Growth and survival of sea scallops *Placopecten magellanicus*: effects of culture depth

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ABSTRACT: We combined extensive water sampling with monthly growth measurements of juvenile sea scallops held in cages 0 to 200 cm above the bottom to (1) construct predictive empirical models of shell and soft-tissue growth based on oceanographic variables, and (2) determine whether scallops on or near the bottom can derive a food supplement from resuspended sediment when seasonal phytoplankton production is low. Variation in growth was strongly dependent on depth, but this relationship was not consistent over time or tissue type. In late fall, when phytoplankton biomass was generally low (~1 µg chl l⁻¹), the adductor muscle of scallops on the bottom lost mass (−1.5 mg dry wt d⁻¹), but for scallops held only 20 cm higher in the water column, growth was 2.5 mg d⁻¹. During the winter, soft-tissue growth on the bottom was significantly lower than that of scallops held above the sediment surface. At this time, there was no variation in shell growth with respect to depth. At the end of the study, soft-tissue weight (excluding muscle tissue) of scallops on the bottom was ~40 % less than that of scallops growing ≥50 cm above bottom. Rather than providing an energetic benefit, results suggest that high concentrations of seston near the bottom inhibit growth. Empirical regression models of scallop growth using data from water sampling every 2 wk accounted for up to 68% of growth variation, with temperature and seston quality being the most important predictor variables. Marginal improvements to the model using data collected hourly with *in situ* probes suggest that estimates of food supply should be corrected, i.e. reduced, when high flows or high seston concentrations limit filtration rates. In addition, results indicate that attention to the magnitude and variation of predictor variables without consideration of their seasonal coherence may be a primary factor limiting the ability to construct truly predictive models of bivalve growth.

KEY WORDS: *Placopecten magellanicus* · Resuspension · Production · Aquaculture

INTRODUCTION

Predictions of bivalve growth and survival based on laboratory data may have little relevance to natural or cultured populations since combined and potentially synergistic effects of many oceanographic variables remain unknown. For scallops, flume experiments have shown that the direction and magnitude of water currents affect growth by controlling seston supply or altering filtration rates (Eckman et al. 1989, Wildish & Saulnier 1992), but not all field studies can link flow to soft-tissue growth (e.g. Fréchette 1989). In the laboratory, Grant & Cranford (1991) found seston quality to be directly proportional to scallop growth, yet in the field, Andersen & Naas (1993) indicated that cultured scallop growth may decrease with increasing concentrations of particulate organic matter. Others have found no correlation between the level of particulate organic carbon and scallop growth (Monical 1980, Wilson 1987). Laboratory studies have also implicated temperature fluctuations, seston size structure, phytoplankton species composition, oxygen concentration, and resuspension of bottom sediments as factors controlling scallop growth (see review by Bricelj & Shumway 1991), but rarely have the combined effects of these and other oceanographic variables been assessed *in situ*. An empirical field study combining extensive environmental monitoring with measurements of growth and mortality should be undertaken so that the true hierarchy of factors influencing scallop production may be distinguished.

By documenting the performance of scallops grown at several heights above the bottom, the influence of several depth-stratified oceanographic processes can

be evaluated at a single site. The response of sus-
pended scallops to position in the water column has
been examined previously, but factors affecting
growth have not always been established due to inad-
equate sampling of environmental variables. Some
studies found scallop growth to be uniform throughout
the water column (Duggan 1973, Richardson et al.
1982), but others observed that scallops closer to the
bottom grew more slowly (e.g. Wallace & Reinsnes
1984, MacDonald 1986, Dadswell & Parsons 1991) or
exhibited higher mortality (Duggan 1973). When envi-
ronmental data were available, similar observations
were attributed to either poor food conditions
(Leighton 1979, Wallace & Reinsnes 1985) or in several
cases a turbidity stress from resuspended sediments
(e.g. Monical 1980). During periods of low phytoplank-
ton production, however, Cranford & Grant (1990)
hypothesised that the organic matter within resus-
pended sediment may contribute significantly to the
net energy gain of scallops. If true, existing energy
flow models of communities dominated by benthic sus-
pension feeders should be reassessed. Moreover, com-
mercial scallop growers may be able to improve stock
production by selecting culture sites where tidal
or wind-forced resuspension can offset seasonal de-
creases in phytoplankton.

To resolve discrepancies of environmental limitations
to scallop production, and specifically, to evaluate the
net effect of resuspension on scallops, growth and sur-
vival of Placopecten magellanicus at several depths
were measured in conjunction with extensive water-
quality monitoring. The resulting environmental data-
base was used to construct predictive empirical models
of scallop production relevant to studies of general ben-
thic energy flow and to the estimation of carrying ca-
pacity of natural and cultured populations. Comparisons
of scallop growth and survival at different heights above
the sediment surface were used to define the environ-
mental conditions under which resuspension is benefi-
cial or detrimental to scallop production.

MATERIALS AND METHODS

Study site. Upper South Cove, off Lunenburg Bay,
Nova Scotia (Fig. 1), was chosen for the study because
of the environmental database established during a
previous study on mussel culture (Dowd 1991), and
because the proximity of a field station allowed water
samples to be processed immediately after collection.
In addition, the shallowness of the water (7 m) enabled
scallops and equipment to be deployed by SCUBA
divers at several discrete depths near the bottom.
Semi-diurnal tidal currents average 12 cm s^{-1} and
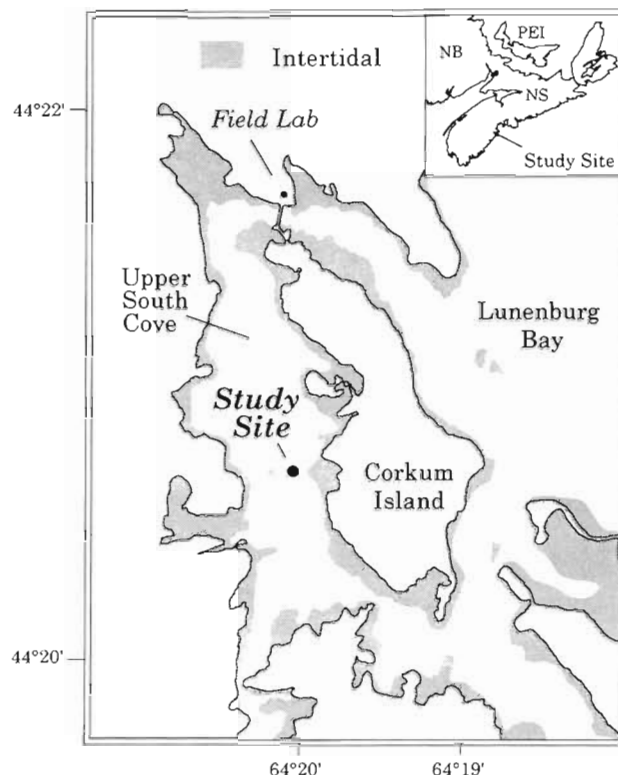flows of 30 to 60 cm s^{-1} during flood tide have been

Fig. 1 Location of study site and field laboratory at Upper
South Cove and Lunenburg Bay, Nova Scotia, Canada. Shad-
ing indicates the intertidal zone. A causeway at the north end
of Corkum Island restricts flushing of the cove to the narrow
channel south of the study site

observed to resuspend the fine component of the
poorly sorted glacial till sediment (median grain size
1000 µm, 5 to 10 % silt content). In summer, water tem-
peratures reach 21°C, but under a 1 m ice cover in Feb-
ruary, temperatures fall to –1.7 °C. Average salinity is
30.5‰ and the minimum oxygen concentration near
the bottom is approximately 80 % of saturation. Pla-
copecten magellanicus is found naturally at low densi-
ties in the area, and a commercial mussel farm (Mytilus
edulis) is located nearby.

Sampling design. – Biological variables: On 20 Sep-
tember 1990, approximately 1000 juvenile scallops
[mean shell height (shell ht) 39.7 ± 5.0 mm SD] from a
single cohort produced on 17 April 1989 were obtained
from the Fisheries Research Development Limited
hatchery at Sandy Cove, Nova Scotia, Canada. Fifteen
scallops were randomly chosen for soft-tissue analysis
and the remainder were distributed evenly among 10
Nortene mesh cages (10 × 50 × 100 cm, 6 mm mesh). To
monitor individual growth, 30 of the 100 scallops in
each cage were measured (shell ht ± 0.05 mm) and
tagged with a plastic label glued to the left valve. Each
cage was secured to a PVC frame standing at 0, 20, 50,
100, or 200 cm above bottom, with 2 replicate cages

per height. Frames were distributed over a 100 m² area.

On 18 October, 15 November, 13 December 1990, and 29 March 1991, each cage was brought to the surface to measure the shell height of the tagged scallops, record mortality, remove and freeze 5 scallops for soft-tissue analysis, and remove any fouling organisms from the cage surface. The 5 subsampled scallops were each partitioned into shell, adductor muscle, and remaining soft-tissue components. The dry weight of muscle and remaining soft tissue was determined by drying at 55 °C until constant weight (±0.0001 g). Ash content was determined by weight difference after heating to 500 °C for 4 h. Although only juveniles were used in the study, gonad tissue was examined to determine whether spawning had occurred. Although gonads appeared to be developed in some individuals, spent gonads were not apparent.

– *Environmental variables:* Seston data were obtained every 2 wk from water samples collected at 10, 20, 50, 100, and 200 cm above bottom using a hand-operated bilge pump connected to a multi-level hose array. Intakes from 5 separate hoses were positioned at the appropriate heights using a weight on the bottom and a subsurface buoy to ensure the array was vertical. Sample collection was delayed until particles resuspended during deployment of the array had settled or been removed by currents, and until each hose was flushed with water from intake depth. Rate of water collection was approximately isokinetic (equivalent to a current speed of ~10 cm s⁻¹). Water was pre-filtered through 110 µm mesh Nitex to eliminate variance associated with large particles or flocs. The concentration of suspended particulate matter (SPM) was determined by filtering replicate water samples through pre-ashed (500 °C for 2 h) and weighed (±0.01 mg) GF/C filters (nominal pore size 1.2 µm). Salt was removed from the filters by rinsing with 20 ml of isotonic ammonium formate. Particulate organic matter (POM) was calculated by subtracting ashed seston weight from total seston dry weight. Particulate organic carbon (POC) and nitrogen (PON) were determined from additional filters processed with a Perkin-Elmer CHN 2400 Elemental analyser. Chlorophyll and phaeopigment concentrations were determined fluorometrically following Parsons et al. (1984).

At 100 cm above the bottom, hourly estimates of temperature, current velocity, salinity, and concentrations of chlorophyll and SPM were determined using a moored instrument array. The array consisted of a thermistor, a SeaTech fluorometer and transmissometer (10 cm path length), a Marsh-McBurney electromagnetic current meter, and a conductivity cell connected to an Applied Microsystems ECM-12 data logger. Stored data were retrieved during instrument maintenance every 2 wk,

when batteries were replaced and optical surfaces cleaned. Ice conditions reduced instrument deployment to a VEMCO temperature probe (4 h sampling frequency) from mid-December to March.

The fluorometer and transmissometer were calibrated *in situ* by comparing voltage data with results of chlorophyll and SPM analyses performed on water samples collected within 10 cm of the instrument array. Laboratory calibrations were also conducted by exposing the fluorometer and transmissometer to a range of monospecific and mixed phytoplankton concentrations (*Chaetoceros muelleri*, *Thalassiosira weissflogii* and T-*Isochrysis galbana*, 0.5 to 60 µg chl l⁻¹) as well as suspended sediment from cores collected at the study site. The transmissometer appeared to be insensitive to mixtures of resuspended particles and phytoplankton in concentrations <0.5 mg l⁻¹. Concentrations of chlorophyll and total seston estimated using the probes were within 5 to 10 % of those estimated from direct water sampling. Bias resulting from biotic fouling of the transmissometer lenses was removed by subtracting an empirical exponential fouling curve from the voltage data. Parameters of the curve were chosen by comparing voltages immediately before and after cleaning, and by comparing corrected voltages (and corresponding SPM estimates) to levels of SPM estimated from the filtration of water samples.

Statistical analyses. On 20 September, 18 October, 15 November, 13 December 1990, and 29 March 1991, the muscle and remaining soft-tissue weights of individual tagged scallops were estimated from shell height versus soft-tissue weight regression equations derived from analysis of the subsampled scallops (Appendix 1). Soft-tissue growth rates of tagged scallops (mg d⁻¹) were calculated by subtracting the estimated weight on one date from the preceding estimate and dividing by the number of days between sampling dates. To determine whether cage height had a significant impact on growth rate during any of the 4 growth intervals, nested analyses of variance were performed at α = 0.05. Before conducting any analysis, homoscedasticity was verified using Bartlett's and Levene's tests (Snedecor & Cochran 1980). Although it was necessary to arc-sine transform the percent-ash data, transformations were unnecessary for measures of shell height and tissue weight. A possible bias originating from differences in initial shell height was minimised by using scallops within a narrow size range from a single cohort. Initial shell heights of the scallops in each treatment were not significantly different (ANOVA, p < 0.001). Nonetheless, a significant relationship between shell height and growth rate was found in some growth intervals. As a result, shell height was employed as a covariate after first testing for homogeneity of slopes. Post hoc comparisons were

performed using the Bonferroni multiple comparison procedure (Wilkinson 1988).

Initial identification of the environmental variables significantly related to scallop growth was accomplished by constructing a Pearson correlation matrix using Bonferroni-adjusted probabilities. Although most predictor variables required no transformation to become homoscedastic, the ratio of organic to inorganic SPM was arc-sine transformed. Stepwise multiple regressions were calculated using variables found to be significantly related to growth. Predictor variables that were strongly colinear ($r^2 > 0.25$) were not considered for analysis.

RESULTS

Shell growth

Over the fall and winter, shell height increased from 40 mm in September to 50 mm in March, with no statistically discernible difference in the slope or intercept of shell height trajectories between different cage levels (Fig. 2A, repeated measures ANCOVA, $p = 0.17$). Even during the fall and winter, linear trajectories indicated that shell height continued to increase by 40 to 60 μm d^{-1} (Fig. 3D). Although shell size on the final day was not related to cage height, the rate of shell growth was dependent on cage height during the second month of growth (Table 1, Fig. 3B). At this time, scallops on the bottom grew faster (140 μm d^{-1}) than all other scallops, including those only 20 cm higher in the water column (70 to 90 μm d^{-1}). Scallops at mid-height (50 and 100 cm above bottom) grew ~30% faster than those immediately below at 20 cm and those above at the 200 cm level. During the remaining 2 growth periods, cage height had no significant effect on growth, although a significant difference in growth rate between the 2 replicate cages at 200 cm was apparent over the winter (Fig. 3D).

Soft-tissue growth

In contrast to the linear increase in shell height over the study, soft-tissue dry weight (excluding muscle) exhibited a significant decline from November to March (Fig. 2B). Soft-tissue weight increased from ~650 mg in September to a high of 1350 mg in December, but fell by 10 to 45% during the next 3 mo. At the end of the study, the weight of soft tissue of scallops on the bottom was approximately 40% less than that of scallops growing more than 50 cm from the bottom. Ash content of soft tissue, generally between 14 and 28% (Fig. 4A), was not related to cage height (ANOVA, $p > 0.05$).
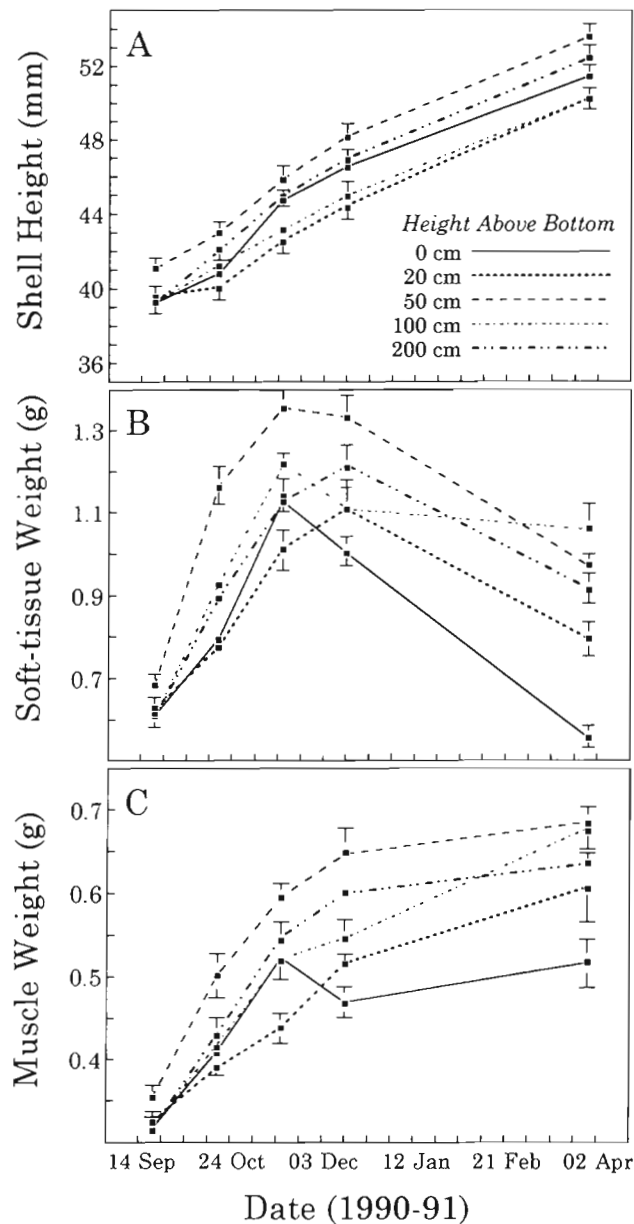

Fig. 2. *Placopecten magellanicus*. (A) Shell height, (B) soft-tissue dry weight (excluding muscle) and (C) muscle dry weight trajectories of sea scallops over the sampling season. Each square represents an average of 60 scallops, 30 from each cage at either 0, 20, 50, 100, or 200 cm above the bottom. For clarity, often only 1 standard error is shown

In early fall (20 September to 14 November), soft-tissue growth ranged from 1 to 17 mg d^{-1} with no detectable effect of cage height. Scallops at 0, 50, and 100 cm above the bottom lost tissue in late fall (~ –2 mg d^{-1}), but again, growth variation between replicate cages was greater than between cage heights, particularly at the 50 and 100 cm levels. Over the winter, however, scallops on the bottom and those at 20 cm grew

Fig. 3. *Placopecten magellanicus*. Shell growth rate of sea scallops between sampling dates as a function of cage height above bottom. Each symbol represents the pooled average daily growth rate of 60 scallops in 2 cages over each sampling period. When 2 symbols appear for 1 cage height, growth rates in 1 cage were significantly different from the other (p < 0.05). Open symbols were significantly different from filled symbols. During the second growth period (B), shell growth in the bottom cage was significantly higher than all other cage heights. When standard error bars are not apparent, they are masked by the symbol
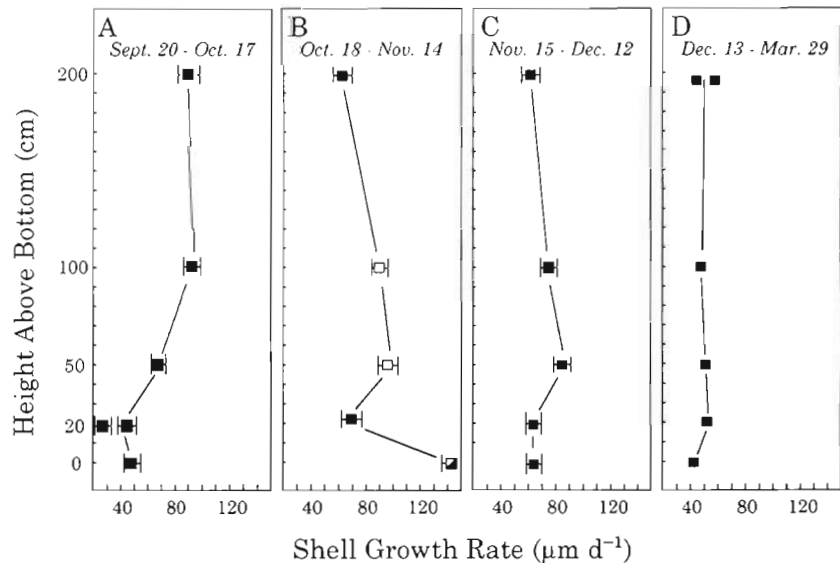
significantly less than those higher in the water column (Fig. 5, Table 1). At all levels, winter soft-tissue growth was negative.

Throughout most of the study period, adductor muscle dry weight increased, but as with the remaining soft tissue, the pattern was nonlinear (Fig. 2C). By the end of the study, muscle weight had doubled from about 300 mg initially to 600 mg. From Fig. 2C, it appeared that the mean muscle weight was lowest for those scallops on the bottom, but there was no statistically significant difference in muscle weight related to cage height at any time. For all scallops, muscle weight was approximately 35 % of total soft-tissue weight, but the preferential loss of other soft tissue during the winter raised this value to 43 %. A temporal pattern in the ash content of the muscle was not apparent (Fig. 4B), although as with soft tissue, these values increased over the winter to ~21 %.

Table 1. *Placopecten magellanicus*. Nested analysis of variance statistics for the comparison of shell, muscle, and remaining soft-tissue growth rates of scallops grown at different heights above bottom during 4 growth periods. Shell height at the beginning of the growth period was used as a covariate. Brackets indicate that replicate cages were nested within height-above-bottom. Sources of variation, degrees of freedom, *F*-ratios and levels of significance are indicated

| Growth period	Source	df	Shell *F*-ratio	p	df	Muscle *F*-ratio	p	df	Remaining soft tissue *F*-ratio	p
20 Sep –	Cage height	4	3.97	<0.05	4	2.67	>0.05	4	2.51	>0.05
17 Oct 1990	Rep{height}	5	3.81	0.002	5	13.24	<0.001	5	10.42	<0.001
	Shell height	1	12.89	<0.001	1	74.47	<0.001	1	329.28	<0.001
	Error	262			253			253		
18 Oct –	Cage height	4	23.43	<0.001	4	1.81	>0.05	4	1.27	>0.05
14 Nov 1990	Rep{height}	5	1.45	0.207	5	10.23	<0.001	5	7.48	<0.001
	Shell height	1	15.50	<0.001	1	213.24	<0.001	1	13.96	<0.001
	Error	252			245			246		
15 Nov –	Cage height	4	1.01	>0.05	4	1.87	>0.05	4	4.04	=0.05
12 Dec 1990	Rep{height}	5	1.94	0.089	5	10.48	<0.001	5	10.42	<0.001
	Shell height	1	0.60	0.439	1	7.12	0.008	1	22.84	<0.001
	Error	246			241			241		
13 Dec –	Cage height	4	0.55	>0.05	4	13.75	<0.01	4	2.41	>0.05
29 Mar 1991	Rep{height}	5	4.79	<0.001	5	3.13	0.009	5	4.28	<0.001
	Shell height	1	1.07	0.301	1	148.61	<0.001	1	23.35	<0.001
	Error	237			235			239		

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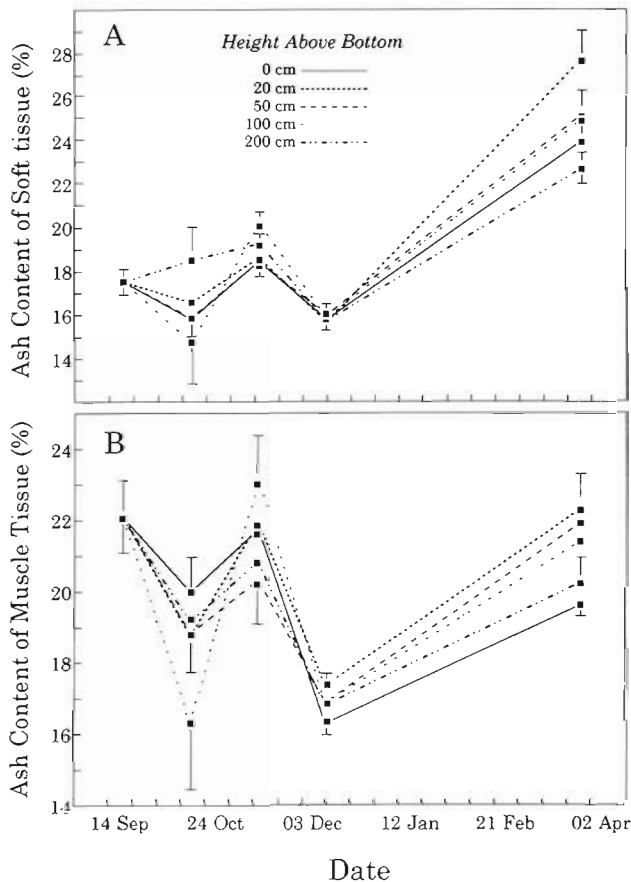
Fig. 4. *Placopecten magellanicus*. Ash content of soft tissue (excluding muscle) and muscle tissue of sea scallops as a percentage of dry weight. Each symbol represents the average ash content of scallops in both cages at each cage depth. The initial value (20 Sep) was determined from 15 scallops randomly subsampled from the stock used to populate each cage. For clarity, often only 1 standard error is shown

Even in winter, growth rate of muscle tissue was maintained at all heights and, in some cases, was greater than during the previous sampling interval (e.g. 0 and 200 cm; Fig. 6, Table 1). From 13 December to 29 March, muscle growth was uniform within the bottom 2 m. Only during late fall (15 November to 12 December) was growth significantly related to cage height. At this time, scallops on the bottom lost muscle tissue by ~1.5 mg d^{-1} while scallops at 20 and 50 cm above bottom grew by ~2 mg d^{-1}. At higher levels, muscle growth appeared to be lower, but significant differences were not detected. Rates of muscle growth in the first 2 mo should be treated with caution since estimated muscle weights on October 18 were singularly poor (Appendix 1).

Mortality

Mortality rates were consistently low, with average monthly losses less than 2% and maximal rates not exceeding 9% of the population (Fig. 7). During each growth period, mortality could not be distinguished statistically by cage height (ANOVAs, p = 0.13 to 0.83). For scallops growing at 200 cm, mortality rates generally decreased during the study, with no observed mortality from mid-November to the end of March.

Suspended particulate matter: direct water sampling

The concentration of total SPM decreased from 5 mg l^{-1} in September to ~1.5 mg l^{-1} through mid-October to December, and increased in spring to ~3 mg l^{-1} (Fig. 8). SPM appeared to be uniform throughout the water
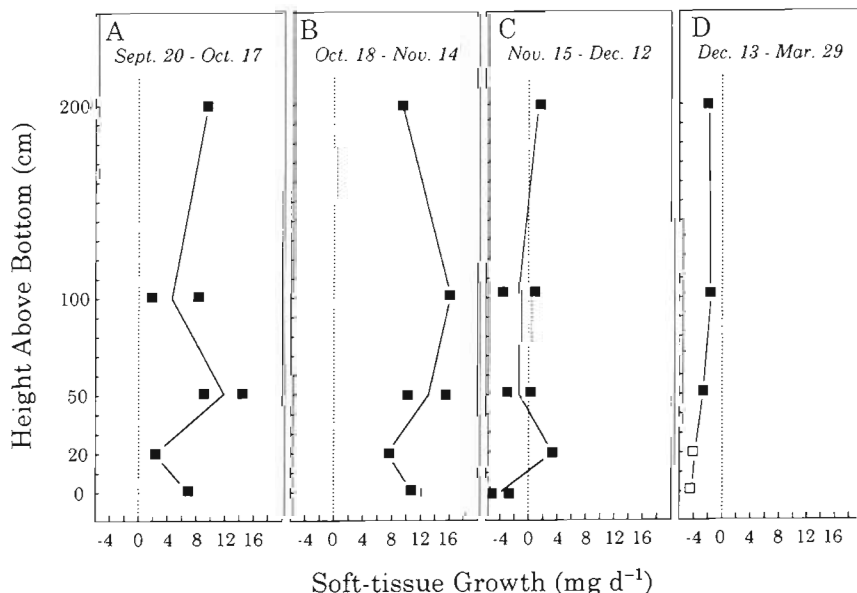

Fig. 5. *Placopecten magellanicus*. Soft-tissue (excluding muscle) growth rate of sea scallops between sampling dates as a function of cage height above bottom. Each symbol represents the pooled average daily growth rate of 60 scallops in 2 cages over the sampling period. When 2 symbols appear for 1 cage height, growth rates in 1 cage were significantly different from the other (p < 0.05). Open symbols were significantly different from filled symbols. When standard error bars are not apparent, they are masked by the symbol

Fig. 6. *Placopecten magellanicus.* Adductor muscle growth of sea scallops between sampling dates as a function of cage height above bottom. Each symbol represents the pooled average daily growth rate of 60 scallops in 2 cages over the sampling period. When 2 symbols appear for 1 cage depth, growth rates in 1 cage were significantly different from the other (p < 0.05). For a given symbol type, open symbols were significantly different from filled symbols. When standard error bars are not apparent, they are masked by the symbol
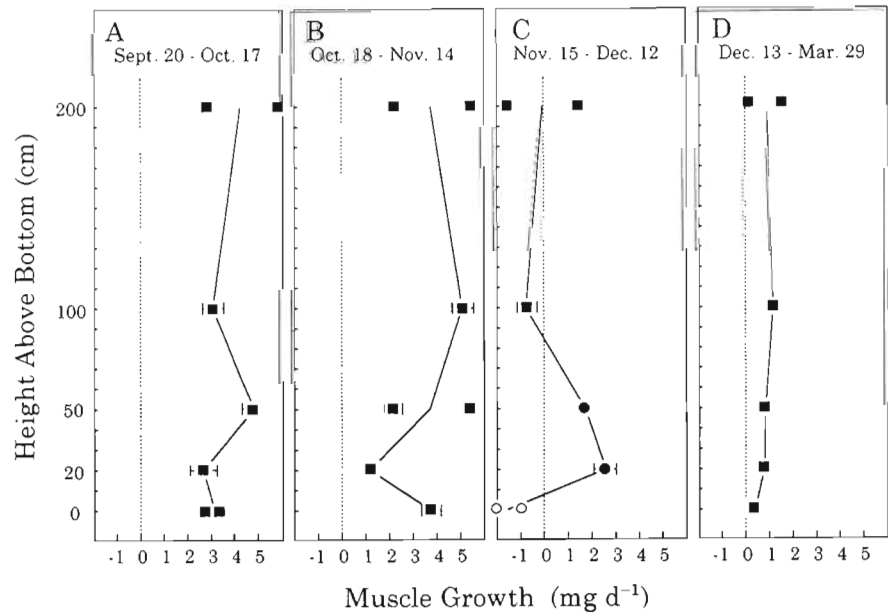
column at most times, but in September, high concentrations were found at mid-height (100 cm). At this time, there was no difference in the growth rate of scallops at different cage heights. When growth was depth-dependent (e.g. for muscle growth between 15 November and 12 December), SPM was apparently uniform throughout the water column. During the last growth period when soft-tissue growth increased with distance from the sediment surface, high levels of low quality SPM were found closer to the bottom. Similar profiles of SPM were present when shell growth was highest in scallops held on the bottom (Figs. 3B & 8B). In general, inorganic material accounted for 55 to 80 % of total seston weight with highest levels in early winter (15 November to 12 December).

Chlorophyll concentrations tracked those of SPM, with highest levels in early fall (4 µg l⁻¹), falling through early December to 0.5 µg l⁻¹, and partially recovering in the spring (2 µg l⁻¹; Fig. 8). The only

deviation in this seasonal pattern for phaeopigment concentration occurred in spring, when levels remained low (~0.5 µg l⁻¹). Again, no apparent relationship to height above bottom could be detected from these pigment profiles derived from averaging data from 4 sampling periods. C:N ratios of seston were very low (4) near the bottom, increased to 6 at 100 cm above the sediment, and decreased to 4 at 200 cm. Between 15 November and 12 December, C:N values were low near the bottom (~5), increasing to ~6 at 200 cm above the bottom. A seasonal pattern in C:N was not evident.

Each profile presented in Fig. 8 was derived by averaging 4 profiles taken within a particular growth period. It should be noted that summary depth profiles which were apparently uniform (Fig. 8) may have consisted of individual profiles that were depth stratified. For example, the single, relatively uniform SPM profile in Fig. 8B is composed of 4 profiles which often varied
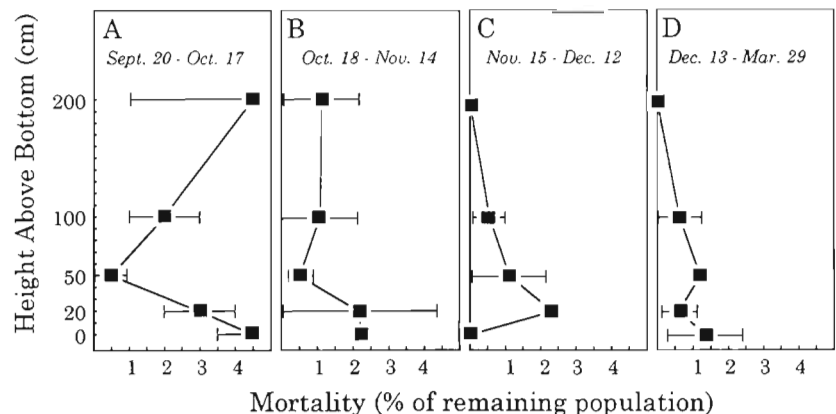

Fig. 7. *Placopecten magellanicus.* Sea scallop mortality during each growth period expressed as a percentage of the population at the beginning of each growth period. Symbols represent the average of 2 replicate cages at each cage height. When standard error bars are not apparent, they are masked by the symbol
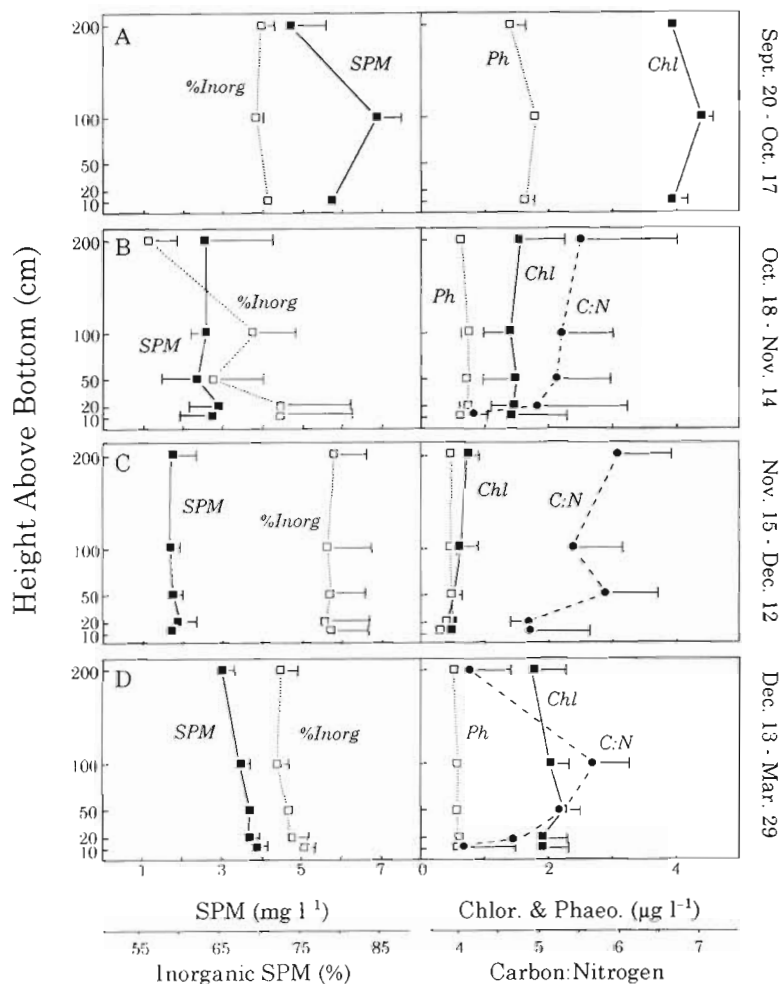
Fig. 8. Water quality variables at each cage height determined from water sampling during each of the 4 growth periods (A to D). Symbols in each panel represent the average of water samples taken at 4 times: low and high tide on 2 days separated by approximately 2 wk (e.g. see Fig. 9). Suspended particulate matter (SPM), percentage inorganic SPM (%Inorg), chlorophyll and phaeopigment concentrations (Chl, Ph), and the carbon:nitrogen ratio of SPM (C:N) are indicated. C:N was not available during the first growth interval. For clarity, often only 1 standard error is shown
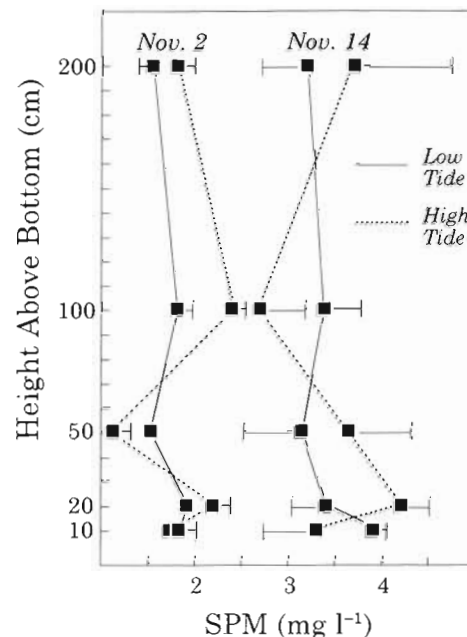

Fig. 9. Suspended particulate matter concentrations determined from water obtained at low and high tides on 2 days. Averages of these data are presented in Fig. 8B, and used in correlation analyses of scallop growth. For clarity, often only 1 standard error is shown

with depth, state of the tide and date of sampling (Fig. 9). Water samples taken on 2 November were lower in SPM than on 14 November, and the increase in SPM away from the bottom during low tide on 14 November was reversed at high tide.

Instrument data

High temporal variability in environmental data was evident from the *in situ* probes which measured temperature, chlorophyll and SPM concentrations hourly at 100 cm above the bed (Fig. 10). Temperature decreased from 16°C in September to a minimum of −1.7°C in January, and subsequently rose to 2°C by

the end of the study. During the development of the fall bloom (max. 13 µg chl l^{-1}) soft-tissue growth at 100 cm was relatively slow, and during the decline of the bloom, an increase in growth was observed. Spawning was not evident during the first period of slow growth of soft tissue (inclusive of gonad tissue). Decreased growth of all tissues in early December corresponded to low chlorophyll levels (1.0 µg l^{-1}) in mid-December. SPM concentrations at this time were highly variable (2 to 10 mg l^{-1}), with a long-period variation corresponding to the spring-neap tidal cycle (e.g. in September and early October). High-frequency variation in both SPM and chlorophyll time series occurred on a tidal period, with high concentrations linked to flood tide and low concentrations associated with ebb tide (insets, Fig. 10). Tidally forced changes in temperature were most apparent in September and early October, when the temperature discontinuity between Upper South Cove and Lunenburg Bay was >3°C.

With the exception of temperature, ice conditions prevented collection of environmental data between mid-December and the end of March. During the previous winter, water sampling every 2 wk indicated that chlorophyll levels ranged from 1.5 µg l^{-1} in mid-
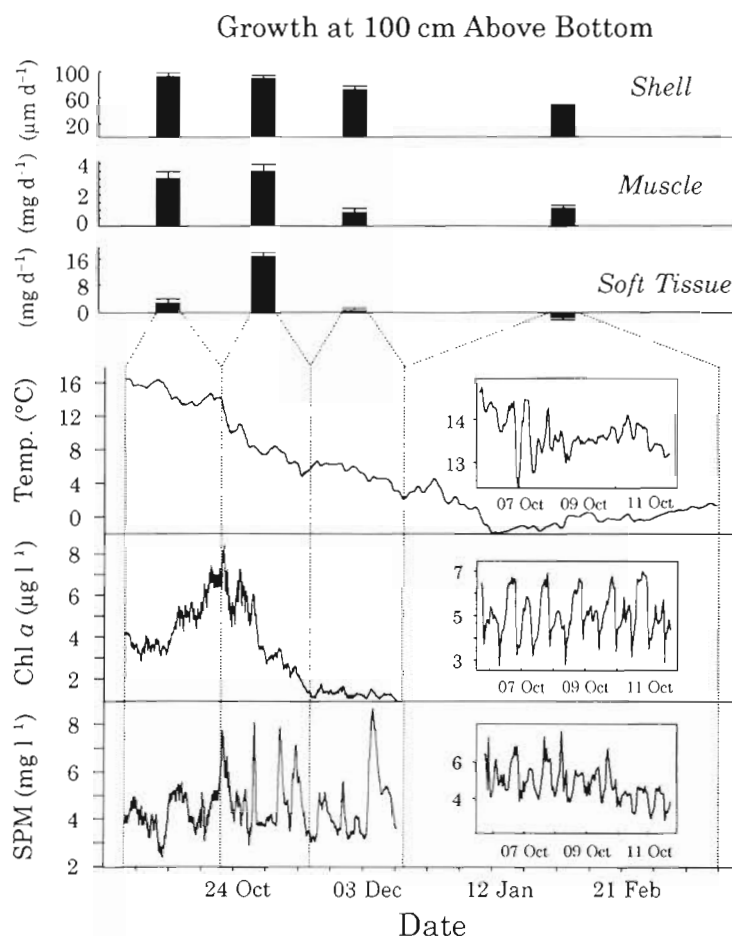
Growth at 100 cm Above Bottom

Fig. 10. *Placopecten magellanicus.* Comparison of sea scallop growth at 100 cm above the bottom with temperature, chlorophyll and suspended particulate matter concentrations measured hourly at the same depth. One standard deviation is indicated at the top of each growth bar. 'Soft tissue' excludes muscle tissue. Fluorometer and transmissometer voltage data were transformed into units of chlorophyll and SPM using laboratory and *in situ* calibrations (see 'Materials and Methods'). Probe data are illustrated with a 6 h running mean; examples of hourly data taken between 1 and 12 October are indicated in the inset panels. Only temperature was recorded during the winter (13 December to 29 March)

January to 0.7 µg l^{-1}, and back up to 1.8 µg l^{-1} in early March. Hourly data from an *in situ* fluorometer indicated the average chlorophyll concentration during the winter was 0.9 µg l^{-1}. SPM concentrations at this time averaged 1.7 mg l^{-1}. Winter water temperature was uniform at all depths.

Empirical models of growth

Without exception, empirical models relating tissue growth to environmental variables were improved when partitioned by cage height (Table 2), however, no model explained more than 68% of the variation in

growth, and most accounted for less than 40%. Changes in shell growth were the most difficult to predict ($r^2 \leq 0.12$), whereas variation in soft-tissue growth was best explained ($r^2 = 0.68$ at 50 cm cage height). The C:N ratio of SPM, POM, and concentrations of chlorophyll and phaeopigment determined from direct water sampling were all significantly correlated with growth (simple linear correlations, p < 0.05), but water temperature, SPM concentration, and the ratio of organic to inorganic SPM (O/I) were the best predictors of growth in the multiple regression models. It should be stressed that although inclusion of secondary and tertiary predictor variables resulted in a significant improvement to the model, these variables were often colinear ($r^2 = 0.02$ to 0.25 for SPM, O/I, and temperature). Temperature and O/I were the best predictors of growth; with the exception of soft tissue at 20 cm cage height, higher temperatures and a higher proportion of organic matter in the seston were related to higher growth. The quantity of seston was an important component in muscle growth models, and for the most part, was also positively correlated with growth.

Empirical models of soft-tissue growth based on environmental data collected hourly performed at least 85% better than those using data collected by water filtration at 4 times during each growth period (Table 3). Unfortunately, even with a data set composed of hourly concentrations of chlorophyll, total SPM, and temperature, empirical models continued to explain relatively little variation in tissue growth. At best, only 40% of the variation in soft tissue could be accounted for using these variables and none of the variation in shell growth could be explained.

DISCUSSION

Growth and mortality: effects of cage height

Within only 2 m of the sediment surface, height above bottom was found to be a significant source of variation in shell and soft tissue growth of caged scallops. However, a consistent relationship between cage height and growth was not found with respect to either time or tissue type. Although uniform growth between 0 and 200 cm above the sediment was prevalent, shell growth in late October was twice as fast in scallops living on the bottom compared to those only 20 cm above.

Table 2. *Placopecten magellanicus*. Stepwise multiple regressions describing the relationship between ln-transformed shell and soft-tissue growth of sea scallops as a function of environmental variables based on direct water sampling. Regressions were calculated using data from all cage heights (All) and for data collected at each of 5 heights above bottom. Potential predictor variables included water temperature (Temp), concentrations of chlorophyll, phaeophytin and suspended particulate matter (SPM), the C:N ratio of SPM, and the ratio of particulate organic matter to particulate inorganic matter (O/I). Variables are listed in order of descending correlation. Variables not listed in the equations were rejected in favour of remaining variables at $\alpha = 0.05$. 'Soft tissue' excludes muscle tissue. Model statements were not included if their level of significance was greater than 0.05

Dependent variable	Cage height (cm)	Model	r^2	p
Shell	All	= 0.04 (Temp) – 0.09 (SPM) + 4.07	0.03	<0.001
growth	0	–	–	0.50
	20	= –0.10 (Temp) + 4.40	0.12	<0.001
	50	–	–	0.15
	100	–	–	0.10
	200	= 0.06 (Temp) + 3.47	0.08	<0.001
Soft-tissue	All	= 0.04 (Temp) + 0.62 (O/I) – 0.05 (SPM) + 2.75	0.37	<0.001
growth	0	= 0.01 (Temp) + 4.15 (O/I) + 1.51	0.58	<0.001
	20	= 0.05 (Temp) – 0.27 (O/I) + 2.88	0.34	<0.001
	50	= 0.04 (Temp) + 0.54 (O/I) + 2.63	0.68	<0.001
	100	= 0.01 (Temp) + 2.23 (O/I) + 2.24	0.23	<0.001
	200	= 0.03 (Temp) + 0.39 (O/I) + 2.69	0.51	<0.001
Adductor	All	= 0.01 (Temp) + 0.13 (O/I) + 0.01 (SPM) + 2.94	0.17	<0.001
muscle	0	= 1.65 (O/I) + 0.004 (SPM) + 2.46	0.56	<0.001
growth	20	= –0.20 (O/I) – 0.04 (SPM) + 3.25	0.13	<0.001
	50	–	–	0.10
	100	= 0.53 (O/I) + 0.002 (SPM) + 2.87	0.13	<0.001
	200	= 0.20 (O/I) + 0.07 (SPM) + 2.78	0.51	<0.001

But change in shell height is not always the best index of overall growth since shell tissue does not respond quickly to adverse conditions and often maintains positive growth when soft-tissue is lost (Kautsky 1982, Hilbish 1986). Seasonal divergence in growth rate between tissue types at Upper South Cove was reflected in the sometimes low or nonsignificant correlation between shell and soft-tissue growth (Table 4). Although cage height was not linked to shell growth in late fall and winter, muscle and remaining soft-tissue growth rates were significantly lower near the bottom in late fall and winter (Figs. 5D & 6C).

Table 3. *Placopecten magellanicus*. Stepwise multiple regressions describing the relationship between ln-transformed shell, muscle and soft-tissue growth of sea scallops at 100 cm above bottom as a function of environmental variables. Two regressions were calculated for each dependent variable; one incorporated values obtained from an *in situ* probe (Probe) which measured variables hourly and the other used estimates derived from direct water sampling (Filter). The potential predictor variables included water temperature (Temp), and concentrations of chlorophyll (Chl) and total suspended particulate matter (SPM). Variables are listed in order of descending correlation. Variables not listed in the equations were rejected in favour of remaining variables at $\alpha = 0.05$. 'Soft tissue' excludes muscle tissue. Model statements were not included if their level of significance was greater than 0.05

Dependent variable	Source	Model	r^2	p
Shell	Filter	–	–	–
growth	Probe	–	–	–
Soft-tissue	Filter	= 0.08 (Temp) –0.21 (SPM) + 3.37	0.16	<0.001
growth	Probe	= 0.01 (Temp) + 0.77 (SPM) – 0.31	0.41	<0.001
Muscle	Filter	= 0.01 (Temp) – 0.02 (SPM) + 3.07	0.07	<0.001
growth	Probe	= 0.03 (Chl) + 2.99	0.13	<0.001

Table 4. *Placopecten magellanicus*. Simple linear regressions describing the relationship between shell growth and both muscle and remaining soft tissue growth of sea scallops during the 4 growth periods: shell growth (μm d^{-1}) = slope (soft tissue growth, mg d^{-1}) + intercept. Coefficients of determination and levels of significance are indicated. Cage height: height above bottom

Growth period	Cage height (cm)	Adductor muscle growth				Soft-tissue growth			
		Slope	Intercept	r^2	p	Slope	Intercept	r^2	p
20 Sep –	0	0.07	3.60	0.37	<0.001	0.02	2.42	0.70	<0.001
17 Oct 1990	20	0.06	3.15	0.08	0.039	–	–	–	0.940
	50	–	–	–	0.239	–	–	–	0.353
	100	0.09	−5.75	0.20	0.001	–	–	–	0.671
	200	0.03	6.90	0.61	<0.001	0.04	0.716	0.30	<0.001
18 Oct –	0	–	–	–	0.37	–	–	–	0.777
14 Nov 1990	20	–	–	–	0.96	0.03	−1.01	0.60	<0.001
	50	0.08	0.24	0.63	<0.001	0.04	−2.58	0.42	<0.001
	100	–	–	–	0.114	0.06	−2.21	0.45	<0.001
	200	–	–	–	0.637	0.04	0.65	0.27	<0.001
15 Nov –	0	0.06	−7.56	0.09	0.033	0.03	−3.53	0.10	0.024
12 Dec 1990	20	–	–	–	0.856	–	–	–	0.980
	50	0.06	−5.09	0.22	<0.001	–	–	–	0.072
	100	0.11	−7.25	0.40	<0.001	0.04	−2.18	0.58	<0.001
	200	0.10	−7.18	0.79	<0.001	0.05	−3.81	0.81	<0.001
13 Dec –	0	0.051	−6.56	0.35	<0.001	0.05	−1.64	0.47	<0.001
29 Mar 1991	20	–	–	–	0.372	0.06	−2.31	0.78	<0.001
	50	0.70	−6.35	0.13	0.007	0.04	−1.23	0.36	<0.001
	100	0.08	−5.68	0.80	<0.001	0.06	−1.71	0.52	<0.001
	200	0.07	−5.53	0.40	<0.001	0.04	−1.07	0.86	<0.001

Many studies which indicate that growth of suspended scallops is less near the bottom do not have concomitant environmental data to explain this observation (e.g. Leighton 1979, Wallace & Reinsnes 1984, Dadswell & Parsons 1991). When such data are available, higher growth away from the bottom is often attributed to differences in food quality (Wallace & Reinsnes 1985, MacDonald 1986, MacDonald & Bourne 1989), but, as indicated previously, the relationship between growth and seston is inconsistent. No index of seston quality or other environmental variables measured in the present study could account for the rapid shell growth of bottom scallops during late October or the reduced muscle growth on the bottom in late November. Chlorophyll, temperature, and seston quality (as POM, POC, chl:SPM) and quantity were vertically homogenous at these times. The C:N ratio was higher at 50 cm than next to the bottom in late November, but because the C:N ratio at 20 cm was equivalent to that just above the bed (~10 cm), it is unlikely that a change in seston quality was responsible for muscle growth differences in the bottom 20 cm of the water column.

Because of low phytoplankton levels, positive winter growth of shell and muscle tissue suggested initially that tidal resuspension of organic-rich sediments (20%

organic matter, 4 μg chl g^{-1} sediment, low C:N) was a seasonally important source of food for scallops. If so, scallops on the bottom should have grown faster than those above, but for shell and muscle tissue, growth was uniform with depth, and for the remaining soft tissue, bottom scallops suffered the greatest biomass loss. These observations do not preclude the possibility that growth would have been reduced further in the absence of resuspension, although it is evident that proximity to the bed does not necessarily confer a growth advantage. The potential benefits of resuspension may have been eliminated or reduced by hydrodynamic sorting (Muschenheim & Newell 1992), filter clogging, or dilution of organic seston with inorganic sediment (reviewed in Stevens 1987, Bricelj & Shumway 1991). The effects of organic dilution were particularly evident in the fall, a period of high particle loading due to the increased frequency of storms at this time (Smith et al. 1978). Despite high particle concentrations, muscle growth of bottom scallops was not depressed when chlorophyll levels were still relatively high in early fall (18 October to 14 November) but in late fall (15 November to 12 December) when phytoplankton were few, muscle growth on the bottom was significantly reduced relative to scallops away from the sediment.

Empirical models

At best, only 68% of the variation in scallop tissue growth could be accounted for by the environmental data obtained from water sampling every 2 wk. Given its strong link to the production of natural stocks (Caddy 1979), it was not surprising that water temperature was a dominant predictor of overall growth, but for muscle growth in particular, food quality was more important. At Upper South Cove, the percentage of organic matter was positively correlated with growth, supporting laboratory experiments using *Placopecten magellanicus* (Grant & Cranford 1991) and field studies of other scallops (e.g. *Chlamys islandica*: Vahl 1981; *Pecten maximus*: Wilson 1987). As discussed previously, however, the relationship between food quality and scallop growth is not always positive, suggesting that the importance of quality is secondary to quantity under high SPM concentrations. Unfortunately, a generalisation on the net effect of quality-quantity interaction is elusive; Andersen & Naas (1993) found growth to be negatively correlated with POM only at sites with low seston concentrations (average 1.1 mg POM l^{-1}) and positively correlated at a site where POM levels reached 30.5 mg l^{-1} (average 7.0 mg l^{-1}).

Chlorophyll concentration has been employed successfully as an index of food quality in studies of bivalve growth (Brown & Hartwick 1988), but it appears that changes in phytoplankton concentration were not always tightly coupled to scallop growth at Upper South Cove. For the bay scallop *Argopecten irradians*, growth can be independent of food supply even when chlorophyll levels are relatively low (1.2 µg l^{-1}; Kirby-Smith & Barber 1974). Similar observations in the field may be an artifact of the often poor correlation between chlorophyll and phytoplankton biomass (see Wildish et al. 1990). Others hypothesize that insensitivity to seasonal variations in chlorophyll may reflect changes in phytoplankton species or size composition (Andersen & Naas 1993). Because we attributed growth variation to changes in phytoplankton concentration (*in re* the dilution effect: see above), the poor predictive value of chlorophyll in the models suggests that biweekly water sampling was inadequate to characterise the amount of phytoplankton available to the scallops. Recent evidence has indicated that many variables important to the growth and survival of benthic suspension feeders can vary on the order of hours, often over a range on par with annual variation (Fegley et al. 1992). Such variation may explain why our empirical models based on hourly sampling of temperature, SPM, and chlorophyll with the probe were more successful than those based on biweekly direct water sampling.

Despite improvements to the models as a result of more intensive water sampling via probes, our selected variables remained poor predictors of growth, not necessarily because they were unimportant to scallops, but possibly because the most relevant statistic to relate to growth was not distilled from the lengthy time series of probe data. Rapid temperature shifts may induce a long-term stress not reflected in our calculations (Dickie 1958), and the food ration derived from a 2 or 3 d peak in phytoplankton biomass may not be represented adequately in mean food concentration. In addition, weighting of the data may be necessary since factors such as temperature, SPM inorganic fraction, and flow rates have critical thresholds (Dickie 1958, Vahl 1981, Wildish & Saulnier 1992). For example, a knowledge of food concentration or quality is of limited value if ambient currents are high enough to inhibit feeding. Lastly, an accurate knowledge of the magnitude and variation of predictor variables will not ensure successful modelling without consideration of their temporal coherence. Hofmann et al. (1992) showed that the timing of the spring or fall bloom relative to temperature fluctuations is crucial in modelling oyster populations since a plentiful food supply may not be converted to oyster biomass if water temperature is too high or too low. These situations highlight the fact that growth is an integrated response of the animal's energy budget. While individual components of energy budgets such as respiration may respond rapidly to temperature changes, net growth may be unaffected. Thus, production models based strictly on correlative analyses may be inherently less predictive than theoretical approaches such as scope-for-growth models.

Recently, there has been a concerted effort to develop general theoretical growth models of bivalves that will be useful to both community ecologists and aquaculturists (e.g. Hofmann et al. 1992, Grant et al. 1993, Herman 1993). To go beyond the identification of general trends and reach true predictive capabilities, such models are developed and subsequently modified on the basis of empirical research. Results from the present study suggest that the effects of resuspension should be incorporated into theoretical models in shallow systems, but as yet, the functional relationship has not been adequately quantified. Comparisons of direct water sampling with instrument data suggest that future studies should include the deployment of a vertical array of sensors to improve the resolution of sediment loading throughout the water column. To this end, a full-scale project is under way at Upper South Cove in which optical backscatter sensors and other particle detectors are being deployed throughout the water column to clarify the functional relationships suggested in the present study.

Appendix 1. *Placopecten magellanicus*. Simple linear regression equations calculated between log-transformed shell height and soft-tissue weights for sea scallops subsampled from cages at each height above bottom: log tissue weight = log shell height × slope + intercept. ('Soft tissue' excludes muscle)

Subsample date	Cage height (cm)	N	Adductor muscle tissue			Soft tissue		
			Slope	Intercept	r^2	Slope	Intercept	r^2
20 Sep 1990	–	15	2.54	-4.56	0.87	2.57	-4.32	0.82
18 Oct 1990	0	10	2.24	-4.01	0.11	1.00	-1.71	0.41
	20	10	3.36	-5.82	0.01	0.39	-0.74	0.94
	50	10	3.41	-5.88	0.52	3.53	-5.77	0.76
	100	10	4.64	-7.95	0.03	-0.87	1.25	0.91
	200	10	3.84	-6.59	0.18	1.50	-2.49	0.87
15 Nov 1990	0	10	4.23	-7.29	0.96	3.99	-6.55	0.91
	20	10	2.71	-4.79	0.65	2.85	-4.65	0.50
	50	10	2.44	-4.32	0.85	2.61	-4.24	0.76
	100	10	2.51	-4.43	0.77	2.18	-3.54	0.78
	200	10	4.96	-7.77	0.84	4.30	-7.01	0.87
13 Dec 1990	0	10	3.30	-5.85	0.89	3.04	-5.14	0.81
	20	10	4.24	-7.31	0.82	4.54	-7.33	0.78
	50	10	3.90	-6.79	0.88	3.71	-6.15	0.86
	100	10	3.19	-5.61	0.74	3.43	-5.66	0.64
	200	10	4.46	-7.69	0.84	4.07	-6.71	0.80
29 Mar 1991	0	10	4.54	-8.07	0.79	4.42	-7.83	0.70
	20	10	4.85	-8.51	0.75	3.86	-6.68	0.83
	50	10	2.79	-4.99	0.89	2.84	-4.93	0.94
	100	10	4.40	-7.76	0.81	4.80	-8.26	0.60
	200	10	3.43	-6.06	0.94	3.42	-5.87	0.86

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