Estimating optimal population density for intermediate culture of scallops in spat collector bags [1]

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Abstract

In a scallop restocking project in Îles-de-la-Madeleine, Québec, we investigated the spat growing within the collector bags, instead of using the usual pearl net method. To estimate optimal population density in the collector bags, we studied yield as a function of spat population density (B–N curves) at three depths in the water column (10, 20, 30 m) and in a nearby lagoon. The B–N curves suggest that for 1-year-old spat, biomass at 10 m depth was maximum at ca. 1900 individual spat per bag. At higher population density, self-thinning occurred and yield decreased. The B–N curve for 20 m did not reach a maximum at the population densities encountered in the experiment. At population density ca. 2000 ind/bag, yield of individuals ≥ 2 cm shell height was greater at 20 m than at 10 m, apparently because of higher food availability at 20 m and presence of interspecific competitors at 10 m depth. Yields in the lagoon and at 30 m depth were not satisfactory. Intermediate culture should be done at 20 m depth, with at least 2000 ind/bag. The upper limit to this estimate could not be determined experimentally. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Wild spat collection is a key step in most, if not all, scallop culture undertakings. The realization that many natural communities appear to be regulated by low settlement rate (Roughgarden et al., 1987; Connolly and Roughgarden, 1998), coupled with the need for obtaining abundant spat in commercial ventures, has oriented research toward maximizing spatfall of scallops. This research has considered choice of depth, site and date of collector deployment (Brand et al., 1980; Giguère et al., 1994, 1995; Harvey et al., 1995a; Chauvaud et al., 1996; Gallager et al., 1996; Pearce et al., 1996); use of natural and chemical attractants (Harvey et al., 1993, 1997; Pearce and Bourget, 1996); effects of modifying structural components of the collectors (Pouliot et al., 1995; Miron et al., 1996; Pearce and Bourget, 1996; Cashmore et al., 1998); and minimizing the presence of competing or predatory species (e.g., Thouzeau, 1991; Claereboudt et al., 1994; Chauvaud et al., 1996; Cashmore et al., 1998). Although in many instances scallop spat settlement has been found to be low, in other cases very high numbers ($> 10^4$ individuals per bag) have been reported (Thouzeau, 1991; Félix-Pico et al., 1997). Heavy spat settlement may eventually lead to intraspecific competition as individual growth proceeds, especially in species where early spat survival is high in collector bags (Giguère et al., 1995; Harvey et al., 1995a).

The scallop fishers' association of Îles-de-la-Madeleine (APPIM), Québec, has been involved in a giant scallop (*Placopecten magellanicus* Gmelin) restocking project since the early 1990s (Cliche et al., 1997). The production scheme envisaged at the beginning of the program involved three steps: (1) wild spat collection in the Fall, (2) intermediate culture in pearl nets for about 1 year, starting the Summer following spat collection (individual size increases from 1 to 3 cm shell height), and (3) sowing on the bottom for final grow-out. Intermediate culture in pearl nets is costly. Consequently, APPIM has been considering keeping the spat within the collector bags for nearly 1 year before sowing, in order to avoid transferring the spat into pearl nets for intermediate culture. This technique has been used extensively in New Zealand (Bull, 1994). It is not known, however, whether intermediate culture can be done efficiently within the spat collector bags. Spat numbers could be too low to provide satisfactory yield, or conversely, so high that competition would result in growth reduction and mortality within the bags, with corresponding loss in yield and decreased post-sowing survivorship owing to the smaller scallop size (Thouzeau and Lehay, 1988; Barbeau and Scheibling, 1994a).

Here we report an experiment designed to assess the effect of scallop population density on the yield of spat kept in the collector bags for the whole duration of intermediate culture.

2. Methods

2.1. Valid competition experiments without controlled population density treatments

Estimating optimal stocking density (OSD; here defined as the population density yielding maximum biomass) is an obligate requirement for efficient culture operations. OSD has typically been estimated in competition experiments where yield (B; biomass)

was estimated for groups of known and experimentally controlled population density (N) at the beginning of the experiments and B is reported as a function of initial N. Expressing yield as a function of population density at harvest, however, allows the generation of $B–N$ curves (Fig. 1A), which lead to a more heuristic analysis of results (Westoby, 1984). In addition to estimating OSD, $B–N$ curves may allow estimation of self-thinning functions, which may be quite useful in aquaculture management (see Fréchette et al., 1996). The point here is that knowledge and control of initial population density is no longer required with $B–N$ curves because yield is expressed as a function of final density. Since initial population density in collector bags is neither known nor controlled, at best, it can be known in a statistical sense only, $B–N$ curves are appropriate for estimating OSD in collector bags. To illustrate this, let us consider the hypothetical experiments depicted in Fig. 1. The $B–N$ curve in Fig. 1A is obtained in a stocking experiment where initial population density of the experimental groups, ranging from $N1$ to $N8$, is known and controlled by the experimenter. Yield increases linearly from density $N1$ to $N3$ because of absence of competition at low density. At higher population density ($N4$ and $N5$), however, yield increase is curvilinear because of competition-induced reduction of individual growth. In Fig. 1A, yield is maximum for group $N5$, which is OSD. As initial population density is increased further, however, yield decreases. This is because competition is so intense that it results not only in growth reduction, but also in mortality. This is the self-thinning region (Yoda et al., 1963; Westoby, 1984).

Fig. 1B depicts a stocking experiment similar to that in Fig. 1A, with the same growth dynamics and environmental conditions. Here the initial population density of groups is unknown, but it spans an array similar to Fig. 1A. We mimic this situation by adding a random term to the treatment groups of $N1$, $N2,\ldots,$ $N8$ individuals shown in Fig. 1A. As individual growth proceeds in each group, biomass increases according to the same constraints as in Fig. 1A. Therefore, the resulting $B–N$ curve in Fig. 1B matches closely that in Fig. 1A, except that the actual position of data points along the curve is different. At population densities $< N3$, the match is perfect since individual growth is not biomass/density-dependent. Maximum yield in Fig. 1B is observed
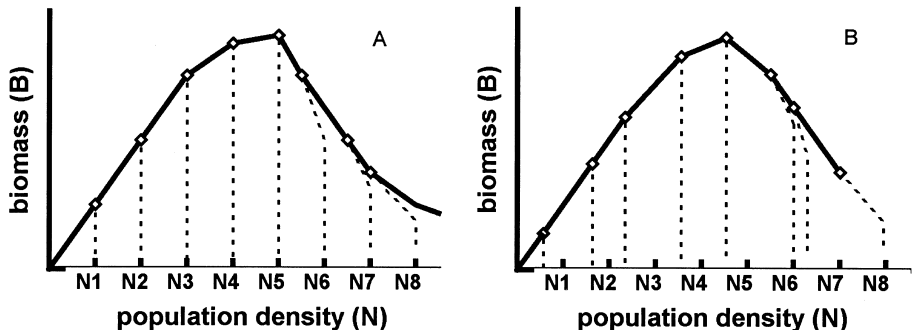

Fig. 1. (A) $B–N$ curve (solid line) for stocking experiment with controlled population density treatments. Broken lines and arrows show the growth trajectories within density groups. (B) Same as in (A), except that the population density treatments are not controlled experimentally.

between $N4$ and $N5$, which is sufficiently close to the true OSD ($N5$ in Fig. 1A) to be a reasonable estimate. For this approach to be useful, however, the unknown initial population density of the groups must span a large range. It is also assumed that competition-independent mortality is negligible, which appears to be a reasonable assumption, at least in some scallop species (Giguère et al., 1995; Harvey et al., 1995a; see Westoby, 1984; Fréchette et al., 1996, for discussions of $B–N$ curves in cases where competition-independent mortality is significant).

Alternative approaches may be preferred to the $B–N$ curve methodology presented in Fig. 1B. For instance, the spat could be induced to detach from the collectors using an appropriate treatment (e.g., Taylor et al., 1997). Subsequently, spat could be induced to resettle at an appropriate density using, for example, various larval densities or attractants of varying efficiency (e.g., Harvey et al., 1995b). A classic stocking experiment could then be performed (e.g., Fig. 1A). This approach assumes, however, that routine operations would involve a similar detachment–reattachment step and that growth conditions within the experimental collectors remain similar to those in unmanipulated bags. We decided to use the simple, non-disruptive methodology depicted in Fig. 1B instead of attempting to manipulate population density.

2.2. Spat collection

Spat collection was made in the Fall of 1995, at a site known as La Perle reef (47°19.51′N, 61°32.00′W). Water depth was 32 m. Spat were collected using onion bags (38 cm × 80 cm; 0.3 cm mesh size) stuffed with three pieces of Netron™. Groups of collectors, six pairs for each line, were attached along lines held vertically above the bottom using an individual buoy for each line. The vertical distance between each pair was 0.8 m. Bottom weights were attached to each vertical line, which themselves were attached to an anchored main line to hold them in place and facilitate retrieval. The collector bags were kept on site until the beginning of the stocking experiment itself, early in the summer following spat collection.

2.3. Initial conditions

In the Fall of 1995 (25/11/95), APPIM found that spat density in collectors held in vertical arrays near the bottom ranged from about 300 individuals/collector to about 4000 individuals/collector. Spat population density increased with height above the bottom (Fig. 2). This provided a large range of initial population densities to study $B–N$ curves according to the methods depicted in Fig. 1B. A preliminary experiment had suggested that within this range of population densities, competition was likely to occur if intermediate culture was attempted within the collector bags (Fréchette, 1996).

2.4. Experimental protocol

For the experiment proper, collectors were deployed in two sites, on La Perle reef (47°19.51′N, 61°32.20′W) and in the lagoon of Havre-aux-Maisons, Îles-de-la-Madeleine, Québec. On La Perle reef, vertical stratification in temperature and a deep maximum in chlorophyll *a* concentration were expected in summer (Vandevelde et al., 1987). Since
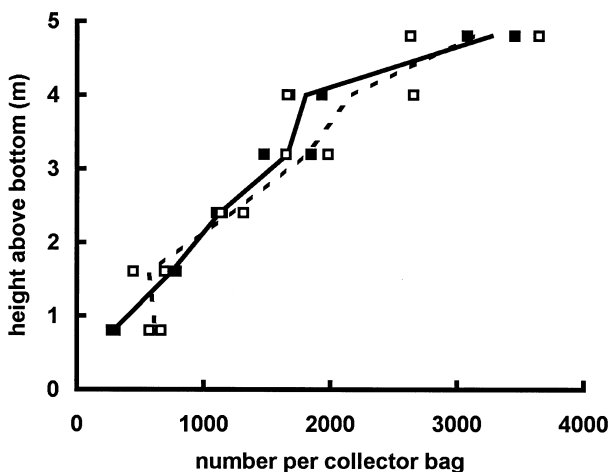
Fig. 2. Relationship between number of individual scallop spat and height above the bottom. Empty and solid squares represent bags from two different collector lines. Solid and broken lines connect the means of each group.

temperature and food affect bivalve growth, the $B-N$ curves were expected to vary with depth. Therefore, we installed collector bags at three depths, above (10 m), at (20 m), and below (30 m) the expected depth of the thermocline. Four lines (48 bags) were installed at each depth. To ensure that conditions would be homogenous among bags, the vertical lines were attached horizontally at each depth. The arrangement of lines was essentially the same in Havre-aux-Maisons lagoon, except that only one depth (1 m below surface) was studied because of shallow water depth. The lines were installed on 18 June 1996. Two lines were retrieved from each depth of each site on 29 August 1996. The remaining lines were retrieved on 8 October 1996.

2.5. Processing of spat samples

At the end of the experiment, collector bags were processed in a field laboratory located near Havre-aux-Maisons. Total spat of all bivalves was weighted. A subsample of known mass was preserved in 95% ethanol and sent to IML, where all individuals of each bivalve species were counted and weighted together. These numbers were then multiplied by the ratio of the mass of the total sample to the weight of the subsample to yield estimates of population density and biomass of each bivalve species. Empty scallop shells and other macrofaunal species such as starfish were counted according to the same method. Size structure of scallops (0.5 cm size classes) was estimated for all of the October samples except those from 30 m depth, La Perle reef.

2.6. Fluorescence and temperature

We estimated fluorescence as a proxy for chlorophyll a concentration. Fluorescence was sampled on five occasions (30 and 31 July, and 1, 27 and 29 August). Six water

samples from each depth were pumped onboard a small ship at 30-min intervals, except on 1 August, where owing to rough weather, sampling was interrupted after taking two samples. These data were not included in the analysis because the pump could not reach the desired depth. Fluorescence was estimated using whole-water samples (1.2 ml seawater extracted in 6.8 ml acetone; see Phinney and Yentsch, 1985). Fluorescence patterns were analyzed in a two-way factorial ANOVA with date (random factor) and depth (fixed factor) as main effects. Half-hourly samples were pooled within days and replicates were pooled within depths and dates. Differences between depths were tested using a priori contrasts. Temperature was monitored hourly at each depth at La Perle reef (VEMCO Minilogs; Armdale, Nova Scotia). Hourly data were averaged on a daily basis. Temperature and chlorophyll *a* in the lagoon were not measured.

2.7. Estimating OSD

The *B–N* curves and OSD were studied in three steps. First, we identified the independent variables to be included in the analysis of yield by stepwise regression (ln–ln data), since both intraspecific and interspecific interactions were to be expected in the bags. The dependent variable was scallop biomass, and the independent variables were scallop population density, mussel biomass and other bivalves' biomass. Scallop population density was forced in the statistical model as the first variable. Second, we tested the *B–N* curves for any evidence of curvilinearity as a criterion for inferring the presence of intraspecific competition. Since the absence of competition is reflected by straight *B–N* curves (e.g., densities $N1$ to $N3$ in Fig. 1A), the value of the regression coefficient for N was tested against the hypothesis of a slope smaller than 1 following Clarke (1980) (Model II regressions; ln–ln data). The analysis of *B–N* curves lacking evidence of competition was not pursued further. In step three, we analyzed yield in the remaining groups in terms of number of individuals larger than 2.0 cm shell length (N_{2+}), as a function of N. Each group was fitted to a quadratic statistical model ($N_{2+} = bN + cN^2$; $c < 0$). Solving for $\partial N_{2+}/\partial N = 0$ yields N_{max}, an estimate of OSD in terms of yield of spat ≥ 2 cm shell length. The equation for the 95% confidence limits of N_{max} is given in Appendix A.

3. Results and discussion

3.1. Environmental conditions

Temperature on La Perle reef decreased with depth (Fig. 3). There were strong seasonal fluctuations with superimposed short-term variations. At 10 m depth, temperature increased from 8°C in mid-June to over 18°C during the second half of August, before declining to 12°C at the end of the experiment. Temperature was about 2°C–4°C lower at 20 m, until early September. Afterwards, temperature was about the same at both depths. At 30 m, there was a slight tendency to increase from about 4°C to about
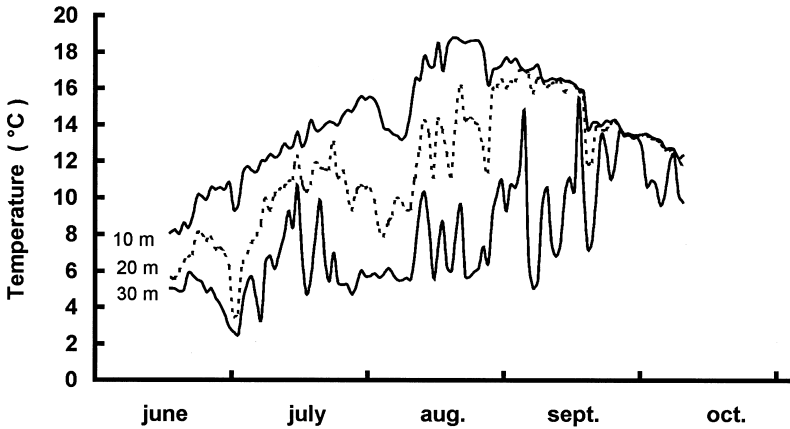
Fig. 3. La Perle reef. Temperature (°C) at 10, 20 and 30 m depth during the experiment, June to October, 1996.

6°C from June to the end of August. During September and early October, the trend was inverted at 30 m as compared to 10 and 20 m, as the thermocline progressively eroded. In early October, temperature was about 10°C at 30 m.

Vertical stratification was obvious in food concentration also (Fig. 4). On all occasions, fluorescence concentration was maximum at 20 m depth. Fluorescence was lower in July than in August. The interaction term ($F_{[6,36]} = 44.3$, $P < 0.001$) was significant. Therefore, contrasts between fluorescence at 20 m on one hand, and at 10 and 30 m on the other hand, were made for each date separately. The contrasts were significant on all dates, with $P \leq 0.0003$ in all cases. This suggests that vertical stratification in food concentration occurred on all dates, but that its intensity varied through time.
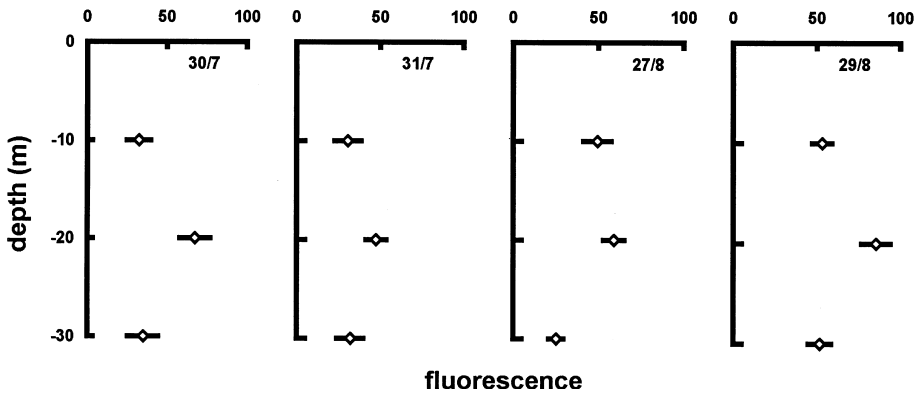

Fig. 4. La Perle reef. Fluorescence (relative units) at 10, 20 and 30 m depth on four occasions in July and August 1996. Means $\pm$ 1 SE.

3.2. Composition of communities within the collectors

In addition to scallops, other bivalves, *Mytilus edulis*, *Hiatella arctica* and *Anomia* sp., were found in the collectors (Table 1). Occasionally, unidentified gastropods were also present in low numbers, but they were not included in data analysis. Starfish occurred in significant numbers only on La Perle reef, 10 m depth on both sampling dates, and at 20 m depth in October. On La Perle reef, scallops dominated the assemblages in the bags, both in terms of biomass and population density, but this was not the case in the lagoon. This was possibly due to heavy spatfall of mussels after the bags had been installed in the lagoon. Giguère et al. (1995) provided an extensive list of species normally encountered in collector bags throughout the year. In contrast to our situation, they found that *P. magellanicus* did not dominate the assemblages. Although the reasons for this are unclear, they may have to do with the fact that the study of Giguère et al. (1995) included samples taken shortly after spat collection, whereas our experiment lasted nearly a year after spat collection. Emigration of species other than scallops out of the collectors may result in significant changes in collector communities (Hortle and Cropp, 1987; Cashmore et al., 1998).

3.3. B–N curves

The B–N curves for scallops are shown in Fig. 5 (La Perle reef) and Fig. 6 (Havre-aux-Maisons lagoon). For all sites and depths, the elevation of the curves increased with time. There was also temporal and spatial variability in the shape of the curves. B–N curves of all groups, except for those from La Perle reef at 30 m, appeared to be curvi-linear with decreasing slope as density increased. Such patterns are consistent with competition as they imply that body size decreased with increasing population density. Biomass increased monotonously with population density in all cases, except at La Perle reef in October, 10 m, where scallop biomass peaked at ≈ 1200 g/collector ($N \approx 1800$ individuals/collector) and decreased at higher population density.

Statistical regression models of the B–N curves (ln–ln data) are shown in Table 2. Collinearity was negligible, the highest condition number being 10.6. In addition to N, which was forced as the first variable in the regression models, mussel biomass (BM) and other mollusc's biomass (BA) significantly affected scallop biomass (B) in some cases, but not in others (Table 2). Since all groups had presumably collected similar spat assemblages in the Fall of 1995, variability in the list of independent variables suggests that larval settlement and community processes occurring after the beginning of the experiment were quite dynamic. For instance, mussels were abundant in bags from the lagoon, but not from elsewhere (Table 1). In addition, starfish were abundant only at La Perle reef, 10 m depth (August and October) and 20 m depth in October. Suspension feeders have been found to negatively affect scallop growth in a number of instances (e.g., Claereboudt et al., 1994; Lodeiros and Himmelman, 1996). Our results support these studies in pointing to the importance of minimizing spatfall of fouling organisms, although scallop population density played a dominant role in explaining variations in scallop biomass.

Table 1
Mean population density (N per bag) and biomass (B, g per bag) of macrobenthic species in the collectors. Standard errors are given in parentheses. S is the proportion of surviving scallops, as computed from the ratio of live scallops to the sum of live plus empty shells

Site	Date	Depth	Scallops			Mussels		Other bivalves		Starfish
			N	B	S	N	B	N	B	N
La Perle	August	10	1658 (254)	421 (42)	0.97 (0.006)	303 (50)	65 (12)	641 (169)	48 (14)	336.4 (62.2)
		20	1912 (337)	241 (36)	0.99 (0.004)	345 (45)	23 (4)	803 (228)	61 (15)	2.6 (2.1)
		30	1623 (259)	51 (8)	0.90 (0.02)	366 (35)	5 (0.8)	906 (241)	59 (17)	0.5 (0.5)
	October	10	1911 (172)	698 (47)	0.78 (0.04)	1054 (105)	238 (27)	1580 (276)	160 (27)	257.5 (44.5)
		20	876 (171)	562 (83)	0.92 (0.02)	475 (53)	210 (28)	213 (49)	16 (5)	233.0 (19.0)
		30	1531 (152)	221 (22)	0.98 (0.005)	500 (37)	28 (3)	878 (197)	94 (22)	1.5 (0.8)
Lagoon	August	1	705 (107)	187 (23)	0.99 (0.02)	12,571 (1786)	312 (24)	617 (123)	30 (7)	1.6 (0.8)
	October	1	752 (89)	287 (24)	0.95 (0.01)	11,634 (1620)	378 (34)	1208 (153)	452 (10)	6.1 (1.5)

28 aug.   **8 oct.**

biomass (g/bag)

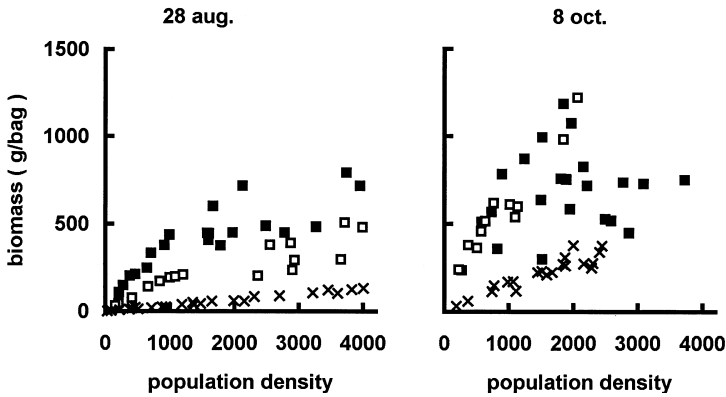population density   population density

Fig. 5. La Perle reef. $B-N$ curves for scallops at 10 m (solid squares), 20 m (empty squares) and 30 m (crosses) depth in August and October 1996.

The general shape of the $B-N$ curve for the 10 m samples from La Perle, October, was non-monotonous, unlike the other curves. A third-order polynomial with BA as a fourth term yielded an excellent fit (Table 2). All three terms for N were significantly different from 0 (N: $F = 66.97$, $P = 0.0001$; N^2: $F = 20.02$, $P = 0.0003$; $N^3 = 11.55$, $P = 0.0032$). Therefore, there was strong evidence of intraspecific and interspecific competition in this group of samples, and self-thinning occurred at high density, as implied by the positive N^3 term in Table 2.

The other groups were tested for intraspecific competition following the procedures outlined in Section 2 (see Section 2.7). The regression coefficients and the test statistics are shown in Table 3. Model II slopes were not smaller than 1 in all August samples and in October samples from La Perle, 30 m depth. This suggests that there was no
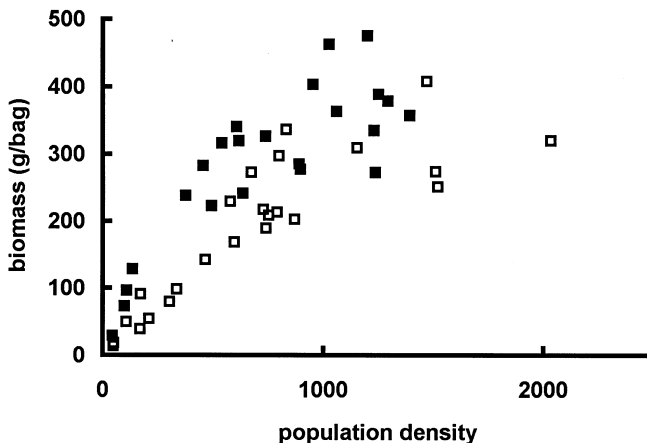
biomass (g/bag)

population density

Fig. 6. Havre-aux-Maisons lagoon. $B-N$ curves for scallops in August (empty squares) and October (solid squares) 1996.

Table 2
Statistical model relating scallop biomass and the independent variables (see Section 2.7). B is scallop biomass; N is scallop population density; BM is biomass of mussels; BA is biomass of other bivalves; n is sample size

Site	Date	Depth	Regression equation	R^2	n
La Perle	August	10	$\ln B = 0.508 + 0.864 \ln N - 0.140 \ln BA - 0.084 \ln BM$	0.93	20
		20	$\ln B = -1.385 + 1.036 \ln N - 0.235 \ln BA$	0.95	16
		30	$\ln B = -2.92 + 0.930 \ln N$	0.98	24
	October	10	$B = 1.277N - 0.00056N^2 - 1.435BA + 8 \cdot 10^{-8} \, N^3$	0.96	22
		20	$\ln B = 1.790 + 0.675 \ln N$	0.93	12
		30	$\ln B = -2.159 + 0.978 \ln N + 0.238 \ln BM - 0.96 \ln BA$	0.97	20
Lagoon	August	1	$\ln B = -0.369 + 0.859 \ln N$	0.92	24
	October	1	$\ln B = 2.144 + 0.710 \ln N - 0.269 \ln BA$	0.93	23

intraspecific competition in these four groups, although interspecific competition occurred in the groups from 10 and 20 m, as inferred from the significant BA and BM terms in Table 2. It is unclear what competition mechanisms were acting, but it is likely that food regulation early in the experiment would have resulted in intraspecific competition as well as in interspecific competition. Since the hypothesis of intraspecific competition was not supported by results in Table 3, we suspect that the curvi-linear patterns in the B–N curves for 10 and 20 m, August (Fig. 5), were attributable to interference competition of *Mytilus*, *Hiatella* and *Anomia* with scallops.

At 30 m depth, individuals were small. Presumably, growth was slow because of low temperature (Fig. 3) and low food availability (Fig. 4), and probably also because resuspended particles retarded growth (Emerson et al., 1994). As a result, body size-density combinations typical of competition were not reached and the B–N curves were straight (Fig. 5). The concept of optimal population density requires that intraspe-

Table 3
Analysis of the regression coefficient for scallops in multispecific B–N curves (ln–ln data)
Model II regression coefficients (m_{II}) were tested against the null hypothesis H_0: $m_{II} = 1$ (H_1: $m_{II} < 1$), following Clarke (1980). Degrees of freedom were calculated as $df = 2 + [(n - i)/(1 + 0.5r^2)]$, where n is sample size, i is the number of independent variables of the statistical model (see Table 2) and r is the correlation coefficient between B and N. Where applicable, r was partialized for all independent variables other than N.

Site	Date	Depth	r	m_{II}	T	df	P
La Perle	August	10	0.92*	0.942	0.600	13.3	n.s.
		20	0.91*	1.155	1.180	11.3	n.s.
		30	0.99*	0.939	2.100	16.8	[0.05, 0.10]
	October	10	†				
		20	0.97*	0.699	4.313	8.8	< 0.01
		30	0.96*	1.015	0.224	12.9	n.s.
Lagoon	August	1	0.96*	0.897	1.787	17.1	n.s.
	October	1	0.91*	0.737	5.083	15.7	< 0.001

*$P < 0.05$. †: The slope was not tested because the relationship was non-monotonous (see Table 2).

cific competition be present. Since the results in Table 3 do not support the hypothesis of intraspecific competition for any of the August samples and for La Perle, 30 m depth in October, the analysis of these groups was not pursued further.

In the remaining groups (October; except La Perle, 30 m depth), there was evidence of intraspecific competition since the regression coefficients for the scallop terms of the $B-N$ curves were smaller than 1 (Table 3). On La Perle reef, 20 m depth, only intraspecific competition occurred, while there was evidence of intraspecific competition and interspecific competition (BA term) at 10 m depth, La Perle, and in the lagoon (Table 2). In the case of the 10 m samples, La Perle, solving for $\partial B/\partial N = 0$ indicates that scallop biomass reached a maximum at $N = 1979$ individuals per bag. Heavier spatfall resulted in self-thinning and loss of yield. Clearly, this provides an upper limit to OSD at 10 m, October.

The relationship between N_{2+} and total population density was dome-shaped (Fig. 7). These results suggest that N_{2+} was maximum (i.e., $\partial N_{2+}/\partial N = 0$) for $N_{max} = 785$ ind/bag in the lagoon (with yield $N_{2+} = 151$), $N_{max} = 1902$ ind/bag at La Perle, 10 m depth (with yield $N_{2+} = 376$), and $N_{max} \geq 2000$ ind/bag at La Perle, 20 m depth (with yield $N_{2+} \geq 640$). If we extrapolate the relationship, we get $N_{max} = 3222$ ind/bag (with yield $N_{2+} = 768$). The latter estimate is based on an extrapolation and therefore should be considered with caution. It is clear from Fig. 7 that maximum yield was lowest in the lagoon, and higher at 20 m than at 10 m at high population density (i.e., at about 2000 individuals per bag). The confidence intervals for N_{max}, which is equivalent to OSD here, were [1614, 2190], [341, 6103] and [688, 882] for 10 and 20 m depth, La Perle, and
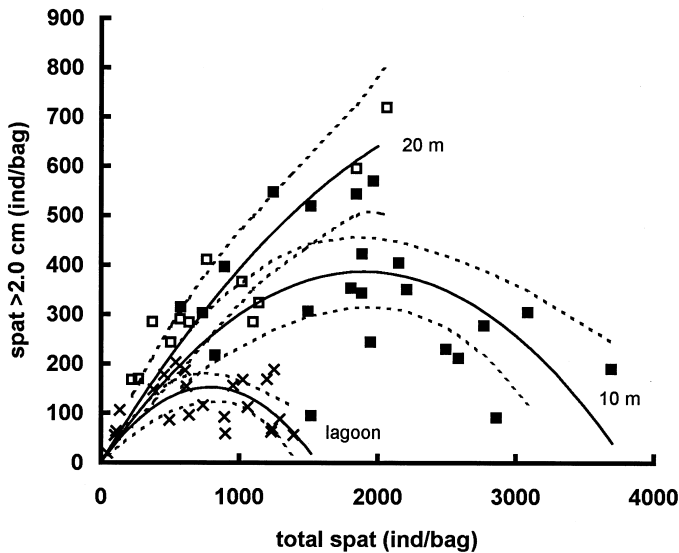

Fig. 7. Number of individual scallop spat equal to or larger than 2.0 cm shell length (N_2), as a function of population density. Empty squares: La Perle reef, 10 m depth. Solid squares: La Perle reef, 20 m depth. Crosses: Havre-aux-Maisons lagoon. Dotted lines are 95% confidence limits.

the lagoon, respectively. Clearly, OSD is larger at La Perle than in the lagoon. The large confidence interval for N_{max} at 20 m do not allow discrimination between 10 and 20 m depths on the basis of OSD. There were differences in yield, however, indicating that growth conditions were better at 20 m than at 10 m. Depth-related differences in growth of giant scallops have been attributed to the combined effect of food availability, temperature and fouling organisms (Côté et al., 1993; Claereboudt et al., 1994). In the Gryllefjord, northern Norway, Wallace and Reinsnes (1985) found that vertical patterns in growth of cultured Iceland scallops were driven by depth-related differences in seston concentration. In the present experiment, temperature was higher at 10 m than at 20 m early in the experiment, and basically the same at both depths from the end of August to the end of the experiment (Fig. 3). However, growth, as measured by N_{2+} at high population density (Fig. 7), was higher at 20 m. Differences between 10 and 20 m reflected higher food availability at 20 m depth (Fig. 4) and the effect of interspecific competition with other molluscs (Table 2). It is likely also that acclimation of feeding dynamics to lower temperature led to growth being relatively more dependent on food availability than on temperature, as suggested by simulation of mussel bioenergetics in cold water situations (Grant, 1996).

It is clear that OSD, as based on N_{2+} (Fig. 7), is quite the same as the value obtained from the $B-N$ curve (Table 2, Fig. 5). The $B-N$ curve, however, is based on the crudest possible measurements, bulk biomass and population density, and thus appears to be quicker and handier than other approaches.

3.4. Competition mechanisms

Size distributions for selected samples are shown in Fig. 8. These samples had lowest, medium and highest population density of their respective groups. Mean size decreased as population density increased. This general pattern was exacerbated by increasing skewness to the right, which is consistent with asymmetric competition (Begon et al., 1986). Asymmetric competition has generally been ascribed to physical interference between individuals, both in mussels (Okamura, 1986) and in plants (Thomas and Weiner, 1989; Weiner, 1990). In contrast to interference, competition for resources such as water and nutrients is less asymmetric in plants (Thomas and Weiner, 1989; Weiner, 1990), or has shown no evidence of asymmetry in food-regulated feeding of benthic suspension feeders (Peterson, 1982; Fréchette and Bourget, 1985a,b). Asymmetry in competition, however, should not be seen as implying that the competition mechanism was interference by physical contact, since small-scale depletion in food resources around mussels grown in the laboratory, free of interference, may lead to asymmetric competition (Fréchette and Despland, 1999). There is no a priori reason to reject the idea that the same mechanism might have been acting in the spat bags.

3.5. Mortality

We used the number of empty scallop shells in the bags as a proxy for mortality. In all cases where the analysis of $B-N$ curves failed to show that intraspecific competition had occurred, survival was very high. It was nearly 100%, since we could barely find
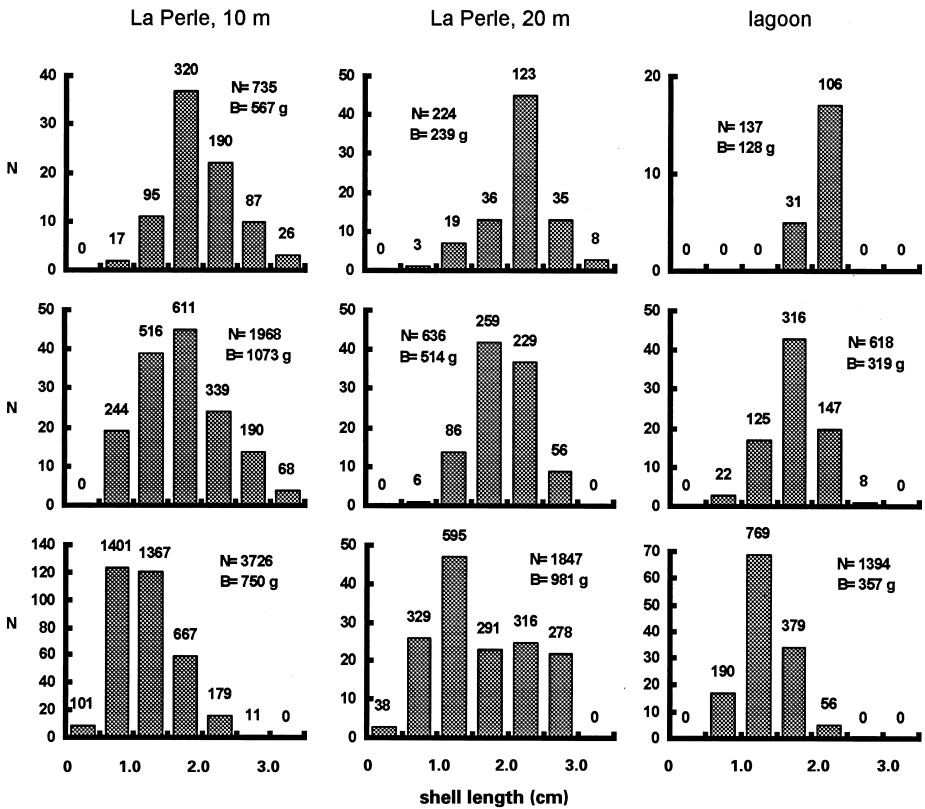
Fig. 8. Size frequencies of scallops in October. Column at the left is from La Perle reef, 10 m depth. Central column is from La Perle reef, 20 m depth. Right hand side column is from the lagoon. Upper, middle and lower rows are for low, medium, and high population density. Vertical axis represents actual scallop numbers in the subsamples. Numbers above the bars are estimated abundance of each size class for the whole bag. *N* is estimated abundance of scallops for the whole bag. *B* is the biomass of the whole bag. Note changes in vertical scale. Width of size classes is 0.5 cm.

any empty shells in these samples (Table 1). There was little pattern in the occurrence of empty shells in August, although they appeared to be more frequent at 30 m depth, especially at low total shell population density (Fig. 9). In October, the proportion of empty shells increased with total number of shells and was highest for La Perle, 10 m depth, where it reached a maximum at about 2000 total shells per bag. At high shell numbers (> 2000/bag), however, the proportion of empty shells was quite variable, and was very low in many bags (Fig. 9). It is unclear why some high population density samples had so few empty shells. Presumably, there were losses through the mesh of the bags or mortality had not yet occurred in these bags. Although this suggests that the analysis of occurrence of dead shells is of limited applicability for detailed study of mortality, these patterns are consistent with competition-driven mortality in October, 10 m depth, in contrast with the other groups. All of the B–N curves were consistent with this interpretation, since there was no evidence of self-thinning except at 10 m depth,
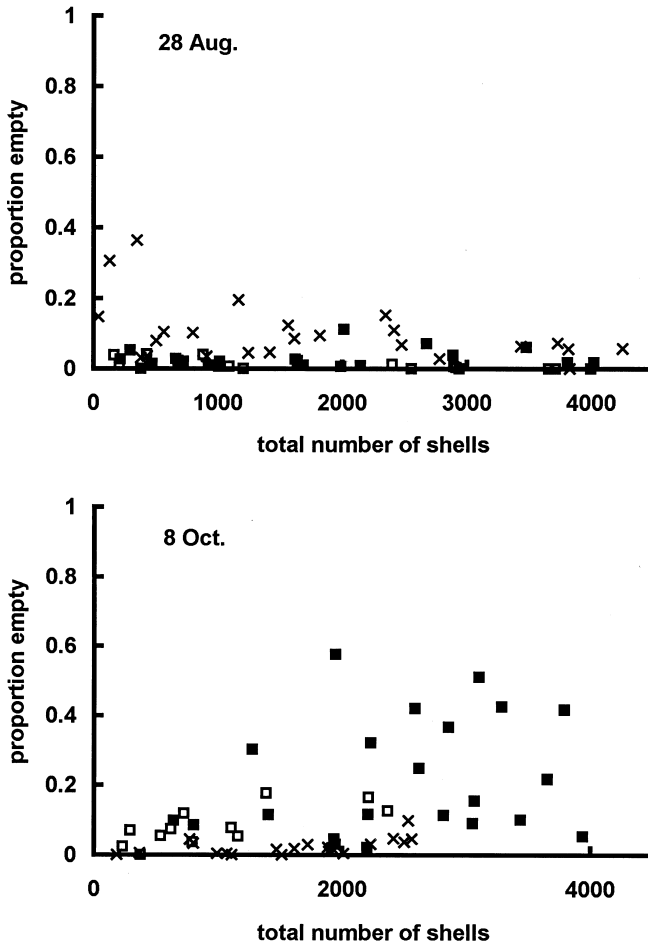
Fig. 9. La Perle reef. Relationship between empty shells and total number of shells (empty + alive). Solid squares: 10 m depth. Empty squares: 20 m depth. Crosses: 30 m depth.

October, where biomass decreased with population density above ca. 2000 ind/bag (Fig. 5). The magnitude of competition-driven mortality could not be estimated from the self-thinning curve because initial population density was unknown and perhaps there were losses of empty shells through the mesh of the bags.

Communities in collector bags typically include potential scallop predators, especially starfish (Naidu and Scaplen, 1976; Thouzeau, 1991; Claereboudt et al., 1994). Starfish occurred in significant numbers on La Perle reef at 10 m on both dates, and at 20 m in October. This raises the possibility that the decreasing part of the *B–N* curve from 10 m depth, which we interpreted as resulting from competition, was partly shaped by predation. Detailed studies of predation by starfish (*Asterias vulgaris*) on juvenile sea scallops in aquaria have shown that predation rate was highest on small-size scallops

and that the scallops' escape response was effective in decreasing predation by starfish (Barbeau and Scheibling, 1994a,b). Starfish were unable to kill scallops larger than about one-third their own size (Fig. 6 in Barbeau and Scheibling, 1994a). We measured the size of the starfish found in the bags with low, medium and high population density from La Perle, 10 m (see Fig. 8), following Barbeau and Scheibling (1994a). Starfish size was 1.59 ± 0.20 cm (mean $\pm$ SD; $n = 16$), 1.61 ± 0.30 cm ($n = 49$) and 1.67 ± 0.45 cm ($n = 3$) in the low, medium and high density bags, respectively. Considering the size of scallops (typically > 1 cm; Fig. 8) relative to that of seastars, it seems unlikely, based on Barbeau and Scheibling (1994a; b), that seastars would have been a major source of mortality. Predation, however, is generally highest against slow-growing, weak prey, and it is likely that scallops in high density bags were indeed in low condition. Furthermore, the escape response of scallops in collector bags was probably hampered by their being in bags crowded with collector material and other organisms, as suggested by the positive effect of tethering on predation rate by starfish (Barbeau and Scheibling, 1994c). Therefore, actual predation rate could have been higher than predicted from laboratory studies. To our knowledge, predation dynamics in collector bags have yet to be studied.

3.6. Management issues

Our results clearly indicate that yield was largely determined by scallop population density, as found in many controlled stocking experiments (e.g., Côté et al., 1993). In addition, yield was strongly influenced by environmental conditions and larval settlement of other species during intermediate culture. To maximize yield from intermediate culture within spat collector bags in the vicinity of Îles-de-la-Madeleine, scallop population density should be at least 2000 individual spat per bag and intermediate culture be made at 20 m depth. Extrapolation suggests that OSD may actually be as high as 3200 individuals per bag.

Investigations of appropriate sites for spat collection in the vicinity of Îles-de-la-Madeleine have shown that spat population density in the bags exceeded 3000 ind/bag in a number of sites (Cliche and Giguère, 1997). In addition, increases in scallop spawning stocks have resulted in positive long-term trends in spatfall intensity in Japan, for instance (Aoyama, 1989). Furthermore, the 2.0 cm target size used in step 3 is somewhat arbitrary. It is a compromise between the need to maximize the number of individual spat obtained and the need to obtain as large as possible animals to minimize the probability of death after sowing (Barbeau and Scheibling, 1994a). Future work may emphasize the need for increasing target size, which can only be attained through lower population densities. Therefore, it is a real possibility that spatfall intensity eventually leads to spat population exceeding OSD.

Spatfall intensity is generally seen as uncontrollable because of annual and spatial variability (Aoyama, 1989; Giguère et al., 1995). On the other hand, field studies have shown that larval distribution may be structured spatially when vertical stratification is strong (Tremblay and Sinclair, 1988, 1990, 1992). Laboratory work has shown that spatfall intensity closely correlates with vertical structure in larval abundance which itself appears to depend on the depth of the thermocline (Gallager et al., 1996; Pearce et

al., 1996). In other situations, however, sea scallop larvae may exhibit stock-related differences in migratory behavior and vertical distribution (Manuel et al., 1996a,b), or the larvae may be dispersed vertically by turbulence (Tremblay and Sinclair, 1988, 1990; Pearce et al., 1998). Therefore, knowledge of larval abundance in a given year and settlement preferences of larvae in relation to the depth of the thermocline, or, alternatively, height above the bottom (Brand et al., 1980) or collection site (Giguère et al., 1995; Cliche and Giguère, 1997), may be combined to provide forecasts of settlement intensity in a given site, depth and year. Spat collecting techniques, such as choice of site and depth of collectors, may be adjusted accordingly in a goal-seeking strategy (e.g., ≈ 3200 individual spat per bag, 20 m depth). Alternatively, any form of control of spatfall abundance may be out of reach. In this case, knowledge of spat abundance shortly after spatfall may provide early information for deciding whether the spat should be thinned out. In practice, this is achieved by removing one or more of the Netron pieces, with its associated spat (Dr. Hideyoshi Sasaki, Osyamanbe, Yamakoshi-gun Prefecture, Hokkaido, Japan, pers. comm.).

Acknowledgements

Appendix A

Confidence limits for N_{max} (where $\partial N_{2+}/\partial N = 0$). Since $N_{max} = -b/2c$, where b and c are adjusted parameters, we estimated the 95% confidence limits for N_{max} with $var(N_{max}) = (var(b/c))/4$, $var(b/c)$ being estimated following Agresti (1990). The confidence limits are given by $(-b/2c) \pm 1.96 \cdot (var(N_{max}))^{0.5}$.

References

Agresti, A., 1990. Categorical Data Analysis. Wiley.

Aoyama, S., 1989. The Mutsu Bay scallop fisheries: Scallop culture, stock enhancement, and resource management. In: Caddy, J.F. (Ed.), Marine Invertebrate Fisheries: Their Assessment and Management. Wiley, New York, pp. 525–539.

Barbeau, M.A., Scheibling, R.E., 1994a. Behavioral mechanisms of prey size selection by sea stars (*Asterias vulgaris* Verrill) and crabs (*Cancer irroratus* Say) preying on juvenile sea scallops (*Placopecten magellanicus* (Gmelin)). J. Exp. Mar. Biol. Ecol. 180, 103–136.

Barbeau, M.A., Scheibling, R.E., 1994b. Temperature effects on predation of juvenile sea scallops [*Placopecten magellanicus* (Gmelin)] by sea stars (*Asterias vulgaris* Verrill) and crabs (*Cancer irroratus* Say). J. Exp. Mar. Biol. Ecol. 182, 27–47.

Barbeau, M.A., Scheibling, R.E., 1994c. Procedural effects of prey tethering experiments: predation of juvenile scallops by crabs and sea stars. Mar. Ecol. Prog. Ser. 111, 305–310.

Begon, M., Harper, J.L., Townsend, C.R., 1986. Ecology. Individuals, Populations and Communities. Sinauer Associates, Sunderland, MA, p. 876.

Brand, A.R., Paul, J.D., Hoogesteger, J.N., 1980. Spat settlement of the scallops *Chlamys opercularis* (L.) and *Pecten maximus* (L.) on artificial collectors. J. Mar. Biol. Assoc. U.K. 60, 379–390.

Bull, M.F., 1994. Enhancement and management of New Zealand's Southern Scallop fishery. In: Bourne, N.F., Bunting, B.L., Townsend, L.D. (Eds.), 9th International Pectinid Workshop, Vol. 2. Nanaimo, B.C., Canada, April 22–27, 1993, pp. 131–136.

Cashmore, D., Learmouth, M.M., MacMillan, J.T., 1998. Improving the efficiency of wild *Pecten maximus* spat collection: potential effects of spat bag design and of species temporarily settling in spat bags. Aquaculture 160, 273–282.

Chauvaud, L., Thouzeau, G., Grall, J., 1996. Experimental collection of great scallop postlarvae and other benthic species in the Bay of Brest: settlement patterns in relation to spatio-temporal variability of environmental factors. Aquacult. Int. 4, 263–288.

Claereboudt, M.R., Bureau, D., Côté, J., Himmelman, J.H., 1994. Fouling development and its effect on the growth of juvenile giant scallops (*Placopecten magellanicus*) in suspended culture. Aquaculture 121, 327–342.

Clarke, M.R.B., 1980. The reduced major axis of a bivariate sample. Biometrika 67, 441–446.

Cliche, G., Giguère, M., 1997. Captage du naissain de pétoncle géant en milieu naturel aux Iles-de-la-Madeleine, Compte-Rendu de la 5ième Réunion annuelle de transfert de technologie. Programme REPERE, Ministère de l'Agriculture, des Pêcheries et de l'Alimentation, pp. 37–50.

Cliche, G., Vigneau, S., Giguère, M., 1997. Status of a commercial sea scallop enhancement project in Îles-de-la-Madeleine, Québec, Canada. Aquacult. Int. 5, 259–266.

Connolly, S.R., Roughgarden, J., 1998. A latitudinal gradient in Northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. Am. Nat. 151, 311–326.

Côté, J., Himmelman, J.H., Claereboudt, M., Bonardelli, J.C., 1993. Influence of density and depth on the growth of juvenile sea scallops (*Placopecten magellanicus*) in suspended culture. Can. J. Fish. Aquat. Sci. 50, 1857–1869.

Emerson, C.W., Grant, J., Mallet, A., Carver, C., 1994. Growth and survival of sea scallops *Placopecten magellanicus*: effects of culture depth. Mar. Ecol. Prog. Ser. 108, 119–132.

Félix-Pico, E.F., Tripp-Quezada, A., Castro-Ortiz, J.L., Serrano-Casillas, G., González-Ramírez, P.G., Villalejo-Fuerte, M., Palomares-García, R., García-Domínguez, F.A., Mazón-Suástegui, M., Bojórquez-Verástica, G., López-García, G., 1997. Repopulation and the culture of the Pacific Calico scallops in Bahía Concepción, Baja California Sur, México. Aquacult. Int. 5, 551–563.

Fréchette, M., 1996. Préélevage du pétoncle dans les sacs de collecte de naissain: présentation d'une approche permettant d'éviter la surpopulation. Compte rendu de la 4e Réunion annuelle de transfert de technologie. Programme REPERE, Ministère de l'Agriculture, des Pêcheries et de l'Alimentation, Gaspé, pp. 87–93.

Fréchette, M., Bourget, E., 1985a. Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. Can. J. Fish. Aquat. Sci. 42, 1158–1165.

Fréchette, M., Bourget, E., 1985b. Food-limited growth of *Mytilus edulis* in relation to the benthic boundary layer. Can. J. Fish. Aquat. Sci. 42, 1166–1170.

Fréchette, M., Despland, E., 1999. Impaired shell gaping and food depletion as mechanisms of asymmetric competition in mussels. Écoscience 6, 1–11.

Fréchette, M., Bergeron, P., Gagnon, P., 1996. On the use of self-thinning relationships in stocking experiments. Aquaculture 145, 91–112.

Gallager, S.M., Manuel, J.L., Manning, D.A., O'Dor, R.K., 1996. Ontogenetic changes in the vertical distribution of giant scallop larvae, *Placopecten magellanicus*, in 9-m deep mesocosms as a function of light, food, and temperature stratification. Mar. Biol. 124, 679–692.

Giguère, M., Cliche, G., Brulotte, S., 1994. Reproductive cycles of the sea scallop, *Placopecten magellanicus*

(Gmelin), and the Iceland scallop, *Chlamys islandica* (O.F. Müller) in Îles-de-la-Madeleine, Canada. J. Shellfish Res. 13, 31–36.

Giguère, M., Cliche, G., Brulotte, S., 1995. Synthèse des travaux réalisés entre 1986 et 1994 sur le captage du naissain de pétoncles aux Iles-de-la-Madeleine. Can. Tech. Rep. Fish. Aquat. Sci., 2061, xii+71.

Grant, J., 1996. The relationship of bioenergetics and the environment to the field growth of cultured bivalves. J. Exp. Mar. Biol. Ecol. 200, 239–256.

Harvey, M., Bourget, E., Miron, G., 1993. Settlement of Iceland scallop spat *Chlamys islandica* in response to hydroids and filamentous red algae: field observations and laboratory experiments. Mar. Ecol. Prog. Ser. 99, 283–292.

Harvey, M., Bourget, E., Legault, C., Ingram, R.G., 1995a. Short-term variations in settlement and early spat mortality of the Iceland scallop, *Chlamys islandica* (O.F. Müller). J. Exp. Mar. Biol. Ecol. 194, 167–187.

Harvey, M., Miron, G., Bourget, E., 1995b. Resettlement of Iceland scallop (*Chlamys islandica*) spat on dead hydroids: response to chemical cues from the protein-chitinous perisarcs and associated microbial film. J. Shellfish Res. 14, 383–388.

Harvey, M., Bourget, E., Gagné, N., 1997. Spat settlement of the giant scallop, *Placopecten magellanicus* (Gmelin, 1791), and other bivalve species on artificial filamentous collectors coated with chitinous material. Aquaculture 148, 277–298.

Hortle, M.E., Cropp, D.A., 1987. Settlement of the commercial scallop, *Pecten fumatus* (Reeve) 1855, on artificial collectors in eastern Tasmania. Aquaculture 66, 79–95.

Lodeiros, C.J.M., Himmelman, J.H., 1996. Influence of fouling on the growth and survival of the tropical scallop, *Euvola (Pecten) ziczac* (L. 1758) in suspended culture. Aquacult. Res. 27, 749–756.

Manuel, J.L., Burbridge, S., Kenchington, E.L., Ball, M., O'Dor, R.K., 1996a. Veligers from two populations of scallop *Placopecten magellanicus* exhibit different vertical distributions in the same mecocosm. J. Shellfish Res. 15, 251–257.

Manuel, J.L., Gallager, S.M., Pearce, C.M., Manning, D.A., O'Dor, R.K., 1996b. Veligers from different populations of sea scallop *Placopecten magellanicus* have different vertical migration patterns. Mar. Ecol. Prog. Ser. 142, 147–163.

Miron, G., Ward, J.E., MacDonald, B.A., Bourget, E., 1996. Direct observations of particle kinematics within a scallop (*Placopecten magellanicus*) spat collector by means of video endoscopy. Aquaculture 147, 71–92.

Naidu, K.S., Scaplen, R., 1976. Settlement and survival of the giant scallop, *Placopecten magellanicus*, larvae on enclosed polyethylene film collectors. FAO Technical Conference on Aquaculture. FAO, Kyoto, Japan, pp. i+5.

Okamura, B., 1986. Group living and the effect of spatial position in aggregations of *Mytilus edulis*. Oecologia (Berlin) 69, 341–347.

Pearce, C.M., Bourget, E., 1996. Settlement of larvae of the giant scallop, *Placopecten magellanicus* (Gmelin), on various artificial and natural substrata under hatchery-type conditions. Aquaculture 141, 201–221.

Pearce, C.M., Gallager, S.M., Manuel, J.L., Manning, D.A., O'Dor, R.K., Bourget, E., 1996. Settlement of larvae of the giant scallop, *Placopecten magellanicus*, in 9-m deep mesocosms as a function of temperature stratification, depth, food, and substratum. Mar. Biol. 124, 693–706.

Pearce, C.M., Gallager, S.M., Manuel, J.L., Manning, D.A., O'Dor, R.K., Bourget, E., 1998. Effect of thermoclines and turbulence on depth of larval settlement and spat recruitment of the giant scallop *Placopecten magellanicus* in 9.5 m deep laboratory mesocosms. Mar. Ecol. Prog. Ser. 165, 195–215.

Peterson, C.H., 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. Ecol. Monogr. 52, 437–475.

Phinney, D.A., Yentsch, C.S., 1985. A novel phytoplankton chlorophyll technique: toward automated analysis. J. Plankton Res. 7, 633–642.

Pouliot, F., Bourget, E., Fréchette, M., 1995. Otimizing the design of giant scallops (*Placopecten magellanicus*) spat collectors: field experiments. Mar. Biol. 123, 277–284.

Roughgarden, J., Gaines, S.D., Pacala, S.W., 1987. Supply side ecology: the role of physical transport processes. In: Gee, J.H.R., Giller, P.S. (Eds.), Organization of Communities: Past and Present. Blackwell, London, England, pp. 459–489.

Taylor, J.J., Rose, R.A., Southgate, P.C., 1997. Inducing detachment of silver-lip pearl oyster (*Pinctada maxima*, Jameson) spat from collectors. Aquaculture 159, 11–17.

Thomas, S.C., Weiner, J., 1989. Including competitive asymmetry in measures of local interference in plant populations. Oecologia (Berlin) 80, 349–355.

Thouzeau, G., 1991. Experimental collection of postlarvae of *Pecten maximus* (L.) and other benthic macrofaunal species in the Bay of Saint-Brieuc, France: I. Settlement patterns and biotic interactions among the species collected. J. Exp. Mar. Biol. Ecol. 148, 159–179.

Thouzeau, G., Lehay, D., 1988. Variabilité spatio-temporelle de la distribution, de la croissance et de la survie des juvéniles de *Pecten maximus* (L.) issus des pontes de 1985, en baie de Saint-Brieuc. Oceanologica Acta 11, 267–283.

Tremblay, M.J., Sinclair, M., 1988. The vertical and horizontal distribution of sea scallop (*Placopecten magellanicus*) larvae in the Bay of Fundy in 1984 and 1985. J. Northwest Atl. Fish. Sci. 8, 43–53.

Tremblay, M.J., Sinclair, M., 1990. Sea scallop larvae *Placopecten magellanicus* on Georges Bank: vertical distribution in relation to water column stratification and food. Mar. Ecol. Prog. Ser. 61, 1–15.

Tremblay, M.J., Sinclair, M., 1992. Planktonic sea scallop larvae (*Placopecten magellanicus*) in the Georges Bank region: broadscale distribution in relation to physical oceanography. Can. J. Fish. Aquat. Sci. 49, 1597–1615.

Vandevelde, T., Legendre, L., Therriault, J.-C., Demers, S., Bah, A., 1987. Subsurface chlorophyll maximum and hydrodynamics of the water column. J. Mar. Res. 45, 377–396.

Wallace, J.C., Reinsnes, T.G., 1985. The significance of various environmental parameters for the growth of the Iceland scallop, *Chlamys islandica* (Pectinidae), in hanging culture. Aquaculture 44, 229–242.

Weiner, J., 1990. Asymmetric competition in plant populations. TREE 5, 360–364.

Westoby, M., 1984. The self-thinning rule. Adv. Ecol. Res. 14, 167–225.

Yoda, K., Kira, T., Ogawa, H., Hozumi, K., 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions (Intraspecific competition among higher plants XI). J. Biol. Osaka City Univ. 14, 107–129.