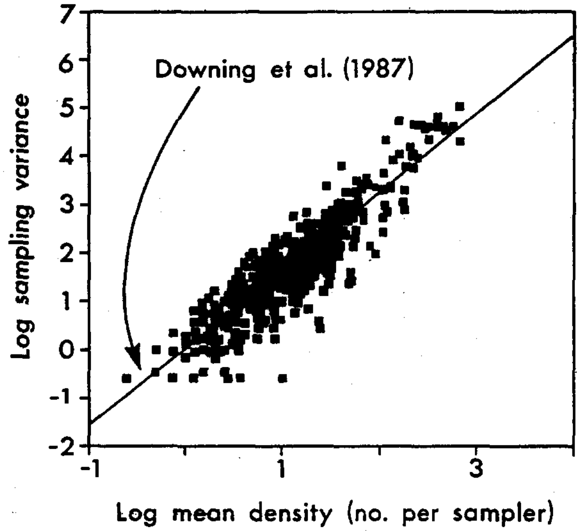


Fig. 1. Relationships between $\log_{10}s^2$ and $\log_{10}m$ densities of zooplankton collected in Lake Cromwell (Québec) compared to the relationship predicted by Downing *et al.*, (1987) from published marine and freshwater zooplankton data. (From Pinel-Alloul *et al.*, 1988).

Zooplankton spatial heterogeneity is of great ecological significance since the distribution patterns, abundance heterogeneity and swarming behavior of zooplankters strongly influence nutrient regeneration (Paffenhofer & Knowles, 1979; Lehman & Scavia, 1982) and feeding activity of herbivores (Tessier, 1983; Marrase *et al.*, 1990), omnivores (Paffenhofer & Knowles, 1980; Williamson & Butler, 1986), and predators (Landry, 1978; Greene, 1983). For example, swarm formation, swimming behavior and grazing of marine krill and copepods are mediated by phytoplankton patchiness (Price, 1989; Tiselius, 1992). Conversely, freshwater cladoceran patchiness increases grazing activity and sustains phytoplankton heterogeneity (Tessier, 1983). Zooplankton patchiness also influences invertebrate and fish predation rates (Neil

Table 1. Types, applications, advantages and limitations of the advanced technologies recently developed to study zooplankton vertical and horizontal patchiness.

Instruments	Types	Applications	Advantages	Limitations	References
Acoustic sounding	Single-beam	Distribution	Non-invasive	No taxonomic	Smith *et al.*, 1992
	ADCP system	Abundance		information	
			Vertical and		
			horizontal	Open water	
	Multi-beam	Distribution	distributions	Pelagic zone	
	NNLS inversion	Abundance			
	technique	Size	Fine- and large-scales	Large zooplankton	
Optical Plankton Counter	OPC system	Distribution	Large-scale	invasive	Sprules *et al.*, 1992
		Abundance	Continuous survey		
		Size	Sinusoidal pattern	No taxonomic	
				information	
			Direct estimation of		
			density per unit volume	Counting coincidence	
				Orientation effect	
Video Plankton Recorder	VPR system	Distribution	Taxonomic and behavior	no automated data	Schulze *et al.*, 1992
		Abundance	information	processing	
		Size			
		Behavior	Swimming patterns	not suitable for survey	
			Predator-prey interactions		
				intermediate invasive	
			Fine-scale, mesocosms		
			Laboratory experiments		

Table 2. Indices of spatial heterogeneity applied to marine and freshwater zooplankton and their formula, calculation and range of observed values in 1200 replicate zooplankton samples. (From Downing, 1991). : range of values according to Downing (1991), Pinel-Alloul & Pont (1991) and Pace *et al.* (1991).

Index	Formula	Calculation	Range of values
Variance mean ratio	s^2/m	s^2/m	1–10 000
Coefficient of variation	CV	s/m	0.3–2.6
k of the negative binomial distribution	k^b	$m^2/(s^2 - m)$	0–50
Lloyd's mean crowding index	$m^\bullet$	$m + (s^2/m) - 1$	1->10 000
Lloyd's index of patchiness	$m^\bullet/m$	$1 + s^2 - m^{-1}$	
Morisita's Index	I_d	$\frac{n(\sum X^2 - \sum X)}{(\sum X)^2 - \sum X}$	1–13
Slope of the s^2/m power function	b	$s^2 = a + m^b$	1.24–1.89^a

& Peacock, 1980; Rothschild & Osborn, 1988; Davis *et al.*, 1991; Noda *et al.*, 1992; Williamson, 1993), and as a corollary, zooplankton exhibits vertical migration behavior in response to low food availability (Johnsen & Jakobsen, 1987) or as a defence against invertebrate and fish predation (Neill, 1990; Levy, 1990; Tjossem, 1990). Others studies also suggest a relationship between zooplankton patchiness and their reproductive activity, as reproducing crustaceans are more likely to be found in patches (Colebrook, 1960b; De

Table 3. Patchiness scales for marine zooplankton, and their abiotic and biotic generative processes as recorded in selected studies.

Spatial scale	Zooplankton taxa	Abiotic processes	Biotic processes	References
Mega-scale (10^3-10^4 km)	145 zooplankton taxa	Climatic regions Oceanic gyres Surface circulation patterns	Primary productivity patterns	McGowan, 1971
Meso-scale (10^2-10^3 km)	Euphausiids	Warm-core eddies Cold-core eddies California current		Simard & Mackas, 1989
Macro-scale (10-10^2 km)	Euphausiids	Coastal eddies Coastal upwelling	Migratory behavior	Simard & Mackas, 1989 Simard *et al.*, 1986
	Calanus, Temora	St. Lawrence outflow		Sameoto & Herman, 1992
	Copepods, tunicates and shrimps	Coastal upwelling Nutrient intrusion	Phytoplankton intrusion	Paffenhofer, 1980
Coarse-scale (10^2-10^4 m)	Shrimps	Bottom features Oceanic currents	Migratory behavior	Crawford *et al.*, 1992
	Crustacea	Tidal fronts	Phytoplankton patterns	Pingree *et al.*, 1974
	Decapoda	Internal waves		Zeldis & Jillett, 1982
	Appendicularia	Langmuir circulation	Phytoplankton patchiness	Alldrege, 1982
	Crustacea	Langmuir circulation	Algae convergence zones	Jillett & Zeldis, 1985
	Zooplankton	Langmuir cells		Schneider & Bajdik, 1992
	Zooplankton community	Hydroclimatic events Hydrodynamic energy		Jouffre *et al.*, 1991
	Copepods and euphausiids	Warm-core ring	Migratory behavior	Wiebe *et al.*, 1992
Fine-scale (1-100 m)	Mysids	Microscale turbulence	Algae-herbivore interactions Swimming behavior	Clutter, 1969 Price, 1989
Micro-scale (10^{-2}-1 m)	Copepods and fish larvae	Microscale turbulence	Food concentration Prey patches	Davis *et al.*, 1991

Nie *et al.*, 1980). Finally, zooplankton spatial heterogeneity is also a species- and size-specific property (Pinel-Alloul *et al.*, 1988). Among macrozooplankton taxa, within-lake spatial distribution patterns in a small canadien lake, has been shown to vary in relation to their feeding behavior and their vulnerability to invertebrate predation (Pinel-Alloul & Pont, 1991). Larger zooplankters are less heterogeneously distributed than small zooplankters; greater spatial aggregation may allow small zooplankters to avoid predators and locate mates while reduced spatial heterogeneity in large species may decrease competition.

Advanced technologies for sampling zooplankton spatial heterogeneity

To understand the role of zooplankters in structuring spatial heterogeneity of planktonic ecosystems, we have to resolve their distributions on a wide range of spatial scales. In addition to being labor-intensive and time-consuming, conventional sampling methods using vertical or horizontal integrating samplers (Wisconsin plankton net, Clarke-Bumpus sampler, integrated pumping or tubing) or discrete-depth samplers (Schindler-Patalas trap) have limitations in their ability to resolve both zooplankton fine- and large-scale patchiness. In the last two decades, three advanced technologies (acoustic devices, the Optical Plankton Counter (OPC), and video systems) have been developed and tested in both marine and freshwater ecosystems (Table 1). An excellent review of the application of these new devices for studying zooplankton distribution and behavior has recently been edited by Williamson *et al.* (1992). In this section, my emphasis will be on the comparison of their potential applications and limitations, as illustrated by studies of freshwater and marine zooplankton.

The application of acoustical methods for studying zooplankton began using single-beam techniques which gave only information on the distribution and

Table 4. Patchines scales for freshwater zooplankton, and their abiotic and biotic generative processes as recorded in selected studies (suite). ^{a}: for species taxa see Malone & McQueen (1983) and Pinel-Alloul & Pont (1991)

Spatial scale	Zooplankton taxa	Abiotic processes	Biotic processes	References
Type I	Rotifers^a	Lake basin morphometry	Shore avoidance	Langford, 1938; Davis, 1969;
Large scale	Bosmids, Chydorids^a	Current patterns	Reproductive and	Patalas, 1969; Leach, 1973;
(>1 km)	*Daphnia* spp.^{a}	Current upwelling	growth recruitements	Gannon, 1975; Watson, 1976;
	Diaphanosoma spp.^{a}	Inshore-Offshore	Food abundance	Patalas, 1981; Urabe, 1990;
	Ceriodaphnia spp.^{a}	Advective currents	Phytoplankton growth	Hart, 1990; Johannsson *et al.*, 1991;
	Leptodora kindtii	River Inflow	Competition	Patalas & Salki, 1992; Pace *et al.*, 1992;
	Diaptomids^a		Invertebrate predation	Gliwicz & Rykowska, 1992
	Eurytemora spp.		Vertebrate predation	
	Epischura lacustris			
	Limnocalanus macrurus			
	Cyclopids^a			
Type II	Rotifers^a	Wind current patterns	Vertical migration	Birge, 1897; Ragotzkie & Bryson, 1953
Coarse scale	Bosmids, Chydorids^a	Internal seiches	Horizontal migration	Berzins, 1958; Tonolli, 1958;
(10 m–1 km)	*Daphnia* spp ^{a}	Vertical stratification	Phytoplankton patterns	Colebrook, 1960b; McNaught & Hasler, 1961;
	Diaphanosoma spp ^{a}	Physical gradients	Invertebrate predation	Dumont, 1967; George, 1974;
	Ceriodaphnia spp ^{a}	Downind accumulation	Active swimming	Richerson *et al.*, 1978;
	Holopedium gibberum			De Nie *et al.*, 1980; Tessier, 1983;
	Polyphemus pediculus			Pinel-Alloul *et al.*, 1988; Levy, 1991;
	Leptodora kindtii			Pinel-Alloul & Pont, 1991
	Bythotrephes			
	Diaptomids^a			
	Cyclopids^a			
	Mysids			
Type III	*Daphnia* spp ^{a}	Langmuir circulation	Reproductive behavior	Neess, 1949; Colebrook, 1960b;
Fine-scale	*Diaphanosoma* spp ^{a}	Physical gradients	Co-active interactions	McNaught & Hasler, 1961; Stavn, 1971;
(1–10 m)	Diaptomids^a		Swimming behavior	George & Edwards, 1973;
	Cyclopids^a		Phototactism	Pont, 1986; Pinel-Alloul & Pont, 1991
			Vertical migration	
			Phytoplankton patterns	
Type IV	Bosmids^a	Convection currents	Swarms patterns	Birge, 1897; Künne, 1925;
micro-scale	*Daphnia* spp ^{a}		Reproductive behavior	Southern & Gardiner, 1926;
(<1 m)	*Scapholeberis* spp.		Social interactions	Colebrook, 1960; Kelmetsen, 1970;
	Polyphemus pediculus		Predator avoidance	Byron *et al.*, 1983; Butorina, 1986;
	Ceriodaphnia pulchella		Prey/predator ratio	De Nie *et al.*, 1980; Arditi *et al.*, 1991
	Diaptomids^a			

abundance of target organisms. A recent application of single-beam acoustics is the ADCP (acoustic Doppler current profiler) system. Compared to conventional net tows, this acoustic device gave accurate abundance estimates of zooplankton with correlation coefficients ranging from 0.85 to 0.98 between both sampling methods (Flagg & Smith, 1989). Single-beam echo integration provided an accurate evaluation of the diel pattern of vertical migration for the shrimp *Pandalus montagui* (Fig. 2a & b) in the eastern Hudson Strait (Québec) (Crawford *et al.*, 1992). It was also successfully used to map the mesoscale aggregation of euphausiids on the continental shelf of Vancouver Island (Simard & Mackas, 1989) and the spatial distribution of the pelagic amphipod *Macrohectopus branickii* in Lake Baikal (Rudstam *et al.*, 1992). More recent development of multiple-frequency acoustics offers the possibility of detecting distributional patterns of different sized

Table 5. Contributions of each significant environmental factors retained in the model developed to explain the environmental control of lake zooplankton in Québec (Pinel-Alloul *et al.*, unpublished data).

Environmental factors	Variable	Variance explained (%)	Significance P
Physical and chemical	Ca^{++}	0.11	0.01**
	SO_4^-	0.06	0.01**
	Mg^{++}	0.06	0.01**
	Mn^{++}	0.05	0.01**
	pH	0.04	0.01**
	Al^-	0.04	0.01**
	Transparence	0.04	0.01**
Morphometry	Altitude	0.07	0.01**
	Mean depth	0.05	0.02*
	Morphoedaphic index	0.04	0.03*
Phytoplankton	*Merismopedia minima*	0.06	0.04*
	Kephyrion sp.	0.05	0.04*
	Cosmarium sp.	0.04	0.04*
Fish	*Perca flavescens*	0.09	0.01**
	Salvelinus fontinalis	0.06	0.01**
	Catostomus commersoni	0.05	0.01**

**: $P \leq 0.01$; *: $P \leq 0.05$

organisms, in addition to their abundance. It has been used to estimate the vertical distribution of 40 size classes of marine zooplankton ranging from nauplii to small euphausiids (Fig. 2c) (Holliday *et al.*, 1989; Pieper *et al.*, 1990). All these acoustic devices are non-invasive since they make measurements from a distance of several meters from the target organisms, and data processing is relatively rapid although the raw data must be converted to counts per unit volume. However, these acoustic devices still do not provide taxonomic information, and they are inefficient in detecting organisms close to the bottom or surface of the water column, as well as small zooplankters <1–4 mm.

Applications of optical particle counters for the characterization of zooplankton spatial patterns began two decades ago. Earlier technologies such as the opto-electronic plankton sizer (Cooke *et al.*, 1970) and the Hiac Particle Size Analyser (Pugh, 1978) were not routinely used in zooplankton research although they facilitated large-scale studies of plankton distribution and abundance. As an alternative to these instruments, Herman (1988) developed the Optical Plankton Counter (OPC) which permits large- scale continuous sampling of zooplankton size and density spectra. The OPC can detect organisms from 250 μm to about 4 mm, and enables sampling of both linear and sinusoidal transects. Coupling the OPC with a fluorometer and with conductivity-temperature-depth sensors (Fig. 3A) allows the concomitant measurement of zooplankton patchiness and the potential biotic and abiotic processes responsible for this spatial heterogeneity. The OPC has been used to study large-scale horizontal and/or vertical distribution of marine zooplankton on the Nova Scotia Shelf (Herman *et al.*, 1991), and freshwater zooplankton in Lake Ontario (Sprules *et al.*, 1992). Like the acoustic devices, the OPC does not provide taxonomic information, but unlike acoustics, the OPC is intrusive since detected organisms must physically pass through its sensor. Technical limitations and biases can also arise from coincidental counting of organisms at high zooplankton density and from orientation errors during zooplankton size estimation. Furthermore, this instrument must be carefully calibrated with comparative analysis of net samples.

Video systems and zooplankton recording by image analysis can be divided into two classes: survey instruments intended primarily for measuring population distributions and abundances over large and fine scales, and instruments designed to measure individual behavior (Schluze *et al.*, 1992). Remotely operated vehicles (ROV) equipped with video cameras (Fig. 3B)

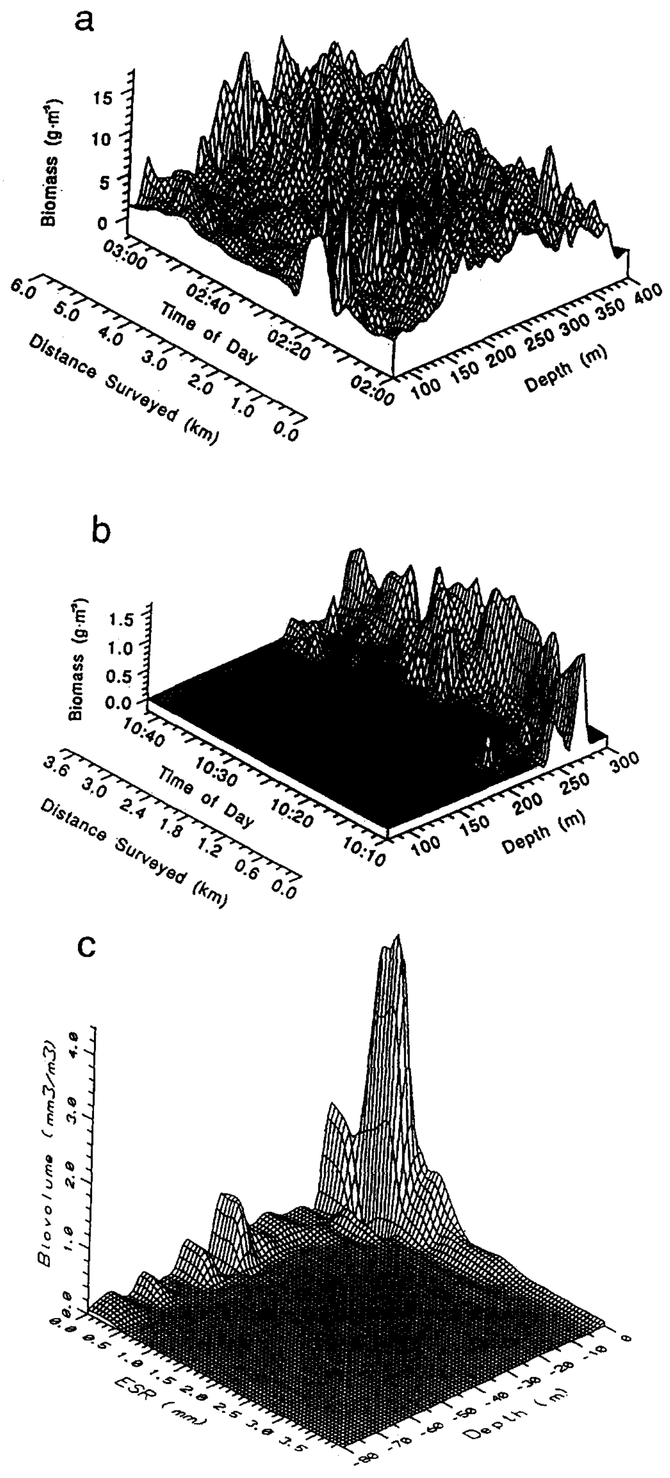


Fig. 2. Vertical distribution of total biomass of the shrimp *Pandalus montagui* detected with a single-beam acoustic device at night (a) and in the morning (b). (From Crawford *et al.*, 1992). (c) Size-class specific zooplankton biovolume as a function of depth estimated by a multiple-frequency acoustic device. (From Holliday *et al.*, 1989).

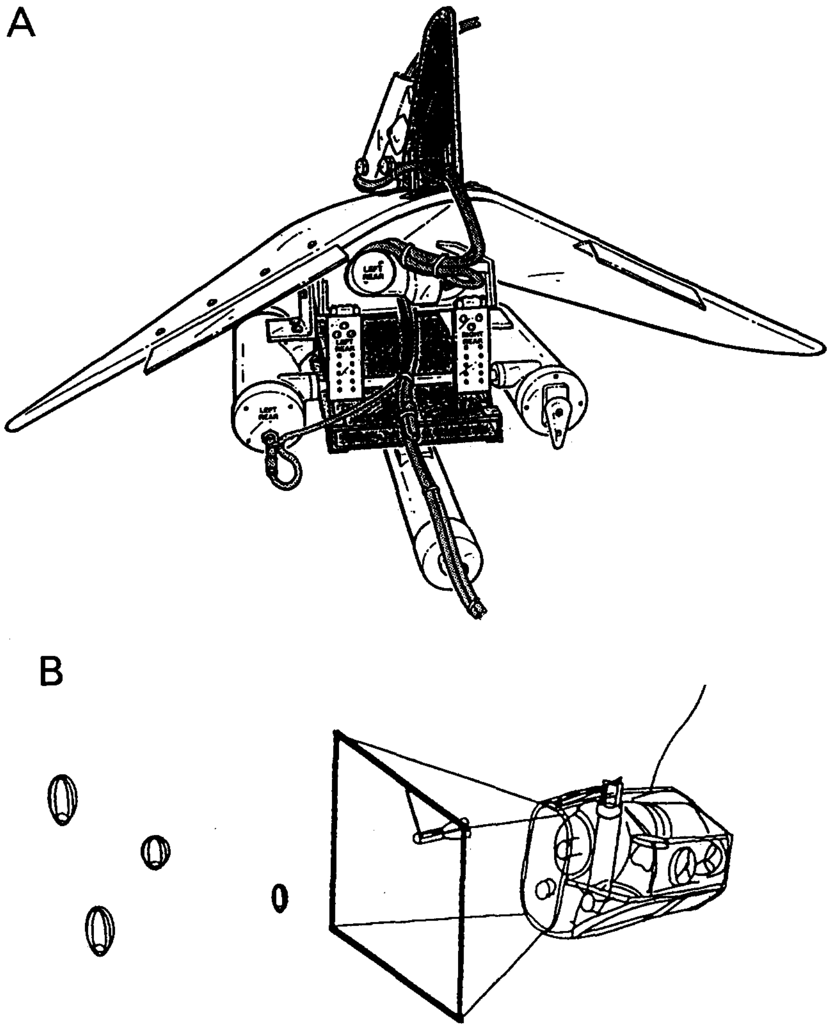


Fig. 3. A: V-FIN underwater vehicle equipped with Optical Plankton Counter (OPC), fluorometer, and conductivity-temperature-depth (CTD) sensor. View is from the rear. (From Sprules *et al.*, 1992). B: Remotely operated vehicle equipped with video camera for quantification of gelatinous zooplankton. (From Bergstrom *et al.*, 1992).

and acoustic devices permitted the study of *in situ* mysid and tunicate aggregation patterns over various vertical and horizontal scales (Lee & Hall, 1989; Paffenhofer *et al.*, 1991). However, these methods also have shortcomings and limitations due to the behavioral responses of organisms (attraction or repulsion) to the instrument and its white light, and to the lack of contrast between transparent organisms and their environment under conditions of high ambient light. Small video devices have also been developed to assess individual behavior (EcoSCOPE, DynIMAGE, CritterCam^{TM} underwater microscope, Infrared video, Motion-sensing holocamera), and enable direct observation of swimming and aggregation patterns (Strickler, 1977), abundance distributions (Bergstrom *et al.*, 1992), and predatory-prey interactions (Kils, 1992). These video instruments are unique in providing taxonomic and behavioral information, but are best suited for small-scale studies in clear water lakes, and for mesocosms and laboratory experiments.

Measurement of zooplankton spatial heterogeneity

Spatial heterogeneity is a concept whose definition depends on the nature of the underlying patterns (Dutilleul & Legendre, 1993). The most common statistical models concern variation of organisms or variables among sites or subregions. A point pattern process concerns the discontinuous distribution of individual organisms or variables through space whereas a surface pattern process, which is spatially continuous, refers to the variability of organisms or variables among subregions over large or fine spatial scales. Two types of statistical approaches have been developed to characterize these patterns of spatial heterogeneity. Indices of spatial aggregation and the variance:mean ratio were primarily developed to assess point patterns whereas spatial analysis methods were used for describing and interpreting surface patterns.

Many indices of spatial aggregation have been developed to estimate marine and freshwater zooplankton heterogeneity based on point pattern distributions (Table 2). All of these indices are related to the variance (s^2) and the mean (m) of population estimates, and are based on the assumptions of the Poisson random distribution model which corresponds to spatial homogeneity and a variance:mean ratio equal to 1. Hurlbert (1990) has pointed out, however, that many other processes than the Poisson distribution model can give rise to a variance:mean ratio equal to 1. All these indices show systematic variation with m, either with a positive (s^2/m, m^*, m^*/m, k) or a negative trend (CV, I_d). Such indices of spatial aggregation are often used to make comparisons of spatial distributions of populations that occur at different densities, and in different environments, but they lead to conficting interpretations. Indeed, using k of the negative binomial distribution (small values implying high heterogeneity), the Morosita's Index I_d, and the coefficient of variation (CV) would lead to the conclusion that sparser and low density populations are the most aggregated, whereas the other indices (s^2/m, m^*, m^*/m) lead to the contrary conclusion (Downing, 1991). Except for Morisita's Index which tends to be constant at around 2 when m and n number of samples) are high, and which has been recommended by Hurlbert (1990) as a reliable index of spatial aggregation, all the other indices cannot be used for comparative purposes of zooplankton spatial heterogeneity. These limitations on the use of most of the s^2-based indices, have led to a search for a better index of spatial variation.

The index b (corresponding to the slope of the $s^2 = a\ m^b$ power function), has been considered to be a true population specific index of aggregation and was better accepted because it seemed more independent of m than the other indices. Indeed, the range of the exponent b of the s^2/m power function extends only from 1.24 to 1.89 for marine and freshwater zooplankton over large- and fine-scales (Pace *et al.*, 1991; Downing, 1991; Pinel-Alloul & Pont, 1991). However, the use of b as an index of spatial aggregation has been questioned since differences in levels of replication and ranges of mean can lead to bias in b values (Downing, 1986, 1991). Furthermore, the Taylor's power law (Taylor, 1961) is based on the premise that all the variable estimates are influenced by a single generative process, which is not met by the environmental control models based on multiple ecological forces. The simple solution to this problem is to compare entire s^2/m relationships established for different populations or different scales using standard methods for the comparison of two or more bivariate relations (see Gujarati, 1978). Examples of this type of analysis have been presented recently for within-lake spatial heterogeneity of freshwater zooplankton (Pinel-Alloul *et al.*, 1988; Pinel-Alloul & Pont, 1991). These studies have indicated that the degree of spatial heterogeneity for the zooplankton community in Lake Cromwell, a small Canadian Shield lake, is consistent with that found in other freshwater and marine zooplankton communities (Fig. 1). However, comparisons of the s^2/m relationships for macrozooplankton species in a single lake demonstrated that the degree of spatial heterogeneity on the horizontal scales using integrated water samples collected at fine-scale (8 m) or coarse-scale (40 m) was similar, whereas higher heterogeneity was observed on the vertical scale compared to the horizontal scale when using discrete-depth samples at fine-scales (5 m) (Fig. 4).

Spatial analysis methods enable the description of surface patterns such as patches, and one or two-dimensional trends; they also allow to infer the process responsible for the spatial structure. Various methods such as mapping, correlograms and variograms, numerical methods of clustering with spatial contiguity constraint, gradient analysis, spectral analysis, and canonical correspondence analysis have been put forward in recent years for detecting and measuring surface patterns, and for including space in ecological modelling of zooplankton spatial heterogeneity (Mackas & Boyd, 1979; Mackas, 1984; Pinel-Alloul & Pont, 1991; Jouffre *et al.*, 1991). A theoretical dis-

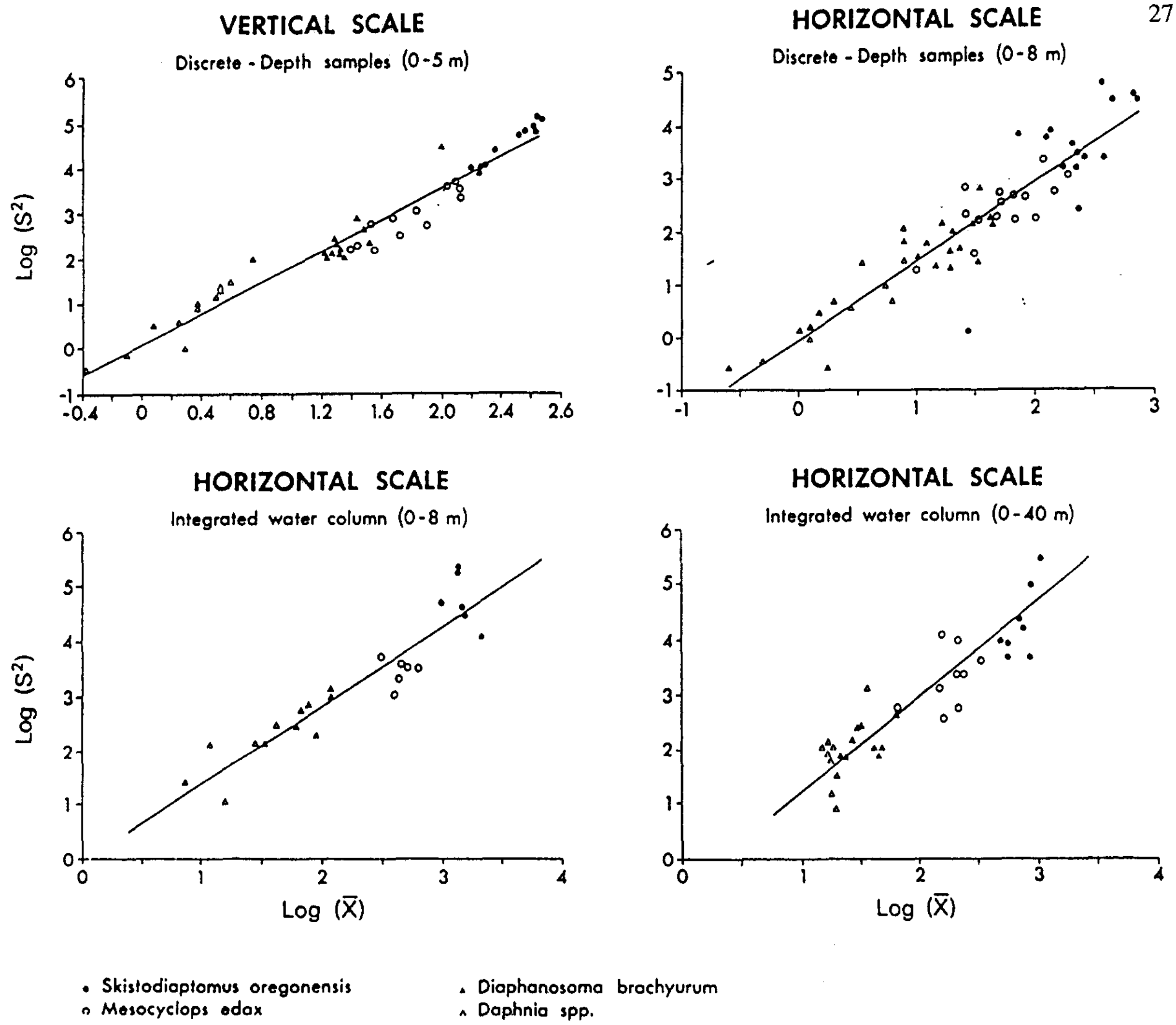


Fig. 4. Relationships log S^2:log $\bar{X}$ for macrozooplankton species collected at different vertical and horizontal scales in Lake Cromwell. (From Pinel-Alloul & Pont, 1991).

cussion of the relevance of these methods for assessing and interpreting spatial surface patterns is presented by Legendre (1987), Sokal & Thompson (1987), Legendre & Fortin (1989), Dutilleul & Legendre (1993), and Legendre (1993).

Here, I discuss and illustrate (Fig. 5) the application of three different methods of spatial analysis (constrained spatial clustering, correlograms and variograms) which give complementary information for assessing macrozooplankton heterogeneity over a whole-lake scale (Pinel-Alloul & Pont, 1991). Constrained spatial clustering (Fig. 5A) suggests that while there was no identifiable spatial distribution pattern for either *Skistodiaptomus oregonensis* and *Daphnia* spp. (only one group) over the whole-lake scale, *Diaphanosoma brachyurum* (2 groups) occurred at lower density in the west part of the transect and at higher density in the east part of the transect. At least, four main subgroups characterized the spatial distribution of *Mesocyclops edax* which demonstrated shore avoidance behavior and a bowl-like depression in the central part of the transect. Correlograms (Fig. 5B) agreed with the constrained clustering results. No significant autocorrelation was detected for *S. oregonensis* and *Daphnia* spp., while spatial autocorrelation occurred at lake-size scales for *M. edax* and *D. brachyurum*. The former showed a patchy spatial structure with circular patches of 90–100 m diameter separated from each other by a 100 m distance interval, while the latter depicted a monotonic decreasing abun-

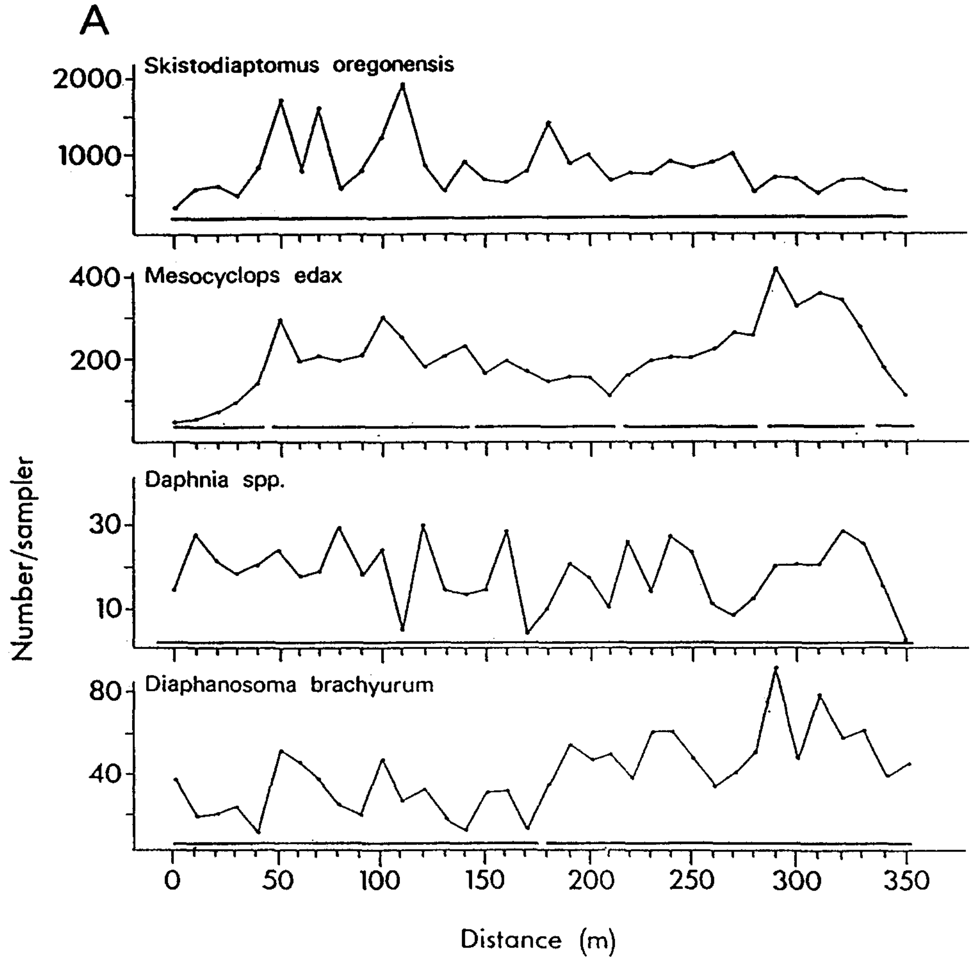


Fig. 5. Spatial analysis methods applied to assess macrozooplankton heterogeneity over a whole-lake scale. A: Plots of four macrozooplankton species abundances against distance with 10-m intervals; the horizontal lines indicate the subgroups of samples determined by constrained spatial clustering, if any. B: Correlograms for four macrozooplankton species over 10-m interval distance classes. C: Variograms for four macrozooplankton species over 10-m interval distance classes. (From Pinel-Alloul & Pont, 1991).

dance trend from west to east. Variograms (Fig. 5C) also supported these results. *S. oregonensis* and *Daphnia* spp. exhibited horizontal variograms without spatial structure at lake-size scales, although irregular discontinuities (nugget effects) suggested micro-scale spatial variations occurring at spatial scales smaller than the sampling interval. The linear model representing a continuous regular gradient fitted well the variogram of *D. brachyurum*. The 'hole effect' model representing a fairly continuous distribution of successive patches fitted the variogram of *M. edax*. Kriging and mapping techniques are additional powerful tools for identifying zooplankton patchiness scales and interpreting the mechanisms controlling pattern formation; these techniques have been used to assess large-scale patchiness of marine zooplankton (Simard *et al.*, 1992).

All the above statistical methods attempt to determine the 'measured heterogeneity' in spatial structuring of ecological entities. However, these tools have limited value for the assessment of 'functional heterogeneity', although direct gradient analysis and canonical correspondence analysis can be used to determine relationships between community spatial structuring and environmental processes (ter Braak, 1987). As the spatial structure of natural communities results from both the spatial distribution of the organisms, independently of ecological forces, and the effects of generative processes at the same scale, the estimation of the true 'functional heterogeneity' is a difficult task. In

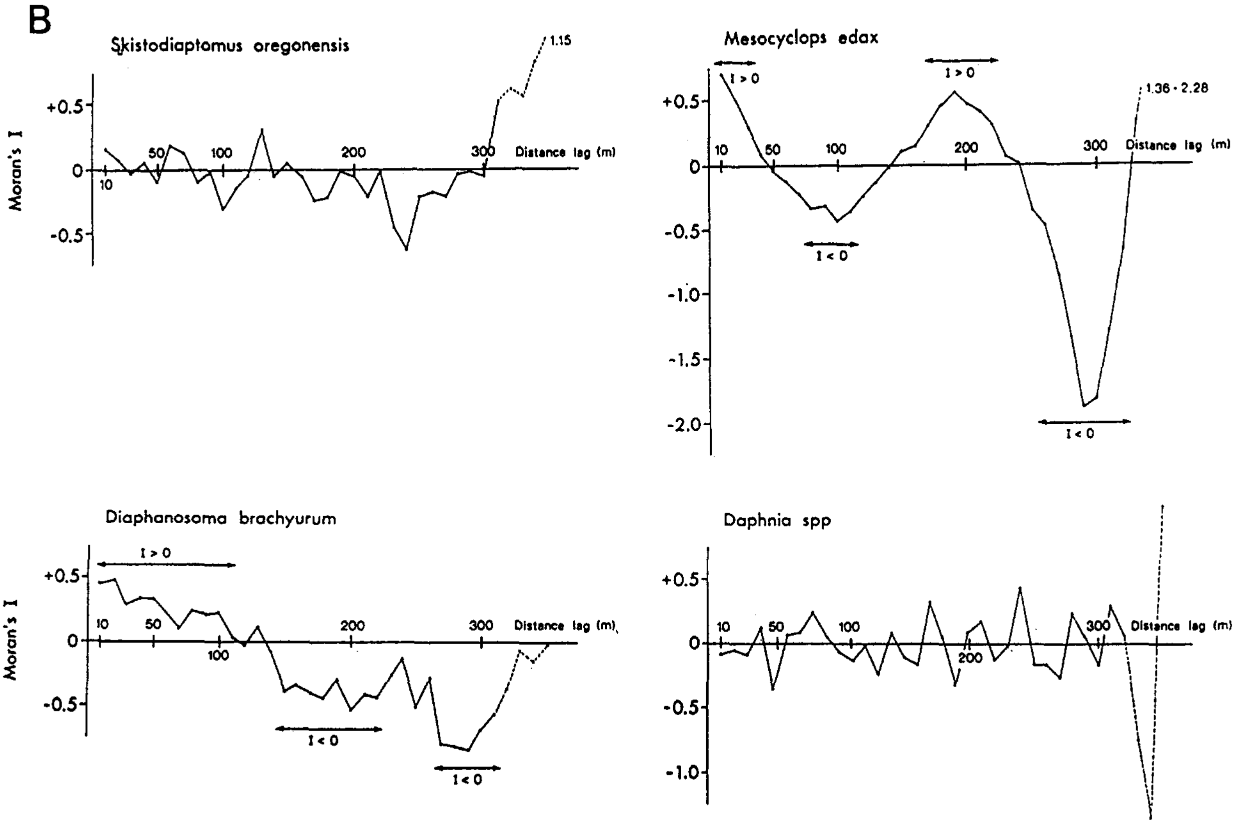


Fig. 5 B.

order to have an accurate evaluation of the 'functional heterogeneity' arising from the interactions between the ecological entities and their environment at any scale of ecological interest, the intrinsic spatial component of heterogeneity (spatial autocorrelation) must be partialled out of the species-environment relationships. Borcard *et al.* (1992) and Borcard & Legendre (1993) have developed a new method for this purpose, using partial canonical correspondence analysis; it allows partitioning of the respective effects of environmental factors and spatial structure of the samples. The spatial variation in ecological entities is partitioned into four independent fractions: (a) a fraction that is attributed to the non-spatially-structured part of the environmental processes (local environmental effects); (b) a second fraction explained by the spatially-structured part of these environmental processes (environmental gradients); (c) a pure spatial component (space structure), unexplained by any of the environmental variables included in the analysis, which may result from spatial structuring within the community due to behavioral factors, or else other spatially-structured physical or biological processes not included in the analysis; and (d) a fraction of the spatial variation that remains unexplained (undetermined) (Fig. 6). This method also enables the user to partition the effects of different generative processes of spatial heterogeneity (for example, abiotic *vs* biotic processes). This statistical tool looks promising for assessing 'functional heterogeneity', and recently it has been successfully applied to test the relative importance of abiotic and biotic forces driving the spatial heterogeneity of lacustrine zooplankton over both small regional and large geographic scales in Québec (Rodriguez *et al.*, 1993; Pinel-Alloul *et al.*, unpublished data).

Hierarchy of zooplankton patchiness across scales

Nested patchiness is a common feature of natural habitats (Kolasa & Rollo, 1991), and zooplankton spatial heterogeneity occurs at hierarchical spatial scales in both marine and freshwater environments (Haury *et al.*, 1978; Pinel-Alloul & Pont, 1991). The range of aggregated patterns may be considered as a continuum since driving forces originating from the various physical, chemical and biological factors of the envi-

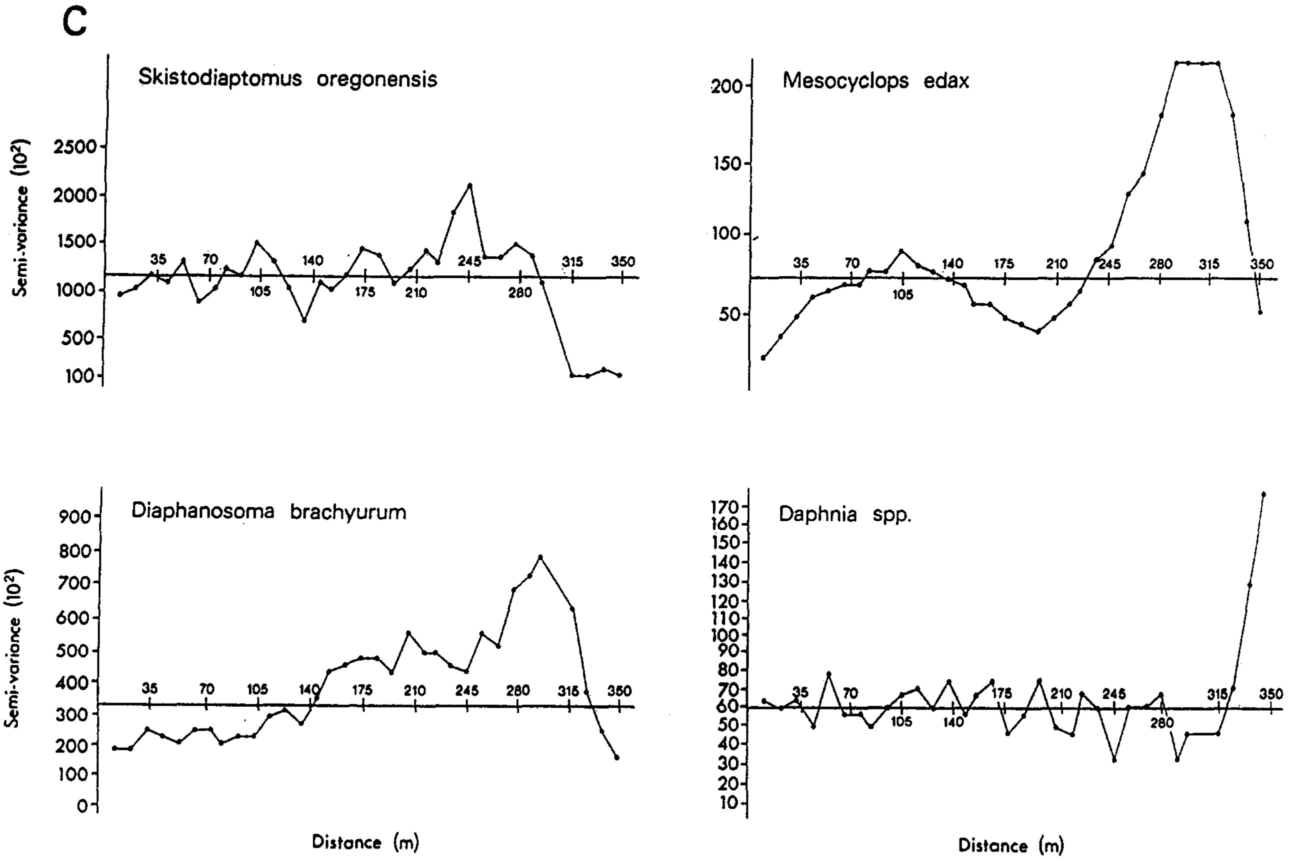


Fig. 5 C.

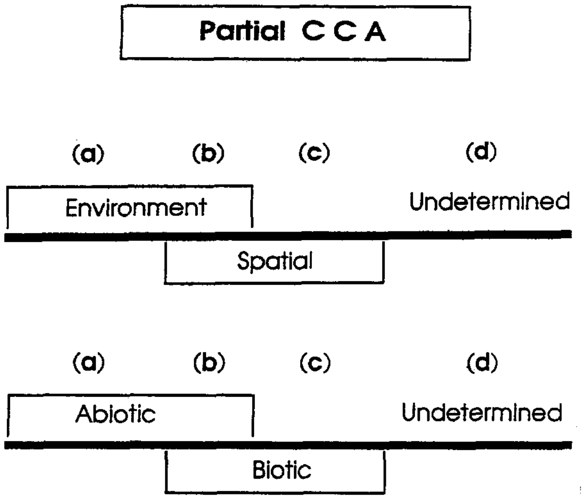


Fig. 6. Spatial variance partitioning of species-community data table following the method of Borcard *et al.* (1992).

ronment cascade from larger to smaller scales (Horne & Platt, 1984; Mackas *et al.*, 1985; Barry & Dayton, 1991).

In marine ecosystems, Haury *et al.* (1978) suggested that zooplankton patchiness exists in six different spatial scales from mega- to micro-scales (Table 3) and illustrated their scale-continuum concept over spatial and temporal axes with the Stommel diagram (Fig. 7). This diagram clearly shows that marine zooplankton patchiness occurs simultaneously at interdependent temporal and spatial scales. Heterogeneity on spatial micro-scales remains unchanged over very short-time scales, from minutes to hours, whereas heterogeneity over large spatial scales have higher temporal stability, from months and even centuries in the case of biogeographic patterns such as the zooplankton faunal provinces in the Pacific Ocean (Fig. 8). One exception to the temporal and spatial coupling, is the pattern of diel vertical migration which ranges over a wide variety of spatial scales.

In freshwater ecosystems, Malone & McQueen (1983) and Pinel-Alloul & Pont (1991) have reviewed

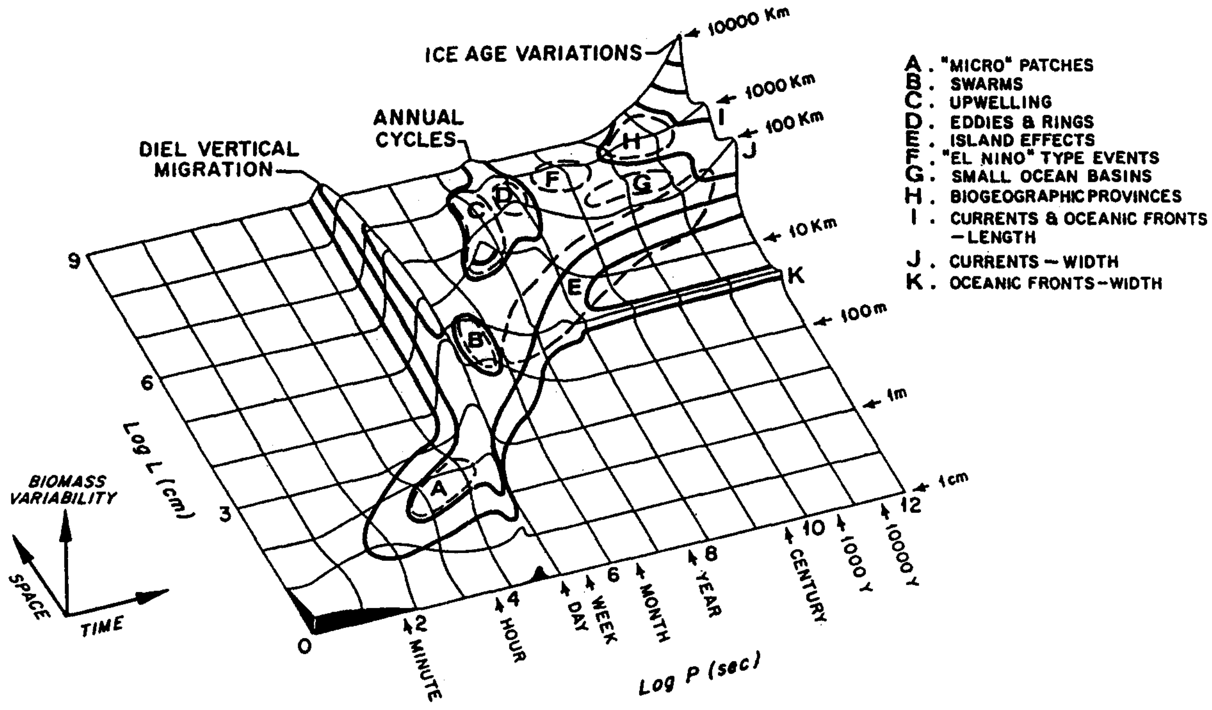


Fig. 7. Stommel diagram of space and time scales of marine zooplankton patchiness. (From Haury *et al.*, 1978).

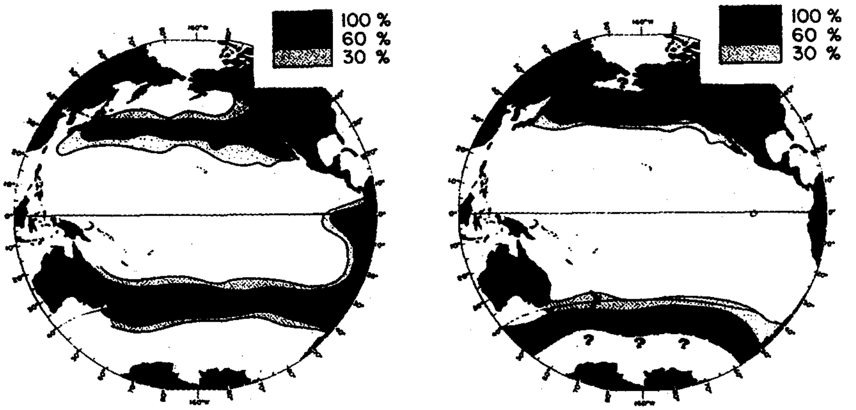
the literature on zooplankton patchiness scales. Four types of patch scales have been identified ranging from large-scale patches Type I: >1 km) to micro-scale patches (Type IV: <1 m), with coarse- (Type II: 10 m–1 km) and fine- (Type III: 1–10 m) scales as intermediate patch sizes (Table 4). None of these four spatial scales is necessarily associated with a given species-group, since the same taxonomic entity may exhibit different spatial scales in different water bodies and even within the same lake under different trophic conditions. However, large-scale patterns have all been identified on the horizontal axis of large lakes whereas coarse- to micro-scales patterns have been observed in smaller lakes either on their horizontal or vertical dimensions. The type IV pattern involves mostly swarms which are stable only in non-turbulent environments, and for littoral cladocerans as *Polyphemus pediculus* and *Scapholeberis.*

Abiotic processes leading to zooplankton heterogeneity

Environmental processes reported in literature to drive zooplankton patchiness in both marine and freshwater ecosystems are presented in Tables 3 and 4, respectively.

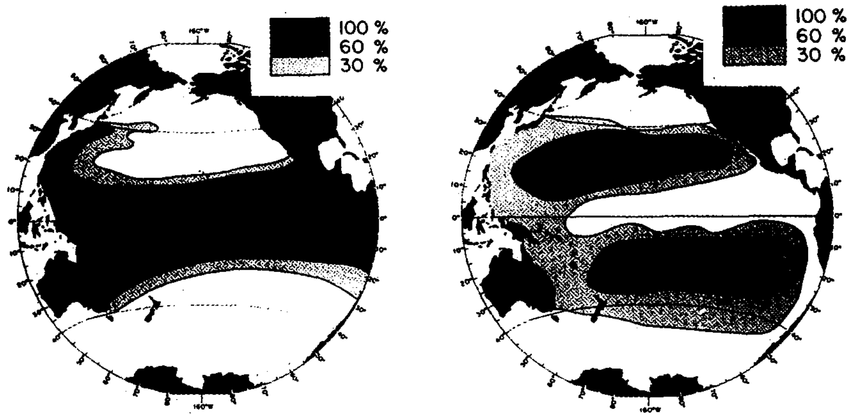
In marine systems, patterns of zooplankton patchiness at mega- to macro-scales are mostly linked to physical processes: climatic and hydrodynamic regimes, tidal and regional wind forces, and bottom and continent topography can generate oceanic gyres, coastal and upwelling eddies, surface circulation currents, and inflows or outflows which affect the distribution of pelagic and coastal zooplankton. At the largest scale, zooplankton oceanic faunal provinces are very stable and overlap directly the distribution patterns of primary production and the climatic regions defined by oceanic gyres (Fig. 8). Cascading across scales, from the largest to the smallest, leads to an increasing importance of coastal eddies, rings, upwelling, fronts, internal waves, and Langmuir circulation cells which have a more complex hydrodynamic structure and less temporal stability than the oceanic gyres. Barry & Dayton (1991) presented a detailed description of these hydrodynamic features relevant to marine plankton patchiness.

Several studies demonstrated a close relation between zooplankton spatial distribution and physical features of advective processes over meso-, macro-



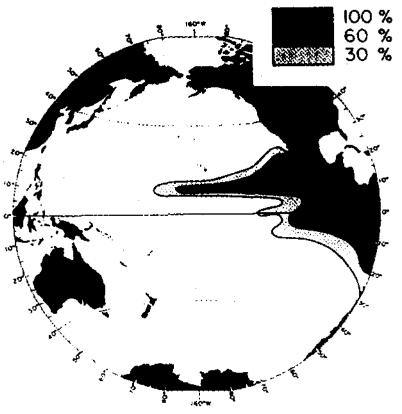
ESTIMATED PERCENT OF TRANSITION ZONE FAUNA PRESENT

ESTIMATED PERCENT OF SUBARCTIC OR SUBANTARCTIC FAUNA PRESENT



ESTIMATED PERCENT OF EQUATORIAL FAUNA PRESENT

ESTIMATED PERCENT OF CENTRAL FAUNA PRESENT



ESTIMATED PERCENT OF EASTERN

Fig. 8. Faunal provinces in the Pacific Ocean, defined from the distributions of 175 species of zooplankton. Darker shading indicates that a higher percentage of species characteristic of that province are present in samples. These provinces correspond directly to the major pattern of surface circulation in the Pacific. (From McGowan, 1971)

and coarse-scales. In the Atlantic Ocean, mesoscale eddies are formed by diversions of the Gulf Stream current. The cold-core rings in the North, and the warm-core rings in the South, constitute biologically isolated systems. Coastal eddies, as the California Current, affect the productivity and distribution of planktonic organisms by inducing vertical advective currents which increase the input of nutrients to the euphotic zone. Coastal upwelling often produces extreme patchiness of phytoplankton leading to high zooplankton grazing rates and productivity. An even tighter coupling was observed for the euphausiids in the continental shelf of Vancouver Island where their horizontal distribution and daytime depth of greater occurrence correspond to the California Current underwaters of 6–7 °C temperature and 33.75–34 ‰ salinity (Simard & Mackas, 1989). At coarse-scales, gelatinous zooplankton (ctenophores and medusae) concentrate in parallel lines along the convergent zones of Langmuir cells in Bonavista Bay, Nova Scotia (Hammer & Schneider, 1986; Schneider & Bajdik, 1992). In coastal lagoon environments, inversion of water flows between the laggon and the sea plays a major role in structuring zooplankton communities (Jouffre *et al.*, 1991). Finally, in estuaries and embayments, intrusion or outflow of saline or rich-nutrient waters, by increasing phytoplankton growth, result in higher zooplankton standing stocks (Paffenhofer, 1980; Sameoto & Herman, 1992). At fine- and micro-scales (Table 3), short-term physical turbulence can also cause zooplankton patch formation which may have important biological consequences for the feeding of pelagic fish larvae (Noda *et al.*, 1992) and the nutrient regeneration for phytoplankton in oligotrophic environments (Paffenhofer & Knowles, 1979).

In freshwater environments, large-scale patterns (Type I) as observed in very large lakes are related to structural and advective physical forces such as the morphometry of the lake basin, the river inflows, and the upwellings or inshore-offshore gradients (Table 4). For instance, the very diverse patterns of zooplankton horizontal distribution in Lake Winnipeg reflect the complexity of the water masses structured by lake morphology and configuration of river inflows (Patalas & Salki, 1992). The zooplankton structure in Lake Winnipeg comprises a core-community of 12 species distributed throughout the whole-lake scale and several marginals sub-groups characteristic of the river inflow inputs (Fig. 9). There was a higher similarity within the same basin than between the North and South basins, and climatic regimes and lake morphometry were the major factors explaining zooplankton structuring. In Lake Geneva, we examined horizontal structures both within the crustacean community and the abiotic factors related to water temperature, stability and nutrients. We found that temperature directly influences zooplankton distribution (path analysis: $r=0.43$, $P=0.0001$) which, in turn, affects ammonium concentration (path analysis: $r=0.53$, $P=0.00001$) as one of the excretion products (Guay, Pinel-Alloul, Angeli, Balvay & Legendre, unpublished data). In Lake Ontario, nearshore-offshore gradients in zooplankton abundance have been partly attributed to earlier warming in the nearshore water column (Johannsson *et al.*, 1991). Furthermore, the dynamics of river zooplankton is considered to be controlled by advective transport and tidal currents (Pace *et al.*, 1992), and in reservoirs, Hart (1990) showed that horizontal distribution of zooplankton reflected the turbidity gradient and associated changes in limnological abiotic attributes from the head-waters to the dam.

In smaller lakes, physical causal forces inducing coarse-scale patterns (Type II), are more variable and involve wind drift currents causing down-wind accumulation, internal seiches, and spiral Eckman currents, as well as the physical and chemical vertical stratification of lakes (Table 4). Our studies of zooplankton patchiness in a small Canadian lake (Pinel-Alloul *et al.*, 1988; Pinel-Alloul & Pont, 1991) showed that surface turbulence and advective processes in epilimnetic layers had a randomizing effect, whereas thermal stratification induced the highest degree of spatial heterogeneity. A number of processes have been suggested as the sources of variation in lake zooplankton spatial heterogeneity between the horizontal and vertical scales. Zooplankton have little directed movement on the horizontal scale beyong a few meters but can move more than 10 m vertically in response to diel changes in light level, predation and food resources (Bollens & Frost, 1989; Leibold, 1990; Ringelberg, 1991; Neill, 1992). Interaction between vertical shear or random turbulence and vertical migration allows zooplankton organisms to forage widely separated areas at little energy cost, but produces horizontal spreading of patches (Evans, 1978). Furthermore, physical and chemical gradients directly influence zooplankton vertical distributions. Recently, Hanazato (1992) demonstrated that a vertical physical gradient associated with low-oxygen hypolimnetic layers, limited the distribution of zooplankton over fine- and coarse-scales, in eutrophic lakes (Fig. 10). Finally, Langmuir circulation patterns and short-term convection currents in lakes are large-

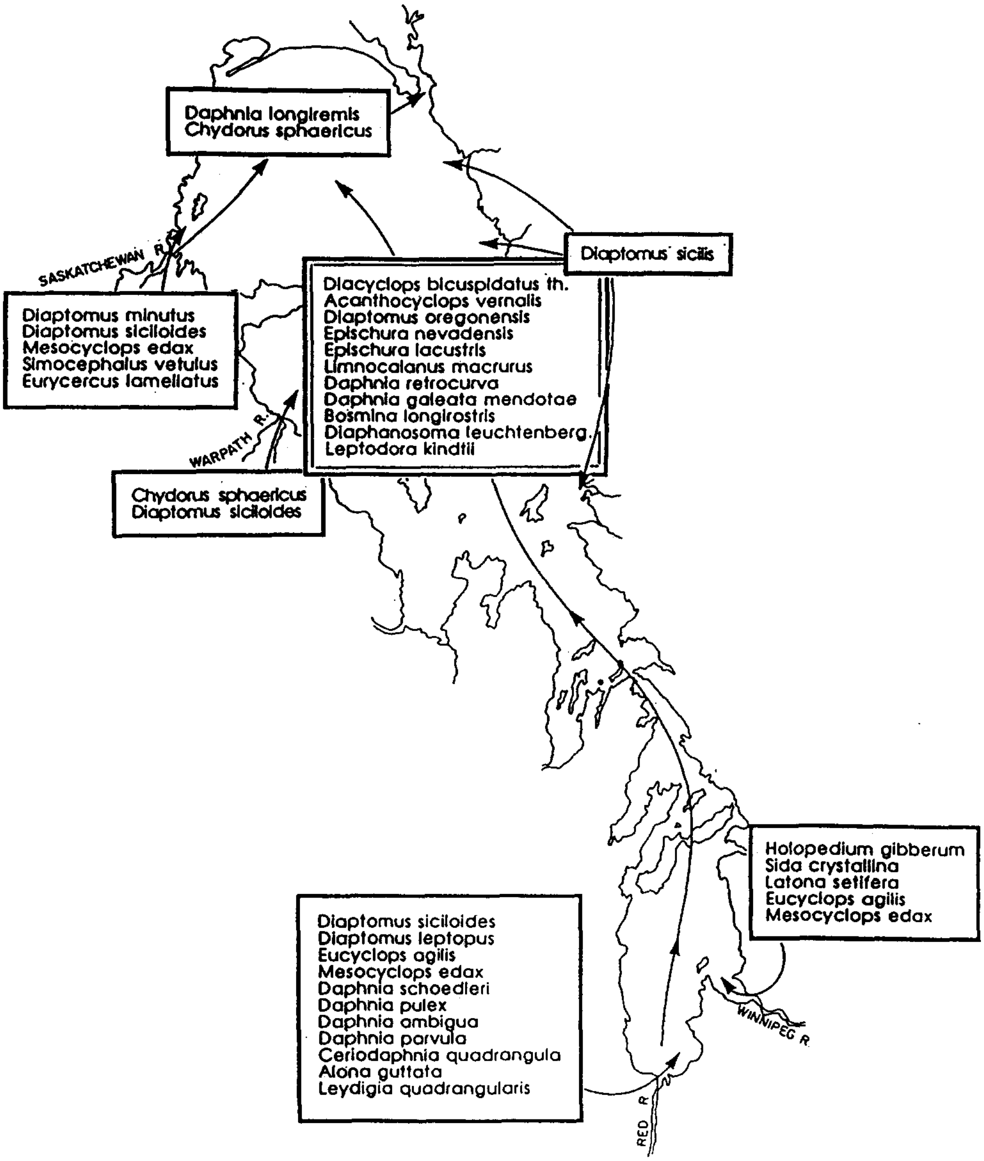


Fig. 9. Schematic diagram of the crustacean community structure in Lake Winnipeg. Core species (double frame) are established all over the lake whereas marginal unsuccessfull invaders (single frame) are brought in by river inflows. (From Patalas & Salki, 1992).

ly responsible for fine- and micro-scales zooplankton patchiness (Table 4).

Biotic processes leading to zooplankton heterogeneity

In addition to physical forces, biogenic environmental factors and biotic interactions may be partly responsible for marine and freshwater zooplankton patchiness, especially at smaller scales. In general, the relative importance of the biotic processes increases inversely with scale. However, even though the megascale oceanic faunal provinces are stable and bounded by hydrodynamic features, the processes that control the structure of marine zooplankton community within each province are, by lack of contrary evidence, thought to be biological (Barry & Dayton, 1991).

In macro- and coarse-patterns, zooplankton vertical and reproductive migratory behavior as well as phytoplankton intrusion and concentration produced

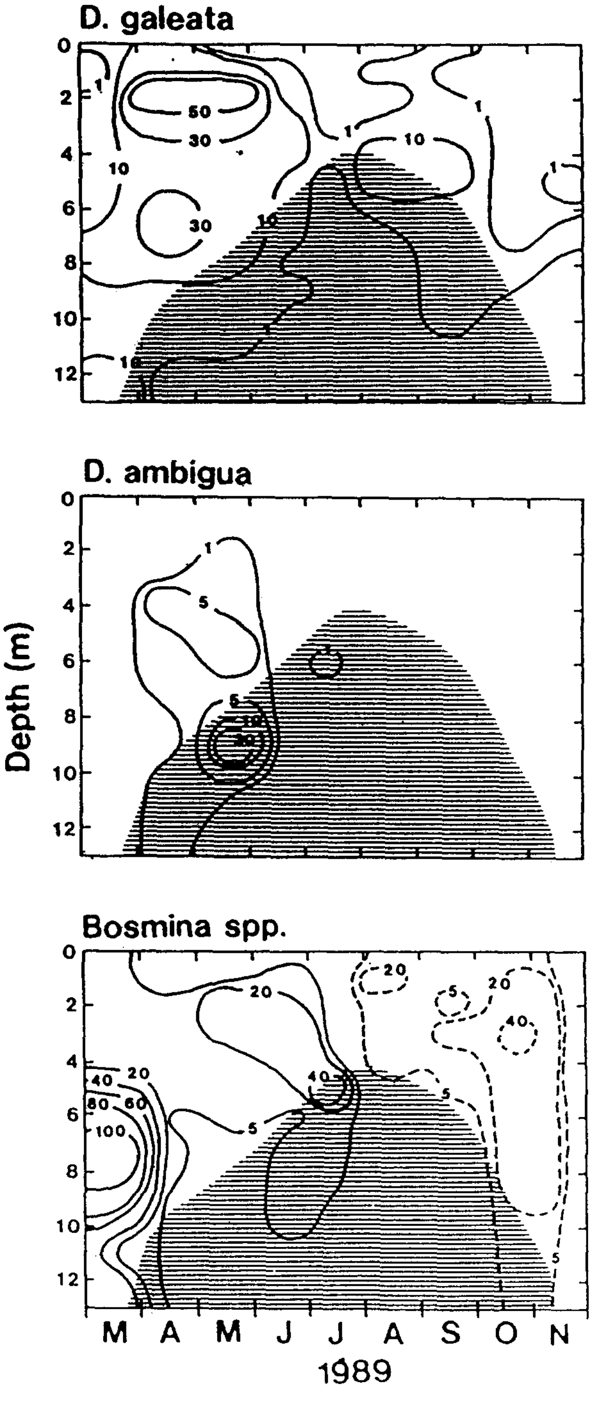


Fig. 10. Depth-time distribution of isopleths of number of the dominant Cladocera in Lake Nakanuma Japan). Shaded area shows the low oxygen layer (<3 mg. O_2 L^{-1}). (From Hanazato, 1992).

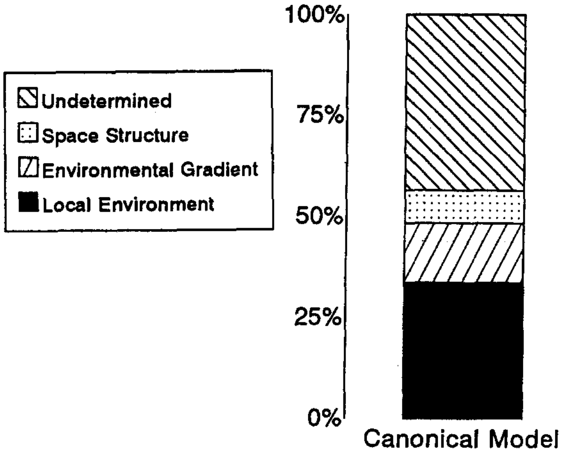
by coastal upwellings and eddies, outflows and Langmuir circulation cells are the main biotic processes enhancing zooplankton patchiness (Table 3). In marine ecosystems, euphausiid distribution patterns in the continental shelf of Vancouver Island are coincident with those of upwelled regions characterized by high phytoplankton biomass (Simard & Mackas, 1989). In freshwater ecosystems, the inshore-offshore decreasing gradient in zooplankton abundance in Lake Ontario could result either from increased vertebrate planktivory or from reduced food resources in the pelagic zone (Johannsson *et al.*, 1991). As a corollary, whole-lake patterns and shore avoidance behavior of macrozooplankton in small lakes could be related to invertebrate (Pinel-Alloul & Pont, 1991) or vertebrate (Gliwicz & Rykowska, 1992) predation, respectively. Both predation and exploitative competition explain the horizontal variation in the zooplankton community of the Ogochi Reservoir in Japan (Urabe, 1990). The horizontal and vertical scales of zooplankton patchiness are also interdependent. For example, in the core of the Gulf Stream ring 82-H, a region of low physical variability, a sharp transition occurred after sunset in the horizontal spatial heterogeneity of euphausiids and copepods as dielly migrating organisms moved into surface waters (Wiebe *et al.*, 1992).

At finer scales, predator-prey interactions mediated by swimming, and migratory or reproductive behavior, are the most important biotic forces driving zooplankton patchiness. The ability of the krill *Thysanoessa raschii* to detect algal patches and to change their swimming behavior in the presence of algal patchiness has been video-taped in mesocosms (Price, 1989). After the introduction of an algal patch, swimming speed of the krill doubled for individuals within the patch and the krill remaining in the algal patch over the 24-h experimental period turned back as they encountered the edge of the patch. A similar behavior has also been observed in marine and freshwater copepods (*Pseudocalanus minutus*, *Acartia tonsa*, *Mesocyclops edax*) which exhibit an increase in turning and looping in the presence of high food concentrations (Buskey, 1984; Wiliamson, 1981; Tiselius, 1992). Both mechanosensory and chemosensory cues contribute to the recognition of food and patch formation on high food conditions. Tessier (1983) observed an extreme zooplankton patchiness in a population of *Holopedium gibberum* which formed a single mobile patch on a scale of tens of meters; this type of cohesive patch moving over the lake could induce alternating periods of grazing and nutrient regeneration which have important effects on phytoplankton dynamics. Finally, micro-aggregations at scales from centimeters to a few meters in pelagic and littoral cladocerans have been usually associated with sexual reproduction, phototaxis and swarming behavior (Table 4).

Coupling of abiotic and biotic processes: the multiple driving forces hypothesis

Neither physical advective forces nor biological forces alone, can explain the complexity of zooplankton spatial heterogeneity observed in marine and freshwater ecosystems. Zooplankton patchiness over large and fine scales is the product of many physical processes interacting with many biological processes (Richerson *et al.*, 1978; Malone & McQueen, 1983; Pinel-Alloul & Pont, 1991). Legendre & Demers (1984) pointed out this physical-biological coupling in marine systems, which they termed hydrodynamic biological oceanography. They emphasized that the various physical, chemical, and biological factors of the environment are considered as the proximal agents through which hydrodynamic variability is transmitted to living organisms. A similar argument founded on hierarchy theory was presented by Allen & Star (1982) and Amanieu *et al.* (1989). They stated that physical processes *sensu lato* constitute the first step of the hierarchy of processes controlling ecosystems and influencing biological sub-systems while conversely, physical processes are less influenced by biological systems.

In this context, we recently introduced the 'multiple driving forces hypothesis' to explain spatial heterogeneity of lake zooplankton in Québec, and tested the primacy of abiotic factors in the model. The method of Borcard *et al.* (1992) was applied to partition the zooplankton variance into four fractions: a) local environmental effects, b) environmental gradient effects, c) pure spatial structure effects and d) undetermined variance. The results of this study indicate that both the abiotic factors related to water-chemistry gradients and the biotic bottom-up (phytoplankton structure) and top-down (fish community) factors significantly contribute to the observed zooplankton heterogeneity (Table 5). The effects of these environmental factors operating at local scale (fraction a) or over geographic gradients (fraction b) explain 48.2% of the zooplankton variance (Fig. 11). When considering only one of the environmental factors sets (physical and chemical characteristics, phytoplankton or fish community structure) in the model, abiotic physical and chemical factors, taken alone, explain 30.7% of the large-scale zooplankton variability, and have primacy over biotic factors which can only explain from 11.2 (phytoplankton) to 15.6% (fish) of zooplankton variance. The non-significance of the pure spatial effects indicates that most of the among-lake spatial zooplankton variation have been explained by the environmental gradients of water chemistry and lake morphology included in the study. However, the large amount of unexplained variance (d: 44%) suggested that other factors operating at the within-lake sampling scale, and not taken in account in the study, could exert influence on lake zooplankton variability as observed in another studies conducted at coarse- and fine-scales (Pinel-Alloul *et al.*, 1988; Pinel-Alloul & Pont, 1991).



Undetermined	43.7	
Space Structure	8.1	NS
Environmental Gradient	14.7	
Local Environment	33.5	

Fig. 11. Percentages of zooplankton spatial variance explained by local effects of environmental factors (a), environmental gradients (b), spatial structure (c) and undertermined variance (d) for Québec lakes. (From Pinel-Alloul *et al.*, unpublished data).

Comparisons of results of our study and that of Rodriguez *et al.* (1993) conducted at a smaller spatial scale suggest a scaling effect on the relative importance of abiotic and biotic factors in the environmental control of zooplankton community. Over large geographic scale, abiotic forces should be predominant and, in contrast, the biotic forces should have the primacy at small spatial scales (Fig. 12). In marine ecosystems, primacy of physical advective processes over biological ones has been well supported by several studies.

Haury *et al.* (1978) suggested a shift from physical to biological forces from large to small spatial scales. They stated that climatic, advective and vectorial processes occur at the largest scales (mega-, meso- and macro-) while reproductive, behavioral and co-active patterns occur only at the smallest scales (coarse-, fine- and micro-). On large-scale features such as oceanic gyres and meso-scale eddies, physical advective factors exert a strong control over biological patterns (Barry & Dayton, 1991). Simard & Mackas (1989) also explain euphausiid distribution patterns first by the direct effects of the advective forces, and secondarily by their interaction with patterns of vertical migration. In freshwater environments, although the role and primacy of physical and chemical forces have been greatly demonstrated in eutrophication and acidification studies, we do not deny or diminish the importance of the many biotic forces known to structure communities. In a conceptual framework of the effect of scaling on processes structuring community composition, one should view the structuring factors (abiotic and biotic), events and processes as a series of mutual filters acting on the communities at continental, regional, lake-type, and local scales to produce different patterns of community composition or species distribution (Tonn *et al.*, 1990).

Henceforth, the zooplankton community should be perceived as a spatially well-structured and dynamic system that requires a combination of both abiotic and biotic explanatory factors for a better understanding and more realistic and reliable predictions of its ecology (Carpenter, 1988). It is very important for ecologists to consider physical as well as biological processes in their sampling design because they constitute the fundamental constraints to which individuals, populations and communities respond. As most biotic and abiotic processes are scale-dependent, this concept implies the necessity for comprehensive sampling programs that take into consideration the pertinent spatial scales of physical and biological heterogeneities.

Conclusions

1. Nested patchiness is a common feature of zooplankton community and spatial heterogeneity occurs in hierarchical clusters of spatial scales in both marine and freshwater environments. In marine ecosystems, zooplankton patchiness exists at six different spatial scales (mega-: 10^3–10^4 km; meso-: 10^2— 10^3 km; macro-: 10–10^2 km; coarse-: 10^2–10^4 m; fine-: 1-10^2 m; micro-: 10^{-2}–1 m) which interact with temporal scales of heterogeneity. In freshwater ecosystems, four types of patch scales have been identified, ranging from large-scale patches (Type I: >1 km) to micro-scale patches (Type IV: <1 m), with coarse- (Type II: 10 m–1 m) and fine- (Type III: 1–10 m) scales as intermediate patch sizes.
2. Since the last two decades, new sampling methods based on advanced technologies (acoustic devices, the Optical Plankton Counter (OPC), and video systems) have been developed to assess zooplankton patchiness in both marine and freshwater ecosystems. On the one hand, acoustic devices and optical particle counter are more suitable for large-scale survey but do not provide taxonomic information. On the other hand, video systems are intended for studying both large and small scales and they have the unique advantage of providing taxonomic and individual behavior information. In many instances, data requirements of studies of zooplankton spatial heterogeneity on different scales should be satisfied by taking advantage of the complementary characteristics of a combination of devices.
3. Studies on zooplankton spatial heterogeneity refer both to the quantification of the degree of heterogeneity ('measured heterogeneity') and to the estimation of the heterogeneity resulting from the interactions between the organisms and their environment ('functional heterogeneity'). Most earlier works have dealt with the estimation of the 'measured heterogeneity' and led to the development of statistical tools as indices of spatial aggregation, variance:mean relationships and spatial analysis methods. More recent studies have investigated the 'functional heterogeneity', using a method of variance partioning which allows to single out the respective effects of different driving processes.
4. Neither physical advective forces nor biological forces alone, can explain the complexity of zooplankton spatial heterogeneity observed in both marine and freshwater ecosystems. Zooplankton patchiness over large- and fine-scales is the product of many physical processes interacting with many biological processes. My review clearly supports the 'multiple driving force hypothesis', and confirms the primacy of abiotic factors in the models of environmental control of zooplankton spatial heterogeneity at large spatial scales, and suggests a

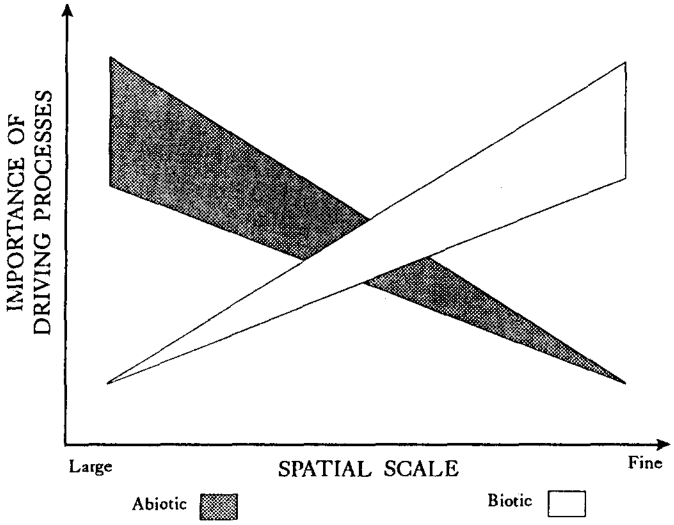


Fig. 12. Hypothetical model of relations between sampling spatial scale and the relative importance of abiotic and biotic processes controlling zooplankton spatial heterogeneity in marine and freshwater ecosystems.

greater importance of biological processes at smaller scales.

5. The zooplankton community must be perceived as a spatially well-structured and dynamic system that requires a combination of abiotic and biotic explanatory factors for a better understanding and more realistic and reliable predictions of its ecology. In ecological study of zooplankton spatial heterogeneity, sampling design must take into consideration the pertinent spatial scales of physical and biological variability because they constitute the fundamental constraints to which individuals, populations and communities respond.

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