Vol. 250: 183–195, 2003 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published March 26

Comparison of cultured and wild sea scallops *Placopecten magellanicus*, using behavioral responses and morphometric and biochemical indices

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ABSTRACT: As the survival of juvenile scallops released onto the seabed is of critical importance in programs seeking to enhance scallop populations, the basis of the vulnerability of seeded cultured scallops needs to be understood. High mortality rates following seeding operations could reflect weaker predator escape responses by cultured scallops. Thus, we compared behavioral responses as well as morphometric and biochemical measurements of cultured and wild sea scallops *Placopecten magellanicus* (35 to 45 mm shell height) sampled in August 1999 in the Gulf of St. Lawrence, eastern Canada. Cultured scallops had larger somatic tissues and higher muscle energetic contents than their wild counterparts. This may reflect the more favorable temperatures and better food supply during suspension culture. When faced with the starfish predator *Asterias vulgaris*, cultured scallops responded with a greater number of claps, longer clapping period and faster recuperation of clapping performance. However, wild scallops had stronger shells and showed more intense escape responses (higher clapping rate) to the starfish. These differences contribute to making cultured scallops more vulnerable to predation by grasping predators (crabs) and asteroids.

KEY WORDS: Scallop · *Placopecten magellanicus* · Muscle · Escape response · Culture · Predation

INTRODUCTION

Juvenile mortality is a major factor determining the population dynamics of marine invertebrates, particularly in the case of broadcast spawners with a large reproductive output. High mortality due to predation can be a major obstacle to effective seeding of juveniles to enhance populations of heavily fished species. During culture of pectinids, juveniles are either collected by natural settlement onto artificial collectors or produced in a hatchery (Young-Lai & Aiken 1986, Tremblay 1988, Naidu et al. 1989, Barbeau et al. 1996, Cliche & Giguère 1998). Subsequent liberation of these juveniles into the natural habitat (during 'seeding-ranching' operations) exposes them to high rates of predation (Minchin 1991, Cliche et al. 1994, Barbeau et al. 1996, Hatcher et al. 1996). Since exposure to the threat of predation can lead to phenotypic defensive adaptations in many aquatic invertebrates (reviewed by Havel 1987), artificially reared juveniles may be more susceptible to predation if their defenses are less efficient than those of wild juveniles.

Despite the increasing reliance upon seeding juvenile scallops as a means of enhancing scallop production, surprisingly few studies have compared the performance of cultured and wild scallops. One such study shows that cultured *Pecten maximus* have weaker shells and are more susceptible to predation than wild *P. maximus* (Haugum et al. 1999). As the survival of juvenile scallops released onto the seabed is a critical determinant of the success of the 'seeding-ranching' strategy (Tremblay 1988, Naidu et al. 1989,

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Hatcher et al. 1996), the factors underlying the vulnerability of cultured scallops need to be understood. As a case in point, in the Îles-de-la-Madeleine, Gulf of St. Lawrence, eastern Canada, predation on seeded sea scallop *Placopecten magellanicus* is the main factor reducing their survival (Cliche et al. 1994).

Scallops are unique among bivalve mollusks in possessing an excellent swimming capacity which they use upon contact with predators (see Wilkens 1991). This response is most effective for escape from slow-moving predators such as starfish and gastropods. Cultured *Placopecten magellanicus* juveniles show a strong escape response to starfish (Barbeau & Scheibling 1994a,b), suggesting that its escape responses are at least partly innate. Nonetheless, the nature of scallop swimming changes with size (Gould 1971, Dadswell & Weihs 1990, Carsen et al. 1996). Smaller *P. magellanicus* swim in a spiral, whereas adults swim in more or less a straight line (Caddy 1968, Manuel & Dadswell 1991, 1993). As scallop swimming responses are variable, we reasoned that the escape response to starfish (clapping rate, total number of claps until fatigue) may differ between wild and cultured juvenile *P. magellanicus*.

Reproductive investment and spawning markedly slow recuperation from exhaustive escape responses by adult *Chlamys islandica* and *Euvola ziczac* (Brokordt et al. 2000a,b). In both species, reproductive investment leads to a decline in muscle carbohydrate levels, as well as in muscle activities of glycolytic and mitochondrial enzymes, along with a decline in the capacity for recuperation from exhausting exercise. These changes suggest that the physiological status of the adductor muscle markedly influences its capacity for recuperation. As cultured and wild juvenile scallops have experienced different rearing densities, environmental conditions and manipulations, their physiological status is likely to differ, and this should affect their capacities for recuperation from exhausting escape responses.

In the present study, we compared cultured and wild scallops (35 to 45 mm shell height) at a period targeted for seeding by growers, to examine whether weaker behavioral and mechanical defenses and physiological status make cultured scallops more vulnerable to predation than their wild congeners present on the seeding grounds. We compared shell strength, escape responses, recuperation from exhausting escape responses, righting responses, anatomical measurements, levels of macromolecular reserves and enzyme activities in the muscle of wild and cultured juvenile *Placopecten magellanicus*. Our underlying hypothesis was that cultured scallops would perform less well than wild scallops in the parameters related to predation avoidance, since cultured scallops were grown in an environment without immediate contact with predators. We used the levels of macromolecular reserves and muscle metabolic capacities to assess whether the physiological capacities of muscle were linked with performance capacities in these wild and cultured juvenile scallops.

MATERIALS AND METHODS

Sampling and maintenance of scallops. The wild population studied was located south of the Îles-de-la-Madeleine, in the 'Chaine-de-la-Passe' fishing area (47° 08′ N, 61° 43′ W). A Digby drag with 2 standard baskets lined with Vexar™ (19 mm mesh) was used for sampling wild juvenile scallops at a depth of 30 m.

The cultured scallops were collected and grown at Newhall (Fig. 1). In autumn 1997, spat settled into collector bags in which they grew until October 1998. Then they were transferred to pearl nets (35 cm square base, with a 6 mm mesh netting) for 8 mo of intermediate culture at a density of 100 ind. net^{-1}. Thereafter, from June to August 1999, the juveniles were maintained at a density of 20 ind. net^{-1} (35 cm square base, with a mesh size of 9 mm). From the beginning, cultured scallops fed on wild phytoplankton. At the time of study, the cultured scallops were 2 yr old.

After harvesting on August 24, the wild and cultured scallops were transported to the wet laboratory at the Cap-aux-Meules Research Station, where they were separately placed in continuously aerated 200 l tanks and maintained at 12.5°C and in a natural photoperiod for 1 wk before experimentation. We chose 12.5°C since it was halfway between the lagoon temperature (19°C; Lafrance et al. 2002) and the bottom temperature (7°C, measured with a thermograph attached to the dredge). Seawater was filtered (1 µm) and UV-sterilized. No food was supplied. Fecal material was removed daily and water was changed twice a week. Salinity ranged from 29.0 to 30.5‰ during this study, both in the laboratory and at the collection sites.

To minimize the impact of size in our comparisons, we selected 76 individuals of 35 to 45 mm in shell height (maximum distance between the dorsal hinge and ventral margin; size range frequently used for seeding) for both the wild and cultured scallops. Scallops were tagged (4 × 8 mm Hallprint™ labels glued on the upper valve using cyanoacrylate adhesive) to facilitate identification of individuals when measuring escape responses, righting responses, shell strength and biochemical and anatomic characteristics. We first measured the righting response (n = 75 for both wild and cultured scallops; missing datum for 1 scallop in each group), escape response and recuperation from exhausting escapes, then recorded the shell mass,

height (dorsal-ventral), length (anterior-posterior diameter) and width (lateral diameter), and finally dissected the scallop to determine the mass of body components (n = 76 for both groups of scallops). Escape responses for these scallops were evaluated over a 3 d period. Dissections were carried out after 1 wk of recuperation from the escape response tests. The adductor muscle of each scallop was frozen on dry ice immediately after dissection and was maintained on dry ice for approximately 1 mo before transfer to –80°C at Université Laval. Other soft tissues (including mantle, gills, digestive tract and a tiny gonad) were dried to constant mass at 60°C. The shells were refrigerated in plastic bags containing seawater for maximally 10 d until determination of shell strengths at Université Laval. Additional scallops with a larger range of shell heights (25 to 51 mm; n = 73 and 64 for wild and cultured scallops, respectively) were used for shell strength determinations. Righting responses were also determined for individuals measuring 45 to 55 mm (n = 30 for both groups of scallops). Several anatomical indices were calculated to examine the relative changes of the variables measured. Muscle indices 1 (muscle mass/mass of total soft tissues minus muscle mass) and 2 (muscle mass/shell mass), a condition index (mass of total soft tissues/shell volume) and the aspect ratio [(shell length/shell height) × 100] are presented in Table 1. The shell volume [π × (height/2) × (length/2) × (width × 0.38)] was estimated by modifying the formula for the volume of a cone with an empirically estimated constant (0.38) assessed from the water displaced by a clay model of a shell of known dimensions.

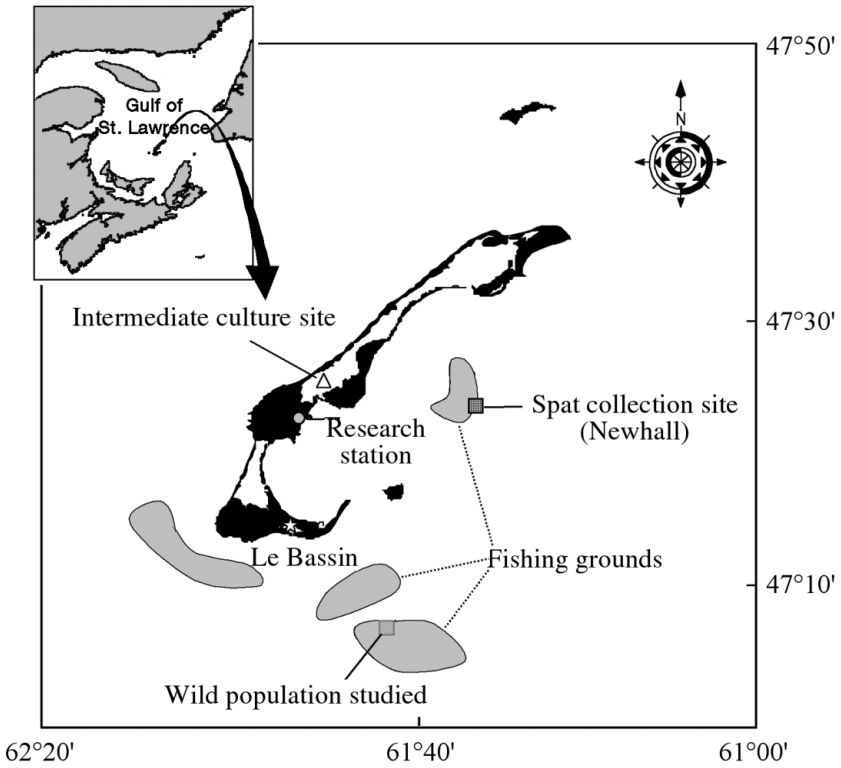

Fig. 1. Location of sites for sea scallop spat collection, intermediate culture in pearl nets and dragging for wild scallops in the Îles-de-la-Madeleine. Starfish were harvested in the lagoon Le Bassin. Inset shows location of the study site in the Gulf of St. Lawrence, eastern Canada

Behavioral tests. ***Evaluation of escape responses:*** Individual scallops were placed in 33 × 28 × 12 cm trays containing ~6 l of filtered seawater at 12°C. Scallops were allowed at least 2 min in the basin before stimulation (Ordzie & Garofalo 1980). We stimulated swimming of a scallop by touching it with the arm of a starfish (*Asterias vulgaris*, 11 to 15 cm in diameter), and then recorded the time and number of valve adductions (claps) until fatigue. We also noted the maximal number of claps in a series during the second and third days of experimentation. In contrast to adults, juvenile *Placopecten magellanicus* do not consistently close their valves when exhausted, so fatigue was defined by the scallops' incapacity to clap within 1 min of the previous clap. Once the scallop was exhausted, it was left in its aerated basin for 15 min. Then the escape response was quantified a second time. Preliminary tests established that 15 min was sufficient for partial recuperation of escape response capacity. If no claps occurred within 2 min of stimulation, the observation was stopped. Seawater in the trays was replaced before starting a test with another scallop.

The *Asterias vulgaris* used to elicit the escape responses had been harvested in the lagoon Le Bassin (south of the Îles-de-la-Madeleine; Fig. 1) and maintained in a tank containing 180 l of filtered and continuously aerated seawater. The starfish were starved for at least 24 h before the experiments, to standardize their hunger level (Elner & Jamieson 1979, Barbeau & Scheibling 1994b). The starfish used in a particular escape response test were haphazardly chosen from 20 individuals. The same starfish was used for the 2 escape response tests of a given scallop.

Righting responses: Righting responses were quantified in two 58 × 118 × 60 cm tanks containing 100 l of filtered and aerated seawater. No gravel was provided. The scallops were placed with their upper (left) valve

on the bottom of the aquarium. All scallops were upside-down at the onset of the test. The number of scallops that had righted themselves was determined at 5 min intervals until at least 95% of the scallops had righted themselves. Thus, the precision for the estimate of the righting time of each scallop was within 5 min. One tank was used for the cultured scallops and a second for the wild scallops.

Evaluation of shell strength. An Instron Model TT Universal testing instrument with a force range of 0.5 to 10 000 kg (5 g precision) was used to crush the scallop shells. A 2 mm steel pin with a shape similar to that of the tip of a crab claw was applied at the region normally attacked by crabs (Elner & Jamieson 1979). We placed the pin on the left valve in a position 1 cm ventral to the ligament, where growth lines typically became visible. We used this approach to simulate the pressure applied during an attack by a crab.

Muscle protein and carbohydrate concentrations. All biochemical determinations examined the phasic portion of the adductor muscle. Total protein concentrations were measured using the bicinchoninic acid method according to Smith et al. (1985), with bovine serum albumin (BSA) as a standard. The total content of carbohydrates was determined using the phenol-sulfuric acid method of Dubois et al. (1956), as modified by Martinez (1991). One aliquot of homogenate was resuspended (1:11) in trichloracetic acid (10%), placed in an incubator at 65°C for 60 min, cooled and centrifuged for 15 min at 4342 × *g* at 4°C; 2 ml of phenol (>99.5%) was added to 1 ml of supernatant; 5 ml sulfuric acid (95%) was then added. After vigorous vortexing, the mixture was heated at 80°C for 20 min. After cooling, the absorbance at 490 nm was determined using a UV-Vis spectrophotometer (Beckman DU-640). Oyster glycogen was used as a standard.

Enzyme assays. Muscle was homogenized in 9 volumes (m/v) of ice-cold imidazole-HCl 50 mM, 2 mM EDTA-Na_2, 5 mM EGTA (ethyleneglycol tetraacetic acid), 150 mM KCl, 0.1% (v/v) Triton x-100 and 1 mM dithiothreitol. Homogenization occurred on ice using a Polytron (Brinkman Instruments) for 3 × 20 s periods separated by 20 s cooling periods. The pH was 6.6 for extracts used to measure octopine dehydrogenase (ODH) and arginine kinase (AK), and pH 7.2 with the addition of 20 mM NaF for phosphofructokinase (PFK), glycogen phosphorylase (GP) and citratre synthase (CS). A portion of this extract was centrifuged at 10 000 × *g* at 4°C for the assay of PFK and GP.

Enzyme activities were measured using a UV-Vis spectrophotometer (Beckman DU-640), with assay temperature controlled at 12.5°C by a refrigerating-circulating water bath (Haake). Enzyme assays were followed at 340 nm to note changes in the concentration of NAD(P)H, except in the case of CS, which was followed at 412 nm to detect the transfer of sulfhydryl groups to 5,5′dithiobis-2-nitrobenzoic acid (DTNB). The micromolar extinction coefficients for NAD(P)H and DTNB were 6.22 and 13.6 cm^2 μmol^{-1}, respectively. All enzyme assays were carried out in duplicate. Enzyme activities were expressed in international units (µmol of substrate transformed to product min^{-1}; U) g^{-1} wet mass, units mg^{-1} protein and as total units in the adductor muscle. We adapted enzyme assay conditions from studies on adult *Placopecten magellanicus* by de Zwaan et al. (1980) and Stewart et al. (1992), as follows:

Glycogen phosphorylase a (EC 2.4.1.1 GP): 50 mM imidazole, 80 mM KH_2PO_4, 5 mM Mg-acetate, 2.5 mM EDTA, 0.6 mM NADP, 0.8 mM AMP, 0.5 mM cyclic AMP, 4 µM glucose-1,6-bisphosphate, 10 mg ml^{-1} glycogen (omitted for controls), pH 7.5. Glucose-6-phosphate dehydrogenase and phosphoglucomutase activities were present in excess.

Phosphofructokinase (EC 2.7.1.11 PFK): 50 mM Tris-HCl, 50 mM KCl, 5 mM Mg-acetate, 1 mM ATP, 0.8 mM AMP, 0.2 mM NADH, 0.08 mM fructose-2,6-bisphosphate, 1 mM fructose-6-phosphate (omitted for controls), pH 7.5. Excess levels of aldolase, triosephosphate isomerase and glycerol-3-phosphate dehydrogenase were used.

Octopine dehydrogenase (EC 1.5.1.11 ODH): 50 mM imidazole-HCl, 2 mM EDTA-Na_2, 5 mM EGTA, 1 mM KCN, 0.2 mM NADH, 5 mM pyruvate-Na, 6 mM L-arginine (omitted for controls), pH 6.6.

Arginine kinase (EC 2.7.3.3 AK): 50 mM imidazole-HCl, 5 mM $MgCl_2$, 0.4 mM ADP, 10 mM glucose, 0.6 mM NADP, 5 mM phosphoarginine (omitted for controls), pH 6.6. Excess levels of hexokinase and glucose-6-phosphate dehydrogenase were used.

Citrate synthase (EC 4.1.3.7 CS): 75 mM Tris, 0.4 mM acetyl CoA, 0.25 mM DTNB, 0.5 mM oxaloacetate (omitted for controls), pH 8.0.

Chemicals. Metabolites and coupling enzymes were purchased from Sigma, Roche Diagnostics and ICN Pharmaceuticals. All other reagents were analytical grade.

Statistical analyses. Statistical analyses were performed using SAS software package (SAS 1999). Prior to the analyses, the data were tested for normality using the Shapiro-Wilk's *W*-test (Zar 1984); homoscedasticity was verified by graphically examining the distribution of the variance residues. A probability level of 0.05 was used.

Anatomical measurements, muscle levels of carbohydrates, proteins and enzymes were compared either by Student's *t*-test or Mann-Whitney *U*-test (Zar 1984), depending on the normality of the data. The shell strengths were compared using analyses of

covariance (ANCOVA) to assess the effect of the shell mass on the slope of the regression line (Snedecor & Cochran 1989). Residual mean squares from the 2 regression lines (i.e. wild and cultured separately) were first compared by the 2-tailed *F*-test to ensure the equality of residual variances. Then, slopes were compared by testing the significance of the interaction term (origin × shell mass) within the ANCOVA. We present non-transformed data (see Fig. 2) to facilitate interpretation since the relation between slopes was very similar to the appropriate log-transformed data.

ANOVA following the GLM procedure tested the effects of the independent factors (origin and day of study) and their interactions on escape response parameters. A total lack of response after the 15 min recuperation was observed for 2 cultured and 4 wild scallops. These individuals were excluded from those analyses. Moreover, after recuperation, certain scallops (≤4) showed responses beyond 200% of their initial values for a given escape parameter and were eliminated from the corresponding analysis. Data were log, square root or reciprocally transformed when necessary to achieve normality and homoscedasticity. Untransformed values are reported in the tables and figures.

To assess the impact of the biochemical and anatomic parameters upon the escape responses, we carried out a multi-step analysis. We initially selected the anatomic (full data set) and biochemical (subset of 56 scallops) variables that least inflated the variance of the parameters quantified during the escape responses, using the REG/vif collin procedure of SAS (1999). Then, we focused on the subset of 56 individuals. The variables previously selected were subjected to a multiple stepwise regression and significantly correlated variables (slstay = 0.15) were retained to perform an ANCOVA with origin and day of study as factors.

RESULTS

Anatomical parameters

For a given shell height, the length, width, volume and aspect ratio were greater for cultured than wild scallops (Table 1). Shell mass did not differ between the 2 groups of scallops. All soft tissue masses (phasic and catch adductor muscle, digestive gland, other soft parts) were heavier in cultured than wild scallops. A condition index evaluating the total soft tissue mass relative to shell volume was also greater in cultured than wild scallops. Water content of the soft tissues (without the digestive gland and muscle) was greater in wild scallops. Shell strength was greater for wild scallops, particularly for larger scallops (Fig. 2). The regression lines from tagged scallops (35 to 45 mm of shell height) and scallops from a wider shell height range (25 to 51 mm) indicate a faster increase in shell strength with shell mass for wild scallops (Table 2).

Behavioral responses

Wild scallops clapped at a higher rate, exhausted faster (could not clap within 1 min) and stayed shut for longer periods than cultured scallops (Table 3). In contrast, cultured scallops made more claps before exhaustion. After 15 min of recuperation from exhaustive escape responses, the cultured scallops maintained their greater number of claps and longer clapping time and, showed a higher maximum number of claps in a series. Wild scallops maintained their higher clapping rate after recuperation.

Table 1. *Placopecten magellanicus.* Anatomical measurements of wild and cultured sea scallops *P. magellanicus* (35 to 45 mm) used in behavioral and biochemical comparisons (mean, SE in parentheses) (n = 76). When not specified, fresh tissue masses are given; p-values are from Student's *t*-tests, or from Mann-Whitney *U*-tests when the data were not normally distributed. T_m = mass of total soft tissues [$M_m + D_m + O_m$]

Variable	Cultured	Wild	p
Shell characteristics			
Height (S_h), mm	40.1 (0.3)	40.2 (0.3)	0.80
Length (S_l), mm	39.1 (0.3)	38.1 (0.3)	0.026
Width (S_w), mm	10.1 (0.1)	8.9 (0.1)	<0.0001
Volume (S_v), cm^3	4.8 (0.1)	4.1 (0.1)	<0.0001
Aspect ratio [(S_l/S_h) × 100]	97.4 (0.3)	94.8 (0.4)	<0.0001
Mass (S_m), g	3.510 (0.080)	3.604 (0.090)	0.36
Soft tissue masses (T_m), g			
Adductor muscle, phasic	0.982 (0.025)	0.601 (0.015)	<0.0001
Adductor muscle, catch	0.105 (0.003)	0.087 (0.002)	<0.0001
Adductor muscle, total (M_m)	1.086 (0.027)	0.688 (0.017)	<0.0001
Digestive gland (D_m)	0.277 (0.008)	0.146 (0.004)	<0.0001
Other soft tissues, wet (O_m)	1.482 (0.034)	1.205 (0.025)	<0.0001
Other soft tissues, dry	0.190 (0.004)	0.140 (0.003)	<0.0001
Water content of other soft tissues, %	87.2 (0.1)	88.3 (0.1)	<0.0001
Muscle index 1 [$M_m/(D_m + O_m)$]	61.9 (0.7)	51.0 (0.7)	<0.0001
Muscle index 2 (M_m/S_m)	31.1 (0.4)	19.3 (0.3)	<0.0001
Condition index [(T_m/S_v) × 100], g cm^{-3}	59.7 (0.5)	49.9 (0.5)	<0.0001

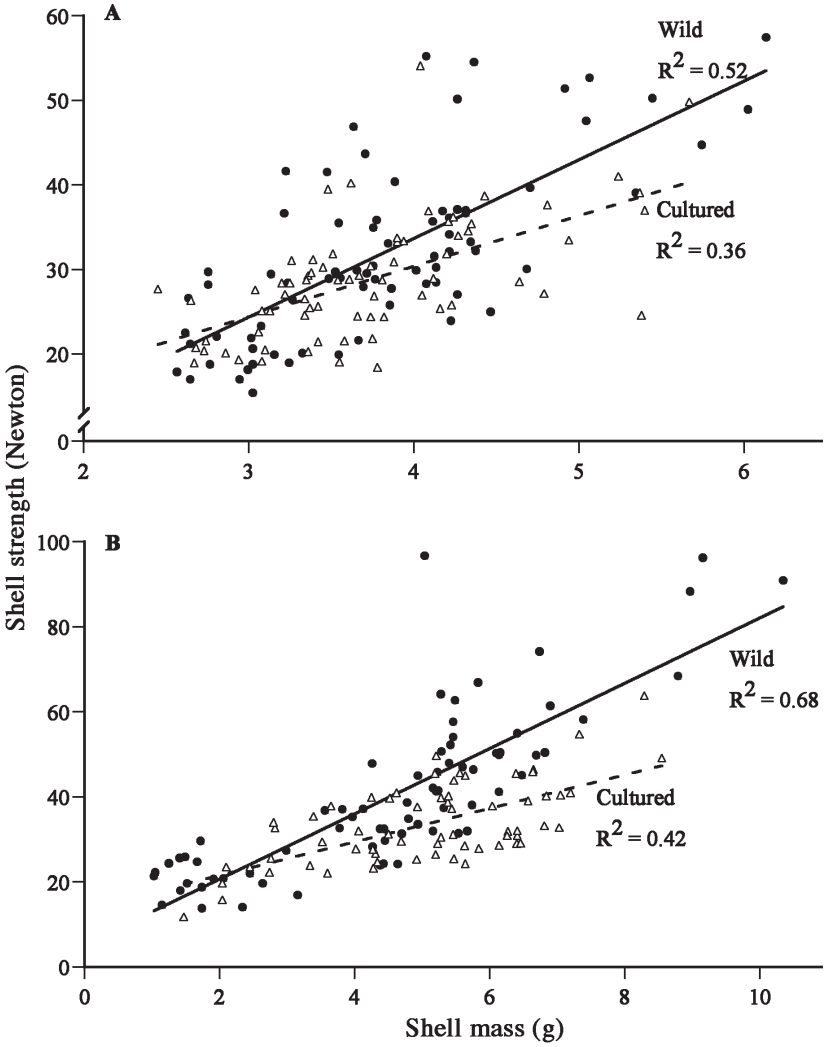

Fig. 2. *Placopecten magellanicus*. Relationship between the pressure causing shell breaking (strength) and shell mass for wild and cultured sea scallops. (A) Scallops (35 to 45 mm) used in all comparisons; n = 75 and 72 for wild and cultured scallops, respectively. (B) Other scallops (25 to 51 mm) used to examine shell strength; n = 73 and 64 for wild and cultured scallops, respectively

Table 2. *Placopecten magellanicus*. ANCOVA statistics on log-transformed shell strength for 35 to 45 and 25 to 51 mm wild and cultured sea scallops with shell mass as the covariate. Log transformations were made to ensure normality and homoscedasticity of residuals

	df	SS	MS	*F*	p
35–45 mm scallops					
Equality of slopes	1	0.031	0.031	4.01	0.047
Residual error	143	1.098	0.008		
25–51 mm scallops					
Equality of slopes	1	0.085	0.085	8.90	0.0034
Residual error	133	1.277	0.010		

When the response after 15 min of recuperation was compared to the first response, wild and cultured scallops did not differ in the percent initial claps and percent clapping time, but cultured scallops showed a more complete recuperation of their initial clapping rate and of the initial maximum number of claps (Table 4).

Cultured and wild scallops did not differ in mean righting time ($p = 0.077$; 27.1 ± 3.5 and 28.7 ± 2.6 min [mean ± SE] for 35 to 45 mm cultured [n = 74] and wild scallops [n = 72], respectively) and most scallops righted themselves within 50 min (Fig. 3a). The righting responses of larger individuals (shell height 45 to 55 mm) were quite similar (Fig. 3b).

Muscle biochemical composition and enzymatic activities

Both total carbohydrate and total protein contents in the phasic muscle were markedly higher in cultured than in wild scallops (Table 5). Cultured scallops showed higher specific activities for phosphofructokinase and octopine dehydrogenase, both as U g^{-1} muscle and U mg^{-1} protein. The other enzymes showed similar activities for both groups. Given the larger size of the adductor muscle in cultured scallops, the total contents of all the enzymes measured were consistently higher in cultured scallops.

Determinants of the escape responses

Among the numerous biochemical and anatomical parameters we measured for each individual, few seemed linked to the performance in the escape responses (Table 6). Most variables were eliminated initially since they inflated the variance of the regression model. Hence, the shell masses, catch muscle masses, protein and carbohydrate content in the phasic muscle and the activities of the five enzymes considered (PFK, GP, CS, ODH, AK) were submitted to multiple stepwise regressions in which each escape parameter was a dependent variable. Muscle carbohydrates and the activity of the ODH partially explained the total number of claps during the initial escape test. CS activity was also significantly associated with the maximal number of claps in a row.

Table 3. *Placopecten magellanicus*. Mean clapping behavior (SE, n) during escape responses by wild and cultured (35 to 45 mm) sea scallops. p-values assigned according to 2-factor ANOVAs (origin and day of study) and show differences due to scallop origin

Origin	Number of claps	Clapping time (min)	Clapping rate (claps min^{-1})	Max number of claps in a series[a]	Time spent closed (min)[b]
Initial response					
Cultured	48.5 (1.5, 76)	1.42 (0.06, 76)	37.5 (1.5, 76)	10.3 (0.8, 52)	5.1 (0.3, 70)
Wild	44.2 (1.0, 76)	0.90 (0.02, 76)	50.7 (1.2, 76)	11.2 (0.6, 52)	6.5 (0.3, 70)
p	0.014	<0.0001	<0.0001	0.17	0.0006
Response after 15 min of recuperation[c]					
Cultured	28.3 (1.0, 74)	1.00 (0.06, 74)	33.1 (1.6, 74)	7.3 (0.4, 50)	–
Wild	23.7 (1.1, 72)	0.66 (0.05, 72)	39.9 (1.3, 72)	5.8 (0.3, 50)	–
p	0.0041	<0.0001	0.0010	0.0054	–

[a]Not measured for 24 individuals from each group on the first day of the experiment
[b]Six individuals from each group not taken into account as they did not open after 15 min recuperation
[c]Two cultured and 4 wild individuals removed from the analyses because they did not clap after 15 min recuperation

Table 4. *Placopecten magellanicus*. Mean (SE, n) percentage (%) of initial number of claps, clapping time, clapping rate and maximum number of claps in a series after 15 min recuperation from exhaustive escape responses by wild and cultured (35 to 45 mm) sea scallops. Two cultured and 4 wild individuals were removed from the analyses because they did not clap after the 15 min recuperation period. Up to 4 scallops showing a recuperation beyond 200% were eliminated. p-values showing differences between wild and cultured scallops assigned according to 2-factor ANOVAs (origin and day of study)

Origin	% initial number of claps	% initial clapping time	% initial clapping rate	% initial max number of claps in a series[a]
Cultured	60.8 (2.7, 73)	70.4 (3.9, 72)	93.4 (4.6, 73)	84.7 (6.3, 49)
Wild	56.2 (3.3, 72)	66.1 (3.4, 68)	80.6 (2.6, 72)	58.1 (4.6, 49)
p	0.24	0.57	0.046	0.0013

[a]Not measured for 24 individuals from each group on the first day of the experiment

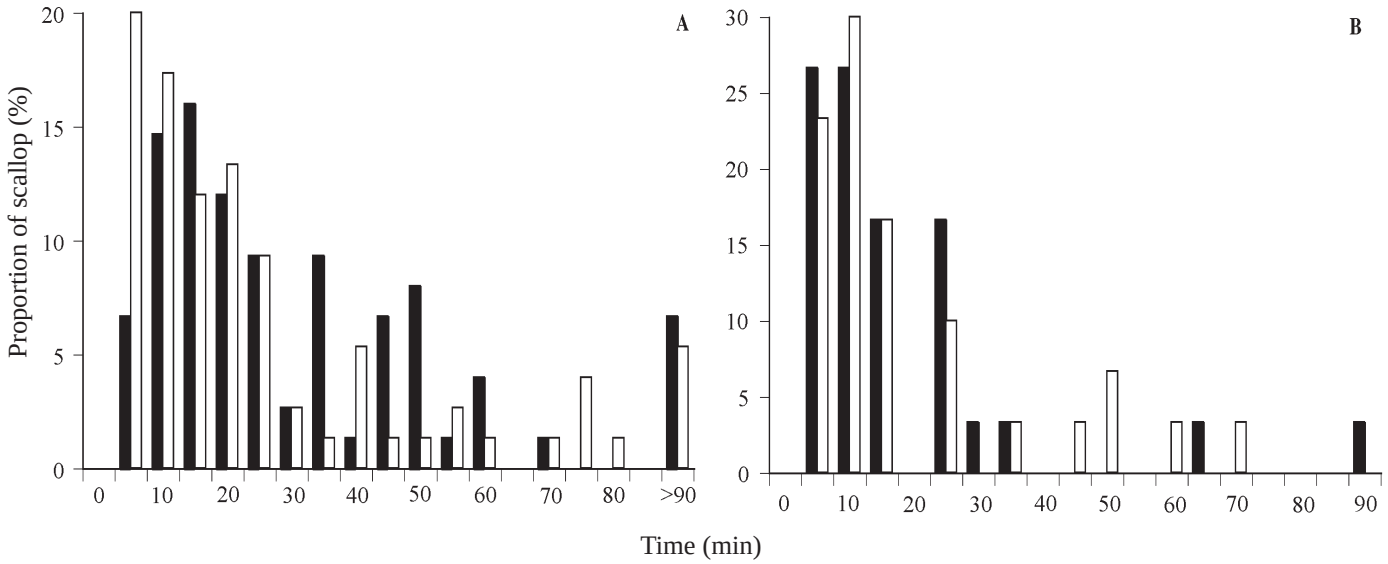

Fig. 3. *Placopecten magellanicus*. Righting time of wild and cultured sea scallops (A) Scallops with a shell height of 35 to 45 mm, used for all comparisons; n = 75 for both wild and cultured scallops. (B) Scallops with a shell height of 45 to 55 mm; n = 30 for both wild and cultured scallops. Solid bars correspond to wild scallops; open bars correspond to cultured scallops

Table 5. *Placopecten magellanicus*. Mean (SE, n) biochemical reserves and maximal enzymatic activities of phasic adductor muscle from wild and cultured (35 to 45 mm) sea scallops. p-values are from Student's *t*-tests, or from Mann-Whitney *U*-tests when the data were not normal

Variable	Units	Cultured	Wild	p
Carbohydrates	mg g^{-1} wet muscle	17.8 (0.6, 76)	3.3 (0.1, 76)	<0.0001
	mg $muscle^{-1}$	17.8 (0.8, 76)	2.0 (0.1, 76)	<0.0001
Proteins	mg g^{-1} wet muscle	133.2 (1.8, 76)	121.1 (1.6, 76)	<0.0001
	mg $muscle^{-1}$	131.2 (3.9, 76)	73.0 (2.2, 76)	<0.0001
Glycogen phosphorylase	U g^{-1} wet muscle	0.75 (0.05, 28)	0.62 (0.03, 27)	0.17
	U × 10^{-3} mg^{-1} protein	5.20 (0.40, 28)	4.69 (0.25, 27)	0.84
	Total U	0.73 (0.06, 28)	0.39 (0.03, 27)	<0.0001
Phosphofructokinase	U g^{-1} wet muscle	0.92 (0.03, 28)	0.73 (0.04, 28)	<0.0001
	U × 10^{-3} mg^{-1} protein	6.34 (0.21, 28)	5.53 (0.27, 28)	0.0048
	Total U	0.90 (0.04, 28)	0.46 (0.03, 28)	<0.0001
Octopine dehydrogenase	U g^{-1} wet muscle	40.5 (1.6, 28)	29.9 (1.2, 28)	<0.0001
	U × 10^{-3} mg^{-1} protein	281 (12, 28)	226 (9, 28)	0.0017
	Total U	40.3 (2.4, 28)	18.6 (1.1, 28)	<0.0001
Arginine kinase	U g^{-1} wet muscle	414 (27, 28)	372 (19, 28)	0.80
	U mg^{-1} protein	2.86 (0.19, 28)	2.82 (0.15, 28)	0.23
	Total U	410 (34, 28)	230 (14, 28)	<0.0001
Citrate synthase	U g^{-1} wet muscle	2.40 (0.05, 28)	2.43 (0.07, 28)	0.63
	U × 10^{-3} mg^{-1} protein	16.59 (0.44, 28)	18.38 (0.52, 28)	0.012
	Total U	2.36 (0.10, 28)	1.50 (0.06, 28)	<0.0001

DISCUSSION

Favorable conditions during suspension culture enhance growth of scallops. The cultured scallops we studied had been grown at low density (<30% of floor coverage, see Ventilla 1982), in a lagoon where temperature and food supply were higher than on the seabed (Cliche et al. unpubl.). Moreover, the density of fouling organisms was low at harvesting and no other species were present inside the pearl nets. Thus after ~2 yr growth, in late August 1999, when animals of the same shell height range were compared, cultured scallops had greater soft tissue masses (digestive gland, muscle, remaining soft tissues) and better condition indices than wild scallops. This result corroborates the finding by Naidu et al. (1989) that sea scallops cultured in suspension grow faster than their wild counterparts. Sea scallops of the size range we used can reach sexual maturity; their reproductive investment may rise to 20% (annual gamete production divided by gamete and somatic tissue production) by their second year (MacDonald 1984, Black et al. 1993). We sampled the scallops in August, a time of gametogenesis (Parsons et al. 1992, Bonardelli et al. 1996). If reproductive effort was greater in wild than cultured scallops, this could have reduced the mass of tissues, notably muscle, relative to those of cultured scallops, as found by Rodhouse et al. (1984) in a comparison of mussels on the shore and from suspended culture. However, the experimental scallops, both wild and cultured, had a relatively small and translucent gonad, which prevented sex determination. This suggests that reproductive effort was insignificant.

MacDonald (1986) reported that *Placopecten magellanicus* grown on the bottom had heavier shells than suspension cultured scallops of a given shell height. Studies of the scallop *Crassadoma gigantea* (30 to 80 mm) (MacDonald & Bourne 1989) and the mussel *Mytilus edulis* (Rodhouse et al. 1984) also show that wild individuals from the bottom have heavier shells than those in suspended culture. While the shell heights and masses of the wild and cultured scallops were the same, the other linear dimensions and the volume enclosed by the shells of wild scallops were smaller, indicating that the shells of wild scallops were either thicker or denser than the shells of cultured scallops. Thus, the shells of wild scallops resisted greater pressures. This difference in shell strength is consistent with the suggestion that wild individuals are better protected against grasping predators such as crabs. As crabs favor prey with shorter handling times, they may prefer cultured scallops (Jubb et al. 1983, Boulding 1984, Sanchez-Salazar et al. 1987, Juanes 1992). Morphological responses to a perceived risk of predation can improve the fitness of some marine invertebrates. Thus, exposure of *Mytilus edulis* to *Asterias rubens* led to the development of more compact and rounded shells, without changes in shell mass (Reimer et al. 1995, Reimer & Tedengren 1996). The mussels also secreted

Table 6. *Placopecten magellanicus*. Impact of the anatomic and biochemical parameters upon escape performances of wild and cultivated sea scallops. Values for *F*-tests from 2-way ANCOVA are shown. Covariates used in these models were variables that least inflated the variance of the parameter, selected by the REG/vif collin procedure (SAS 1999). Probability levels from each stepwise multiple regression are given for all significant covariates. Model R^2 refers to power of indicated factors and covariates in explaining the corresponding escape parameter. $^{*}p < 0.15$; $^{**}p < 0.10$; $^{***}p < 0.05$; $^{****}p < 0.01$. na = not applicable

Escape parameter	Origin	Day	Origin × Day	Muscle proteins	Muscle carbohydrates	PFK	GP	CS	ODH	AK	Shell mass	Catch muscle mass
Initial response												
Number of claps												
Stepwise regression	na	na	na	–	****	–	–	–	**	–	**	–
Model R^2 = 0.36	$F_{1,47}$=0.37	$F_{2,47}$=3.24***	$F_{2,47}$=2.50**	–	$F_{1,47}$=7.51****	–	–	–	$F_{1,47}$=4.31***	–	$F_{1,47}$=3.68**	–
Clapping time												
Stepwise regression	na	na	na	–	****	–	–	–	–	–	–	***
Model R^2 = 0.44	$F_{1,48}$=4.29***	$F_{2,48}$=1.13	$F_{2,48}$=0.06	–	$F_{1,48}$=0.75	–	–	–	–	–	–	$F_{1,48}$=7.85****
Clapping rate												
Stepwise regression	na	na	na	***	–	**	–	–	***	–	–	–
Model R^2 = 0.27	$F_{1,47}$=4.37***	$F_{2,47}$=1.13	$F_{2,47}$=0.88	$F_{1,47}$=5.79***		$F_{1,47}$=0.05			$F_{1,47}$=0.39			
Maximal number of claps in a series												
Stepwise regression	na	na	na	*	–	–	*	**	–	***	–	–
Model R^2 = 0.35	$F_{1,29}$=0.01	$F_{1,29}$=1.94	$F_{1,29}$=0.65	$F_{1,29}$=2.74*	–	–	$F_{1,29}$=2.75*	$F_{1,29}$=6.92***	–	$F_{1,29}$=2.23*	–	–
Time spent closed												
Stepwise regression	na	na	na	–	–	–	–	–	–	–	–	–
Model R^2 = 0.10	$F_{1,50}$=0.05	$F_{2,50}$=0.34	$F_{2,50}$=2.04*	–	–	–	–	–	–	–	–	–
Response after 15 min of recuperation												
Number of claps												
Stepwise regression	na	na	na	–	–	–	–	–	–	–	–	–
Model R^2 = 0.12	$F_{1,50}$=0.22	$F_{2,50}$=0.55	$F_{2,50}$=2.73**	–	–	–	–	–	–	–	–	–
Clapping time												
Stepwise regression	na	na	na	*	–	–	–	–	–	–	–	***
Model R^2 = 0.16	$F_{1,48}$=0.11	$F_{2,48}$=0.56	$F_{2,48}$=0.24	$F_{1,48}$=1.72	–	–	–	–	–	–	–	$F_{1,48}$=1.16
Clapping rate												
Stepwise regression	na	na	na	–	**	–	*	–	–	–	–	–
Model R^2 = 0.32	$F_{1,47}$=2.49*	$F_{2,47}$=3.73***	$F_{2,47}$=4.77***	–	$F_{1,47}$=0.73	–	$F_{1,47}$=3.72**	–	–	–	–	–
Maximal number of claps in a series												
Stepwise regression	na	na	na	–	–	–	**	–	–	–	–	–
Model R^2 = 0.26	$F_{1,32}$=1.50	$F_{1,32}$=2.04	$F_{1,32}$=3.56**	–	–	–	$F_{1,32}$=1.62	–	–	–	–	

more, shorter and thicker byssus threads when placed in water in which a predatory crab had been placed (Côté 1995). Furthermore, slow growth can enhance shell thickness and change shell shape in *Mytilus edulis* (Seed 1968). Chemical cues of crab activity foraging induce development of shell features which help resist predators in the juvenile gastropod *Nucella lapillus* (Palmer 1990). A predatory snail induces bent-over growth in the barnacle *Chthamalus anisopoma*, reducing its vulnerability (Lively 1986). Hence, predators on natural grounds and slower growth may have stimulated a greater investment in shell strength (mass/thickness) in wild scallops, or may have eliminated scallops with thinner shells. The rock crab *Cancer irroratus* is an important predator of *P. magellanicus* and adjusts its predation rates to the availability of juvenile scallops at the seeding sites, thus leading to a density-dependent mortality of scallops (Barbeau et al. 1996). Since *P. magellanicus* often closes its valves in response to encounters with crabs (Barbeau & Scheibling 1994a), the lower resistance to crushing of the shell of cultured scallops may contribute to high mortality in seeding operations.

The higher clapping rate of wild scallops may favor their survival when faced with foraging asteroids, as a vigorous clapping to an initial contact with these non-visual predators may facilitate escape. Survival should be increased by decreased encounter rates with predators (Barbeau & Scheibling 1994a–c). Nonetheless, the cultured scallops clapped more and longer than wild scallops both during their initial escape response and during the response after 15 min of recuperation. Also, the period of valve closure during recuperation was shorter for cultured than wild scallops. Clearly, cultured scallops mounted a strong escape response to starfish. Predator-conditioned juvenile *Buccinum undatum* show increased responsiveness (high intensity escape response) to their natural predator *Leptasterias polaris* (Rochette et al. 1998). Possibly, exposure of wild scallops to starfish in their natural habitat favored the development of a higher clapping rate. Alternately, predation on scallops with lower clapping rates may have led to the difference between wild and cultured scallops. Methodology is unlikely to be the cause of these differences, since we always concluded a test by stimulating the scallop's best area for triggering a swim response: the byssal notch on the right valve, adjacent to the anterior ear region (Ordzie & Garofalo 1980, Wilkens 1981). Further, a reduction in the ability to escape predators has been reported to result from stress caused by the physical impact of dredges (Jenkins & Brand 2001). Our wild *Placopecten magellanicus*, sampled by dredging, seemed undamaged and were tested after being maintained for 7 d in the laboratory. However, if the physiological status of the wild scallops was still affected at the time of the escape tests, their performance may have been lower than that of unstressed wild scallops.

Conditioning to moderately high water temperature can enhance shell growth, adductor muscle condition, and energy reserves in juvenile *Placopecten magellanicus* (Kleinman et al. 1996). The higher reserve levels and soft tissue contents of cultured scallops are likely linked with their greater number of claps, longer clapping period and faster recuperation of clapping performance. The adductor muscles of cultured scallops were larger (both absolute and relative masses), had higher carbohydrate and protein levels and higher ODH and PFK activities than those from wild scallops. The shorter period of valve closure in cultured scallops would have facilitated aerobic recuperation of intracellular metabolites after the initial exhausting escape response (Brokordt et al. 2000a). The shorter valve closure may well be linked with the higher catalytic capacity of enzymes in anaerobic glycolysis. Anaerobic glycolysis produces ATP both during the final portion of escape responses and during the glycolytic recovery period (Thompson et al. 1980, Livingstone et al. 1981). The combination of a higher capacity for anaerobic recuperation and a longer aerobic recuperation allowed the cultured scallops to out-perform wild scallops during the second escape response.

Both muscle carbohydrate and protein levels were similar to values measured in adult *Chlamys islandica*, a sympatric species found in the northern Gulf of St. Lawrence (Brokordt et al. 2000a). The levels of energetic reserves we measured in the muscle were slightly lower than those observed in other scallop species (Martinez 1991, Boadas et al. 1997, Brokordt et al. 2000b, Lodeiros et al. 2001). Since high swimming frequency decreases carbohydrate reserves from adductor muscle in juvenile *Placopecten magellanicus* (Kleinman et al. 1996), the escape responses coupled with a lack of food between escape responses and dissections could explain the somewhat lower carbohydrate levels observed in our study.

The glycolytic capacity in the phasic muscle of adult *Placopecten magellanicus* (de Zwaan et al. 1980) seems slightly greater than that of juveniles from our study. Thermal effects are likely to account for much of this difference since enzyme activities were measured at 25°C by de Zwaan et al. (1980), whereas our determinations were made at 12.5°C. The maximal enzymatic capacities measured by de Zwaan et al. (1980) ranged from 1.58 to 1.82 and from 2.34 to 3.04 U g^{-1} wet muscle mass for GP and PFK, respectively. Size-dependent increases in the activities of glycolytic enzymes as observed in the bay scallop's adductor muscle (Garcia-Esquivel & Bricelj 1993) and in white skeletal fish muscle (Somero & Childress 1990) could

also contribute to the difference between adult and juvenile GP-PFK activity.

Whereas performance during escape responses differed between wild and cultured scallops, the righting responses did not. Our measurements of escape responses were carried out individually, whereas the righting responses were monitored simultaneously for each group of scallops. The activities of neighboring scallops influence the behavior of a given scallop (Brand 1991), and in future studies on righting responses, individual measurements should be carried to prevent pseudoreplication (Hurlbert 1984).

Our attempt to explain escape performances according to the numerous parameters we have measured remained more or less in vain. Only muscle carbohydrates and ODH and CS activities showed links with escape response performance. No correlations were observed between the escape performance and the righting responses. Although muscle substrates and metabolic pathways must be used during escape responses, the weak correlations we observed suggest that these parameters are not limiting escape responses. Elucidation of the physiological determinants of behavior showing marked inter-individual variability may require study of an even greater number of subjects or a wider range of physiological parameters.

In conclusion, cultured and wild juvenile *Placopecten magellanicus* showed strong responses to encounters with starfish, with cultured scallops clapping more and longer than wild scallops. On the other hand, the clapping rate was higher for wild scallops, both initially and after 15 min of recuperation from the first exhausting escape response. The shell of wild scallops was also significantly stronger than that of cultured scallops. Since crabs can decimate juvenile scallop populations more quickly than starfish (Barbeau & Scheibling 1994a, Cliche et al. 1994, Barbeau et al. 1996, Nadeau & Cliche 1998), future studies should examine the mechanisms enhancing scallop shell strength and also explore ways of reducing crab abundance on the reseeding grounds. The greater shell strength and clapping intensity of wild scallops could facilitate their survival during the period of high juvenile mortality.

Acknowledgements. We thank C. Cyr, F. Aucoin and M. Guay for laboratory assistance and Diego Mantovani for facilitating our measurements of shell strength. We are also grateful to M. Giguère for his aid with the sampling of wild scallops, to H. Paradis and R. Côté for their statistical support and to J. H. Himmelman and B. Myrand for helpful comments on the paper. This study was supported by funds from MAPAQ (Ministère de l'Agriculture des Pêcheries et de l'Alimentation du Québec) to M.L. and H.G. and by an operating grant from the NSERC to H.G.

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Editorial responsibility: John Lawrence (Contributing Editor), Tampa, Florida, USA

Submitted: September 10, 2002; Accepted: November 11, 2002
Proofs received from author(s): March 4, 2003