Discriminating between food and space limitation in benthic suspension feeders using self-thinning relationships

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ABSTRACT: Growth and survival have been shown to be density-dependent in many populations of benthic suspension feeders, but it is generally difficult to determine whether food or space is the limiting factor. The study of biomass-density relationships (B-N diagram) in self-thinning situations may provide an additional criterion for such a purpose. It is shown here that the slope of B-N diagrams may vary significantly depending on whether food or space is the limiting factor When food is limiting, it varies as a function of the exponent relating respiration to individual biomass. When space is limiting, the slope varies as a function of the length-weight relationship, roughness of the substrate at scales significant to the organisms, and the relationship between individual size and maximum population density. Testing the slopes of B-N relationships may, therefore, provide evidence concerning the nature of the limiting factor. Further, when food is the limiting factor, the intercept of B-N diagrams is an index of site quality. An example of the use of the B-N diagram for purposes of managing bivalve aquaculture is provided for mussels cultivated on bouchots (intertidal stakes). It is shown that in this particular case, space and food probably alternated seasonally as limiting factors. In addition, under the hypothesis that the entire population is completely harvested on a single occasion, analysis of the B-N diagram provides an estimate of the optimal sowing density in order to minimize competition and avoid subsequent thinning operations. These results illustrate the utility of managing cultivated populations in terms of biomass and density jointly.

INTRODUCTION

Density-dependent regulation of growth rate and reproductive effort has been observed in many populations of infaunal (Peterson 1982, Ólafsson 1986, Peterson & Black 1987, Vincent et al. 1989) as well as epifaunal bivalves (Stiven & Kuenzler 1979, Smalley 1984, Okamura 1986). The relevant evidence was obtained from experiments involving manipulations of density of natural populations, although examination of size of individuals within unmanipulated populations has also yielded results consistent with compensatory growth in some populations (Smalley 1984).

Space or food have been invoked as limiting factors. Space has been pointed out by Peterson & Andre (1980) to be the most important limiting factor to explain the vertical zonation of infaunal bivalves in sediments of a coastal lagoon. The conclusion that infaunal bivalves are space-limited, however, was not verified in a subsequent study (Peterson 1982) where *Protothaca staminea* and *Chione undatella* responded to manipu-

lations of intraspecific densities, but not to changes in density of the other species. As both *P. staminea* and *C. undatella* species occupy the same depth stratum, Peterson (1982) concluded that such patterns were suggestive of food, rather than space, limitation. Indirect evidence of food limitation has also been found in *Anadara granosa* (Broom 1983), *Mytilus edulis* (Kautsky 1982), and *Anthopleura xanthogrammica* (Sebens 1982). Indeed, observations of chlorophyll *a* and phaeopigment concentrations above an intertidal *M. edulis* bed provided evidence of strong depletion of phytoplankton near the bottom (Fréchette & Bourget 1985a), as foreseen by Wildish (1977). Related experiments have shown that mussels held in cages 1 m above the mussel bed grew faster than mussels kept in similar cages, but laid on the bottom, within the mussel bed (Fréchette & Bourget 1985b). Subsequent work on the same population has shown that higher resuspended loads near the bottom were not responsible for the lower growth rate of mussels laid on the bottom (Fréchette & Grant unpubl.). Other examples of food-

limited growth situations have been provided by Bricelj et al. (1987) and Peterson & Black (1987). An eloquent example of space limitation was provided by Dijkema et al. (1987). They observed that under situations of extremely high population density, several individuals of a cockle (*Cerastoderma edule*) population were pushed out of the sediment because of lack of space. It appears, therefore, that either food or space limitation is possible in benthic suspension feeders.

Distinguishing between either cause of competition has proven a difficult task. For instance, Buss (1979) reported that the outcome of interspecific competition for space between bryozoan colonies appeared to be determined by competition for food at the margins of the colonies, which has led to the idea that for benthic suspension feeders, space and food are so intricately linked as to be indistinguishable. Similar views have been presented by Ólafsson (1986) for a deposit-feeding population of *Macoma balthica*. At first glance, the argument seems to be valid in instances such as that of mussels grown on stakes or suspended in the water column. Although the primary purpose of these techniques is to avoid predators (Mason 1976), as mussel growers manipulate space, they also manipulate food by raising the mussels in the water column above the food-depleted zone that would develop if mussels were grown on the bottom. The analogy between food and space no longer holds, however, when one considers that not only bottom populations, but also mussels grown in the water column can deplete phytoplankton when stocking density is sufficiently high (Cabanas et al. 1979, Rodhouse et al. 1985). Space and food are also manipulated independently when high current speed areas are sought in order to enhance the food supply (Fréchette et al. 1989, Grizzle & Lutz 1989) for bottom-cultured animals. Buss' (1979) analogy, therefore, may be of limited generality.

In certain controlled experiments, clear conclusions can be drawn about food and space limitation (e.g Peterson 1982). In others, however, some factors known to affect growth may covary with experimental treatments. For instance, in order to test for interspecific interactions, Peterson & Andre (1980) transplanted individuals of *Sanguinolaria nuttallii* in enclosures containing 2 other deep-dwelling species, *Tresus nuttallii* and *Saxidomus nuttallii*. In unmanipulated situations, however, *S. nuttallii* inhabits coarser sediments than the 2 other species (Peterson & Andre 1980). In a study of *Macoma balthica* population dynamics, Vincent et al. (1989) compared populations of differing intertidal levels. It was reported that the mid and upper intertidal zones contained heterogeneous gravel, sand and mud sediments, whereas the lower intertidal sediments were sandy and very homogeneous. Considering that it was clearly shown by Newell & Hidu (1982) that meat

growth in *Mya arenaria* decreased with grain size per se, differences in sediment grain size in the aforementioned studies were clearly undesirable, although impossible to avoid. It would have been desirable, therefore, to have additional criteria to decide whether food or space was actually limiting growth.

One possible methodology for distinguishing between food and space as limiting factors is to put dead shells in natural positions, so as to occupy space without feeding (Peterson & Andre 1980). However, considering that dead shells are inert, while competition for space (?) may involve behavioural mechanisms (e.g. mussels: Okamura 1986), the applicability of this methodology is probably restricted to endofauna.

It is the purpose of this paper to discuss a possible criterion for discriminating between food and space as factors limiting growth and survival in benthic suspension feeders. The method is based on the study of the relationship between maximum population biomass and density (i.e. self-thinning relationships), but a mathematically equivalent formulation involves the study of body size and density (Westoby 1984, Weller 1987b). The space limitation case has been studied in depth for organisms occupying a 2-dimensional substrate (Weller 1987a, b, Norberg 1988a, Hughes & Griffiths 1988), as well as for water-column dwellers (Duarte et al. 1987). Some results obtained in the field of plant ecology are briefly reviewed in the next section of this paper In a vast survey of the literature, Damuth (1981) found that size in terrestrial animals scaled as the −0.75 power of density (−0.87 in aquatic animals; Damuth 1987), which was interpreted as resulting from metabolic constraints on size and density (see also Agusti & Kalff 1989). These studies have led to the suggestion that the exponent relating size to density may indicate which of metabolic or spatial constraints are actually driving self-thinning situations (Norberg 1988b).

In the following, it is assumed that predation does not significantly influence mortality. Only intraspecific competition is considered. It follows that the caveats expressed by Lawton (1989) concerning the analysis of size-density relationships do not apply, as they concern multi-specific situations. It is concluded below that (1) the slope of self-thinning relationships may indeed indicate which of space or food is limiting, (2) in cases of food limitation, inferences are possible as to the indexing of site quality and stock performance for aquaculture, and (3) both food- and space-driven self-thinning may indicate improper sowing densities.

SELF-THINNING IN PLANTS

Crowded, but actively growing, plant populations undergo density-dependent mortality in such a way

that smaller individuals are suppressed as growth of survivors proceeds further (White & Harper 1970). Assuming isometric growth in plants, Yoda et al. (1963) proposed that plant density (N) and the mean weight of survivors (m) be related according to the power equation $m = kN^\gamma$, with γ taking a value of $-3/2$ (see Westoby 1984). When log m is plotted against log N, a straight line (with slope $= \gamma$ and intercept $= k$) is observed in the range of densities where self-thinning is occurring. This form of the rule will be referred to as the m-N diagram, as opposed to the B-N diagram (see below).

The value of $\gamma = -1.5$ (and k = [3.5, 4.4]) was reported for such a wide variety of plants (White 1981, Westoby 1984) that the relationship was given the status of a law (Hutchings & Budd 1981). The general acceptance of the -1.5 slope was later challenged, however, as Weller (1987b) showed that the m-N diagram was prone to statistical bias, and that much of the evidence reported to support $\gamma = -1.5$ relied on improper regression techniques. Other problems identified were the lack of statistical testing and in some cases, lack of evidence that mortality was density-dependent (Weller 1987b). Weller (1987b), therefore, proposed a different, but mathematically equivalent, representation of self-thinning, the B-N diagram, following Westoby (1984). Since m = B/N, B being biomass, the B-N diagram is obtained from the m-N formulation by substitution. Therefore $B = kN^\beta$, with $\beta = -1/2$ ($\beta = \gamma + 1$). Weller's reanalysis of data in terms of B-N relationships showed that β was far from being invariant. In particular, β ranged from -3.808 to -0.146, with means of -0.847 for experimental and natural populations and -0.876 for forestry yield tables. In a related study, he also showed that thinning exponents are correlated with allometric relationships describing plant geometry (Weller 1987a). His overall conclusion was that the B-N relationship arises from the 'geometry of space filling'. In other words, those self-thinning relationships were considered to describe density-dependent growth and mortality, with space as the limiting factor.

Models presented by Norberg (1988a), explicitly including growth mode (i.e. isometry versus allometry of growth) and space limitation, were successful in reproducing general trends of Weller's (1987a) results. Indeed, for isometric growth, $\gamma = -1.5$ is predicted. For allometric growth, however, γ does not take a constant value, but rather a range of values between asymptotes of -2.00 and -1.33, increasing as individual growth proceeds (Norberg 1988a). Therefore some curvature in m-N diagrams is possible, depending of the ontogenic stage of plants. The most realistic range of exponent values is expected to fall between -1.97 and -1.80.

The value of k has been seen as invariant (White

1981). In some studies, however, it has been possible to ascribe variations in k to differences in plant geometry, light, or site quality (see reviews by White 1981, Westoby 1984, Weller 1987b). Statistical analysis of variations of k among a large body of studies appears to be difficult because of heterogeneity of slopes of B-N relationships (Weller 1987b).

SELF-THINNING RELATIONSHIPS IN BENTHIC SUSPENSION FEEDERS

Space-driven self-thinning (SST)

The original formulation of the mathematical relationship describing SST assumed isometric growth, and assuming 100 % occupation of the substrate, that the substrate surface (S) occupied by an individual is proportional to 1/N, and proportional to the square of one of its linear dimensions. Further, it was assumed that its weight is proportional to the cube of the linear dimension chosen. Thus

$$S \propto L^2 \propto (L^3)^{2/3} \propto (m)^{2/3} \tag{1}$$

Therefore $S \propto m^{2/3}$, and $N^{-1} \propto m^{2/3}$. Then $m \propto N^{-3/2}$, or

$$m = kN^{-3/2} \tag{2}$$

(Yoda et al. 1963). Subsequent work showed that the allometry of growth and of substrate occupation could not be ignored, otherwise accurate predictions were not possible (Weller 1987a, Norberg 1988a, b). Further assumptions in Eqs. (1) and (2) are that the organisms are single-layered, and that the substrate surface is smooth at scales significant to the organisms. Hughes & Griffiths (1988) provided an empirical relationship between population density and mean shell length for a mussel population that they interpreted to reflect multi-layered packing. Shell size and mussel density were related by an exponent $= -1.63$, instead of -2.00, as expected in single-layered situations (Hosomi 1985). In some cases, it is possible that such empirical relationships account not only for multi-layered packing, but also for heterogeneity of the substrate's surface at scales significant to the organisms, for example pebbles and crevices on hard bottom. A significant contribution of roughness to total surface area would mean that the apparent surface area (S_a) recorded would differ from the effective surface (S_e) available to the organisms (Fig. 1).

In the following, N^{-1} is invariant. Multi-layer packing results in density increasing with respect to surface at a faster rate than expected, that is, mussel density and shell size are related by an exponent smaller than 2 (Hughes & Griffiths 1988)

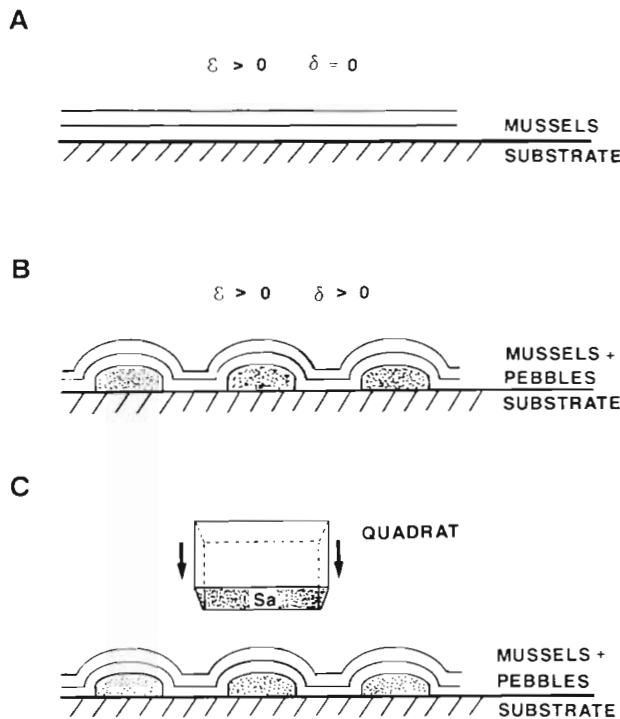$$N^{-1} \propto L^{2(1-\varepsilon)} \tag{3}$$

A

B

C

Fig. 1. Schematic representation of a mussel bed with 2 layers of mussels ($\varepsilon > 0$) and different combinations of substrate roughness (δ). See text for definitions of ε and δ. (A) Substrate roughness is negligible at scales significant to individual mussels ($\delta = 0$). (B) Substrate roughness significant ($\delta > 0$). (C) Effect of substrate roughness on effective surface sampled (S_e) with an apparatus of surface S_a

where ε is positive and has a value smaller than 1, representing the effect of multi-layer packing. Similarly, it is possible to take into account the other effects described above: if the surface of the substrate is rough, the total number of mussels per surface area of quadrat (S_a) may be increased. Again, this results in a proportionality between mussel density and shell size smaller than 2

$$N^{-1} \propto L^{2(1-\delta)} \tag{4}$$

Allometric growth results in individual mass being proportional to length at an exponent different from 3

$$m \propto L^{3(1-\alpha)} \tag{5}$$

It is possible to account for the combined effects of multi-layer packing, substrate heterogeneity, and allometric growth on the relationship between size and density First, Eq. (5) may be rewritten as

$$L \propto m^{\frac{1}{3(1-\alpha)}} \tag{6}$$

Combining Eqs. (3) and (4) allows to quantify the effects of multi-layered packing and of substrate heterogeneity on density

$$N^{-1} \propto L^{2(1-\varepsilon)(1-\delta)} \tag{7}$$

Substituting for L from Eq. (6)

$$N^{-1} \propto m^{\frac{2(1-\varepsilon)(1-\delta)}{3(1-\alpha)}} \tag{8}$$

Therefore,

$$m \propto N^{-\frac{3}{2}\frac{(1-\alpha)}{(1-\varepsilon)(1-\delta)}} \tag{9}$$

Eq. (9) shows how multi-layer packing, substrate heterogeneity and allometric growth modify the $-3/2$ slope in a SST situation. Therefore, comparing the effect of different packing strategies between populations living on substrates with different geometries is possible when the substrate is completely covered with organisms, provided that substrate heterogeneity may be assessed through examination of nearby control areas or clearing of limited parts of the substrate (Bergeron & Bourget 1986). A critical assumption leading to Eq. (7) is that packing configuration and elements of substrate heterogeneity are independent. Such an assumption would be violated if, for example, mussels were packed in 3 layers on the side of pebbles, but only 2 on the top.

Food-driven self-thinning (FST)

To simulate what self-thinning relationship might be expected in a food-limited, unimodal even-aged bivalve population, let us assume a constant supply of food from the overlying water column. The population will remove food until its concentration reaches a critical level (Thompson & Bayne 1972, Winter 1978) below which metabolic demands can no longer be sustained, whereupon the total consumption (C_T) is at equilibrium with energy expenditure,

$$N \ a m^b = C_T \tag{10}$$

where m = individual biomass; and a and b = parameters relating respiration to individual biomass. Rearranging Eq. (10) leads to the formulation $m = (C_T/a)^{(1/b)} \cdot N^{-(1/b)}$. As $b = 0.75$ (Bayne & Newell 1983, Peters 1983), we obtain

$$m = (C_T/a)^{1.33} \ N^{-1.33}, \tag{11}$$

with $(C_T/a)^{1.33}$ constant for a given population in stable environmental conditions. Thus FST is predicted to result in an exponent $\gamma = -1.33$ (Damuth 1981), as compared to $\gamma = -1.5$, or $\sim [-1.97, -1.80]$, if growth is allometric (Norberg, 1988a, b), in the case of SST. Thus the slope of self-thinning relationships may be used as a criterion for identifying which of food or space is actually limiting growth.

The ratio $(C_T/a)^{1.33}$ is interpretable in terms of the combined effects of food availability and respiration on the mean individual biomass attainable at a given density. This ratio is expected to change between environments, since a is sensitive to, or to combinations of, variables such as temperature and salinity (Shumway & Koehn 1982, Bayne & Newell 1983), and since the rates of food replenishment and consumption change with current speed and mixing when food is locally depleted (Wildish 1977, Peterson et al. 1984, Fréchette et al. 1989, Grizzle & Lutz 1989, Grizzle & Morin 1989). In addition, not all genotypes perform equally well energetically (Koehn & Shumway 1982). However, it is not clear whether such differences are reflected in a, b, or both parameters. FST relationships, therefore, appear to be useful for indexing site quality, and perhaps genotype performance, for bivalve culture, especially in view of controlling for density-dependent effects on growth and mortality.

DISCUSSION

Little is known about self-thinning relationships in benthic suspension feeders. Hogarth (1985) found $\gamma = -2.04$ in *Semibalanus balanoides* in Scotland. Hughes & Griffiths (1988) reported data for *S. balanoides* and *Choromytilus meridionalis* which were analysed in terms of B-N and m-N diagrams, respectively. They reported values of $\beta = -0.68$ for barnacles and $\gamma = -1.40$ ($\beta = -0.40$) for mussels. These results were consistent with predicted values based on the allometries of growth and space occupation (following Weller 1987a) for the particular populations under study, and therefore were interpreted as indicating space limitation, in agreement with Griffiths' (1981) original conclusion. Thus SST may be described by slope values different from $\gamma = -1.50$, depending on the length-weight relationships and whether or not the animals occur in single or multi-layer packing. Similarly, FST situations may result in slopes different from the expected -1.33 value, as in many field situations, oxygen consumption appears to be related to size by an exponent b smaller than the value of 0.75, which value seems to be characteristic of laboratory situations (Bayne & Newell 1983). For instance, measurements using ambient seawater yielded annual mean exponent values of 0.445 and 0.584 for 2 populations of *Mytilus edulis* (Bayne & Widdows 1978) and 0.56 in *Cardium edule* (Newell & Bayne 1980). Other examples of exponents smaller than 0.75 are found in Thompson (1984), Emerson et al. (1988) and Widdows & Johnson (1988). Therefore FST relationships in these populations should exhibit steeper slopes than predicted in Eq. (11).

It is possible then that B-N relationships predicted under the hypotheses of FST and SST are similar. Griffiths (1980) gives exponent values relating respiration rate ($b = 1.58$) and dry flesh weight ($b' = 2.29$) to shell length for the mussel population studied by Hughes & Griffiths (1988). The exponent relating respiration rate to dry weight is therefore $b/b' = 0.69$. Using Eq. (11), the predicted slope for a FST m-N diagram is $\gamma = -1.45$. This is very close to that predicted in the case of SST (Hughes & Griffiths 1988; $\gamma = -1.40$). Clearly, such situations impose a major limitation in the use of self-thinning relationships for resolving factors limiting growth. It is therefore necessary to derive decision criteria a priori, and then test observations against the predictions, as in Hughes & Griffiths (1988). However, this must be done for both the SST and FST hypotheses, otherwise the B-N slope may be uninterpretable.

There is a wealth of information in the literature on length-weight relationships in bivalves, from which to estimate α. Typically, $\alpha \sim [-0.35, +0.20]$, and in many cases, is small. However, there is evidence of temporal (annual: MacDonald & Thompson 1985; seasonal: Thompson 1984, Bricelj et al. 1987, Boromthanarat & Deslous-Paoli 1988) and spatial variability (geographic and bathymetric: MacDonald & Thompson 1985). Length-weight relationships may also vary between cultivated and wild animals (MacDonald 1986). Finally, we have noted above that in some instances, slopes of B-N diagrams predicted for FST and SST situations may be similar. In such a situation, the slope of a B-N diagram would be uninterpretable. This problem may be circumvented by taking advantage of the fact that the weight of different body parts may be related to shell length following different relationships. In the giant scallop *Placopecten magellanicus*, for instance, MacDonald (1986) reports slopes of 2.50 and 3.58 for the height-weight relationship for somatic tissues and the gonad, respectively. The corresponding values of α are 0.17 and -0.19, respectively. It follows that the predicted slope of a B-N relationship governed by SST (Eq. 9) is radically different, depending on whether one considers gonad or somatic tissue.

The size-density relationship reported by Griffiths (1981) leads to a value of $\varepsilon = 0.16$. We are not aware of any study of the effect of substrate roughness on the size-density relationship. However, it appears to be reasonable to expect that in cases reflected in Fig. 1, roughness will result in positive values of δ. It appears, therefore, that in SST situations, both multi-layer packing and substrate roughness will result in B-N relationships with steeper slopes.

The hypothetical results depicted in Fig. 2 illustrate the possible use of FST relationships in comparing growth at 2 sites. Let us assume that Site A has lower
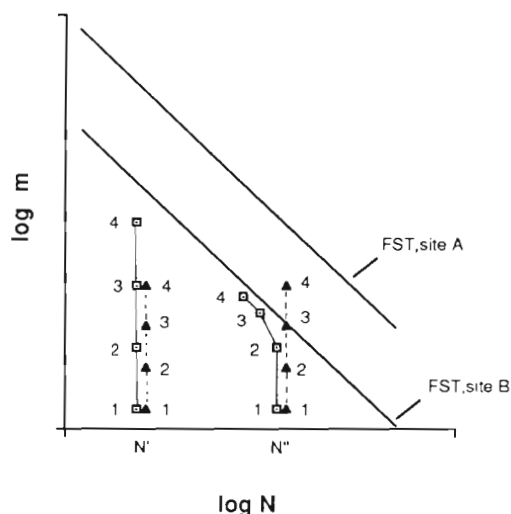
Fig. 2. Hypothetical growth experiment carried out at 2 densities, N' and N", to test which of Site A (▲) or B (◻) has highest growth potential. Numbers near symbols indicate successive sampling times. At low density, growth is density-independent at both sites, and proceeds faster at Site B. At high density, growth becomes food-limited at Site B after Time 2. Subsequent samplings show that local FST limits growth at Site B, but not at Site A. Sites get inverted ratings, therefore, depending on density

food concentration, but higher current speed than Site B. A growth experiment performed at low density (N') would indicate that Site A has lower potential for growth than Site B. If a similar experiment were to be performed at high density (N"), initial growth would still be higher at Site B than at Site A. However, as the experiment progressed, the ranking between sites could converge or be reversed because higher current speed at Site A would result in higher food flux in the otherwise food-depleted benthic boundary layer. As bottom-culture procedures often result in phytoplankton depletion (at least in the case of mussels; Newell et al. 1989), it would be advisable to rank site potential in light of results in high density situations. In practice, however, including the study of self-thinning relationships in stock-site methodologies such as that developed by Dickie et al. (1984) (see also Mallet & Carver 1989) should be undertaken with caution, since it is not known beforehand whether food or space will be limiting the population. It is obvious that the discussion above requires that food be the limiting factor. The alternative manipulation of thinning the organisms prior to an experiment is to be preferred whenever trophic properties of environments are to be compared independently of different hydrodynamic regimes or competition for space (see for example Duggins et al. 1989).

Experiments designed to ascertain the characteristics of self-thinning relationships will yield information on the factor limiting individual size. In addition, they will give insight as to the proper sowing density. Clearly, if an animal is to be harvested at a given size, there is no advantage in sowing at densities that would result in size-density combinations precluded by self-thinning, since all surplus animals would have to be eliminated by competition before the proper size may be attained. Experiments similar to that of Dare & Edwards (1976) provide interesting examples of density manipulations whereby self-thinning may be induced. Care should be taken that such experimental plots are large enough to discount edge effects in growth (C. R. Newell, Great Eastern Mussel Farms, Tenants Harbor, Maine, pers. comm.). Such observations raise the possibility of small-scale spatial heterogeneity in the nature of the factor actually limiting growth and survival. On the other hand, 'natural' experiments are also possible. Navigation buoys and other structures provide uniform substrates from which naturally occurring organisms may be sampled, and site quality assessed (Fradette & Bourget 1980).

Predictions about self-thinning slopes are based on the slope of allometric relationships relating size to weight and size to substrate surface occupied in the case of SST, and respiration to weight in the case of FST. Temporal variability of these relationships may be significant. If thinning is to occur, it may follow varying slopes on a B-N diagram, depending on the variability of the underlying allometric relationships.

It is also conceivable that food and space may alternate through time as factors inducing self-thinning. Boromthanarat & Deslous-Paoli (1988) studied the production of *Mytilus edulis* on intertidal stakes ('bouchots'), depending on whether spat was allowed to settle on bouchots naturally or was transplanted to bouchots after a primary attatchment to coco fiber ropes. The data in the following analysis were supplied by the authors and taken from their Table 1 and their Figs. 2, 3 and 5B. The mussel groups were sampled monthly from August 1983 to August 1984. When the logarithm of mussel biomass on bouchots is plotted against the logarithm of mussel density, a negative relationship is obtained, which is consistent with self-thinning (Fig. 3). An interesting feature in Fig. 3 is the emergence of 2 different patterns. Points 1, 2, 12 and 13 for naturally settled spat appear to form a first group, with Model II regression slope equal to -1.59 ($r \approx -1.00$, $n = 4$, $p < 0.01$). A second group of observations (Points 3 to 11 in naturally settled spat and Points 3 to 10 in transplanted mussels) has a Model II regression slope equal to -0.85 ($r = -0.57$, $n = 15$, $p < 0.05$). The trajectory of the B-N diagram of each of the 2 groups was compared with that expected under the hypothesis of food limitation, using the B-N form of Eq. (11) (Weller 1987b). The value of b was taken from
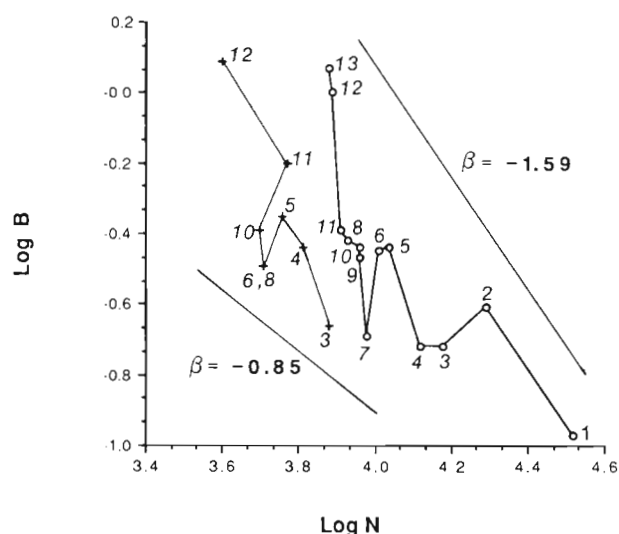
Fig. 3. B-N diagram for mussels cultivated on bouchots. (○) Wild population settling naturally on bouchots; (+) mussels transplanted on bouchots after a primary fixation on coco fiber ropes. Numbers near symbols indicate successive sampling times. Data from Boromthanarat & Deslous-Paoli (1988). The observed slopes for FST ($\beta = -0.85$) and SST ($\beta = -1.59$) are shown

Bayne & Widdows (1978; Appendix 2: the results for both the Lynher and Cattewater were averaged; $b = 0.515$). It follows that the value of β predicted under the hypothesis of FST is equal to -0.94. The observed values of -1.59 and -0.85 for the first and second groups of points, respectively, were tested against the predicted value of -0.94 following Clarke (1980). There was a significant difference between the expected and the observed value of β in the first group of points ($T = 8.76$, $n = 4$, $p < 0.01$). Therefore, it appears that the first group of points describes self-thinning induced by a factor other than food, namely space. The observed value of β in the second group of points was not significantly different from that expected under the hypothesis of FST ($T = 0.46$, $n = 15$, $p > 0.05$). It follows that the B-N relationship in the second group of points is consistent with food limitation. Indeed, low food availability and factors hampering its efficient use by the animals such as high suspended loads, are observed in the Bay of Marennes-Oléron during winter (Héral et al. 1983). It should be noted that the present data offer suggestive evidence only of alternation of food and space as limiting factors, since the slopes of the 2 groups are not significantly different ($T = 1.23$, df $= 22$, $p \approx 0.20$).

It was not possible to compare the observed slopes with predicted values under the hypothesis of SST. In the present state of affairs, a critical point in making predictions about β in SST situations for animals

exhibiting multi-layer packing is that the value of ε cannot be predicted beforehand. Rather, it has to be estimated from sampling of the size-density and length-weight relationships within the population under study, with prior knowledge that the population is space-limited. The next step is to compute the B-N relationship from the size-density and length-weight relationships above. It follows that the B-N relationship is a description of SST, and cannot be used as a prediction against which to test the observed slope. Clearly it is necessary to develop a theory of space occupation as a function of size for organisms exhibiting multi-layering.

The analysis carried out above shows that it is possible to distinguish between food and space limitation of growth and survival on theoretical grounds. Populations of mussels grown on bouchots provide an example of the use of B-N relationships for resolving which of food or space was actually limiting growth. Boromthanarat & Deslous-Paoli (1988) recognized that growth and survival on bouchots were density-dependent, and recommended regular thinning of mussel populations growing on bouchots. Actually, present harvesting strategies may involve more than one harvest per year (G. Bouyé, Les Vignes Marines, 17230 Charron, France, pers. comm.). This is analogous to thinning. However, if we hypothesize that there would be only one, complete, harvest of the population on each bouchot, the B-N diagram on Fig. 3 further suggests that mussel density be adjusted at a level of about 4000 ind. m^{-1} of bouchot from the very beginning of growth. Adjusting density on a single occasion would minimize thinning operations and optimize spat collection operations and cost, while avoiding adverse negative effects of high density during growth. It should be noted that the estimated optimal initial density is valid only for bouchots comparable to those of Boromthanarat & Deslous-Paoli (1988). Recent technical innovations in mussel culture with bouchots involve transplanting seed mussels on cylinders with larger diameter than traditional bouchots (G. Bouyé pers. comm.). In addition, roughness elements are added to the cylinder to prevent sloughing of mussels. It follows that the available surface area for mussels and substrate roughness are increased. Therefore, the optimal sowing density would increase accordingly.

Cultivated populations are generally managed on the basis of models using biomass, population density or size separately. The hypothetical experiment presented in Fig. 2 and the mussel populations studied above provide strong support for the use of biomass and density jointly in managing cultivated populations of benthic suspension feeders. The use of the self-thinning model may provide information on the factor limiting growth, optimal sowing density, and in cases

where food is the limiting factor, it may provide a way of indexing site quality.

Finally, our model ignores the hypothesis that competition for food and space could be interdependent in some instances, in order to point out how they can be distinguished when they are independent. Jørgensen et al. (1986) experimentally reduced gaping in *Mytilus edulis,* and found that filtration rate decreased accordingly. All other things being equal, if competition for space involves lateral forces that reduce gaping, then the resulting reduction of filtration rate would result in a decrease of food intake and growth. This is a possible mechanism conducive to interdependence of competition for food and space.

LITERATURE CITED

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