

Analysis of scale-dependent processes with dimensionless ratios

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Horne, J. K. and Schneider, D. 1994. Analysis of scale-dependent processes with dimensionless ratios. – *Oikos* 70: 201–211.

Awareness of the role of scale in ecological research has increased over the last decade but few tools have been developed to evaluate biological and physical processes that generate scale-dependent biological patterns. We describe a procedure that combines demographic, growth, and kinematic rates to evaluate the spatial and temporal dynamics of population biomass. Values of dimensionless ratios are plotted and contoured as a function of spatial and temporal scale to summarize knowledge of processes that generate variability in a biological quantity. This summary can be used to indicate variance generating processes at any scale of interest, to identify potential research areas and appropriate sampling scales for field studies, and to limit the range of scales over which conclusions can be generalized.

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Recent publications (e.g. Wiens 1989, Menge and Olson 1990, Holling 1992, Levin 1992) re-iterate the importance of scale in the description of ecological variability. The scale-dependence of biological and physical observation is well recognized in both aquatic (Stommel 1963, Smith 1978, Steele 1978a) and terrestrial (Watt 1925, 1947, Greig-Smith 1952, Urban et al. 1987) ecosystems. Many techniques have been developed to quantify scale-dependent ecological pattern (e.g. Platt and Denman 1975, Ripley 1981, Greig-Smith 1983) and the consistency of results has been compared among techniques (O'Neill et al. 1991, Cullinan and Thomas 1992, Turner et al. 1992). However there remains a lack of quantitative tools that evaluate the relative importance of biological and physical processes capable of generating observed patterns.

Scale-dependent physical or biological pattern can be summarized in a diagram by plotting variance as a function of spatial and temporal scale. The first diagrammatic descriptions of scale-dependent physical variability were estimates of sea level and deep ocean current variance (Stommel 1963). Haurly et al. (1978) used this presenta-

tion to develop a conceptual model of zooplankton biomass variability. This was the first comparison of biological variability across a wide range of scales and remains the only published Stommel diagram of an ecological variable (Marquet et al. 1993). Variations of Stommel diagrams show concentrations of spatial and temporal variability as a function of space and time scale for aquatic (e.g. Steele 1978b, 1989, Harris 1986, Dickey 1990) and terrestrial (e.g. Delcourt et al. 1983) ecosystems. These are intuitive diagrams where the boundaries of any feature in a plot indicate the minimum and maximum scales of variability for the quantity of interest. The construction of a true Stommel diagram requires simultaneous variance estimates at all spatial and temporal scales. This is rarely possible at intermediate or large spatial scales as the passage of time during data collection precludes independent calculation of spatial and temporal variance. Stommel diagrams summarize scale-dependent variability in a quantity of interest. They do not indicate the biological or physical processes that generate observed patterns.

Variance generating processes are often inferred from

Accepted 14 December 1993

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ISSN 0030-1299

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observed patterns by identifying spatial and temporal scales of maximum variability. This empirical approach uses variance to mean ratios (Greig-Smith 1952, 1983, Southwood 1978, Andrew and Mapstone 1987), spectral analysis (Jenkins and Watts 1968, Platt and Denman 1975), allometric relations (Huxley 1932, Peters 1983, LaBarbera 1989), or geostatistical tools (Getis and Franklin 1987, Rossi et al. 1992) to quantify scale-dependent spatial or temporal variance of biological quantities. Scales of maximum biological variance are then matched to dominant physical or biological processes at the same scale (e.g. Greig-Smith 1952, Denman and Powell 1984, Mackas et al. 1985). An assumption in this matching approach is that pattern is directly coupled to processes acting at the same scale. This may not be true in all cases. Both theoretical (e.g. May 1976) and experimental (e.g. Dwyer and Perez 1983) evidence suggest that non-linear relationships occur between ecosystem components. An aquatic example is growth of phytoplankton altering the transmission of light in the water column due to self-shading (Shigesada and Okubo 1981). A second assumption of this matching approach is that biological variability and the coupling of physical and biological processes occur at 'characteristic' scales. Single plots of variance as a function of scale show concentrations of variance among terrestrial (Greig-Smith 1952, Kershaw 1957) and marine (Grassle et al. 1975, Schneider 1989, Rose and Leggett 1990) organisms. But when multiple plots are averaged, these scale-dependent concentrations of variance disappear (Weber et al. 1986, Horne 1994, Schneider 1994). In populations of mobile aquatic organisms, plots of variance as a function of scale do not reveal any 'characteristic' scales on average.

As an alternative to inferring process from statistical descriptions of biological variance, we propose the use of dimensionless ratios to evaluate the relative importance of variance generating processes as a function of scale. Comparison of scale-dependent rates within a dimensionless ratio assesses the relative contribution of biological or physical processes in the generation of biological variability. Similar comparisons using a complete set of ratios identify all potential processes that regulate variability in a biological quantity of interest. Dimensionless ratios have been used in ecology to identify mechanisms of plankton variability (O'Brien and Wroblewski 1973, Denman and Platt 1976, Okubo 1978), examine growth and physiological rates as a function of body size (Günther 1975, Platt and Silvert 1981, Heusner 1987), summarize spatial variability in marine nekton (Schneider 1991, 1993), and evaluate complex problems in wildlife management (Schneider et al. 1993).

In this paper we use dimensionless ratios to summarize knowledge of variance generating processes across spatial and temporal scales. This summary identifies dominant variance generating processes at any scale of interest and can be used to improve the design of field sampling programs. The application of dimensional reasoning to evaluate competing processes complements the quantitative

description of scale-dependent biological pattern. It neither replaces statistical techniques, nor is it directly comparable to them.

Methods

Prior to any field sampling, a crucial task is to identify variables to be measured and appropriate scales of measurement for each variable. A scale of measurement has two components – a resolution and a range. The resolution or grain is the minimum sample unit (e.g. quadrat size) while the range is the maximum extent of the sample (O'Neill et al. 1986, Wiens 1989). To summarize the relative importance of biological or physical processes that generate scale-dependent biological variability, we propose a 'generic' procedure consisting of 4 steps: 1) state the quantity of interest. 2) write an equation incorporating all potential sources of variability for this quantity. 3) calculate dimensionless ratios. 4) plot and contour ratio values in rate diagrams using existing data.

To illustrate this procedure, we examine the spatial and temporal dynamics of capelin (*Mallotus villosus*) biomass distribution in the northwest Atlantic. Capelin are a pelagic, schooling fish species inhabiting sub-Arctic and Arctic waters in the Atlantic and Pacific oceans (Jangaard 1974). In the northwest Atlantic, adult capelin (≥ 3 yr) migrate from offshore to coastal waters to spawn on gravel beaches during June and July (Carscadden 1983). During this period, capelin form the basis of a multimillion dollar commercial fishery (Carscadden 1983). They are a key forage species for marine mammals, fish, and marine birds (Bailey et al. 1977), and they experience spawning mortality in excess of 80% (Carscadden and Miller 1980). Eggs hatch within the beach gravel in 9–20 d (Templeman 1948, Frank and Leggett 1981) and are transported offshore (Fortier and Leggett 1982, 1983). Surviving adults and juveniles remain offshore during autumn and winter (Bigelow and Schroeder 1963, Bailey et al. 1977). In summary, changes in the distribution of capelin biomass are a result of demographic (recruitment, mortality), growth, and kinematic (active and passive movements) processes acting within a wide range of spatial and temporal scales.

The quantity of interest in this example is the proportional rate of change of capelin biomass in the northwest Atlantic. The rate of change of biomass has dimensions time^{-1} . The biomass B of a group of organisms (i) is the product of the number of animals N multiplied by their individual mass M :

$$B = \sum_{i=1}^n N_i M_i \quad (1)$$

The concentration of biomass is defined as:

$$[B] = \frac{NM}{V} \quad (2)$$

where V is the volume occupied. To simplify the notation we use a dot over a symbol to signify the proportional rate of change in the quantity represented by the symbol. Hence, the proportional rate of change in the concentration of biomass $[B]$ is:

$$[\dot{B}] = [B]^{-1} \frac{d[B]}{dt} \quad (3)$$

The second step is to write an equation containing potential processes that affect the concentration of capelin biomass. Change in the concentration of biomass $[\dot{B}]$ is a function of change in biomass due to recruitment and mortality \dot{N} , somatic growth \dot{M} , the divergence due to fluid motions \dot{V}_F , and the divergence due to individual motions relative to the fluid \dot{V}_I as shown in Appendix A. Five research areas are integrated by the equation that expresses the rate of change in biomass concentration:

$$[\dot{B}] = \dot{N} + \dot{M} - \dot{V}_F - \dot{V}_I$$

biomass
demo-
growth
fluid
behaviour
distribution
graphics
mechanics

(4)

The third step combines terms from eq. (4) to form dimensionless ratios. If terms in an equation are dimensionally heterogeneous, a complete set of ratios is obtained by dimensional analysis (Bridgman 1922). If all terms in an equation have the same units then ratios can be combined from any pair or group of terms. This flexibility enables the formation of ratios relative either to a process of interest (e.g. Schneider 1992) or to the combination of multiple terms into functionally important single terms (Fischer et al. 1979). In eq. (4) we can form 3 ratios relative to the fluid mechanics term or combine demographic and kinematic terms to form population dynamics and construct a single ratio with somatic growth.

In the capelin biomass example, all terms in eq. (4) have dimensions time^{-1} and so we formed ratios from the equation. We used biological reasoning to select pairs of terms to compare. For example we were more interested in comparing the two kinematic terms, \dot{V}_F and \dot{V}_I , than comparing one of the kinematic terms to demographics \dot{N} or somatic growth \dot{M} . A formal approach illustrating the use of dimensional analysis to form ratios from eq. (4) is provided in Appendix B. The formal approach ensures that redundant ratios are not included.

The first dimensionless ratio compares somatic growth \dot{M} to the net result of demographics \dot{N} and kinematics \dot{V} .

$$\frac{\dot{M}}{\dot{N} - \dot{V}} \quad (5)$$

Biomass concentration increases if animals grow ($\dot{M} > 0$), increase in number ($\dot{N} > 0$), or contract into a smaller volume of water ($\dot{V} < 0$). At small time scales relative to the life span of the organism, changes in population biomass due to somatic growth are limited and the value of the ratio is expected to be much less than 1. Spatial or temporal variability of a sample becomes a function of the change in number of individuals or the volume in which they occur rather than a change in mass of organisms. Over longer temporal scales the value of the ratio is expected to approach 1. Large positive changes in growth \dot{M} and a ratio greatly exceeding 1 are typical for long-lived (\dot{N} small) species that are managed in large geographic areas (\dot{V} small). Small changes in somatic growth \dot{M} coupled with a ratio much less than 1 (\dot{N} large, \dot{V} small) are expected at spatial and temporal scales associated with the capelin spawning season.

The demographic to kinematic ratio relates recruitment and mortality to movements.

$$\frac{\dot{N}}{\dot{V}} \quad (6)$$

If the ratio is greater than 1 then demographics prevail over kinematic processes. A ratio less than 1 indicates that kinematics will dominate over demographic processes. Values of the ratio can be expected to be near unity at time scales of a cohort and at space scales comparable to the range of the population. In many populations, kinematic processes dominate at small temporal and spatial scales, while demographic processes dominate at larger temporal and spatial scales.

The kinematic ratio compares locomotory velocities of the organism to passive velocities within the fluid.

$$\frac{\dot{V}_I}{\dot{V}_F} \quad (7)$$

If individual motions dominate, the kinematic ratio will exceed 1. The magnitude of \dot{V}_I is a function of the locomotory capacity and life history stage of the organism. An example is the relative mobility of fish larvae compared to adults. As the mobility of an organism decreases, \dot{V}_I approaches 0. When organisms drift passively with the fluid, the value of the ratio is much less than 1. Values of \dot{V}_F are sensitive to study location and spatial scale. Lentic and lotic environments will differ in the potential for passive drift of any organism. Passive drift may also be important to terrestrial organisms, including seeds, small insects, and spiders. At large spatial scales, the range of a study may encompass autonomous circulation features associated with the fluid (e.g. gyres), thereby making \dot{V}_F small and the kinematic ratio large. If the value of the ratio is approximately equal to 1, changes in the distribution of biomass due to movement may depend on the

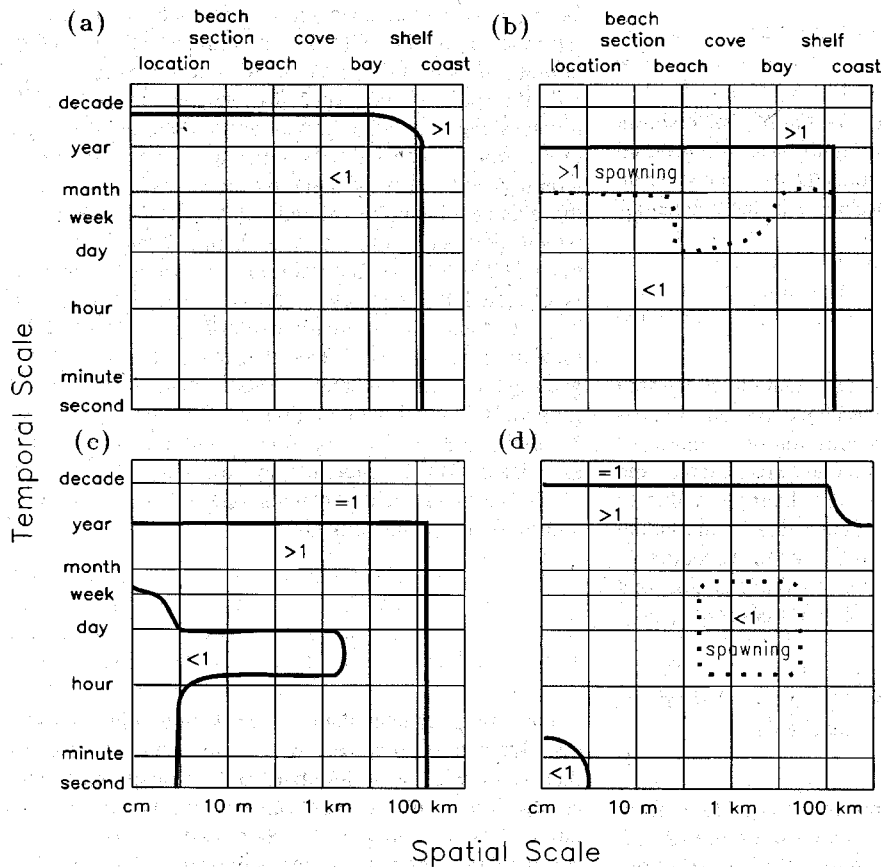


Fig. 1. Contoured rate diagrams of dimensionless ratio values for adult capelin biomass distribution in the northwest Atlantic. Ratios are contoured less than 1 (<1), equal to 1 (=1), and greater than 1 (>1). a) Growth to population dynamics (demographics - kinematics) ratio, $M/(N-V)$. b) Demographics (recruitment + mortality) to kinematic (locomotory + passive motions) ratio, N/V . Dotted line indicates shift in contour during spawning season. c) Locomotory to fluid (passive) motion ratio, V_f/V_p . d) Recruitment to natural and harvesting mortality ratio, $N_r/(N_m + N_f)$. Dotted line indicates scales of mortality during spawning season.

interaction between biological and physical processes. High, intermediate, and low values of this ratio correspond to Wiebe and Flierl's (1983) biological, physical-biological, and physical distributional mechanisms.

The demographic ratio measures the importance of recruitment N_r relative to mortality N_z . In capelin, as in other commercially important species, mortality N_z is partitioned into natural N_m and harvesting N_f mortality:

$$\frac{N_r}{N_m + N_f} \quad (8)$$

Over short time scales, this ratio is greater than 1 during the breeding season of capelin and less than one during the remainder of the year. At the spatial scale of the population range and the temporal scale of a cohort, the value of the ratio will approach unity. In unexploited populations, maintenance of biomass levels at equilibrium is indicated by a value of 1. Increased mortality due to predation or the onset of harvesting reduces this value below unity unless a compensatory increase in recruitment occurs at low densities. Commercial fisheries managers maintain the value of this ratio near unity at time

scales of several years by regulating harvest mortality N_f through quotas and gear restrictions.

The fourth step in the procedure is the plotting of each dimensional ratio as a function of spatial (x-axis) and temporal (y-axis) scale using existing data. In many ecological systems precision of calculations may be limited by a paucity of data at large spatial and temporal scales. We suggest an iterative procedure that uses order of magnitude calculations to estimate initial values of dimensionless ratios. If data are limited or unavailable, calculations can be made at 'benchmark' spatiotemporal scales. Nominal (<1, 1, >1) contours are then drawn based on these benchmarks. If data are available over a wide range of scales, spatiotemporal scales where transitions between dimensionless ratio values occur are marked. Contour lines are then drawn to connect transition points. Location of dimensionless ratio contours are refined as additional data are obtained from field studies. The inability to calculate dimensionless ratio values at a specific scale indicates a potentially important research area.

Independent plotting of rate diagrams makes perceptions of the relative importance of competing processes explicit. Comparison of independent rate diagrams high-

lights discrepancies between ratio values and can be used to focus the discussion of large research groups on dominant scale-dependent processes. In this study each of us independently calculated dimensionless ratio values and plotted a set of rate diagrams for adult capelin in the northwest Atlantic. Diagrams for each ratio were compared and then combined to form a composite. When comparing diagrams, we found that plots were repeatedly similar with only minor differences. For example one author omitted tidal processes when estimating values of the kinematic ratio and so this was included in the composite.

Results

We used data from capelin assessment documents and published velocities of the Labrador and Newfoundland inshore currents to estimate scale-dependent ratios in rate diagrams. Order of magnitude calculations showed whether the absolute value of any dimensionless ratio was less than, equal to, or greater than 1 at a given spatiotemporal scale. Contour lines marked the spatial and temporal scales where dimensionless ratios changed value.

The major feature in the rate diagram of capelin growth to population dynamics ratio (Fig. 1a) reflects the persistence of Newfoundland-Labrador capelin populations at large scales. At spatial scales larger than the continental shelf and temporal scales larger than a year the value of the ratio is greater than 1. This is a result of changes in the concentration of biomass due to somatic growth exceeding changes due to population dynamics. Capelin growth, as indicated by length, increases an average of 40 900% or 10 225% of initial hatch length per year during the first 4 years of life (Templeman 1948). This rate exceeds that of partial recruitment to the adult stock – 53% per year (Carscadden and Miller 1981), spawning mortality – 80% of spawning stock per year (Carscadden and Miller 1980), fishing mortality – 0.05% of estimated biomass per year (Carscadden et al. 1991), and the net kinematic rate – 0% since the population remains on the continental shelf. Recruitment, mortality and kinematic rates exceed somatic growth rates at smaller scales and the value of the ratio is less than 1.

Values of the demographic to kinematic ratio (Fig. 1b) vary depending on capelin reproductive status. At temporal scales of a year and spatial scales of the continental shelf changes in the concentration of capelin biomass due to demographic processes exceed changes due to kinematics and the value of the ratio is greater than 1. Partial recruitment to the adult population (4 years) is 53% per year (Carscadden and Miller 1981). Natural mortality is typically assumed to be 30% per year in capelin (e.g. Carscadden and Miller 1980). Changes in the volume occupied by capelin populations are negligible at these scales and therefore the value of the kinematic term is

near zero. At sub-annual scales passive and active movements of capelin increase the value of the kinematic term and the value of the ratio is less than 1. During the spawning season, the location of the unity contour shifts to the spatial scale of a spawning beach or cove (100–1000 m) on a day to week scale. This is a result of increased mortality due to spawning – approximately 2% of spawning fish per day (Carscadden and Miller 1980) and inshore harvesting – 0.001% of total estimated biomass per day (Carscadden et al. 1991). Concentrated predation on capelin by fish, seabirds and marine mammals also occurs during this period (c.f. Carscadden 1983) but lack of data prevented an estimate of mortality rates due to natural predation.

The unity contour in the diagram of the kinematic ratio (Fig. 1c) is also located at the scale of the entire population. On the continental shelf over an annual cycle, passive drift associated with the Labrador Current – typical surface speed of inshore branch 0.1 ms^{-1} (Helbig et al. 1992), is balanced by the annual migratory cycle of adult fish (c.f. Carscadden 1983). At temporal scales less than a year and the continental shelf, changes in biomass concentration due to swimming exceed changes due to passive drift and the value of the ratio is greater than 1. At spatial scales of kilometres to metres and temporal scales of weeks to seconds, potential changes in the concentration of biomass due to passive drift with tides, currents and internal waves (Yao 1986, de Young et al. 1993) exceed changes due to active movements. Hence the value of the ratio is less than 1. The dominance of passive movements at these scales disappears during the spawning season when aggregations of adult capelin migrate to coastal waters.

At the largest scales in the rate diagram of the demographic ratio (Fig. 1d), persistence of a population requires a balance between recruitment and mortality. The resulting value of the demographic ratio must equal 1. On an annual scale over the spatial range of the population, recruitment generally exceeds natural and harvesting mortality. Large decreases in recruitment combined with increased natural and harvesting mortality may reduce the value of the ratio below unity at these scales in any particular year. For example, capelin recruitment measured as 2-year-olds dropped by a factor of 35 between the 1973 and 1976 year-classes in NAFO Division 2J3K (Carscadden and Miller 1981). During the spawning season, mortality exceeds recruitment to the adult population. This reduces the value of the demographic ratio to less than one at spatial scales of hundreds of metres to tens of kilometres and temporal scales of hours to weeks. At the scale of an individual capelin, natural and harvesting mortality exceeds recruitment and occurs at scales less than a metre and lasts no more than minutes.

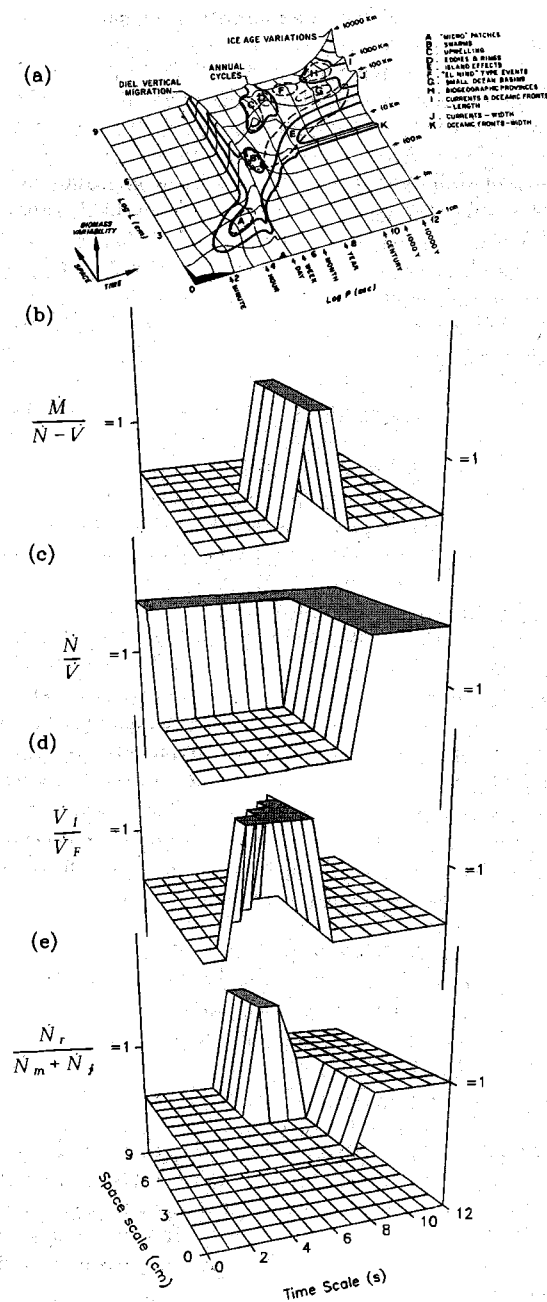


Fig. 2a). Stommel diagram of zooplankton biomass variability (from Haury et al. 1978). Nominal contoured rate diagrams (<1 , $=1$, >1) of b) growth to population dynamics dimensionless ratio, $M/(N-V)$ c) demographic to kinematic dimensionless ratio, N/V d) locomotory to fluid (passive) motion dimensionless ratio, V_l/V_f and e) recruitment to natural and harvesting mortality dimensionless ratio, $N_r/(N_m + N_f)$. Shaded regions indicate a ratio value greater than 1.

Discussion

The proposed framework is not a panacea for evaluating pattern generating processes. It is a technique that summarizes and displays existing knowledge of scale-dependent processes in any ecological system. Rate diagrams can be used to evaluate the relative importance of variance generating processes at any scale of interest and to identify sampling scales in process oriented research. This is an iterative procedure where ratio values and contour locations are refined as new data are gathered.

A plot depicting biological variability as a function of space and time combined with a set of rate diagrams synthesizes all knowledge of scale-dependent pattern and process for a biological quantity. Comparison of scale-dependent variability to dimensionless ratio values identifies processes that are likely to generate variability at that scale. This presentation avoids the assumption that a single biological or physical process is directly linked to pattern at any scale, and that coupling of biological and physical processes occurs at characteristic spatial and temporal scales. To further illustrate the advantages of using dimensionless ratios we constructed a set of zooplankton rate diagrams to identify potential variance generating processes in the Haury et al. (1978) Stommel diagram of zooplankton biomass variability (Fig. 2a). Dimensionless ratio values were estimated across the same range of scales and nominal contours (<1 , $=1$, >1) were plotted in a column of rate diagrams (Fig. 2b-2e). Zooplankton were assumed to be an unexploited population of mid-latitude, zooplanktonic organisms with the limited locomotory capability of copepods. As with the capelin diagrams, we calculated and plotted ratio values independently, then compared and discussed differences to form a composite for each ratio.

The rate diagram of the growth to population dynamics ratio (Fig. 2b) shows greater change in the concentration of biomass due to somatic growth than due to demographic and kinematic processes at spatial scales up to a kilometre and temporal scales from days to a month. The value of the ratio is less than 1 at all other scales. In the demographic to kinematic rate diagram (Fig. 2c) at the scale of the population, biomass changes due to the succession of generations exceed biomass changes due to movement. At scales below annual cycles and smaller than the continental shelf, biomass changes due to swimming and passive movements dominate over demographic changes and the value of the ratio is less than 1. The rate diagram of the kinematic ratio (Fig. 2d) reflects the locomotory capacity of the organism. Changes in biomass due to swimming and diel migration dominate at scales of days and hundreds of metres, resulting in a ratio value greater than 1. At larger scales passive motions associated with flow structures (e.g. currents, gyres, upwelling) determine the distribution of biomass and the value of the ratio is reduced below 1. In the rate diagram of the demographic ratio (Fig. 2e), changes in biomass due to recruitment and natural mortality are approxi-

mately equal at all spatial scales over annual and larger temporal scales. The value of the ratio is greater than 1 at spatial scales greater than a kilometre and at temporal scales of weeks to months as a result of the turnover in generations. Changes in biomass due to predation and natural mortality dominate at all other scales, thereby reducing the value of the ratio below 1.

Comparison of the rate diagrams with the zooplankton Stommel diagram showed that of the 11 features in the Stommel diagram (designated by letters A–K), 6 were attributable to dominant processes in rate diagrams at the same spatial and temporal scales. The remaining 5 features (C, F, I, J, K) in the Stommel diagram are attributed to fluid motions, while plots of rates indicate that demographic processes should prevail at the space and time scales of these features. Based on our rate diagrams, we hypothesize that variability in zooplankton concentration at the space and time scales of features C, F, I, J, K in the Stommel diagram are due more to demographic than to fluid processes. Biomass distribution, locomotory capacity and passive drift data at large temporal scales are needed to test this speculation.

Identifying appropriate sampling scales

If a research program is focused on a particular process (e.g. somatic growth), rate diagrams can be used to identify relevant sampling scales for a field program. For example the rate diagram of the growth to population dynamics ratio (Fig. 1a) indicates that somatic growth exceeds demographic and kinematic rates at a spatial scale of hundreds of kilometres and a temporal scale of several years. This spatiotemporal scale is a logical choice of sampling resolution when quantifying the contribution of somatic growth to changes in capelin biomass concentration. At smaller spatiotemporal scales, changes in capelin biomass concentration are dominated by demographic and kinematic processes. Scales where interaction between competing processes may be important are indicated by dimensionless ratio values approximately equal to 1. Interactions between growth and population dynamic processes are likely to occur at annual and continental shelf scales (Fig. 1a).

The plotting of dimensionless ratios can also be used to quantify the range of scales over which research conclusions can be generalized. Ecosystem process models should not be generalized across scales, just as regression models should not be extrapolated beyond limits of sampled data. For example, the capelin biomass rate diagrams indicate that a spatial variance model for the capelin spawning season over spatial scales less than 10 kilometres should include fishing and spawning mortality (Figs 1b, 1d). If the range of the model was expanded to annual cycles over the continental shelf, the model must also be expanded to include recruitment and growth processes (Figs 1a, 1b, 1d).

Evaluating variance generating processes

Comparison of ratios derived from dimensional analysis provides considerable insight into the relative importance of pattern generating processes. After setting the temporal and spatial scales of interest, a set of rate diagrams and order of magnitude calculations can be used to identify potentially dominant processes prior to field sampling. To illustrate by way of example, what sampling scales should be used and which processes should be measured to quantify the spatial variance of capelin distribution in nearshore waters during the spawning season? From capelin life history we know that the spawning season lasts approximately six weeks every year and occurs along most of the Newfoundland coast. Onset of spawning may follow a south to north latitudinal trend (Templeman 1948) but suitable spawning habitat is assumed along the entire coast. Therefore the temporal scale at which to evaluate competing processes is approximately six weeks. Logistic sampling constraints set the spatial scale to that of a bay (20–40 km). At this spatiotemporal scale, the rate diagram of the growth to population dynamics ratio (Fig. 1a) indicates that demographic and kinematic processes are more important than growth processes. The ratio of demographic to kinematic rates (Fig. 1b) is near 1, indicating both demographic and kinematic processes may be important to capelin spatial dynamics during the spawning season. Further comparison shows that kinematic processes are dominated by divergence due to swimming motions (Fig. 1c) and that mortality exceeds recruitment in the demographic ratio (Fig. 1d) at this time of year.

Order of magnitude calculations can be used to compare the relative importance of individual motion (V_i) to mortality ($\dot{N}_m + \dot{N}_r$) at this scale. Using the relation between body size and swimming speed (Okubo 1987), a 15 cm capelin has a range of approximately 24 km d⁻¹. Mortality averages approximately 2% d⁻¹ due to spawning (Carscadden and Miller 1980) and 0.00125% of the total biomass d⁻¹ in NAFO divisions 2J3KL during 1989 due to harvesting (Carscadden et al. 1991). Using 20 and 40 km sampling ranges, there is a 60%–119% d⁻¹ rate of capelin divergence compared to a total mortality of 2% d⁻¹. At the scale of a bay, research effort on the spatial dynamics of capelin during the spawning season should examine kinematics.

Plotting dimensionless ratios within rate diagrams can be used to define time and space scales required to manage renewable resources. The ratio of growth to population dynamics (Eq. 5) assesses the effects of resource management policy. Large positive changes in somatic growth (\dot{M}) combined with a ratio greatly exceeding 1 indicate a potential for growth overharvesting. Small changes in somatic growth coupled with a ratio much less than 1 indicates recruitment overharvesting. Widely-used fishery models (Ricker 1954, Beverton and Holt 1957) were developed for situations where \dot{M} was large and the ratio in eq. (5) greatly exceeded 1. This is

typical for long-lived, demersal species that are managed over large areas. In contrast, heavy fishing pressure on pelagic species increases both \dot{N} and V as mortality increases and the spatial range is contracted to maintain school densities (Murphy 1966, Winters and Wheeler 1985, Csirke 1988). The size of management areas for demersal and some pelagic fish stocks are typically on the order of hundreds of km². These are chosen to contain population movements over an annual cycle. This reduces the value of the demographic to kinematic ratio (Eq. 6) below 1 and the kinematic ratio (Eq. 7) becomes indeterminate because V_f has a value of 0. Wide ranging species (e.g. whales, tuna) clearly require much larger management areas to maintain similar values in ratios with kinematic terms.

The management of exploited populations is summarized by the demographic ratio (Eq. 8). Resource populations are regulated through the allocation of quotas (\dot{N}_r). Natural mortality (\dot{N}_m) is rarely measured for commercial fish stocks. It is traditionally assigned a constant value in stock assessments, typically 0.2 yr⁻¹ for demersal species. Fisheries research has largely focused on recruitment processes (\dot{N}_r) in an effort to predict conditions of high recruitment. Fluctuations in annual recruitment of fish species have ranged from a factor of 2 to a factor of 100 (Cushing 1982) but the process is not well understood. The demographic ratio can also be used to calculate harvesting rates needed to maintain or increase resource levels. The onset of harvesting dramatically increases \dot{N}_r relative to \dot{N}_r . If the recruitment rate is known, resource managers can prevent recruitment overharvesting by limiting harvesting at levels equal to or below recruitment rates during the long-term management of the resource.

Contouring dimensionless ratio values as a function of space and time scales provides a comprehensive method to summarize knowledge of pattern generating processes in complex ecological systems. It can be used by individuals conducting research programs or by agencies managing renewable resources. This technique summarizes the spatial and temporal dynamics of any organism, evaluates the relative importance of pattern generating processes at single or multiple scales, identifies potential research areas and appropriate sampling scales for field studies, and quantifies the range over which spatiotemporal models can be generalized. Aquatic examples were used to demonstrate the method but the same procedures can be applied to organisms in terrestrial or aerial environments. As a brief terrestrial example we examine factors affecting the rate of change in the concentration of seed producing, balsam fir (*Abies balsamea*) trees. The rate of change in the concentration of trees [\dot{S}] is a function of recruitment \dot{N}_r , natural \dot{N}_m and harvesting \dot{N}_h mortality, and the lateral divergence of trees due to seed dispersal A_D .

$$[\dot{S}] = \dot{N}_r + \dot{N}_m + \dot{N}_h - A_D \quad (9)$$

or simply:

$$[\dot{S}] = \dot{N} - \dot{A} \quad (10)$$

A forest manager or conservationist may be interested in changes in the density of fir trees. Changes in density reflect the relative importance of demographic and kinematic processes, indicated by the change in number of trees relative to the areal spread of a balsam stand or of the species \dot{N}/\dot{A} . If for example recruitment to the balsam tree population \dot{N}_r is approximately 0.1% yr⁻¹, then mortality $\dot{N}_m + \dot{N}_h$ might be expected to exceed recruitment at small spatiotemporal scales. At scales greater than 100 km and the lifespan of a tree (100 yr) recruitment is expected to equal mortality. At spatial and temporal scales of a single tree values of the ratio are predicted to equal 1, although soil conditions and stand succession stage will influence local values. At annual scales the ratio will exceed unity due to blowdown, disease, insect damage, and seed movement. At the scale of centuries kinematic changes due to lateral divergence might be expected to exceed those due to demographics and the ratio will be less than 1. This sketch of the relative importance of competing processes in balsam fir tree distribution could be depicted in a rate diagram such as Fig. 1 or Fig. 2, based on estimates of rates and the resulting dimensionless ratios plotted as a function of scale.

The use of dimensionless ratios is highly useful to researchers collecting data in diverse ecosystems, such as the Long-Term Ecological Research (LTER) sites (c.f. Magnuson et al. 1991). Variance generating processes of several species can be summarized and compared within or among terrestrial and aquatic environments over a wide range of spatial and temporal scales.

Acknowledgements – This work was supported by the Natural Sciences and Engineering Research Council of Canada and also by the Ocean Production Enhancement Network (National Centres of Excellence, Canada). We thank J. Hutchings, S. Levin, P. LeBlond, P. Pepin, I. Perry, and M. Turner for comments that improved the manuscript. This is Ocean Sciences Centre contribution 223.

References

- Andrew, N.L. and Mapstone, B.D. 1987. Sampling and the description of spatial pattern in marine ecology. – *Oceanogr. Mar. Biol. Annu. Rev.* 25: 39–90.
- Bailey, R.J.F., Able, K.W. and Leggett, W.C. 1977. Seasonal and vertical distribution and growth of juvenile and adult capelin (*Mallotus villosus*) in the St. Lawrence estuary and western Gulf of St. Lawrence. – *J. Fish. Res. Board Can.* 34: 2030–2040.
- Beverton, R.J.H. and Holt, S.J. 1957. On the dynamics of exploited fish populations. – *Fish. Invest. London* 2, pp. 533.
- Bigelow, H.B. and Schroeder, W.C. 1963. Family Osmeridae. – In: *Fishes of the Western North Atlantic*. Mem. Sears.

- Found. Mar. Res. 1(3). Yale Univ., New Haven, CT, pp. 553-597.
- Bridgman, P.W. 1922. Dimensional analysis. - Yale Univ. Press, New Haven, CT.
- Carscadden, J.E. 1983. Population dynamics and factors affecting the abundance of capelin (*Mallotus villosus*) in the northwest Atlantic. - FAO Fisheries Report No. 291: 789-811.
- and Miller, D.S. 1980. Analytical and acoustic assessment of the capelin stock in Subarea 2 and Div. 3K, 1979. - Northwest Atl. Fish. Org. SRC Doc. 80/13. Ser. No. N045: 1-19.
- and Miller, D.S. 1981. Analytical assessment of the capelin stock in Subarea 2 + Div. 3K using SCAM. - Northwest Atl. Fish. Org. SRC Doc. 81/4. Ser. No. N268: 1-8.
- , Nakashima, B.S. and Miller, D.S. 1991. Capelin in NAFO division 2JK and division 3L. - CAFSAC Res. Doc. 91/68: 1-25.
- Csirke, J. 1988. Small shoaling pelagic fish stocks. - In: Gulland, J.A. (ed.), Fish population dynamics. Wiley, New York, pp. 271-302.
- Cullinan, V.I. and Thomas, J.M. 1992. A comparison of quantitative methods for examining landscape pattern and scale. - Landscape Ecol. 7: 211-227.
- Cushing, D.H. 1982. Climate and fisheries. - Academic Press, New York.
- Delcourt, H.R., Delcourt, P.A. and Webb, T. 1983. Dynamical plant ecology: the spectrum of vegetational change in space and time. - Q. Sci. Rev. 1: 153-175.
- Denman, K.L. and Platt, T. 1976. The variance spectrum of phytoplankton in a turbulent ocean. - J. Mar. Res. 34: 593-601.
- and Powell, T.M. 1984. Effects of physical processes on planktonic ecosystems in the coastal ocean. - Oceanogr. Mar. Biol. Annu. Rev. 22: 125-168.
- de Young, B., Otterson, T. and Greatbatch, R.J. 1993. The local and non-local response of Conception Bay to wind forcing. - J. Phys. Oceanogr. 23: 2636-2649.
- Dickey, T.D. 1990. Physical-optical-biological scales relevant to recruitment in large marine ecosystems. - In: Sherman, K., Alexander, L.M. and Gold, B.D. (eds), Large marine ecosystems: patterns, processes, and yields. Am. Assoc. Advanc. Sci. Publ. No. 90-30s, Washington, DC, pp. 82-98.
- Dutton, J.A. 1975. The ceaseless wind. - McGraw-Hill, New York.
- Dwyer, R.L. and Perez, K.T. 1983. An experimental examination of ecosystem linearization. - Am. Nat. 121: 305-323.
- Fischer, H., List, E.J., Koh, R.C.Y., Imberger, J. and Brooks, N.H. 1979. Dimensional analysis. - In: Mixing in inland and coastal waters. Academic Press, New York, pp. 23-29.
- Fortier, L. and Leggett, W.C. 1982. Fickian transport and the dispersal of fish larvae in estuaries. - Can. J. Fish. Aquat. Sci. 39: 1150-1163.
- and Leggett, W.C. 1983. Vertical migrations and transport of larval fish in a partially mixed estuary. - Can. J. Fish. Aquat. Sci. 40: 1543-1555.
- Frank, K.T. and Leggett, W.C. 1981. Wind regulation of emergence times and early larval survival in capelin (*Mallotus villosus*). - Can. J. Fish. Aquat. Sci. 38: 215-223.
- Getis, A. and Franklin, J. 1987. Second-order neighborhood analysis of mapped point patterns. - Ecology 68: 473-477.
- Grassle, J.F., Sanders, H.L., Hessler, R.R., Rowe, G.T. and McLellan, T. 1975. Pattern and zonation: a study of the bathyal megafauna using the research submersible Alvin. - Deep-Sea Res. 22: 457-481.
- Greig-Smith, P. 1952. The use of random and contiguous quadrats in the study of structure of plant communities. - Ann. Bot. Soc. Lond. NS 16: 293-316.
- 1983. Quantitative plant ecology. - Univ. of California Press, Berkeley, CA.
- Günther, B. 1975. Dimensional analysis and theory of biological similarity. - Phys. Rev. 55: 659-699.
- Harris, G.P. 1986. Phytoplankton ecology: structure, function and fluctuation. - Chapman and Hill, London.
- Haury, L.R., McGowan, J.A. and Wiebe, P.H. 1978. Patterns and processes in the time-space scales of plankton distributions. - In: Steele, J.H. (ed.), Spatial pattern in plankton communities. Plenum Press, New York, pp. 277-327.
- Helbig, J., Mertz, G. and Pepin, P. 1992. Environmental influences on the recruitment of Newfoundland/Labrador Cod. - Fish. Oceanogr. 1: 39-56.
- Heusner, A.A. 1987. What does the power function reveal about structure and function in animals of different size. - Annu. Rev. Physiol. 49: 121-133.
- Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. - Ecol. Monogr. 62: 447-502.
- Horne, J.K. 1994. Spatial variance of capelin (*Mallotus villosus*) in coastal Newfoundland waters. - J. Northw. Atl. Fish. Sci. in press.
- Huxley, J.S. 1932. Problems of relative growth. - Methuen, London.
- Jangaard, P.M. 1974. The capelin (*Mallotus villosus*) biology, distribution, exploitation, utilization and composition. - Bull. Fish. Res. Board Can. 186.
- Jenkins, G.M. and Watts, D.G. 1968. Spectral analysis and its applications. - Holden-Day, San Francisco.
- Kershaw, K.A. 1957. The use of cover and frequency in the detection of pattern in plant communities. - Ecology 38: 291-299.
- LaBarbera, M. 1989. Analyzing body size as a factor in ecology and evolution. - Annu. Rev. Ecol. Syst. 20: 97-117.
- Langhaar, H.L. 1980. Dimensional analysis and the theory of models. - Krieger Publishing, Huntington, NY.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. - Ecology 73: 1943-1967.
- Mackas, D.L., Denman, K.L. and Abbott, M.R. 1985. Plankton patchiness: Biology in the physical vernacular. - Bull. Mar. Sci. 37: 652-674.
- Magnuson, J.J., Kratz, T.K., Frost, T.M., Bowser, C.J., Benson, B.J. and Nero, R. 1991. Expanding the temporal and spatial scales of ecological research and comparison of divergent ecosystems: Roles for LTER in the United States. - In: Risser, P.G. (ed.), Long-term ecological research. Wiley, New York, pp. 45-70.
- Marquet, P.A., Fortin, F.-J., Pineda, J., Wallin, D.O., Clark, J., Wu, Y., Bollens, S., Jacobi, C.M. and Holt, R.D. 1993. Ecological and evolutionary consequences of patchiness: A marine-terrestrial perspective. - In: Levin, S.A., Powell, T.M. and Steele, J.H. (eds), Patch dynamics. Springer, Berlin, pp. 277-304.
- May, R.M. 1976. Simple mathematical models with very complicated dynamics. - Nature 261: 459-467.
- Menge, B.A. and Olson, A.M. 1990. Role of scale and environmental factors in regulation of community structure. - Trends Ecol. Evol. 5: 52-57.
- Murphy, G.I. 1966. Population biology of the Pacific sardine (*Sardinops caerulea*). - Proc. Cal. Acad. Sci. 34: 1-84.
- O'Brien, J.J. and Wroblewski, J.S. 1973. On advection in phytoplankton models. - J. Theor. Biol. 38: 197-202.
- Okubo, A. 1978. Horizontal dispersion and critical scales for phytoplankton patches. - In: Steele, J.H. (ed.), Spatial pattern in plankton communities. Plenum Press, New York, pp. 21-42.
- 1987. Lecture notes in biomathematics. Number 71. - Springer, New York.
- O'Neill, R.V., De Angelis, D.L., Waide, J.B. and Allen, T.F.H. 1986. A hierarchical concept of ecosystems. - Princeton Univ. Press, Princeton, NJ.
- , Turner, S.J., Cullinan, V.I., Coffin, D.P., Cook, T., Conley, W., Brunt, J., Thomas, J.M., Conley, M.R. and Gosz, J. 1991. Multiple landscape scales: An intersite comparison. - Landscape Ecol. 5: 137-144.
- Peters, R.H. 1983. The ecological implications of body size. - Cambridge Univ. Press, Cambridge.

- Platt, T. and Denman, K. L. 1975. Spectral analysis in ecology. – *Annu. Rev. Ecol. Syst.* 6: 189–210.
- and Silvert, W. 1981. Ecology, physiology, allometry and dimensionality. – *J. Theor. Biol.* 93: 855–860.
- Ricker, W. E. 1954. Stock and recruitment. – *J. Fish. Res. Board Can.* 11: 559–623.
- Ripley, B. D. 1981. *Spatial statistics*. – Wiley, New York.
- Rose, G. A. and Leggett, W. C. 1990. The importance of scale to predator-prey spatial correlations: An example of Atlantic fishes. – *Ecology* 71: 33–43.
- Rossi, R. E., Mulla, D. J., Journel, A. G. and Franz, E. H. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. – *Ecol. Monogr.* 62: 277–314.
- Schneider, D. C. 1989. Identifying the spatial scale of density-dependent interaction of predators with schooling fish in the southern Labrador Current. – *J. Fish Biol.* 35: 109–115.
- 1991. The role of fluid dynamics in the ecology of marine birds. – *Oceanogr. Mar. Biol. Annu. Rev.* 29: 487–521.
- 1992. Thinning and clearing of prey by predators. – *Am. Nat.* 139: 148–160.
- 1993. Scale-dependent patterns and species interactions in marine nekton. – In: Giller, P. S., Hildrew, A. G. and Raffaelli, D. (eds), *Aquatic ecology: scale, pattern and process*, in press.
- 1994. Distribution of capelin (*Mallotus villosus*) in relation to coastal upwelling in the Avalon Channel. – *J. Northw. Atl. Fish. Sci.* in press.
- , Duffy, D. C., MacCall, A. D. and Anderson, D. W. 1993. Seabird-fisheries interactions: evaluation with dimensionless ratios. – In: McCullough, D. R. and Barrett, R. H. (eds), *Wildlife 2000*, Elsevier, London, pp. 602–615.
- Shigesada, N. and Okubo, A. 1981. Analysis of the self-shading effect on algal vertical distribution in natural waters. – *J. Math. Biol.* 12: 311–326.
- Smith, P. E. 1978. Biological effects of ocean variability: time and space scales of biological response. – *Rapp. P.-v. Réun. Cons. Int. Explor. Mer* 173: 117–127.
- Southwood, T. R. E. 1978. *Ecological methods with particular reference to the study of insect populations*. – Chapman and Hall, London.
- Steele, J. H. (ed.) 1978a. *Spatial pattern in plankton communities*. – Plenum Press, New York.
- 1978b. Some comments on plankton patches. – In: Steele, J. H. (ed.), *Spatial pattern in plankton communities*. Plenum Press, New York, pp. 1–20.
- 1989. The ocean 'landscape'. – *Landscape Ecol.* 3: 185–192.
- Stommel, H. 1963. Varieties of oceanographic experience. – *Science* 139: 572–576.
- Taylor, E. S. 1974. *Dimensional analysis for engineers*. – Clarendon Press, Oxford.
- Templeman, W. 1948. The life history of the capelin (*Mallotus villosus* Müller) in Newfoundland waters. – *Nfld. Gov. Lab. Bull.* 17: 1–151.
- Turner, S. J., O'Neill, R. V., Conley, W., Conley, M. R. and Humphries, H. C. 1992. Pattern and scale: statistics for landscape ecology. – In: Turner, M. G. and Gardner, R. H. (eds), *Quantitative methods in landscape ecology*. Springer, New York, pp. 17–49.
- Urban, D. L., O'Neill, R. V. and Shugart Jr., H. H. 1987. Landscape ecology. – *BioScience* 37: 119–127.
- Watt, A. S. 1925. On the ecology of British beechwoods with special reference to their regeneration. – *J. Ecol.* 13: 27–73.
- 1947. Pattern and process in the plant community. – *J. Ecol.* 35: 1–22.
- Weber, L. H., El-Sayed, S. Z. and Hampton, I. 1986. The variance spectra of phytoplankton, krill and water temperature in the Antarctic Ocean south of Africa. – *Deep-Sea Res.* 33: 1327–1343.
- Wiebe, P. H. and Flierl, G. R. 1983. Euphausiid invasion/dispersal in Gulf Stream Cold core rings. – *Aust. J. Mar. Freshw. Res.* 34: 625–652.
- Wiens, J. A. 1989. Spatial scaling in ecology. – *Funct. Ecol.* 3: 385–397.
- Winters, G. H. and Wheeler, J. P. 1985. Interaction between stock area, stock abundance, and catchability coefficient. – *Can. J. Fish. Aquat. Sci.* 42: 989–998.
- Yao, T. 1986. The response of currents in Trinity Bay, Newfoundland, to local wind forcing. – *Atmos.-Ocean* 24: 235–252.

Appendix A: Spatial dynamics of biomass

Changes in the concentration of biomass $[B]$ of an organism in a fluid environment are a function of recruitment \dot{N}_r , natural \dot{N}_m and harvesting \dot{N}_f mortality, somatic growth \dot{M} , divergence due to motions within the fluid \dot{V}_F , and divergence due to individual motions relative to the fluid \dot{V}_I :

$$[\dot{B}] = \dot{N}_r - \dot{N}_m - \dot{N}_f + \dot{M} - \dot{V}_F - \dot{V}_I$$

Definition of terms:

$[\dot{B}]$ instantaneous time rate of change in concentration of biomass. Dimensions are time^{-1} .

$$[\dot{B}] = [B]^{-1} \frac{d[B]}{dt} = \left(\frac{NM}{V} \right)^{-1} \frac{d(NM/V)}{dt}$$

$\dot{N} = \dot{N}_r - \dot{N}_m - \dot{N}_f$ instantaneous time rate of change in biomass due to births (r), natural mortality (m) and harvesting mortality (f). Dimensions are time^{-1} .

$$\dot{N} = (NM)^{-1} M \frac{dN}{dt}$$

\dot{M} instantaneous time rate of change in biomass due to growth. Dimensions are time^{-1} .

$$\dot{M} = (NM)^{-1} N \frac{dM}{dt}$$

$\dot{V} = \dot{V}_F + \dot{V}_I$ instantaneous time rate of change in volume occupied by a group of organisms due to the velocity of the fluid (\dot{V}_F) and the velocity of individuals relative to the fluid (\dot{V}_I). The divergence theorem can be used to describe the kinematics of biomass in a fluid environment (Schneider 1991). This theorem relates the local rate of change in a volume (dV/dt) occupied by a group of organisms to horizontal ($u = dx/dt$, $v = dy/dt$) and vertical ($w = dz/dt$) velocities in an x, y, z co-ordinate system. In compact notation, the rate of change in volume occupied (\dot{V}) is $\dot{V} = (\nabla \cdot \mathbf{u})$ where \mathbf{u} is the vector of velocities (u, v, w), the dot indicates scalar multiplication, and ∇ is the gradient operator (see Dutton 1975: chapter 5). Dimensions are time^{-1} .

$$\dot{V} = V^{-1} \frac{dV}{dt} = \frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = \nabla \cdot \mathbf{u}$$

This equation states that rate of change in the volume occupied by a given biomass is equal to the divergence of biomass, where divergence can be positive (diverging) or negative (converging). Movement of organisms in a fluid environment is a result of displacement due to motions of the fluid (u_i) and movement of individuals relative to the fluid (v_i). For many terrestrial organisms $V_r = 0$ and divergence is a function of organism locomotion.

Appendix B: Dimensional analysis

Dimensionless ratios are calculated by arranging a two-way table where the variables of interest are columns and all fundamental dimensions (e.g. mass, length, time, number of organisms) are rows. Exponents of each variable form the elements of a dimensional matrix (e.g. volume has dimensions length +3). Variables are then combined using the linear algebra (Langhaar 1980) or the successive elimination method (Taylor 1974) to make all values of exponents zero. This results in a set of dimensionless products.

In the capelin biomass example, quantities of interest are: demographic \dot{N} , growth \dot{M} , and kinematic \dot{V} rates. The fundamental quantities are: length L , mass M , time T , and number of organisms $\#$. The dimensional matrix is:

		\dot{N}	\dot{M}	\dot{V}
Dimension	L	0	0	0
	M	0	0	0
	T	-1	-1	-1
	$\#$	0	0	0

Since all quantities are rates, dimensions other than time

can be dropped. Dividing through by \dot{V} the revised matrix becomes:

		$\frac{\dot{N}}{\dot{V}}$	$\frac{\dot{M}}{\dot{V}}$
Dimension	T	0	0

Dimensionally homogeneous terms can be combined to form logical groups (Fischer et al. 1979). Demographics and kinematics are combined to form the quantity population dynamics $\dot{N} - \dot{V}$ with dimensions time⁻¹. Replacing \dot{N} and \dot{V} by $\dot{N} - \dot{V}$ and dividing the original matrix by $\dot{N} - \dot{V}$ the revised matrix becomes:

		$\frac{\dot{M}}{\dot{N} - \dot{V}}$
Dimension	T	0

Analysis results in two ratios:

$\frac{\dot{N}}{\dot{V}}$ Ratio of demographics (recruitment, natural mortality, harvesting mortality) to kinematics (active movement, drift).

$\frac{\dot{M}}{\dot{N} - \dot{V}}$ Ratio of growth to population dynamics (demographics, kinematics).

Two additional ratios result if demographic and kinematic processes are examined individually.

$\frac{\dot{N}_r}{\dot{N}_m + \dot{N}_f}$ Ratio of recruitment to natural and harvesting mortality.

$\frac{\dot{V}_l}{\dot{V}_r}$ Ratio of locomotory to fluid (passive) motions.