

Effect of thermoclines and turbulence on depth of larval settlement and spat recruitment of the giant scallop *Placopecten magellanicus* in 9.5 m deep laboratory mesocosms*

Christopher M. Pearce^{1,2,**}, Scott M. Gallager³, Joan L. Manuel²,
Darlene A. Manning², Ron K. O'Dor², Edwin Bourget¹

¹GIROQ, Département de Biologie, Université Laval, Sainte-Foy, Québec G1K 7P4, Canada

²Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

³Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, USA

ABSTRACT: An experiment was conducted from December 1992 to February 1993 in a 10.5 m deep, 3.7 m diameter tank to examine the effect of thermoclines and water column turbulence on the depth of larval settlement and spat recruitment of the giant scallop *Placopecten magellanicus* (Gmelin). Polyethylene tube mesocosms set up within the tank were used to enclose 9.5 m deep columns of seawater which were then used as experimental replicates. Five different treatments were established as follows: (1) no turbulence and a 1.5°C thermocline, (2) no turbulence and no thermal gradient, (3) low level of turbulence with a 1.5°C thermocline, (4) medium level of turbulence with a 0.5°C thermocline, and (5) high level of turbulence with no thermal gradient. Various turbulence levels simulated turbulent energies ranging from open oceanic environments to near-shore and coastal conditions with vertical dissipation rates ranging from 10^{-7} to 10^{-3} cm² s⁻³. Ropes with collectors positioned at every 1 m depth interval were suspended the length of the water column in each replicate tube to collect settled spat. Spat counts varied significantly with both depth and turbulence treatment and were dependent on the interaction between the 2 factors. Numbers of spat generally increased with increasing depth in the static and low turbulence treatments, but this relationship became less evident with increasing turbulence; spat recruitment in the high turbulence tubes appeared random with respect to depth. It is suggested that the trend of increasing recruitment with depth in the static and low turbulence tubes was driven primarily by larval behaviour at settlement. There was no indication of increased recruitment at or above the thermocline, in contrast to a previous mesocosm experiment with a stronger thermal gradient and a different population of larvae, suggesting that stratification intensity may affect depth of larval settlement and spat recruitment. Settlement rate did not appear to be a strict function of larval encounter rate with the spat collectors. Higher spat counts in treatments with a 1.5°C thermocline than in other turbulence treatments, even when results were corrected for differences in competency among the various treatments, suggest that thermal gradients have a potential commercial importance in both the collection and hatchery production of scallop spat.

KEY WORDS: Depth of larval settlement · Larval scallop behaviour · Mesocosm study · *Placopecten magellanicus* · Spat recruitment · Thermocline · Turbulence

INTRODUCTION

The vertical distribution of planktonic larvae of benthic marine invertebrates can be influenced both by active larval responses to environmental stimuli on a small scale and passive transport by water movements within the water column on meso and/or large scales. The degree to which these 2 mechanisms control larval

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**Present address: Ross Island Salmon Ltd, PO Box 21, North Head, Grand Manan, New Brunswick E0G 2M0, Canada.
E-mail: anderel@nbnet.nb.ca

vertical distribution will depend on the strength of vertical mixing—or degree of water column stratification—and the swimming ability of the larva (see review by Mileikovsky 1973). Many species of benthic invertebrates produce larvae which undertake vertical migrations at some point during their pelagic existence and a wide variety of environmental stimuli [both biological (e.g. food, predators, prey) and/or physical (e.g. gravity, light, pressure, salinity, temperature, tides)] are known to influence these larval vertical movements (see reviews by Thorson 1964, Crisp 1974, Sulkin 1984, Young & Chia 1987). A large number of studies have shown how vertical discontinuities in physical factors such as salinity and temperature (i.e. haloclines and thermoclines, respectively) can influence the vertical distribution and movement of planktonic invertebrate larvae. Species from a wide variety of taxonomic groups including polychaetes, gastropods, bivalves, cirripedes, decapods, bryozoans, and echinoderms produce larvae whose vertical position in the water column has been shown to be influenced by vertical discontinuities in salinity and/or temperature (e.g. Harder 1968, Oshurkov et al. 1982, Scrope-Howe & Jones 1986, Boudreau et al. 1991, 1992, Thiébaud et al. 1992, Raby et al. 1994, Gallagher et al. 1996, Manuel et al. 1996b). Although the scientific literature on the vertical distribution of invertebrate planktonic larvae in the water column in relation to vertical boundaries and water column mixing is substantial, very little work has been conducted to examine how these factors influence settlement of larvae [but see Boudreau et al. (1992) who found that laboratory thermoclines significantly reduced the number of post-larval lobster *Homarus americanus* settling in comparison with control columns of water with no temperature discontinuities].

Very little is known about the settlement requirements of larvae of the giant or sea scallop *Placopecten magellanicus* (Gmelin). Only 3 laboratory studies to date have been published on the settlement preferences of this species. Culliney (1974) found that larvae settled on fragments of conspecific adult shells, glass shards, and small pebbles. Pearce & Bourget (1996) tested a variety of artificial materials as settlement substrata (including onion bags, monofilaments, Astroturf, Vexar® meshes, scallop shells, filter-wool) under hatchery-type conditions and found that polyester filter-wool was, by far, the best substratum for collecting settled spat. They also reported that microbial films enhanced larval settlement rate. Pearce et al. (1996) found that giant scallop larvae settled predominantly at or above a thermal gradient (i.e. ~11°C established over a 1 m depth interval) created in 9 m deep mesocosms. Settlement rate on artificial (i.e. polyester filter-wool) and natural (i.e. red filamentous alga *Polysiphonia*

lanosa) substrata were similar (Pearce et al. 1996). The scant information available on the settlement requirements of this species is surprising given its economic importance for the fishing industry in Atlantic Canada and the northeastern United States (Bourne 1964, Sinclair et al. 1985, Naidu 1991) and the recent interest in its aquacultural development (Couturier 1990, Dadswell & Parsons 1991). The paucity of laboratory data on larval settlement of giant scallops may be due to a number of factors including: (1) the species has a relatively long larval developmental time of at least 28 to 50 d at 15°C (Culliney 1974, Naidu et al. 1989, Couturier 1990) and (2) the species is relatively difficult to rear through settlement as high mortality generally occurs during this period (Tremblay 1988, C. M. Pearce pers. obs.).

In the field, natural spat settlement of *Placopecten magellanicus* has been recorded on a variety of substrata including: navigation buoys (Merrill & Posgay 1967, Naidu 1970, Merrill & Edwards 1975), gravel and pebbles (Kenchington et al. 1991, Thouzeau et al. 1991), shells of adult *P. magellanicus* (Naidu 1970), mussel byssal threads (Merrill & Edwards 1975), red macroalgae (Naidu 1970), bryozoans (Baird 1953, Caddy 1972, Merrill & Edwards 1975), hydrozoans, amphipod tubes, and sand grains (Larsen & Lee 1978). Various field studies have collected giant scallop spat on artificial substrata such as polyethylene sheets and monofilament (Naidu & Scaplen 1979, Naidu et al. 1981, Naidu & Cahill 1986, Robinson et al. 1992, Parsons et al. 1993, Pouliot et al. 1995). While some of these studies have examined collector design and compared the efficiency of various substrata in collecting spat (e.g. Naidu et al. 1981, Pouliot et al. 1995), little information is available on how physical factors in the water column affect larval settlement distribution. Robinson et al. (1992) reported that horizontal spatial patterns of giant scallop settlement reflected known oceanographic circulation within Passamaquoddy Bay, Canada, but no known scientific research has examined the direct effect of physical oceanographic conditions on depth of larval scallop settlement on artificial spat collectors.

Aggregation of larvae of *Placopecten magellanicus* at or above thermoclines/pycnoclines has been documented both in the field (Tremblay & Sinclair 1988, 1990a) and in laboratory mesocosms (Gallagher et al. 1996, Manuel et al. 1996b). In a previous study, Pearce et al. (1996) found that settlement of giant scallop larvae—spawned from adults collected from Newfoundland, Canada—in 9 m deep thermally stratified mesocosms (i.e. ~11°C thermocline at a depth of 4.0 to 5.0 m with temperatures of 16°C above and 5°C below the thermal gradient) was greatest in collectors at or above the thermocline. The authors hypothesized that depth

of settlement of scallop larvae in the field may be affected by such processes as water column stratification and vertical mixing, but were uncertain as to how settling larvae might respond to weaker gradients of temperature or under conditions of turbulent mixing.

The present study follows the previous work of Pearce et al. (1996) and examines the effect of weaker thermoclines and turbulence on the depth of settlement of larvae produced from giant scallops collected from a population located on Georges Bank, Canada. The results are discussed considering the applications to field spat collection, natural recruitment, and hatchery production of giant scallops.

MATERIALS AND METHODS

Tower Tank parameters. The experiment was conducted from December 1992 to February 1993 in a cylindrical Tower Tank (depth: 10.5 m; inner diameter: 3.7 m; volume: 117 m³) located in the Life Sciences Centre of Dalhousie University. The tank is constructed of reinforced concrete and lined with multiple, sprayed coatings of polyvinyl chloride (PVC). It was filled with seawater passed through a sandbed filtering system which removed particles above 50 µm in size (nominal). Polyethylene bags (length: 9.5 m; diameter: 0.60 m; thickness: 150 µm), filled with 2686 l of 1 µm cartridge-filtered seawater and suspended at the water surface using styrofoam flotation collars, were used to divide the tank into replicate columns of seawater (Fig. 1). Salinity of seawater in the tubes, at the time of filling, ranged from 30.4 to 30.6‰. While measurements were not conducted during the experiment, salinities would not be expected to vary substantially. Any slight increase in salinity due to surface evaporation, which was minimal, would have been compensated for by the addition of phytoplankton and periodically topping up tubes with ~30‰ seawater. Vertical profiles of oxygen concentration, conducted in previous static mesocosm experiments run in 9.0 m deep tubes, indicate that dissolved oxygen concentration remains relatively stable at 8.5 to 9.0 ppm throughout a 50 d experimental period, indicating that there is no problem with static tubes turning anoxic.

A thermocline was established in the Tower Tank at a depth of 4.0 to 5.0 m by circulating chilled seawater (~4°C) through a titanium ring placed around the inner cir-

cumference of the tank at a depth of 4.5 m and running hot freshwater (~30°C) through a PVC ring set up at a depth of 4.0 m (Fig. 1). Actual thermal gradients in the experimental tubes varied with treatment manipulation (see 'Experimental protocol' section). Light was provided solely by an overhead array of three 1000 W phosphor-coated metal halide lamps set on a 12 h dark/12 h light photoperiod that were phase shifted so that 2 lights came on and switched off ~30 min before the other one. A gradual increase in light intensity during dark to light transition was afforded by the lamps' slow warm-up time. Light measurements taken a few

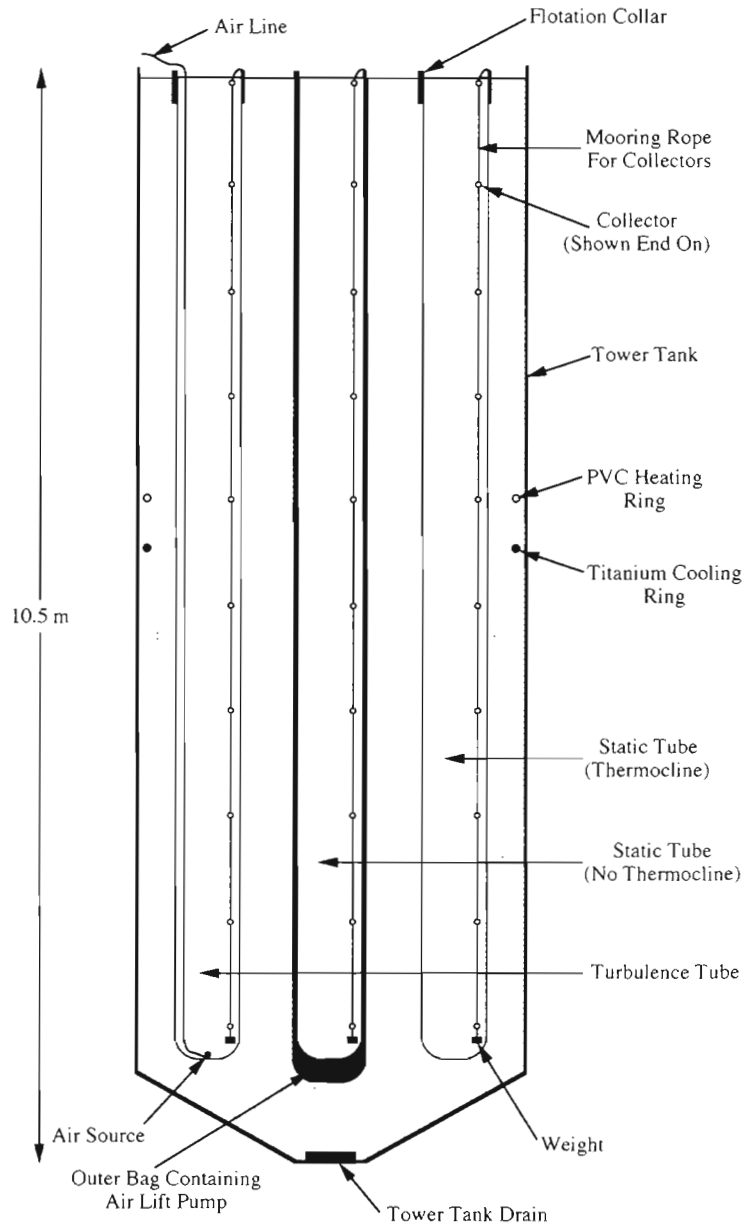


Fig. 1. Side view of Tower Tank, drawn to scale, showing set up of different treatment tubes

centimetres above the water surface using a Weston Instruments Inc. model 756 illumination meter and a Gossen Lunasix 3 intensity meter showed light intensities ranging from ~1800 to 7000 lux or ~15 to 60% normal midday summer sun. Light intensity was greater in the center of the tank (6026 ± 701 lux, mean \pm SD, $n = 5$) than around the perimeter (3425 ± 931 lux, mean \pm SD, $n = 20$).

Spawning and larval development. Adult giant scallops from a Georges Bank population were collected and maintained at an aquaculture site in suspended pearl nets at Mahone Bay, Nova Scotia for a period of at least 1 yr prior to the experiment. Ripe individuals were transported to the laboratory in coolers and spawned the same day. Seven females and seven males were scrubbed clean and induced to spawn in 0.2 μ m filtered seawater by thermal stimulation and agitation of the water with a small submersible pump. The eggs from all females were mixed together and fertilized with a sample of mixed sperm of all 7 males. At 5.5 h post-fertilization, approximately 50 million developing embryos were added to the surface of a 9 m deep polyethylene tube in the Tower Tank, which was thermally stratified so that temperature in the top half of the tank was 15 to 16°C while that below the thermocline was 8 to 9°C. The vertical distribution of the embryos was monitored during the next few days with the use of a profiling video camera (Polarized Larval Recorder, PLR; see Gallagher et al. 1996). The embryos gradually sank, distributing themselves predominantly in the upper half of the water column; they were most dense in a region just above the thermocline. Four days after the addition of the embryos, large numbers of veligers were seen swimming at the surface of the tube, indicating developmental progression. At this time the tube was drained and the larvae collected on a 63 μ m Nitex® mesh. The larvae were rinsed into a 50 l plastic bucket containing ~35 l of 1- μ m cartridge-filtered seawater at 15 to 16°C for counts of individuals. Approximately 540 000 D-stage larvae were introduced into each replicate 9.5 m deep tube in the Tower Tank, giving a final larval concentration in each tube of ~0.20 larvae ml^{-1} . This concentration is somewhat lower than typical hatchery larval rearing densities of 1 to 5 larvae ml^{-1} (Tremblay 1988), but at least 2 orders of magnitude greater than maximum densities found on Georges Bank [Tremblay & Sinclair (1990a) reported peaks in larval concentration within the water column as high as 0.002 larvae ml^{-1}]. While experimental larval concentration was markedly greater than natural densities, it represents approximately the lowest concentration at which workable numbers of spat can be collected under such conditions.

Cultured phytoplankton *Isochrysis galbana* (Tahitian variety; clone designation TISO) was added to the

tubes to produce a concentration throughout the whole tube of 5.0×10^3 cells ml^{-1} . The density of phytoplankton cells in the tubes was monitored during the course of the experiment with a multi-sizer Coulter Counter® and additional TISO was added to maintain this density when needed (i.e. at larval ages 10, 14, 22, and 30 d). Phytoplankton was gravity fed throughout the length of each tube via the use of a vinyl sprinkler hose (inner diameter: 1.3 cm) which ran the entire length of the tubes. This hose had small perforations every 2 cm of its length and distributed the phytoplankton evenly throughout the tube. This was confirmed by conducting Coulter counts on vertically stratified water samples.

Experimental protocol. Five different treatments, each with 3 replicate tubes, were established as follows: (1) no turbulence and a well-developed thermocline: 'Static Therm'; (2) no turbulence and no thermocline: 'Static'; (3) relatively low level of turbulence: 'Low Turb'; (4) medium level of turbulence: 'Med Turb'; and (5) relatively high level of turbulence: 'High Turb'. Distribution of the 15 tubes within the Tower Tank was completely randomized and their positions within the tank were constant throughout the duration of the experiment (Fig. 2).

Turbulence in the Low, Med, and High Turb tubes was created by pumping compressed air through a small, single-point orifice (2 mm diameter capillary tube) positioned in the center at the bottom of each tube (Fig. 1). The position of the bubble stream rising up through the tubes was random (i.e. uncontrollable and not directed in any particular area of the tube). The different levels of turbulence were created by

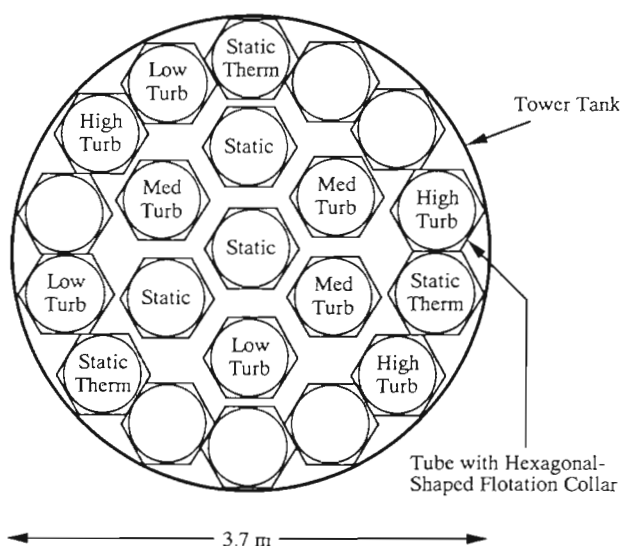


Fig. 2. Overhead view of Tower Tank, drawn to scale, showing position of treatment replicates. Tubes without treatment names were part of a separate experiment

using different air pressures. Rates of turbulent energy dissipation (ϵ) were calculated for each replicate tube using recorded profiles of the entire water column taken with the PLR combined with a modification of the theoretical approach of Dickey & Mellor (1980). Particle images on the video tapes were integrated over 1/60 s to produce streaks. Streak lengths were proportional to the sum of the PLR profile speed and the speed of the particle movement. For each particle i within a single video field f , the x , y , and z components of the instantaneous velocity (cm s^{-1}) were calculated—assuming isotropy in the horizontal diffusional field—as:

$$u_i = [(x_2 - x_1) - p]/t \quad (1)$$

$$v_i = [(y_2 - y_1) - p]/t \quad (2)$$

$$w_i = [(z_2 - z_1) - p]/t \quad (3)$$

where x_1, z_1 and x_2, z_2 are the 2-dimensional coordinates for the beginning and end of a streak, p is the particle diameter, and t is the time (1/60 s). Fluctuating components of the velocities for each particle were calculated as:

$$u'_i = u_i - U_x \quad (4)$$

$$v'_i = v_i - U_y \quad (5)$$

$$w'_i = w_i - U_z \quad (6)$$

where U_x , U_y , and U_z are the mean particle velocities in each direction of a given field:

$$U_x = \sum u_i / N \quad (7)$$

$$U_y = \sum v_i / N \quad (8)$$

$$U_z = \sum w_i / N \quad (9)$$

and N is the number of particles in the field. For a given video field f , the average of the fluctuating components of the velocities was calculated as:

$$\sigma u_f = [\sum (u'_i)^2 / N]^{0.5} \quad (10)$$

$$\sigma v_f = [\sum (v'_i)^2 / N]^{0.5} \quad (11)$$

$$\sigma w_f = [\sum (w'_i)^2 / N]^{0.5} \quad (12)$$

The 3-component turbulent velocity Q was calculated for each field as:

$$Q_f = [(\sigma u_f)^2 + (\sigma v_f)^2 + (\sigma w_f)^2]^{0.5} \quad (13)$$

The vertical turbulent diffusion VTD ($\text{cm}^3 \text{s}^{-3}$) is the cube of the turbulent velocity:

$$\text{VTD} = Q^3 \quad (14)$$

and the turbulent energy dissipation rate ϵ ($\text{cm}^2 \text{s}^{-3}$) is:

$$\epsilon = d\text{VTD}/dz \quad (15)$$

where z is 0.6 m, the width of a tube (i.e. largest eddy size is constrained to the width of a tube).

The PLR was profiled at 10 cm s^{-1} and data were recorded at 60 fields s^{-1} . Data on ϵ values were calculated as 10-cm averages for 60 individual fields. Mean

ϵ values ($\text{cm}^2 \text{s}^{-3}$) reported in this paper are the vertical averages from surface to bottom of each replicate tube and are as follows: Static Therm (7.1×10^{-7} , 1.2×10^{-6} , 4.3×10^{-6}), Static (1.6×10^{-6} , 2.0×10^{-6} , 7.0×10^{-6}), Low Turb (9.4×10^{-6} , 2.5×10^{-5} , 2.9×10^{-5}), Med Turb (6.8×10^{-5} , 1.5×10^{-4} , 2.3×10^{-4}), and High Turb (1.1×10^{-3} , 2.7×10^{-3} , 4.4×10^{-3}). Typical intensities of oceanic turbulence span several orders of magnitude: open ocean 10^{-6} to 10^{-2} , shelf 10^{-3} to 10^{-2} , coastal zone 10^{-3} to 10^0 , tidal front $10^{-1} \text{ cm}^2 \text{s}^{-3}$ (Kjørboe & Saiz 1995). The turbulence intensities used in the present experiment, thus, ranged from open ocean (i.e. Static Therm, Static, Low Turb, Med Turb) to shelf or moderate coastal conditions (i.e. High Turb) and were typical of giant scallop larval habitats.

Temperatures within the tubes during the first 7 d of the experiment (i.e. larvae 4 to 11 d old) were somewhat variable as the thermal regimes were being established in the various treatments. During this period, temperatures were generally 12 – 13°C just below the water surface and gradually decreased to 9 – 10°C at the bottoms of the tubes (Fig. 3). An exception to this generalization was the High Turb treatment which was vertically homogeneous with respect to temperature (i.e. 11°C at all depths at 7 d old). By the time larvae were 12 d old, all treatments had developed their characteristic thermal structures. A 1.5°C thermocline was established in the Static Therm and Low Turb tubes at a depth of 4.0 to 5.0 m while the Static treatment remained unstratified. The latter treatment was created by housing the tube containing the larvae within another polyethylene bag and mixing seawater between the two using an air lift pump (Fig. 1). This procedure was sufficient to completely break down the thermocline within these tubes. A thermal gradient was established in the Med Turb tubes at a depth of 4.0 to 5.0 m, but the temperature differential was only $\sim 0.5^\circ\text{C}$ due to stronger vertical mixing. Higher rates of turbulence within the High Turb treatment produced unstratified conditions. The temperature in all the tubes gradually increased by 2°C over the following week (Fig. 3) due to a gradual warming of the water column. This was most likely a result of surface heating by the overhead lights and transfer of this heat to depth by water column mixing in some of the tubes. To prevent temperatures in the upper part of the water column from becoming excessive for larval development, when larvae were 28 d old the flow rate in the chilling coil was increased. By larval age 48 d, the temperatures had been brought back down to original levels. During these gradual shifts in temperature, the thermal gradients in the various treatments remained unchanged (Fig. 3).

Spat collectors were added to the tubes when larvae were 9 d old. A collector consisted of an open cylinder

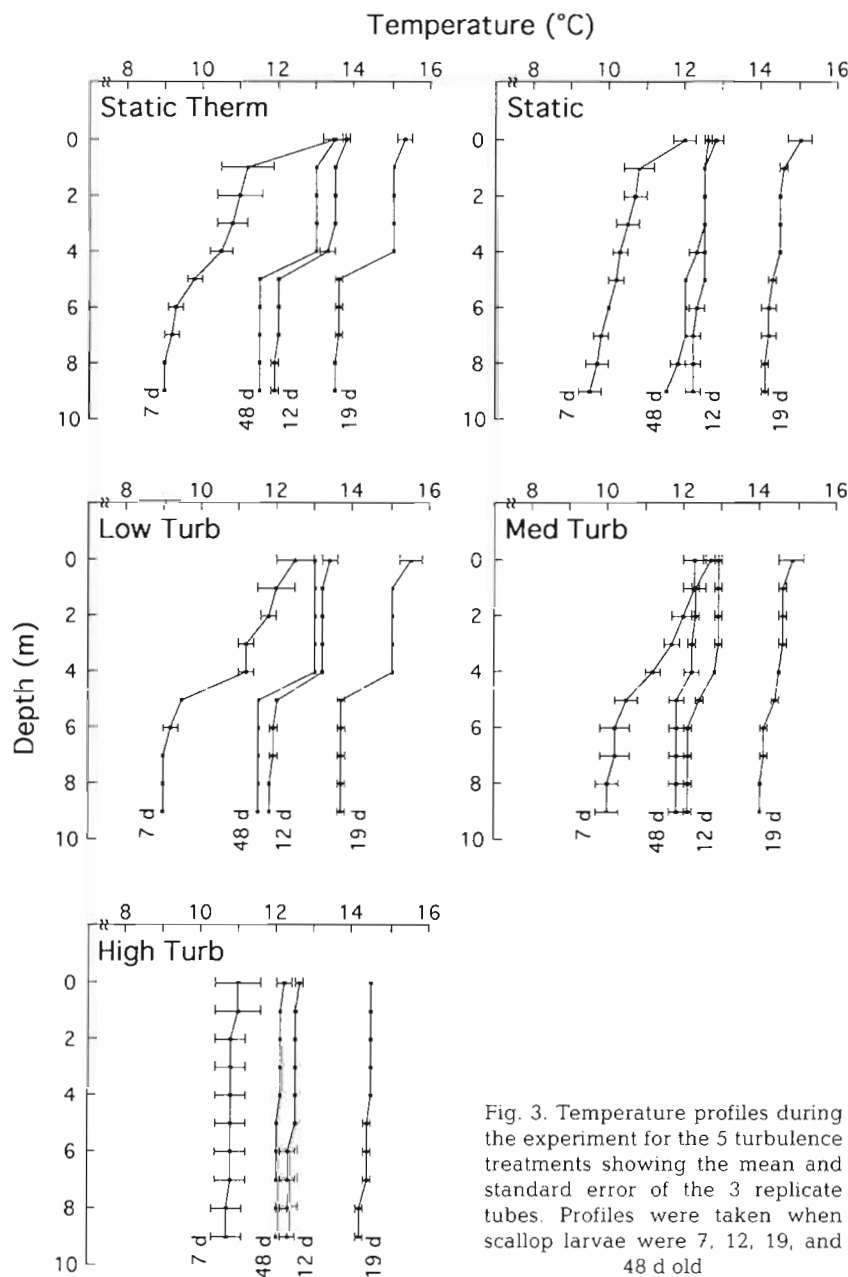


Fig. 3. Temperature profiles during the experiment for the 5 turbulence treatments showing the mean and standard error of the 3 replicate tubes. Profiles were taken when scallop larvae were 7, 12, 19, and 48 d old

(length: 12 cm; diameter: 4 cm) of black, low-density, polyethylene mesh (Vexar® brand made by DuPont Canada Inc.; mesh size 3.8 mm) stuffed with a tangle of 6 m of 0.40 mm diameter, aquamarine monofilament (12 lb or 5.5 kg test). Collectors were hung from a 5 mm diameter, yellow polypropylene rope which extended the length of each tube and was weighted at the bottom. One collector was placed at every metre interval starting just below the water surface and continuing down to 9 m (i.e. 0.5 m above the bottom of tube). One 'string' of collectors was hung in each replicate tube close to the tube wall (total of 150 collectors). All col-

lectors and ropes were soaked in 0.2- μ m cartridge-filtered seawater for 12 h prior to deployment in the Tower Tank.

During the course of the experiment, the monofilament in some of the spat collectors was lost. The collectors were open-ended cylinders and, occasionally, protruding monofilament was snagged by the feeding tube or by the PLR. This occurred in the following turbulence treatment/depth combinations: Static (1 replicate at a depth of 2 m), Low Turb (1 replicate at depths of 0, 5, and 7 m), Med Turb (1 replicate at depths of 4 and 6 m and 2 replicates at a depth of 7 m), and High Turb (1 replicate at depths of 4, 7, and 8 m). The loose monofilaments were recovered, but counts from these were not included in the statistical analyses. Spat collected from the mesh tube itself, without monofilament, were counted and included in the analyses, however, since all of these tubes remained in place on their respective mooring ropes (i.e. n remained equal for all treatment combinations). A t -test comparing numbers of spat on collectors with and without monofilament at 7 m depth in the Low Turb, Med Turb, and High Turb treatments revealed no significant difference between the two ($p = 0.4$), suggesting that collectors with monofilament did not consistently collect more spat than those without.

When the larvae were 55 d old and very few planktonic individuals were evident in video profiles of

any of the tubes, the collectors were slowly and carefully pulled to the surface, removed from the rope, placed into separate specimen bags, and preserved with 70% ethanol. The polypropylene rope itself was carefully cut into 1 m lengths, bagged, and preserved with 70% ethanol as well. Just prior to counting, the collectors and ropes were soaked in a 1% bleach solution in 0.2- μ m cartridge-filtered seawater (i.e. ~0.05% sodium hypochlorite) for at least 10 min to ensure that any remaining byssally attached spat were dislodged (Bourne et al. 1989, Heasman et al. 1994) and then rinsed with a jet of hot freshwater (5 l in total) to

remove all spat and larvae. Previous studies had shown that this technique removed all individuals from similar substrata (Pearce & Bourget 1996, Pearce et al. 1996). The ethanol that the collectors and ropes were originally preserved in, the bleach that they were soaked in, and the freshwater rinsings were all passed through a 75 μm Nitex[®] mesh to collect the spat and larvae. Counts of individuals were made with the use of a dissecting microscope set up for polarized light viewing as larvae and young juveniles of giant scallop are birefringent (see Gallagher et al. 1989 for technique).

Individuals were counted as spat only if new dissoconch (i.e. post-metamorphic) shell growth was evident, otherwise they were classified as larvae. This type of classification is somewhat conservative in estimating numbers of spat present, since individuals which are in the process of metamorphosis, but have yet to lay down a visible layer of new shell growth, will be classified as larvae. Other indicative signs of scallop metamorphosis include the loss of the larval velum, the development of gill bars, and the repositioning of the foot, but these are all features that are often hard to distinguish in preserved individuals—especially samples treated with solutions of hypochlorite. Thus, the most definitive measure of successful larval metamorphosis is the production of new dissoconch.

At the end of the experiment the tubes were completely drained using a high speed electrical pump (Jacuzzi[®] SP125, 3450 RPM; pump speed: $\sim 107 \text{ l min}^{-1}$) and the contents of each tube were collected on screens. The tubes were drained down to a depth of 8.5 m, filtering the water through a 100 μm Nitex[®] mesh (denoted as the 'water' sample). The bottom 1.5 m was filtered separately through Nitex[®] meshes varying in size from 60 to 100 μm depending on the tube. This 'bottom' sample included rinsings of the bottom of the tubes with a jet of 1- μm filtered seawater. Water and bottom samples were preserved separately in 1% buffered formalin. Shell lengths of a random allotment of larvae from both samples were later measured using the computer image-analysis system BioScan OPTIMAS[®] 4.02. Shell length was defined as the greatest distance measured from the anterior to the posterior end of the larval shell, approximately parallel to the larval hinge. These larval shell lengths were used to standardize for varying levels of competency across tubes (see 'Statistical analyses' section).

Statistical analyses. Slight non-normality (judged by normal probability plots) and significant heterogeneity of variances (Cochran's test: $\alpha < 0.01$) were evident in the raw data of numbers of spat on the collectors and ropes. A log transformation [$\ln(x+1)$] was sufficient to both normalize the data and reduce the heteroscedasticity to non-significant levels. Counts of spat were

analysed with a mixed model nested analysis of variance which was constructed as follows:

$$Y_{ijkl} = \mu + M_i + D_j + MD_{ij} + T(M)_{k(i)} + \epsilon_{ijkl} \quad (16)$$

where M = effect of mixing or turbulence (fixed factor with 5 levels), D = effect of depth (fixed factor with 10 levels for collectors and 9 levels for rope), and T = effect of tube (random factor with 3 levels nested within mixing factor).

Multiple comparisons among depths and turbulence treatments were made with Least Significant Difference (LSD) tests with $\alpha = 0.05$ (Sokal & Rohlf 1981). The relationship between transformed numbers of spat and depth was further examined through linear regression analysis.

Although the effect of depth could be examined directly by simply using the transformed counts of spat found on the collectors and ropes, analysis of the effect of turbulence was complicated by the fact that differential larval growth rates in the various treatments (S. M. Gallagher pers. obs.) led to different proportions of competent larvae available for settlement at the end of the experiment. In order to standardize settlement rates for variations in the percentages of competent larvae among treatments, the proportion of larvae $\geq 230 \mu\text{m}$ in shell length taken from the tubes at the end of the experiment was calculated for each replicate tube. To calculate this proportion, larvae collected from both water and bottom samples were combined (N.B. the original separation of the 2 samples was done because information on numbers of planktonic versus benthic larvae was required for another study). The active substrate-seeking phase of larval development, termed the pediveliger, where larvae alternate between periods of crawling and swimming and have the capacity for weak byssus attachment to substrata, generally does not occur until a larval shell length of 230 to 280 μm has been attained (Culliney 1974, Naidu et al. 1989, Couturier 1990; but see also Pearce et al. 1996 who reported finding metamorphosed individuals slightly smaller than 230 μm). The proportion of larvae $\geq 230 \mu\text{m}$ was used to estimate how many spat would have been present in the tubes if 100% of the individuals had been competent, thus standardizing across tubes and treatments. These standardized values were used in a nested ANOVA as described above. Slight non-normality (judged by normal probability plots) and significant heterogeneity of variances (Cochran's test: $\alpha < 0.01$) were evident in these standardized values for both the collector and rope data. A log transformation [$\ln(x+1)$] was, again, sufficient to both normalize the values and reduce the heteroscedasticity to non-significant levels in both data sets. Comparisons among turbulence treatments were made with LSD tests with $\alpha = 0.05$.

Table 1. *Placopecten magellanicus*. Analysis of variance tables for log-transformed raw (Raw) and standardized (Stand) numbers of scallop spat on (A) collectors and (B) ropes. N.B. Raw counts of spat were standardized among tubes by taking into consideration the proportion of competent larvae in each tube (see text for full explanation of procedure). M = effect of mixing or turbulence (fixed factor with 5 levels), D = effect of depth (fixed factor with 10 levels for collectors and 9 levels for rope), T = effect of tube (random factor with 3 levels nested within mixing factor), df = degrees of freedom, SS = sum of squares, MS = mean square

Source	df		SS		MS		F-value		p-value	
	Raw	Stand	Raw	Stand	Raw	Stand	Raw	Stand	Raw	Stand
(A) Collectors										
M	4	4	152.21	153.94	38.05	38.49	8.31	7.35	≤ 0.005	≤ 0.005
D	9	9	17.83	26.88	1.98	2.99	4.52	3.39	≤ 0.0001	≤ 0.005
M × D	36	36	17.98	42.09	0.50	1.17	1.14	1.33	= 0.30	= 0.14
T(M)	10	10	45.81	52.37	4.58	5.24	10.46	5.95	≤ 0.0001	≤ 0.0001
Residual	90	90	39.40	79.19	0.44	0.88				
(B) Ropes										
M	4	4	88.05	83.38	22.01	20.85	6.10	3.78	≤ 0.01	= 0.04
D	8	8	16.70	19.12	2.09	2.39	7.10	2.68	≤ 0.0001	≤ 0.01
M × D	32	32	16.28	29.46	0.51	0.92	1.73	1.03	= 0.03	= 0.44
T(M)	10	10	36.06	55.22	3.61	5.52	12.27	6.20	≤ 0.0001	≤ 0.0001
Residual	80	80	23.52	71.26	0.29	0.89				

One-way ANOVAs, followed by Tukey tests with $\alpha = 0.05$, were used to analyse the size of larvae in the various tubes, the proportion of competent larvae in the various treatments, and the number of planktonic larvae counted by the PLR in the various treatments. All data were verified for normality and homogeneity of variances using normal probability plots and Cochran's test with $\alpha < 0.01$, respectively. All statistical analyses and graphing were carried out using either the SuperANOVA 1.11 (Abacus Concepts 1989) or the SYSTAT 5.2.1 (Wilkinson 1992) computer packages for the Macintosh computer.

RESULTS

Effect of depth

Collectors

A nested ANOVA on the log-transformed number of spat found on the collectors showed that the effect of depth was highly significant ($F = 4.52$, $df = 9, 90$, $p \leq 0.0001$; Table 1A) and was not significantly dependent on the interaction with turbulence treatment ($F = 1.14$, $df = 36, 90$, $p = 0.30$; Table 1A). An LSD multiple comparisons test on data pooled across all turbulence treatments revealed an increase in spat numbers with increasing depth (Fig. 4). While the analysis of variance revealed a non-significant interaction between depth and turbulence treatment, changes in depth profiles of spat counts among turbulence levels were suggested when interaction results were examined. Numbers of spat generally increased with depth in

the Static Therm, Static, and Low Turb treatments, whereas spat were more evenly dispersed across depths in the Med Turb tubes and randomly distributed in the High Turb tubes (Fig. 4). Coefficients of determination (r^2) from individual regression analyses of spat numbers and depth within each turbulence treatment confirmed this trend; coefficients were greatest for Low Turb (0.538), Static Therm (0.180), and Static (0.110) treatments, lower for Med Turb tubes (0.058), and lower still for High Turb tubes (0.002) (Table 2). The slight peak in spat numbers in the 0 m deep collectors in the Static Therm treatment was the result of a relatively high spat count in the surface collector from one of the 3 replicate tubes. If this value is left out of the regression analysis, r^2 for the Static Therm treatment increases to 0.458 (Table 2).

Ropes

A nested ANOVA on the log-transformed number of spat found on the ropes showed that the effect of depth was, again, highly significant ($F = 7.10$, $df = 8, 80$, $p \leq 0.0001$; Table 1B). The interaction between depth and turbulence treatment was slightly significant ($F = 1.73$, $df = 32, 80$, $p = 0.03$; Table 1B). Depth profiles of numbers of spat in the 5 turbulence treatments generally exhibited the same trends as shown for the collector data (Fig. 5). Spat numbers increased with depth in the Low Turb ($r^2 = 0.471$) and Static Therm ($r^2 = 0.393$) treatments, whereas spat were more evenly distributed among depths in the Med Turb ($r^2 = 0.050$) and High Turb ($r^2 = 0.039$) tubes (Table 2, Fig. 5). As with the collector data, there was a slight peak in numbers

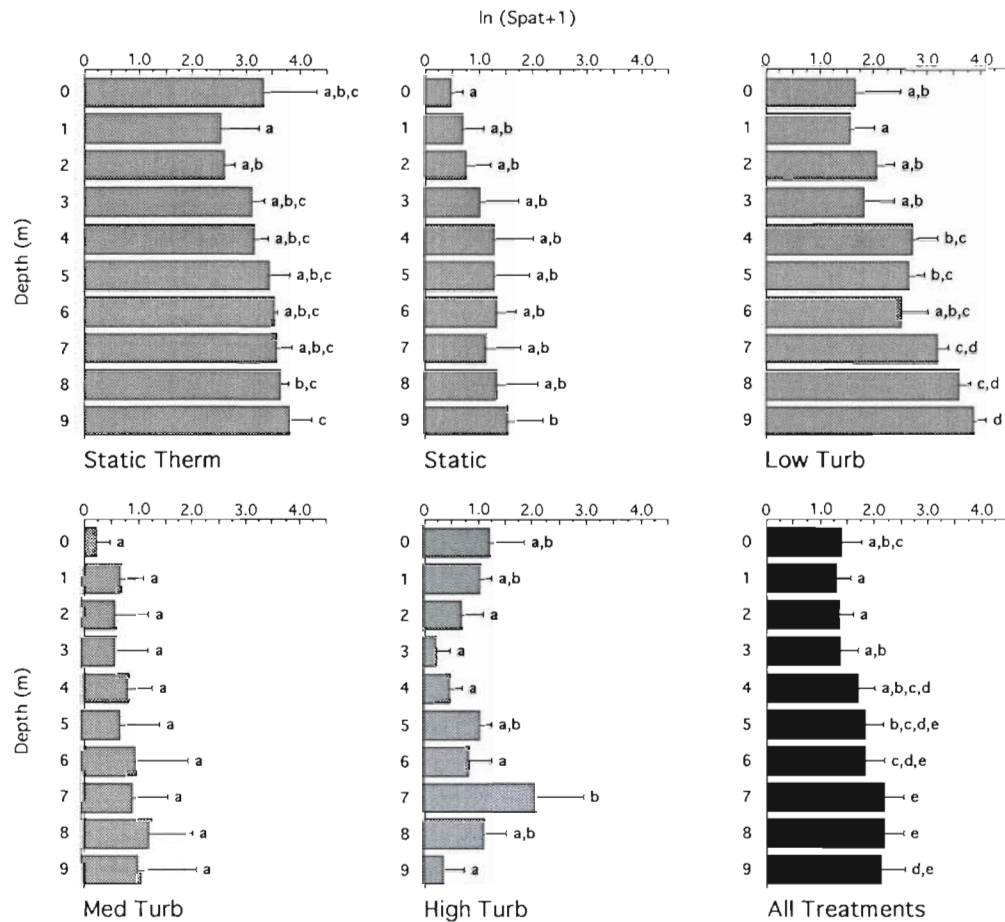


Fig. 4. *Placopecten magellanicus*. Depth profiles of log-transformed number of spat on collectors. Profiles are for the 5 separate turbulence treatments (i.e. Static Therm, Static, Low Turb, Med Turb, High Turb) as well as for the data pooled across all turbulence levels (i.e. All Treatments). Bars are the means of 3 (individual treatments) or 15 (all treatments) replicates and error bars are standard errors of the means. Letters by error bars represent the results of separate LSD tests examining the effect of depth within each turbulence treatment. Bars with the same letters within each profile are not significantly different (i.e. $p > 0.05$)

of spat near the surface (i.e. 1 m deep rope portion) in the Static Therm treatment that was due to elevated spat counts in one of the 3 replicate tubes. If this value is left out of the regression analysis, r^2 for the Static Therm treatment increases to 0.520 (Table 2). Two major differences between the rope and collector data should be noted. Firstly, the correlation between spat numbers and depth in the Static treatment is lower for the rope data set ($r^2 = 0.046$; Table 2) and there is no discernible increase in numbers of spat with depth on the ropes in this treatment (Fig. 5). Secondly, the collectors caught more spat than the ropes (compare Figs. 4 & 5). An LSD multiple comparisons test on data pooled across all turbulence treatments in the rope data set (N.B. interaction effect was only slightly significant at $p = 0.03$) shows an increase in numbers of spat with depth (Fig. 5).

Effect of turbulence

Collectors

The log-transformed number of spat on the collectors varied significantly with turbulence treatment ($F = 8.31$, $df = 4, 10$, $p \leq 0.005$; Table 1A). As mentioned previously, there was no significant interaction between turbulence treatment and depth in the collector data set. An LSD multiple comparisons test on data pooled across all depths revealed that significantly more spat were collected in the Static Therm and Low Turb treatments than in the Static, Med Turb, and High Turb tubes, the latter 3 treatments not differing significantly from one another (Fig. 6). LSD tests on turbulence data at each depth showed the same general trend as with the pooled data

Table 2. *Placopecten magellanicus*. Coefficients of determination (r^2) and p-values for linear regressions of transformed numbers of spat on depth in each separate turbulence treatment for both the collector and rope data sets. Values of r^2 and p in brackets listed in Static Therm treatment represent those resulting from a regression with 1 high value in the surface collectors/ropes deleted from the analysis

Treatment	r^2	p-value
Collectors		
Static Therm	0.180 (0.458)	≤ 0.05 (≤ 0.0001)
Static	0.110	= 0.07
Low Turb	0.538	≤ 0.0001
Med Turb	0.058	= 0.20
High Turb	0.002	= 0.83
Ropes		
Static Therm	0.393 (0.520)	≤ 0.0005 (≤ 0.0001)
Static	0.046	= 0.28
Low Turb	0.471	≤ 0.0001
Med Turb	0.050	= 0.26
High Turb	0.039	= 0.33

(Fig. 6), as would be expected with a non-significant interaction term.

As mentioned in the 'Materials and methods', larvae grew at varying rates within the different turbulence treatments (S. M. Gallagher pers. obs.) which resulted in differences in larval sizes at the end of the experiment. A 1-way ANOVA on the untransformed larval size data revealed a highly significant effect of tube ($F = 30.64$, $df = 14, 1066$, $p \leq 0.0001$) with a subsequent Tukey test showing a number of significantly different pairwise comparisons (Fig. 7). Larvae in 1 of the Static tubes and in all 3 of the High Turb tubes were significantly smaller than in any of the other mesocosms. None of the other tubes were significantly different from one another. This difference in growth rate led to varying proportions of competent larvae (i.e. $\geq 230 \mu\text{m}$ shell length) among the turbulence treatments (1-way ANOVA on untransformed data: $F = 5.10$, $df = 4, 10$, $p \leq 0.05$; Fig. 8). The High Turb treatment had a smaller proportion of competent larvae than the 4 other treat-

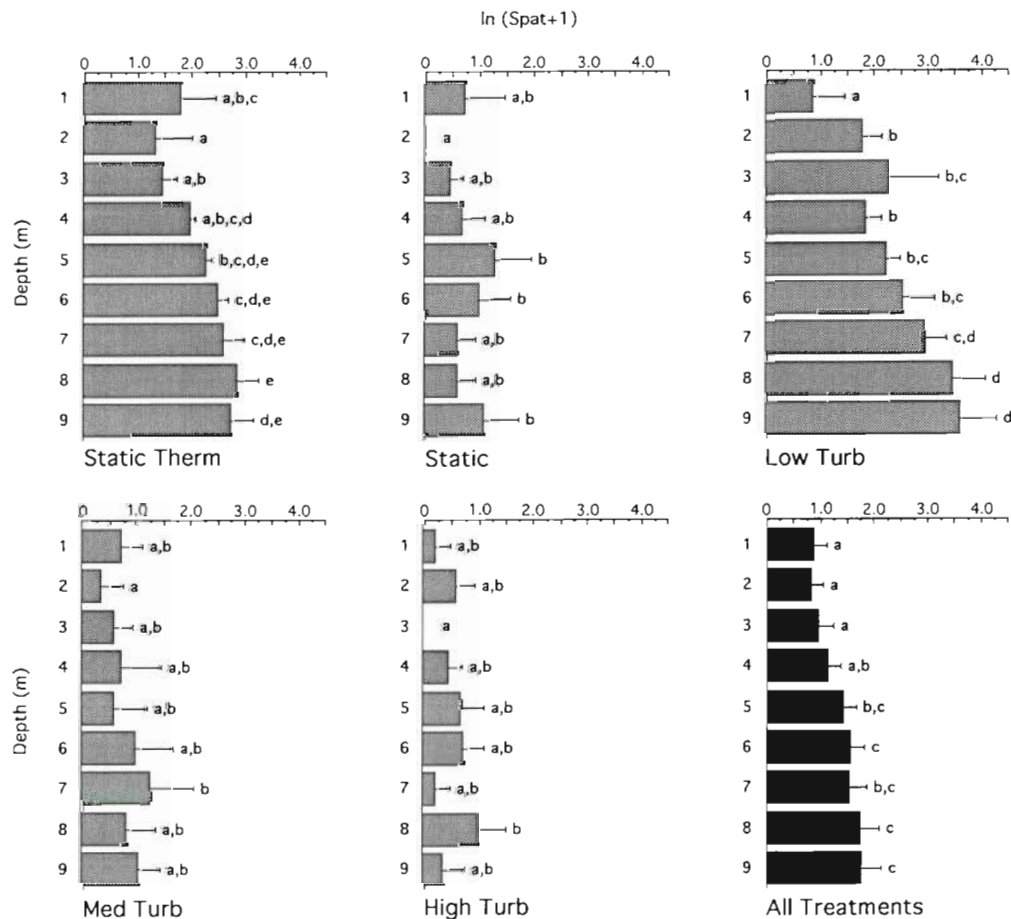


Fig. 5. *Placopecten magellanicus*. Depth profiles of log-transformed number of spat on ropes. Profiles are for the 5 separate turbulence treatments (i.e. Static Therm, Static, Low Turb, Med Turb, High Turb) as well as for the data pooled across all turbulence levels (i.e. All Treatments). Bars are the means of 3 (individual treatments) or 15 (all treatments) replicates and error bars are standard errors of the means. Letters by error bars represent the results of separate LSD tests examining the effect of depth within each turbulence treatment. Bars with the same letters within each profile are not significantly different (i.e. $p > 0.05$)

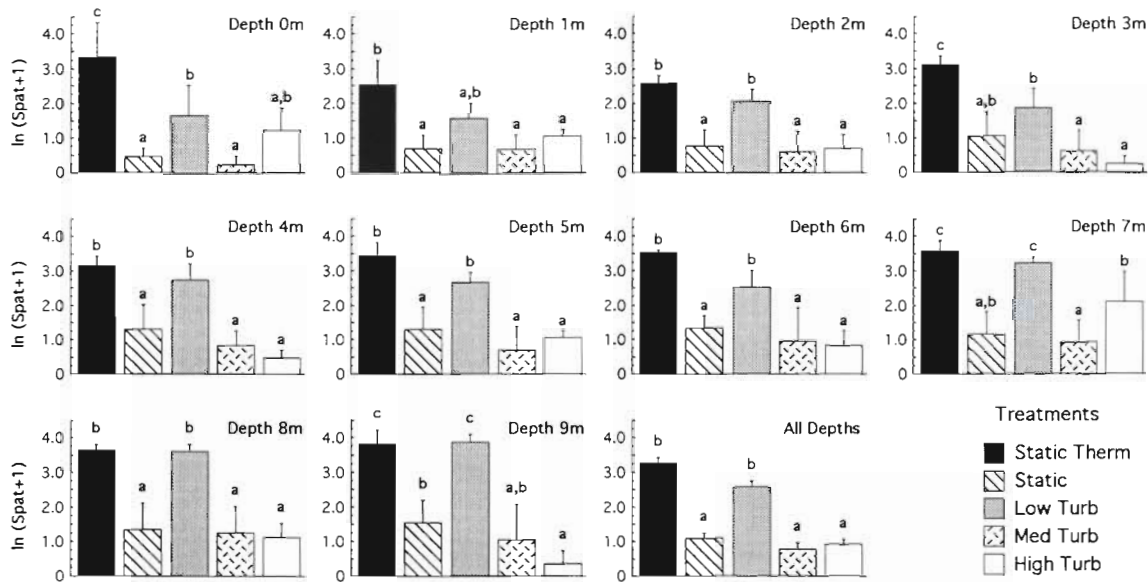


Fig. 6. *Placopecten magellanicus*. Log-transformed number of spat on collectors in the 5 turbulence treatments at each depth. Data pooled across all depths is shown in the last graph labeled 'All Depths'. Bars are the means of 3 (individual depths) or 30 (all depths) replicates and error bars are standard errors of the means. Letters above error bars represent the results of separate LSD tests examining the effect of turbulence treatment within each depth (or depths pooled). Bars with the same letters within each graph are not significantly different (i.e. $p > 0.05$)

ments—significantly smaller than the Low Turb and Med Turb treatments (Tukey analysis: $p \leq 0.05$). No other pairwise comparisons were significantly different.

If the results in Fig. 6 are standardized for the varying proportions of competent larvae, we see only a slight change in the interpretation of the results. For spat on collectors, the effect of turbulence treatment remains highly significant ($F = 7.35$, $df = 4, 10$, $p \leq 0.005$; Table 1A) and not dependent on the interaction with depth ($F = 1.33$, $df = 36, 90$, $p = 0.14$; Table 1A). An LSD multiple comparisons test on the data pooled across all depths revealed only 1 change in pairwise comparisons from the unstandardized data: the High Turb treatment was no longer significantly different from the Low Turb treatment (Fig. 9A). All other pairwise comparisons remained the same as for the unstandardized spat counts.

Ropes

The log-transformed number of spat on the ropes also varied significantly with turbulence treatment ($F = 6.10$, $df = 4, 10$, $p \leq 0.01$; Table 1B). As mentioned previously, there was a marginally significant interaction (i.e.

$p = 0.03$) between turbulence treatment and depth in the rope data set. LSD tests performed on turbulence data at each depth interval revealed, for the most part, a similar trend as seen with the collector data (Fig. 10). Significantly greater numbers of spat were collected in the Static Therm and Low Turb treatments than in the Static, Med Turb, and High Turb treatments at depths of 4, 5, 6, 7, 8, and 9 m. Greater numbers of spat were

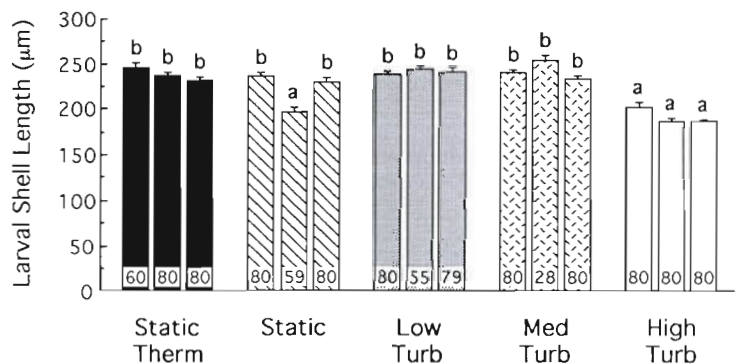


Fig. 7. *Placopecten magellanicus*. Shell lengths of larvae in each of the 3 replicate tubes of the 5 turbulence treatments. Bars are the means of 28 to 80 measurements (dependent on tube; see number at the bottom of each bar) and error bars are standard errors of the means. Letters above error bars represent the results of a Tukey test examining the effect of tube. Bars with the same letters are not significantly different (i.e. $p > 0.05$)

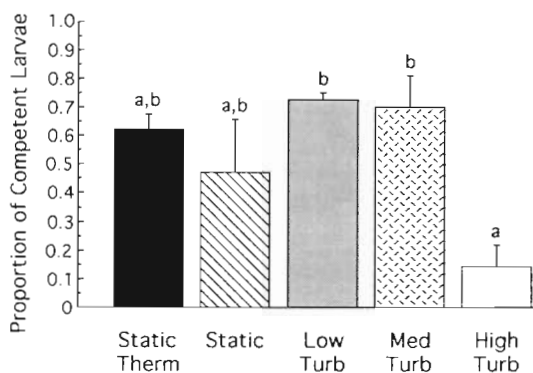


Fig. 8. *Placopecten magellanicus*. Proportion of larvae that were $\geq 230 \mu\text{m}$ in shell length and deemed to be competent in the 5 turbulence treatments. Bars are the means of 3 replicates and error bars are standard errors of the means. Letters above error bars represent the results of a Tukey test examining the effect of turbulence treatment. Bars with the same letters are not significantly different (i.e. $p > 0.05$)

collected in the Static Therm and Low Turb treatments than in the other 3 treatments at depths of 2 and 3 m, but the differences between Static Therm and High Turb at 2 m and Static Therm and Med Turb at 3 m were not significant. At a depth of 1 m, Static Therm had significantly more spat than any of the other 4 treatments which did not differ significantly from one another. If the results are pooled across all depths, which could be justified with the marginally significant interaction term, the same pattern emerges—i.e. significantly greater numbers of spat collected in the Static Therm and Low Turb tubes than in the Static, Med Turb, and High Turb tubes with no significant differences between the former 2 treatments and the latter 3 treatments (Fig. 10).

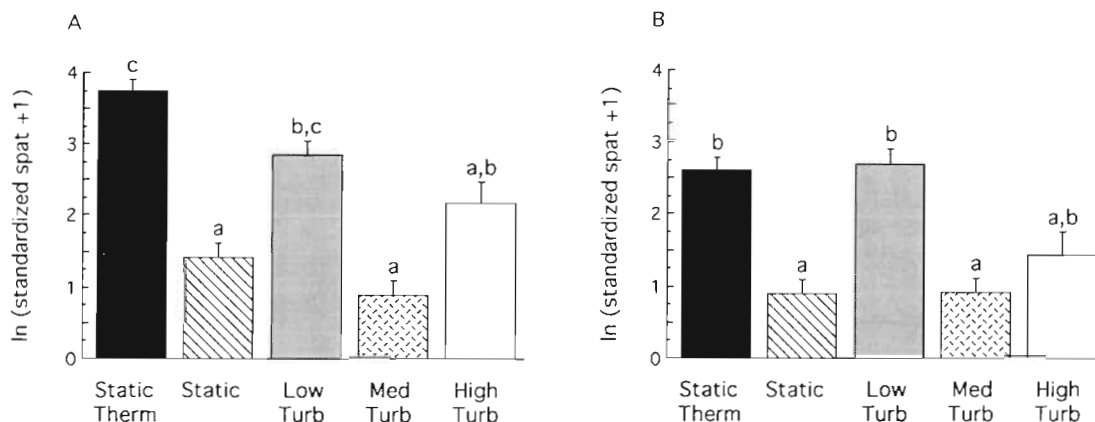


Fig. 9. *Placopecten magellanicus*. Log-transformed number of standardized spat (i.e. numbers of spat were standardized among treatments for differing levels of competency) on (A) collectors and (B) ropes in the 5 turbulence treatments. Bars are the means of 30 (A) or 27 (B) replicates and error bars are standard errors of the means. Letters above error bars represent the results of separate Tukey tests examining the effect of turbulence treatment within A and B. Bars with the same letters are not significantly different (i.e. $p > 0.05$)

Standardizing spat counts on the ropes for varying proportions of competent larvae across turbulence treatments only changes the results slightly. The effect of turbulence treatment is still significant ($F = 3.78$, $df = 4, 10$, $p = 0.04$; Table 1B), but the interaction between turbulence treatment and depth becomes non-significant ($F = 1.03$, $df = 32, 80$, $p = 0.44$; Table 1B). An LSD multiple comparisons test on the standardized data pooled across all depths revealed only 2 changes in pairwise comparisons from the unstandardized pooled data: the High Turb treatment was no longer significantly different from the Static Therm treatment or the Low Turb treatment (Fig. 9B). All other pairwise comparisons remained the same as for the unstandardized spat counts.

DISCUSSION

Effect of vertical mixing on depth of larval settlement

The depth distribution of spat on the collectors and ropes was a function of the intensity of vertical mixing or turbulence. Spat recruitment to collectors increased with increasing depth in the Static, Static Therm, and Low Turb treatments, but this trend became progressively disrupted as turbulence increased (i.e. spat were more evenly distributed with respect to depth in the Med Turb treatment and more randomly distributed in the High Turb treatment). In the collector data set, however, differences in spat depth distributions among the 5 different turbulence treatments were not sufficient to produce a significant depth/turbulence interaction in the nested analysis of variance (N.B. a slight increase in numbers of spat with collector depth was

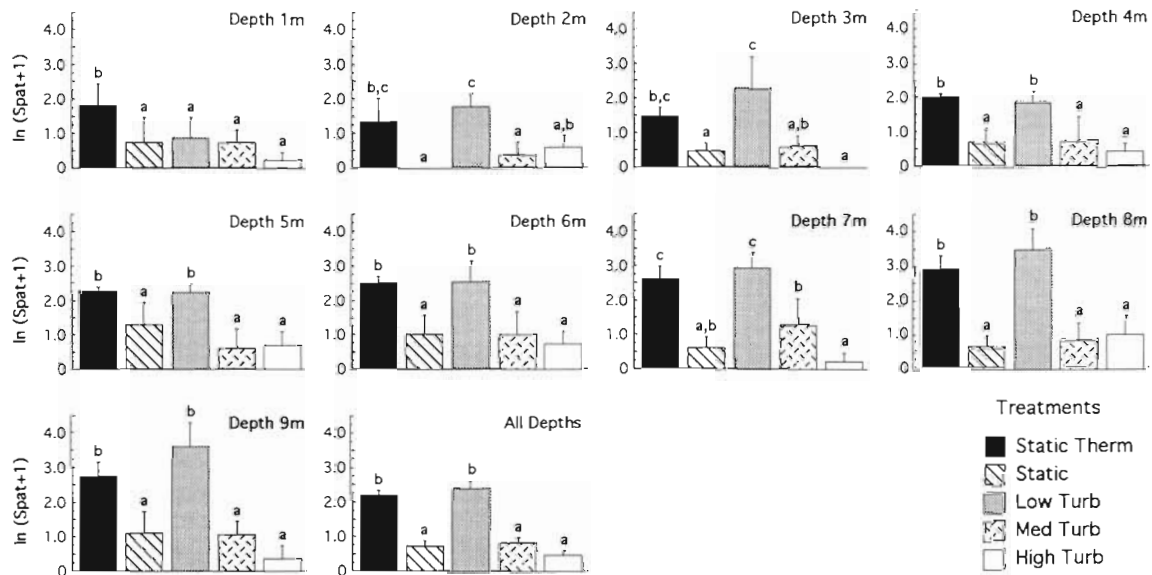


Fig. 10. *Placopecten magellanicus*. Log-transformed number of spat on ropes in the 5 turbulence treatments at each depth. Data pooled across all depths is shown in the last graph labeled 'All Depths'. Bars are the means of 3 (individual depths) or 27 (all depths) replicates and error bars are standard errors of the means. Letters above error bars represent the results of separate LSD tests examining the effect of turbulence treatment within each depth (or depths pooled). Bars with the same letters within each graph are not significantly different (i.e. $p > 0.05$)

still evident in the Med Turb treatment even though there was no significant pairwise comparisons among depths and r^2 was only 0.058; Fig. 4).

Similarly, spat recruitment on the mooring ropes increased with increasing depth in the Static Therm and Low Turb treatments, with progressive disruption of this trend as turbulence increased in the Med Turb and High Turb mesocosms. However, numbers of spat on the ropes in the Static treatment did not increase with depth as they did on the collectors. The reason for this is not entirely clear. Since collectors and ropes were hauled out of the water column at the end of the experiment, more spat were likely to be lost on the deeper collecting surfaces as these passed through the greatest length of water column and were exposed to the longest periods of physical agitation during the sampling procedure. Spat may have been more easily lost from the rope surfaces than the more heterogeneous collectors which were filled with a tangle of monofilament (N.B. although the mesh size of the collectors was not small enough to retain loose spat, the entanglement of monofilament would be expected to entrap dislodged individuals). If a trend of increasing spat recruitment with depth had been established on the ropes in the Static treatment, it probably would have been relatively weak (compare Static depth distribution with those in Static Therm and Low Turb treatments in the collector data set), and may have been disrupted by the sampling process. If deeper collecting surfaces did lose more spat than shallower sur-

faces, then trends of increasing spat numbers with increasing depth will tend to be underestimated in all turbulence treatments in both data sets. The relatively weaker linear relationship of spat with depth in the Static treatments of both collector and rope data sets, as compared to the Static Therm and Low Turb treatments, may be due to lower numbers of recruiting spat (see 'Effect of turbulence on spat recruitment' section below).

Factors controlling vertical spat distributions: evidence for larval behaviour and physical water-column mechanisms

Larval behaviour

Field studies that have examined the recruitment of pectinids to artificial collectors placed at various depths in the water column have generally found that spat collection is greatest in mid-water (Brand et al. 1980, Hortle & Cropp 1987, Sause et al. 1987, Sumpton et al. 1990, Margus 1991, Burnell et al. 1995) or closer to the sea floor (Mason 1969, Ventilla 1977, Buestel et al. 1979, Naidu & Scaplen 1979, Wallace 1982, Fraser 1983, Ruiz-Verdugo & Cáceres-Martínez 1991, Thouzeau 1991, Ambrose et al. 1992, Young et al. 1992, 1995, Harvey et al. 1993, Peña et al. 1995). Recruitment to collectors very close to the sea floor can be reduced, however, due to the effects of siltation (Naidu &

Brand et al. (1980) reported lower recruitment of the scallops *Chlamys opercularis* and *Pecten maximus* in

What is most plausible for the present study, then, is that larval behaviour at settlement was primarily responsible for the increase in recruitment with depth in the Static Therm, Static, and Low Turb treatments. Giant scallop larvae have been shown to undertake diel vertical migrations both in laboratory mesocosms (Silva-Serra & O'Dor 1988, Silva-Serra 1995, Gallagher et al. 1996, Manuel et al. 1996b) and in the field (Trem-

[illegible]

blay & Sinclair 1990b), indicating that depth regulation can be behaviourally controlled. Like many other larval invertebrates, giant scallop larvae are generally distributed lower in the water column as they approach competency (Culliney 1974, Gallagher et al. 1996)—a behaviour probably associated with a substratum-searching phase as the larvae attain metamorphic competency. Greater larval abundance with depth, as competency approaches, has been demonstrated in other species of pectinids as well, including *Patinopecten yessoensis* (Maru et al. 1973) and *Pecten maximus* (Cragg 1980, Mason 1983), and may be associated with larval behaviours such as positive geotaxis and/or negative photokinesis (Kaartvedt et al. 1987, Gallagher et al. 1996). Two other pieces of evidence suggest that larval settlement depth may be determined by active larval choice under conditions of limited vertical mixing. Firstly, under static mesocosm conditions, competent giant scallop larvae can vertically migrate and are not limited to a strictly benthic existence (Manuel 1996). Secondly, settlement depth can be affected by sufficiently strong vertical stratification and spat numbers may not increase positively with depth under such conditions (Pearce et al. 1996). Although giant scallop larvae are negatively buoyant and will sink if ciliary beating is arrested, a trend of increasing spat numbers with increasing depth may not be simply a function of larvae passively sinking to the bottom and being unable to choose among depths.

Vertical mixing

While depth of larval settlement and spat recruitment may be determined by larval behaviour under static or low turbulence conditions (i.e. $\epsilon \leq 10^{-7}$ to $10^{-5} \text{ cm}^2 \text{ s}^{-3}$), it also appears to be affected by physical processes such as vertical mixing at higher levels of turbulence (i.e. $\epsilon \geq 10^{-4}$ to $10^{-3} \text{ cm}^2 \text{ s}^{-3}$). Spat in the Med Turb and High Turb treatments were more evenly or randomly distributed with depth than in the static or low turbulence treatments, suggesting that competent larvae may have been suspended in the water column, forcing settlement to occur at depths that larvae may not have actively chosen under less turbulent conditions. Although competent giant scallop larvae can delay metamorphosis for at least 1 mo (Culliney 1974), and could potentially choose not to settle on shallower collectors, prolonged periods of vertical mixing and suspension of larvae will force individuals that can no longer delay metamorphosis to settle at their given depth provided an appropriate settlement surface exists. It is not known what may happen to suspended scallop larvae that can no longer delay metamorphosis and that do not contact a suitable settlement substra-

tum. They may spontaneously metamorphose in the water column or perish. In the field, spat recruitment to near-surface collectors under suitably intense conditions of vertical mixing—where larvae are suspended in the upper water column—may be reduced due to factors discussed previously such as fouling of surface collectors by macroalgae, effects of turbulence and wave action near the surface, low salinity surface water, and/or predation by recently settled predators such as starfish.

Very little field research has examined the effects of vertical mixing on depth of larval scallop settlement, but what little information is available suggests that vertical mixing can, indeed, affect spat depth distributions. Ruzzante & Zaixso (1985), for instance, suggested that the lack of an optimum settlement depth of *Chlamys tehuatlensis* on artificial collectors in the San José Gulf, Argentina, may have been due to variable conditions in the water column such as high tidal range and shallow depths. In Bass Strait, Australia, Young et al. (1992) found that *Pecten fumatus* showed a trend of greater settlement in deeper spat bags early in the settling season, but noted that this trend became much more variable later in the settlement period. This change in spat depth distribution as the settlement season progressed may have been linked to changes in hydrographic conditions within the water column, although the authors did not test this hypothesis. The highest intensity of turbulence used in the present experiment ($\sim 10^{-3} \text{ cm}^2 \text{ s}^{-3}$) is representative of weaker intensities found in coastal and shelf regions, but is 2 to 3 orders of magnitude lower than those that can typically occur in high energy zones such as fronts. In such areas of extreme, prolonged vertical mixing, larval settlement may be expected to be relatively random with respect to depth.

Vertical stratification

As noted previously, strong vertical stratification can also influence the depth of larval scallop settlement. In a subsequent Tower Tank experiment, giant scallop larvae, spawned from Georges Bank stock, settled primarily above a 5°C thermocline established at a depth of 5 to 6 m in 9 m deep mesocosms (Pearce 1996). Similarly, larvae spawned from a Newfoundland population settled predominantly at or above an 11°C thermocline established at a depth of 4 to 5 m in 9 m deep mesocosms (Pearce et al. 1996). It has been hypothesized that larval settlement may be enhanced in areas where vertical discontinuities or fronts intersect with the sea floor and that recruitment in such habitats would be beneficial due to elevated food levels and/or temperatures resulting in increased post-settlement

growth rates (Pearce et al. 1996). Field evidence for such recruitment patterns was presented by Walossek (1991) who found large aggregations of *Chlamys patagonica* on the Argentinean shelf in a zone coinciding with the boundary of the summer thermocline, a region characterized by high productivity.

In the present study, there was no indication of increased settlement of Georges Bank larvae at or above the 0.5 to 1.5°C thermoclines established in the Med Turb, Low Turb, or Static Therm treatments (Figs. 4 & 5), suggesting that a critical level of stratification intensity must be achieved before larvae begin to settle at or above a vertical discontinuity. Results from several Tower Tank studies suggest that, for a strict thermal gradient in a 9 m deep water column, this critical threshold of temperature stratification would be $>1.5^{\circ}\text{C m}^{-1}$, but $\leq 5.0^{\circ}\text{C m}^{-1}$ for Georges Bank larvae. It is unknown whether giant scallop larvae react to temperature per se or to other physical properties which change with variations in temperature such as density and viscosity (see discussions in Gallagher et al. 1996, Manuel 1996). Also unknown is the effect of haloclines on the planktonic distribution of larval giant scallops. Salinity gradients have been shown to affect the vertical distribution of larvae of other species of bivalves (Carrier 1951, Feeny 1984, Mann et al. 1991) and it is plausible that giant scallop larvae are affected by an interaction of temperature and salinity and/or the associated changes in density and/or viscosity. Critical thresholds of thermal stratification may be lower than predicted if larvae react to changes in salinity, density, and/or viscosity rather than temperature alone. Further research is required in order to determine what physical variables giant scallop larvae are affected by and the response of larvae to combined salinity/temperature gradients.

Critical thresholds of vertical stratification at which larvae settle at or above the discontinuity may also be lower in a deeper water column. For instance, Tremblay & Sinclair (1988) found that in the Bay of Fundy, New Brunswick, Canada, peaks in larval giant scallop concentration were associated with thermoclines with temperature differences of only 1.0 to 2.5°C over a vertical distance of 20 m or a temperature gradient of only 0.050 to 0.125°C m⁻¹ (N.B. the authors did not measure changes in salinity or density). In our 9.5 m deep Tower Tank studies, giant scallop larvae from Georges Bank have been found to aggregate at thermoclines as small as 0.8°C m⁻¹, but do not appear responsive to gradients less than this (Manuel 1996). That pelagic larvae are affected by thermal gradients of 1.5°C while settling larvae are not suggests an ontogenetic shift in gradient sensitivity and/or behavioural response.

In addition, there is also the possibility that critical thresholds may be dependent on larval population.

Larvae from Georges Bank, Passamaquoddy Bay (New Brunswick), and Mahone Bay (Nova Scotia) show dissimilarities in their vertical migration behaviour in laboratory mesocosms (Manuel et al. 1996b) which may be linked to genetic differences (Manuel et al. 1996a). While larvae from these 3 populations show similar settlement depth distributions in 9.5 m deep mesocosms with a 1.5°C thermocline established at a depth of 4 to 5 m (i.e. increase in settlement with depth with no peak at the thermocline; Pearce 1996), the possibility that differences in critical thresholds exist among the 3 populations cannot be entirely discounted.

For field collection of scallop spat in areas of relatively high stratification, Pearce et al. (1996) concluded that it may be most beneficial to place spat collectors within or around the layer of discontinuity instead of nearer the sea floor where settlement might be assumed to be greater, based on the general behaviour of competent larvae. The present study suggests that the degree of stratification will have an effect on the depth of settlement and that depth of placement of spat bags in the water column should take into account stratification intensity and vertical mixing. If stratification intensity is high, maximum recruitment may be expected at or above the discontinuity. However, under conditions of weak stratification and limited vertical mixing, spat collection should be greatest nearer the sea floor. In areas of intense turbulence spat may be collected throughout the water column if mixing conditions are prolonged or preferentially in deeper collectors if mixing is intermittent. Differences in published accounts of pectinid settlement depth (i.e. mid-water versus closer to the sea floor; see previous references) could be, at least partially, due to variations in water-column stratification intensity.

It should be noted that conditions on Georges Bank do exist where thermal stratification could influence depth of larval settlement. Tremblay & Sinclair (1990a) measured vertical stratification intensities at various locations in the northeastern portion of the bank in October 1986 and 1987, when planktonic scallop larvae were present, and found some frontal zone areas where temperature dropped by as much as 5°C (from 12.5 to 7.5°C) in the upper 40 m of the water column.

Effect of turbulence on spat recruitment

The number of spat found on both the collectors and ropes was significantly greater in the Static Therm and Low Turb tubes than in the Static, Med Turb, or High Turb treatments when results were not standardized for varying levels of competency among tubes. However, larvae grew at varying rates, dependent on the

turbulence treatment, and this led to differing levels of competency among the tubes. Only 27.5, 13.8, and 2.5 % of the larvae measured at the end of the experiment from the 3 replicate tubes of the High Turb treatment were deemed to be competent (i.e. $\geq 230 \mu\text{m}$ shell length). This was in sharp contrast to most other tubes in the other turbulence treatments that had from 50 to 70 % competency (N.B. one replicate tube of the Static treatment was an exception with only 11.9 % larvae $\geq 230 \mu\text{m}$ in shell length). Adjusting spat numbers for varying levels of larval competency among the tubes had a slight effect on the overall comparisons among turbulence treatments. The Static Therm and Low Turb treatments still remained greater than the Static, Med Turb, and High Turb treatments, but pairwise comparisons between Low Turb and High Turb in both data sets and Static Therm and High Turb in the rope data set became non-significant when results were standardized for competency differences. These results suggest that settlement rate may not be a simple function of larval encounter rate with the collectors as more spat were collected in the Static Therm tubes than in the Med or High Turb treatments.

It is interesting to note that the number of recruited spat was greatest in the treatments with the strongest thermoclines (i.e. Static Therm and Low Turb). This treatment effect could be due to several factors, working alone or in combination, including: (1) reduction of larval settlement and/or post-settlement survival in higher turbulence treatments as a result of negative effects of microalgal films, (2) differences in larval growth rates among the various turbulence treatments, (3) increased spat dislodgment with increased turbulence, and/or (4) increased larval survivorship due to thermal gradients in stratified treatments. Since visible films of microalgae were most developed on collectors and ropes in the Med Turb and High Turb tubes (Table 3), lower spat recruitment in those treatments could have been due to potential negative effects of these films leading to lower rates of larval settlement and/or increased post-settlement mortality. Inhibition of larval settlement by certain strains of bacteria has been shown for the bay scallop *Argopecten irradians* (Xu et al. 1991), but no research has been conducted with *Placopecten magellanicus* on settlement inhibition by biofilms. Since the diatom film was equally well developed in both the Static and Low Turb treatments, but the latter collected more spat than the former, microalgal filming of settlement substrata cannot be the sole factor responsible for the differences in spat recruitment among the turbulence treatments.

The low spat recruitment in the High Turb treatment was, at least partially, due to reduced larval growth. At the end of the experiment only High Turb tubes had planktonic larvae (albeit very few) still evident in video

profiles of the water column. Veligers in the High Turb tubes were significantly smaller than those in the other turbulence treatments leading to a smaller percentage of larvae being competent to metamorphose. Standardizing for larval competency among the turbulence treatments increased potential spat numbers in the High Turb tubes and reduced the pairwise differences between Static Therm and High Turb as well as Low Turb and High Turb treatments (compare Figs. 6 & 10 with Fig. 9). However, even with using standardized spat values, the High Turb tubes still had fewer potential recruited spat than the Static Therm and Low Turb treatments in both the collector and rope data sets—significantly fewer when compared with the Static Therm treatment in the collector data set. It should be noted that spat recruitment in the High Turb treatment may have been greater if the experiment had been continued to allow all larvae in these tubes to settle, although the probability of survival through metamorphosis of slow-growing veligers, as compared to faster-growing individuals, is not known. In the field, however, a prolonged planktonic developmental period would most likely lead to reduced recruitment rates as a result of greater larval losses due to predation and potential advection away from suitable settlement sites. Thus, it might be expected that recruitment of larvae entrained in highly turbulent areas such as upwelling and downwelling zones, mixing fronts, and coastal mixing zones would be reduced in comparison to that of larvae undergoing development in stratified, calmer waters. Reduced larval growth rate may also be partially responsible for lower spat recruitment in the Static treatment as one of the Static tubes had significantly smaller larvae than those in the Static Therm, Low Turb, and Med Turb treatments. Possible reasons for differences in larval growth rates among the replicate Static tubes are not evident, but must be linked with some tube effect. Interestingly, larvae grew best in the Med Turb treatment (S. M. Gallagher pers. obs.) indicating that differences in larval growth rate can only partially explain differences in spat recruitment among the various turbulence treatments.

Brand et al. (1980) suggested that reduced spat recruitment of the scallops *Chlamys opercularis* and *Pecten maximus* in surface spat collectors in the field may have been a result of increased turbulence near the surface which may have reduced post-settlement survival. In the present experiment, spat could have been dislodged from collectors and ropes by the bubbling action in the turbulence treatments. Obviously, the intensity of turbulence in the Low Turb tubes was not sufficient to significantly impact on recruitment in this manner, but turbulence intensities in the Med Turb and High Turb tubes may have been great enough to dislodge settled individuals. However, the

relatively low rate of recruitment in the Static treatment, which was not subjected to mixing, suggests that dislodging of settled spat by turbulence was not the sole factor responsible for differences in spat recruitment among the turbulence treatments.

Thermoclines may increase larval survivorship—and, hence, numbers of competent larvae available for settlement—by creating a barrier between the larvae and the bottom of the tubes, which may be a rather inhospitable environment for veligers due to accumulations of debris, detritus, bacteria, and protozoans. Young larvae in the Static Therm and Low Turb tubes were predominantly distributed above the thermal gradient and undertook diel vertical migrations between the surface and thermocline. Larvae in the Static treatment, however, were scattered throughout the water column during daylight hours and concentrated near the surface at night, while larvae in the Med Turb treatment were distributed throughout the water column during both day and night (S. M. Gallagher pers. obs.). Thus, veligers in the Static Therm and Low Turb treatments remained out of the debris, detritus, bacteria, and protozoans that may have accumulated at the bottom of the tubes while those in the Static and Med Turb treatments made excursions, or were mixed, into this potentially deleterious bottom environment. Exposure to these detrimental conditions most likely reduced larval survivorship in the Static and Med Turb treatments and, thus, total larvae available for settlement.

Counts of 28- and 29-d-old planktonic larvae taken throughout the water column in each replicate tube of

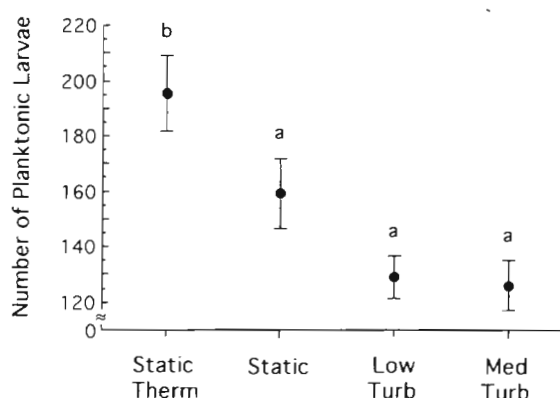


Fig. 11. *Placopecten magellanicus*. Number of larvae in the water column at age 28 to 29 d in 4 of the 5 turbulence treatments (High Turb excluded) as visualized by the Polarized Larval Recorder (PLR). Values are the means of 25 (Static, Low Turb, Med Turb) or 26 (Static Therm) profiles taken from the 3 replicate tubes over a period of 22 h and error bars represent the results of a Tukey test examining the effect of turbulence treatment. Values with the same letters are not significantly different (i.e. $p > 0.05$)

each treatment using the PLR give some indication of decreased larval survivorship in the Static and Med Turb tubes in comparison with the Static Therm tubes (Fig. 11). From a series of profiles taken over 22 h in each tube, significantly more planktonic larvae were counted in the Static Therm tubes than in the Static, Low Turb, or Med Turb treatments (1-way ANOVA on log-transformed data: $F = 11.44$, $df = 3, 65$, $p \leq 0.0001$; Tukey analysis: $p \leq 0.05$). Data retrieval from the High Turb videotapes was hindered by air bubbles, so the results for this treatment were not included in the analysis. No significant difference in numbers of larvae was evident between the Low Turb tubes and the Static Therm and Med Turb treatments, however, indicating that it is not larval survivorship alone creating differences in spat collection among treatments. Interestingly, young veligers in the High Turb tubes primarily concentrated near the surface (S. M. Gallagher pers. obs.). Thus, low spat recruitment in this treatment was more likely due to reduced larval growth rates and/or lowered settlement rates/increased spat mortality due to microalgal films (see discussions above) than to decreased survivorship due to larval mixing into inhospitable bottom environments, although the latter possibility cannot be entirely discounted.

Other larval studies have alluded to the importance of larval distributions, with respect to the bottom of rearing vessels, in determining larval survivorship. Culliney et al. (1975), for instance, noted that it is beneficial to use relatively tall vessels for rearing larvae of *Placopecten magellanicus*. They remarked that, in greater water depths, veligers could remain well above the bottom of the containers where accumulations of debris, faeces, pseudofaeces, and protozoa led to deleterious conditions for the larvae. Barker (1978) reared larvae of the asteroids *Stichaster australis* and *Coscina nasterias calamaria* under stirred conditions and remarked that water movements prevented larvae from concentrating on the bottoms of rearing containers where they were at higher risk of bacterial infection. The use of thermal gradients as a barrier to prevent larvae from mixing with the bottom of static rearing vessels may be of commercial importance to larval hatcheries aiming to increase larval survivorship and juvenile recruitment.

CONCLUSIONS

Many studies have examined pectinid recruitment in the field on artificial collectors placed in the water column. Most of these have focused on the temporal and spatial variations in spatfall and how to maximize spat collection by varying the quality and quantity of collector materials. Very little scientific research has

examined how physical factors in the water column, such as thermoclines and degree of turbulence, affect depth of larval settlement and spat recruitment. Results from this mesocosm study showed that, under conditions of limited vertical mixing and weak or no thermal stratification ($\epsilon = 10^{-7}$ to $10^{-5} \text{ cm}^2 \text{ s}^{-3}$), spat recruitment generally increased with increasing depth, a pattern most likely established by planktonic larval behaviour at settlement. Increasing levels of turbulence disrupted this pattern so that spat recruitment in tubes with the highest turbulence ($\epsilon = 10^{-4}$ to $10^{-3} \text{ cm}^2 \text{ s}^{-3}$) was random with respect to depth. There was no increase in recruitment at or above the 0.5 to 1.5°C thermoclines established in this study as was shown in a previous paper by Pearce et al. (1996) for a thermocline of 11.0°C. Results from the present study and subsequent experiments indicate that a critical level of stratification must be attained before larvae settle at or above a vertical discontinuity. To optimize the field collection of spat, either for scientific or commercial purposes, a broad knowledge of the physical oceanographic features of the system are required. In highly stratified regions, maximum recruitment may be expected at or above the discontinuity as discussed in Pearce et al. (1996), while in weakly stratified zones with limited vertical mixing, spat collection should be enhanced by the placement of collectors at greater depths. In areas of high turbulence, spat may be collected throughout the water column if mixing conditions are prolonged or in deeper collectors if mixing is intermittent.

Results of this experiment showed that total spat recruitment was also dependent on the degree of vertical mixing. The greatest recruitment occurred in the 2 treatments with the largest thermal gradients and may have been, at least partially, the result of increased larval survivorship in these treatments. It is hypothesized that thermoclines may act as a barrier to larvae, keeping them off the bottoms of their rearing containers and out of potentially deleterious environments containing debris, detritus, faeces, bacteria, and protozoans. Further research is required to more closely examine vertical distribution of larvae, larval survivorship, and larval settlement rates under various conditions of thermal stratification to fully understand the mechanism(s) by which recruitment may be increased under thermally stratified regimes. The effect of thermal gradients on the recruitment of spat could be extremely beneficial for scallop hatchery facilities concerned with optimizing larval survivorship and juvenile recruitment.

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