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Separating effects of limited food and space on growth of the giant scallop *Placopecten magellanicus* in suspended culture

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ABSTRACT: Effects of limitations in space and food resources on the growth of the giant scallop *Placopecten magellanicus* (Gmelin, 1791) were examined by growing juveniles in pearl nets at different densities in 2 series, one in which density was increased by adding living scallops and a second in which density was increased by adding 'dummy' (non-living) scallops. The dummies occupied space but did not compete for food resources. For the first series, increasing the density from 25 to 250 ind. net^{-1} caused a marked decrease in growth. In contrast, no significant decrease occurred in the series in which density was increased by adding dummies. This demonstrated that food depletion is the major factor causing decreased growth at high densities. The only evidence suggesting an effect of space was a decrease in the mass of the muscle and other soft tissues with increasing density in the series with dummies; however, this decrease was not significant. Density did not affect rates of mortality, either in the absence or presence of dummy scallops.

KEY WORDS: Food/space competition · Density effect · Bivalve growth · Aquaculture · *Placopecten magellanicus*

INTRODUCTION

Competition for food and space are known as major factors determining growth and survival for suspension feeders. Numerous field studies of bivalves demonstrate that growth decreases with increasing density (Okamura 1986, Peterson & Beal 1989, Vincent et al. 1989). This may be explained by the decrease in food resources per individual with increasing density, possibly because of depletion of food particles within the benthic boundary layer (Wildish & Kristmanson 1984, Fréchette & Bourget 1985, Fréchette et al. 1989). Competition for space may also cause decreased growth at higher densities. This is suggested because sessile suspension feeders in rocky habitats are often strongly limited by space (Connell 1961, Dayton 1971, Harger 1972). Peterson & Andre (1980) further suggest that competition for space largely determines the vertical zonation of infaunal bivalves in a coastal lagoon of California, USA, and Dijkema et al. (1987) report that in extremely dense populations, the cockle *Cerastoderma edule* can even be pushed out of the sediment by conspecifics.

Intraspecific competition may also limit growth of bivalves maintained in suspended culture by aquaculture industries, as studies demonstrate that growth decreases with increasing stocking density for scallops (Duggan 1973, Monical 1980, Parsons & Dadswell 1992, Côté et al. in press) and other bivalves (Jarayabhand & Newkirk 1989, Eversole et al. 1990, Mallet & Carver 1991, Holliday et al. 1993). These studies emphasize food as a potential limiting factor. Competition for space, involving physical interference among individuals, may also explain reduced growth at high densities. This is suggested by Duggan (1973), Monical (1980), Widman & Rhodes (1991) and Côté et al. (in press), although Parsons & Dadswell (1992) reject this hypothesis in a study of the giant scallop *Placopecten magellanicus*. Parsons & Dadswell did not observe signs of competition for space, such as decreased survival or a higher proportion of deformed individuals at high densities. It is difficult to separate the importance

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of competition for food and space, since both cause a reduction in growth with increasing density (Olafsson 1986, Fréchette & Lefaivre 1990, Lesser et al. 1992) and none of the above experiments were specifically designed to do so.

The present paper investigates, in the field, the relative effect of limitations of food and space on the growth of bivalves reared at various densities in suspended culture. The giant scallop *Placopecten magellanicus* (Gmelin, 1791) was studied because previous reports demonstrate that its growth is affected by food availability (MacDonald & Thompson 1985), food quality (Cranford & Grant 1990, Lesser et al. 1991) and current velocity (Wildish et al. 1987, Wildish & Saulnier 1992) and because 2 recent studies provide data on the effect of density on its growth in suspended culture (Parsons & Dadswell 1992, Côté et al. in press). The effect of space was separated from that of food by comparing growth at different densities in 2 series of pearl nets. In one, density was increased by adding 'dummy' (non-living) rather than living scallops.

MATERIAL AND METHODS

Field experiment. The study was conducted from 15 July to 11 October 1992 near Gascons (48° 10' 55" N, 64° 54' 58" W) on the north shore of the Baie des Chaleurs, southwestern Gulf of St. Lawrence, Canada (Fig. 1). During this period the water column at Gascons is thermally stratified, the mean current velocity is ca 6 to 7 cm s^{-1} (Bonardelli et al. 1993) and small phytoplankton cells (<5 µm) dominate (Claereboudt et al. unpubl. data).

Increase in shell height and in the mass of shell, muscle and other soft tissues were quantified for juvenile scallops maintained in pearl nets (6 mm mesh size, square bottom with a surface area of 0.16 m^2) at densities of 25, 50, 75, 100, 150, 200 and 250 ind. net^{-1} in 2 series. In the first, all scallops were living individuals and 25 were tagged with a small number glued to the inferior valve. In the second series, the pearl nets contained only 25 living scallops net^{-1}, all tagged, and the density was completed to 50, 75, 100, 150, 200 and 250 ind. net^{-1} using dummy scallops. The dummy scallops were shells, from dead individuals of similar size, which were glued together (valves closed) with non-toxic silicon sealant. This technique was adapted from the studies by Peterson & Andre (1980) and Okamura (1986). After being glued, the dummy scallops were dried in the air for 3 d and then thoroughly washed to ensure that living scallops would not be harmed by chemicals from the sealant. The living scallops came from spat collectors which had been placed in the water in autumn 1990. After 1 yr on the collectors, they were placed in pearl nets and reared in suspended culture at a density of ca 100 scallops net^{-1} and at a depth of 15 m. The range of densities examined was based on the data of Parsons & Dadswell (1992) and Côté et al. (in press) showing that for juvenile giant scallops the effect of density becomes apparent at densities exceeding 100 scallops net^{-1}.

SCUBA divers placed the pearl nets in the water column on 15 July 1992. Pairs of pearl nets with the same stocking density, one with dummy and one with living scallops only, were suspended one under the other, separated by ca 30 cm. A buoy attached to the upper net maintained them in the water column and a line attached to the lower one anchored them to a bottom line (Fig. 2). The pearl nets were suspended at 9 m above the bottom, which was approximately 15 m below the surface at low tide. This depth was chosen as a compromise between shallower depths where conditions favour enhanced growth and greater depths where the negative effects from fouling are reduced (Claereboudt et al. in press). The pearl nets were retrieved on 11 October 1992. Tagged living scallops were counted and, for each, the increase in shell height was determined to calculate the daily rate of increase. The dry mass of the shell, adductor muscle and other soft tissues

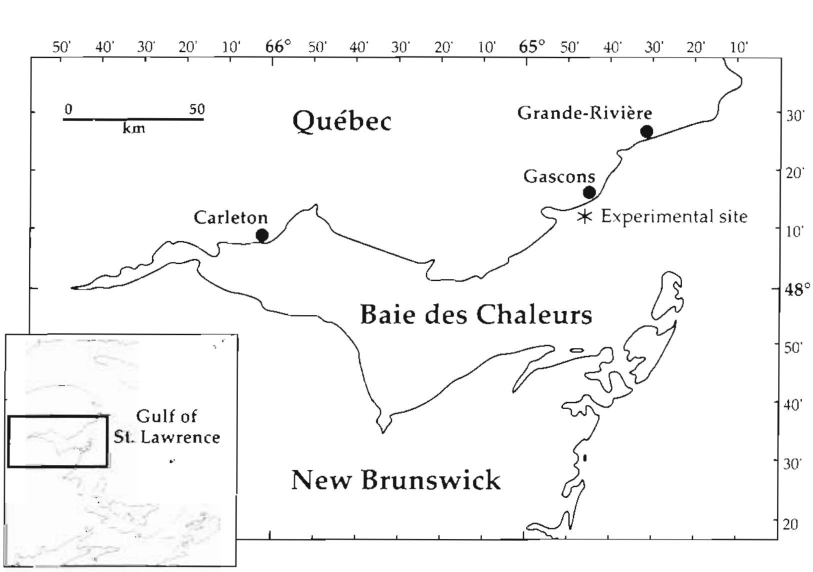

Fig. 1. Location of the study area at Gascons, in the southwestern Gulf of St. Lawrence, Canada

were also quantified after dissecting the scallops and drying tissues at 60 °C to a constant mass.

Statistical analysis. A 1-factor analysis of variance (ANOVA) of the data on initial shell height was first made to verify whether the scallops in different pearl nets were of similar size. At the end of the study, to determine the effect of the presence or absence of dummy scallops, the rate of growth of the shell and final dry mass of the shell, muscle and other soft tissues at each experimental density were compared using Student *t*-tests. Linear regressions were further used to examine the effect of density. That 25 tagged scallops were used in each net allowed us to obtain individual data and a higher number of degrees of freedom in statistical analysis. Individual rates of shell growth and final mass values (shell, muscle and other soft tissues) were used as dependent variables and stocking density as the independent variable. A logarithmic transformation was made of density to linearize the relation of growth and dry mass values to density, and further to respect the assumptions of homogeneity of variances or normality of error terms. Regression analyses were done separately for each series of pearl nets. Variations in mortality among pearl nets were examined using a chi-square analysis applied to a 3-dimensional contingency table, as described by Zar (1984). The significance level of $\alpha = 0.05$ was used in all tests.

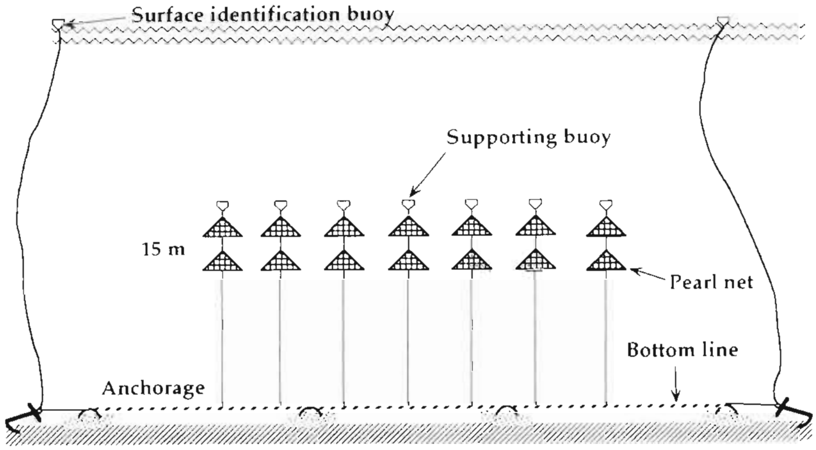

Fig. 2. Underwater structure maintaining the pearl nets at a depth of 15 m from the surface

RESULTS

The mean initial shell height (dorsal/ventral axis) for the living tagged scallops in the different pearl nets varied from 28.1 to 31.8 mm (Fig. 3) and the mean for all tagged scallops was 29.6 mm (SE = 0.3, n = 325). The 1-factor ANOVA applied to shell height demonstrated that the scallops were of similar size at the onset of the experiment ($p = 0.354$; Fig. 3). At the end of the study, the rate of growth in shell height, as well as the dry mass of the shell, muscle and other soft tissues, all showed a clear separation of values between treatments with and without dummy scallops, particularly at the higher densities (Fig. 4). At densities of 100 scallops net^{-1} and greater, mean growth rate of the shell and dry mass of the various body components were always significantly lower in treatments without dummies ($p < 0.05$; Table 1, Fig. 4).

For the series of pearl nets with living scallops only, the regression of rate of shell height growth to log-

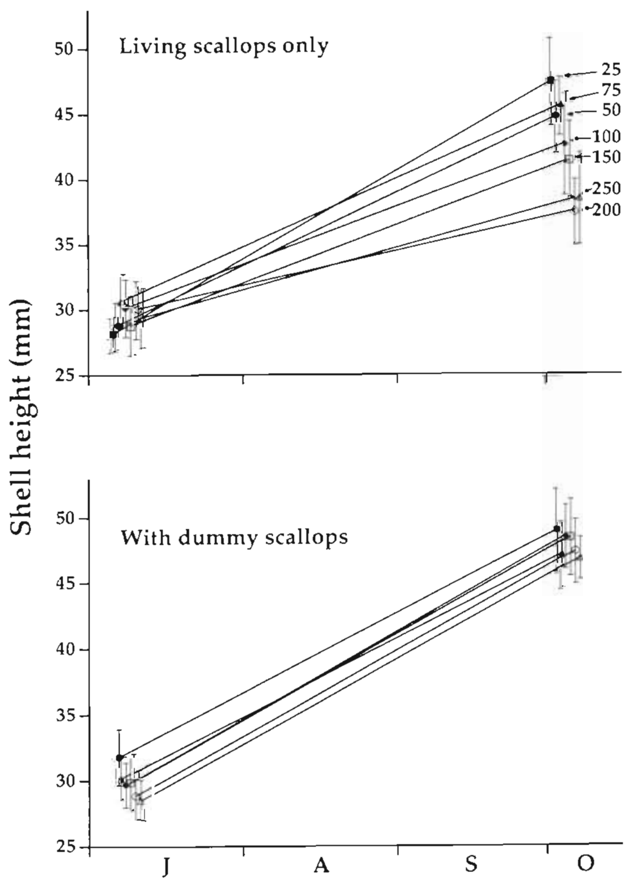

Fig. 3. *Placopecten magellanicus*. Initial and final mean shell height of scallops grown in pearl nets with dummy or living scallops at densities ranging from 25 to 250 scallops net^{-1}, from 15 July to 11 October 1992. There were initially 25 tagged scallops in each net. Vertical lines indicate 95 % confidence intervals

Table 1. *Placopecten magellanicus*. Student *t*-tests comparing, at 6 different densities, the growth rate (increase in shell height) and mass of the shell, muscle and other soft tissues for scallops grown in the presence or absence of dummy scallops. Values in table are *t*-value and their associated probabilities (p)

Density (ind. net^{-1})	df	Shell growth		Shell mass		Muscle mass		Other tissue mass	
		t	p	*t*	p	*t*	p	*t*	p
50	36	0.103	0.918	-1.741	0.902	-1.909	0.064	-2.05	0.044
75	38	-2.891	0.006	-0.878	0.386	-0.414	0.681	-0.744	0.462
100	33	-3.238	0.003	-2.261	0.031	-2.518	0.017	-2.161	0.038
150	34	-6.618	0.0001	-3.502	0.001	-3.786	0.0006	-3.458	0.001
200	37	-15.0	0.0001	-4.603	0.0001	-4.389	0.0001	-5.411	0.0001
250	36	-10.0	0.0001	-4.658	0.0001	-3.634	0.0009	-4.396	0.0001

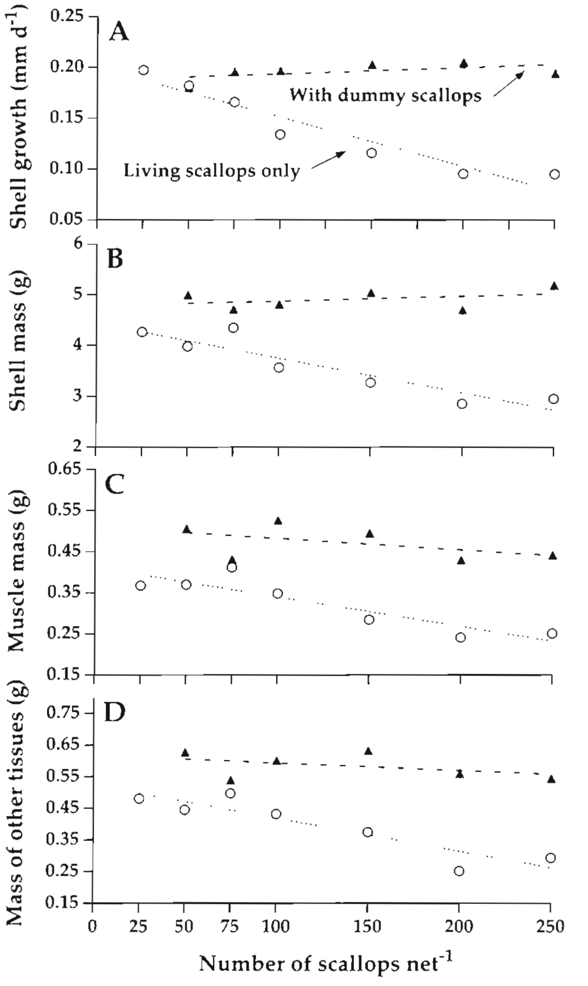

Fig. 4. *Placopecten magellanicus*. Mean daily growth in shell height during the study (A), and mean dry mass of the shell (B), the muscle (C) and the other soft tissues (D) at the end of the study for scallops grown in pearl nets with dummy or living scallops at densities ranging from 25 to 250 scallops net^{-1}, from 15 July to 11 October 1992. There were initially 25 tagged scallops in each net. Vertical lines indicate 95% confidence intervals

transformed stocking density was strongly negative ($p = 0.0001$; Table 2). The mean rate of growth decreased from 0.22 mm d^{-1} at a density of 25 scallops net^{-1} to 0.10 mm d^{-1} at densities of 200 to 250 scallops net^{-1} (Fig. 4A). Regressions of mass of the shell, muscle and other soft tissues to the log-transformed stocking density, in the absence of dummies, similarly showed a significant decrease with density (Table 2, Fig. 4B, C, D). In contrast, the series in which density was increased by adding dummy scallops did not show a significant relationship of growth, or of the various mass parameters, to log-transformed stocking density ($p > 0.1$; Table 2). The low determination coefficient (R^2) indicated a large scatter of points around the regression line, due to the variability in the growth rate and dry masses of scallops, especially in the series with dummies (Table 2).

Mortality in the various treatments varied from 20 to 36% (5 to 9 scallops net^{-1}; Table 3), except for one pearl net where there was 60% mortality. The latter unexpectedly occurred in the pearl net which had the lowest density, 25 scallops net^{-1}. The mortality was

Table 2. *Placopecten magellanicus*. Intercept (*a*), slope (*b*), associated probabilities (p) and determination coefficient (R^2) for linear regressions of the relation of growth rate (increase in shell height) and dry mass of the shell, muscle and other soft tissues to stocking density (log), for individuals grown in the presence or absence of dummy scallops. All regressions are expressed as $y = a + bx$

Dependent variable	*a*	*b*	p	R^2
With dummy scallops (n = 113)				
Shell growth	0.150	0.023	0.166	0.017
Shell mass	4.531	0.176	0.769	0.001
Muscle mass	0.621	-0.072	0.321	0.009
Other tissue mass	0.705	-0.059	0.505	0.004
Without dummy scallops (n = 118)				
Shell growth	-0.396	-0.125	0.0001	0.580
Shell mass	6.618	-1.483	0.001	0.089
Muscle mass	0.627	-0.148	0.0001	0.070
Other tissue mass	0.818	-0.206	0.0007	0.095

Table 3. *Placopecten magellanicus*. Percentage survival of 25 tagged scallops grown in series of pearl nets in which density was increased with living scallops compared to series in which density was increased with dummy scallops

Density (ind. net^{-1})	Living scallops only	With dummy scallops
25	40	–
50	72	80
75	80	80
100	76	64
150	72	72
200	84	72
250	68	84

probably related to colonization by *Tubularia larynx*, since this was the only net heavily colonized by this hydrozoan. It was attached to most of the scallops as well as to the pearl net. When this sample was removed from the analysis, a chi-square test indicated that survival was not affected by either density or the presence or absence of dummy scallops (chi-square value = 5.95, p = 0.989).

DISCUSSION

The present study demonstrates that density affects the rate of shell growth, as well as the mass of the shell, muscle and other soft tissues, for juvenile giant scallops maintained in suspended culture. The most striking effect was on shell height, since the growth rate at 25 to 50 scallops net^{-1} was nearly twice that at 200 to 250 scallops net^{-1}. The strong effect of density agrees with previous investigations of the effect of stocking density on growth for giant scallops (Parsons & Dadswell 1992, Côté et al. in press) and numerous other bivalves (Duggan 1973, Monical 1980, Mallet & Carver 1991, Holliday et al. 1993). An inverse relationship of growth to density has also been documented for bivalves in natural bottom habitats (Peterson & Black 1987, Vincent et al. 1989, van Erkom & Griffiths 1993).

The experimental design employed, in which density in one series of pearl nets was increased using dummy scallops that occupied space but did not compete for food resources, permitted us to separate effects of limited space from the effect of food depletion with increasing density. This is the first application of this technique to a bivalve in an aquaculture context. Simulated animals were used in 2 earlier studies which examined the growth of infaunal bivalves in bottom habitats. Peterson & Andre (1980) showed that growth of the sanguine clam *Sanguinolaria nuttallii* is limited by both food and space. Adding dummy clams has an effect equivalent to adding half as many living clams. Okamura (1986) used dummies to examine growth of individual mussels *Mytilus edulis* living in groups of different sizes. Surprisingly, he found that at low densities growth was reduced when dummies were present, whereas at high densities growth was increased when dummies were present. In our study, if space was an important limiting factor, the growth rate of the shell and the dry mass of soft tissues should have been similar at different densities in the 2 series; however, marked differences between the 2 series were observed. These parameters sharply decreased when density was increased by adding living scallops (particularly at densities of 100 scallops net^{-1} and greater) whereas no significant change occurred when density was increased by adding dummies. This indicates that competition for food is the principal limiting factor.

Dummy scallops could affect living individuals merely because of the space they occupy. Reducing space availability increases physical contacts among scallops as the pearl nets are moved about by wave activity and currents. Duggan (1973) considers that such mechanical disturbance could decrease feeding and growth in scallops. The mass of the muscle and soft tissues are the parameters most sensitive to environmental stress (Côté et al. in press) and their tendency to decrease with increasing density when dummies are present, although not significant, may indicate this effect of space.

Dummy scallops, as in the present study, are not capable of behavioural interactions and it is possible that a reduction in space increases behavioural interactions involved in spatial competition (Fréchette & Lefaivre 1990). Juvenile giant scallops are prone to making swimming excursions (Manuel & Dadswell 1991, Parsons et al. 1992) and such activity, within the confines of a pearl net, could induce more frequent contacts among individuals, causing reduced time spent feeding (more frequent valve closure) and less energy available for growth. Another potential behavioural interaction is 'biting', in which the valves of scallops become interlocked (Paul et al. 1981, Wildish et al. 1988). Biting may cause damage to soft tissues, deformation of the shell and higher mortality. The effect of 'biting', if important, should have been detected since it is usually the 'biter' which is harmed. Although behavioural interactions cannot be excluded, there was little to suggest they had an effect, since few interlocked shells were observed, shell margins appeared to be similar between scallops in the 2 series and there were no differences in mortality between the 2 treatments. A lack of evidence of an effect of behavioural interactions among *Placopecten magellanicus* in suspended culture was similarly reported by Parsons & Dadswell (1992).

Additional factors potentially affecting growth in pearl nets are mesh size and organisms fouling the nets. Both reduce water flow to the scallops and fouling organisms, such as *Mytilus edulis* and *Hiatella arctica* which colonized the pearl nets, may further compete with the scallops for food resources. Mesh size was the same and the degree of colonization appeared to be similar for pearl nets in this study, except for the one heavily colonized by *Tubularia larynx*. These factors do not appear to explain differences among treatments. Our experiment shows that food depletion causes a marked decline in growth at high densities. In bivalve aquaculture, the negative effects of increased stocking density could in part be compensated for by selecting sites where food abundance is high.

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