

# Heat waves, baby booms, and the destruction of kelp beds by sea urchins

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## Abstract

Large populations of sea urchins, *Strongylocentrotus droebachiensis* (Müller), destroyed kelp beds along the Atlantic coast of Nova Scotia in the 1960's and 1970's. The origin of these large sea urchin populations is not understood. We have investigated the potential influence of variable growth and development of the planktonic larvae of sea urchins (in response to temperature and food abundance) on recruitment of benthic juveniles. The adult sea urchins were collected at Sandy Cove, Digby County, Nova Scotia, Canada, in December 1986. Temperature strongly affected larval size and the growth of the echinus rudiment within the range 3° to 9°C, and larvae grew most rapidly at 14°C. Food abundance had a smaller effect on larval growth, and these effects were apparent only at high temperature. Larvae fed the same concentration of two different algal food species grew and developed similarly. Correspondence between spring temperature variation and qualitative variation in sea urchin recruitment, as well as strong temperature effects on larval growth in culture, and the occurrence of a large, positive temperature anomaly in June 1960, all suggest that temperature effects on larval growth and development may have led to intense sea urchin recruitment in 1960 and the appearance of large adult populations 4 to 6 yr later. This result invites further research.

## Introduction

Grazing by sea urchins influences both the extent and composition of kelp communities in many parts of the world (Lawrence 1975, Lawrence and Sammarco 1982, Chapman 1986). Sea urchins in sufficient numbers can denude large areas of all fleshy macroalgae, and prevent the recoloniza-

tion of these areas by grazing (e.g. North and Pearse 1970, Breen and Mann 1976b, Hagen 1983). Along the Atlantic coast of Nova Scotia, Canada, sea urchin-dominated barren grounds may persist until sea urchin populations are decimated by disease (Miller and Colodey 1983, Scheibling 1984, Scheibling and Stephenson 1984). In the absence of sea urchins, kelp beds recover quickly from the effects of destructive grazing (Scheibling 1986).

The factors that control (or fail to control) the size of adult sea urchin populations are poorly understood (see Lawrence 1975). Mann and his co-workers argued in a series of papers (Mann and Breen 1972, Breen and Mann, 1976a, b, Evans and Mann 1977, Mann 1977, 1982, Wharton and Mann 1981) that reduction of predation pressure on sea urchin (*Strongylocentrotus droebachiensis*) populations through overfishing of lobster (*Homarus americanus*) stocks off Nova Scotia allowed sea urchin populations to grow unchecked, resulting in the destruction of kelp beds. Others have argued strongly against this predator hypothesis (Elner 1980, Miller 1985a, Vadas et al. 1986). Mann (1985) recently concluded that predation is probably not the most important factor regulating sea urchin abundance in Nova Scotia.

Recruitment rates of planktonic larvae may have a large effect on the size of benthic sea urchin populations. Camp et al. (1973) suggest that aggregations of *Lytechinus variegatus* which destroyed seagrass beds off the Gulf coast of Florida, USA, in 1971 were composed of a single, massive cohort of larvae which settled together in 1970. Ebert (1983) has reviewed the episodic nature of sea urchin recruitment patterns. Mann (1985) and Scheibling (1986) have suggested that the intensity of recruitment of larval *Strongylocentrotus droebachiensis* may determine the rate of growth of sea urchin populations off Nova Scotia.

Thorson (1950) emphasized the importance of water temperature and food abundance to the growth of marine invertebrate larvae, and suggested how suboptimal levels of these factors might extend larval development and increase predation pressure on larval populations. Echinoplutei have higher rates of growth, development, and metabolism at

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high temperature (McEdward 1985). Stephens (1972) found that *Strongylocentrotus droebachiensis* embryos and larvae failed to develop above a critical temperature of ca. 10°C, and suggested that this might account for the limited southward extent of benthic *S. droebachiensis* populations in the northwest Atlantic.

Evidence for food limitation of growth and development of larval echinoderms is more equivocal. Fenaux et al. (1985) showed that the abundance of a cultured alga in vitro limited the growth of larval *Paracentrotus lividus*. Lucas (1982) demonstrated a similar effect for brachiolaria larvae of the crown-of-thorns starfish *Acanthaster planci*. Paulay et al. (1985) found that the development of juvenile structures of the sand dollar *Dendraster excentricus* could be delayed or enhanced by the manipulation of naturally-occurring phytoplankton fed to larvae in culture. In contrast, Roller and Stickle (1985) found no effect of cultured algal concentration on the length of larval *Strongylocentrotus droebachiensis*. Olson (1985, and unpublished data) has shown that *A. planci* larvae cultured in situ in shallow reef waters develop normally, and that growth is not appreciably hastened by the addition of cultured algal food. Olson's work argues against the role of larval food limitation in determining the abundance of benthic crown-of-thorns starfish (see Birkeland 1982).

Few attempts have been made to correlate conditions for larval growth with subsequent abundance of newly recruited echinoderms (Birkeland 1982, Ebert 1983). The present paper confirms the effects of temperature and algal food abundance on the larval growth and development of *Strongylocentrotus droebachiensis*. We have also found qualitative correlations between surface sea temperatures and recent recruitment of *S. droebachiensis* off the Atlantic coast of Nova Scotia. These congruent results suggest a causal mechanism that may explain large-scale changes in the abundance of sea urchins and in the structure of the near-shore community in which they live.

## Materials and methods

### Comparing algal food species at high temperature

Adult *Strongylocentrotus droebachiensis* were collected from a shallow subtidal population at Sandy Cove, Digby Co., Nova Scotia, Canada, in winter 1987 and held in flowing seawater in the laboratory. The urchins were fed kelp (*Laminaria* sp.) at intervals of several weeks.

Gametes were obtained from these sea urchins by peristomial injection of 1 to 2 ml of 0.5 M KCl. Eggs from a single female were shed into chilled 0.45 µm Millipore filtered seawater, then washed and resuspended in 400 ml of filtered seawater. Concentrated sperm from three males was combined, and several drops of this mixture were used to fertilize eggs in suspension. Fertilization success (defined as the completion of the extraembryonic fertilization membrane) was 89% after 20 min.

Pre-feeding embryos were reared to the pluteus stage in six groups of several thousand each (to avoid crowding), in glass jars containing 3 l of filtered seawater, immersed in a flowing seawater bath. Gentle agitation was provided by a paddle stirrer similar to the one used by Strathmann (1971).

Four days after fertilization, pluteus larvae with well-developed postoral and anterolateral arms were removed from the embryo cultures and combined into a common pool. From this pool were drawn six groups of 200 larvae each, assigned at random to two treatments (with three replicates): fed 1 000 cells ml<sup>-1</sup> *Dunaliella tertiolecta* (a green flagellate) or *Chaetoceros gracilis* (a small diatom). Groups of larvae were reared in 2 l of filtered seawater in glass jars immersed in the same flowing seawater bath, with agitation provided by paddles as described above, and a combined ambient/fluorescent light regime of approximately 12 light : 12 darkness. Mean daily temperature ( $\pm 1$  standard deviation) was 14.2°C  $\pm$  2.1°C ( $n = 22$  d).

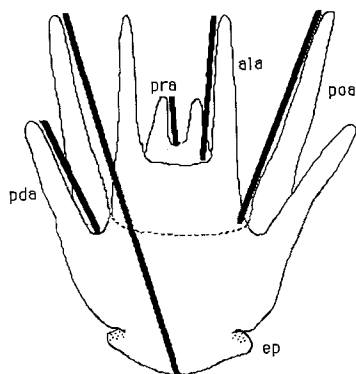
Algae were reared at room temperature under constant fluorescent illumination in Guillard's f/2 nutrient medium. Algal cells were removed from the nutrient medium by centrifugation and resuspended in filtered seawater before feeding them to sea urchin larvae. Algal cells in suspension were counted with a haemocytometer.

Water and algal food in the jars was replaced at 2-d intervals (exceptionally at 3-d intervals) by pouring off the water while retaining the larvae on a submerged nylon mesh filter. Filtered seawater and the appropriate amount of algal food was then added, and the larvae were returned to the jar by gently swirling the filter in the water.

A small number of larvae was removed from each jar by filtration onto a submerged nylon mesh, and placed by pipette into a Petri dish under a dissecting microscope. Ten to twelve larvae were removed from the Petri dish to a glass slide and mounted under a glass cover slip supported at each corner by a bit of plasticine (forming a shallow well). The remaining larvae were returned to the jar.

Mounted larvae were examined under a compound microscope at 100× magnification. Using an ocular micrometer, the following characters were measured on each larva: left and right postoral, anterolateral, posterodorsal, and preoral arm lengths (from the medial base to arm tip); left and right larval lengths (from the posterior end to the tips of the postoral arms); diameter of the echinus rudiment. The geometry of arm measurements is shown in Fig. 1.

Measurements were made on 10-, 15-, and 22-d-old larvae. Cultures were terminated when many larvae with large, well-developed echinus rudiments were observed: larvae were removed and counted, then set in a plastic Petri dish with 20 ml filtered seawater and 1 to 2 g of an encrusting coralline alga (*Lithothamnium glaciale*) which is known to induce settlement of competent *Strongylocentrotus droebachiensis* larvae (Raymond 1985). Settled larvae (attached to the algal or plastic substratum by podia of the juvenile sea urchin) were counted in each dish after 24 h. Survival was calculated as the proportion of larvae alive at the end of the experiment, out of the original number less those removed for growth measurements.



**Fig. 1.** *Strongylocentrotus droebachiensis*. Sketch (in dorsal view) of eight-arm pluteus larva. Bold lines show measurements made; broken line indicates transverse ciliated band between the postoral arms. Both left and right arm lengths and total length were measured. ala: anterolateral arms; ep: epaulettes; pda: posterodorsal arms; poa: postoral arms; pra: preoral arms

### Combined effect of temperature and food ration on growth and development of plutei

Spawning, rearing and sampling procedures were the same as those described above, with the following exceptions. Four males and four females were used to obtain embryos. Fertilization success was >95% for all females after 25 min. Embryos were reared in filtered seawater at 6°C in a controlled temperature chamber.

Seven-day-old plutei from the embryo cultures were combined into a common pool, and from this pool were drawn 18 groups of 250 larvae each. These groups were assigned at random to one of nine treatments (with two replicates): 3°, 6° or 9°C, fed 500, 1 000, or 5 000 cells ml<sup>-1</sup> of a 1 : 1 mixture of *Dunaliella tertiolecta* and *Chaetoceros gracilis*. These groups were reared as above in controlled temperature chambers under constant fluorescent illumination. Mean temperatures ( $\pm 1$  standard deviation) were 3.1°C  $\pm$  0.3°C, 6.1°C  $\pm$  0.2°C and 9.1°C  $\pm$  0.1°C, respectively ( $n = 39$  d).

Measurements were made on 13-, 19-, 24-, 29-, 34- and 39-d-old larvae. Some groups (at high temperature, fed large amounts of algae) developed and settled more quickly than others. Larvae reared at 9°C and fed 5 000 cells ml<sup>-1</sup> developed most rapidly, and these cultures were terminated after 29 d; larvae in two other treatments (9°C, 1 000 cells ml<sup>-1</sup>; 6°C, 5 000 cells ml<sup>-1</sup>) were terminated after 34 d.

Four groups of larvae were lost during the experiment. Unfortunately, these included both replicate groups reared at 6°C fed 1 000 cells ml<sup>-1</sup>. One of these replicates was lost due to unknown causes after 19 d. The second replicate from this treatment, as well as one replicate group fed 5 000 cells ml<sup>-1</sup> at 3°C were lost after 24 d. One group of larvae reared at 6°C fed 5 000 cells ml<sup>-1</sup> was lost after 29 d due to a handling error.

### Statistics and data analysis

Survival of groups of *Strongylocentrotus droebachiensis* larvae in different treatments were compared using Chi-square

contingency table analysis by pooling observations across replicate jars within food or temperature treatments. For the 2  $\times$  2 contingency table (comparing survival of larvae fed different algal food species), Yates' correction for one degree of freedom was used (Zar 1974). Temperature and food effects on larval survival in the second experiment were analysed separately by pooling across temperatures for the food comparison, and vice versa. Normally, log-linear analysis of a 3-way contingency table (temperature by food by survival) would be in order, but the loss of four groups of larvae from the original 18 (including both replicates from one treatment) made this analysis problematical.

Echinus rudiment diameter, larval length (using the longer of the two measures for each individual), and total arm length (summed over all arm pairs) were analysed by one- or two-way nested analysis of variance (ANOVA), with replicate jars nested within treatments. Analysis of variance was preceded by Bartlett's *F*-test for non-homogeneous variances among treatments. Bartlett's test rarely indicated highly significant heteroscedasticity, and variances did not vary systematically with means. For these reasons, and because ANOVA is considered robust even to large departures from homogeneity of variances (Zar 1974), untransformed data were analysed throughout.

## Results

### Comparing algal food species

Algal species had little effect on either the length of *Strongylocentrotus droebachiensis* larvae or the summed length of larval arms. Plutei had already achieved large size in 10 d, and little increase in larval length was observed subsequently (Fig. 2a). In several groups, length decreased slightly from 15 to 22 d of age. Total arm length increased by 20 to 30% through 15 d, as the anterolateral, posterodorsal, and preoral arms continued to develop (Fig. 2b). Food effects on measures of larval size were small and usually not statistically significant ( $p > 0.05$ ).

Larvae from cultures fed *Chaetoceros gracilis* generally were longer and had greater total arm lengths than those fed *Dunaliella tertiolecta*. These differences approached statistical significance ( $p < 0.01$ ) only on the second sampling date, when larvae in two of the three cultures fed *C. gracilis* were 50 to 70  $\mu$ m longer than those in cultures fed *D. tertiolecta* (Fig. 2a).

Mean total arm length and mean larval length of 22-d-old larvae were in some cases smaller (or at least not much greater) than those of 15-d-old larvae. These decreases were statistically significant (Student's *t*-test,  $p < 0.05$ ) only for one replicate group of larvae fed *Dunaliella tertiolecta*.

Development of the echinus rudiment of plutei was not strongly affected by algal food species. Rudiments appeared first in 10-d-old larvae fed *Chaetoceros gracilis*, and 5 d later these larvae (except for one group which lagged in rudiment development) still had larger rudiments than larvae fed

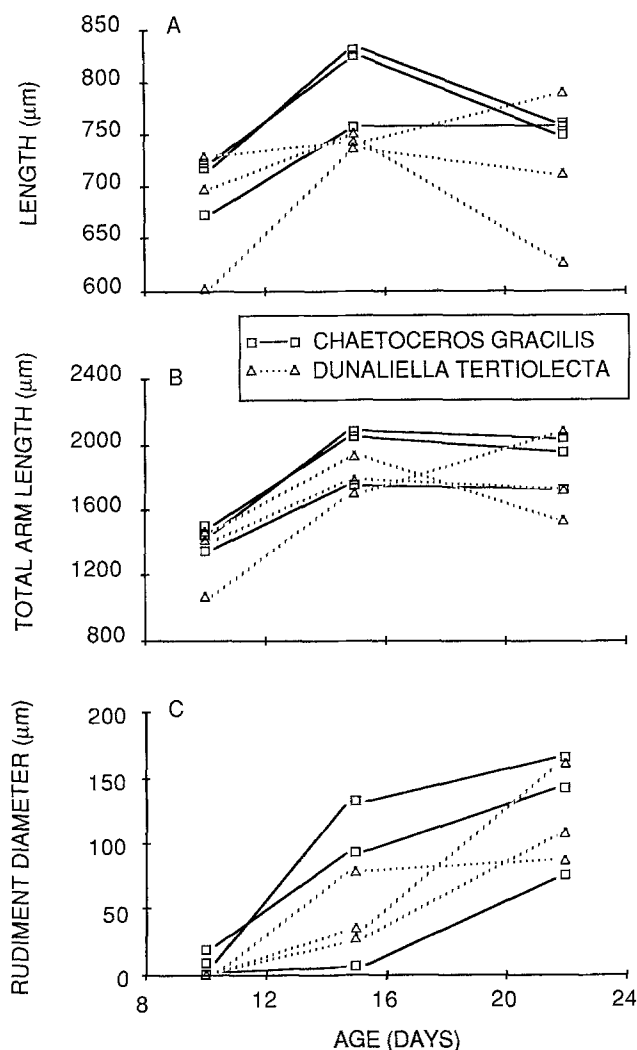


Fig. 2. *Strongylocentrotus droebachiensis*. Changes in A. larval length (from posterior tip to end of postoral arm), B. total arm length (summed over all larval arms), and C. echinus rudiment diameter of larvae fed two different algal species (at 1000 cells  $\text{ml}^{-1}$ ) during development. Means for 7 to 10 larvae from each jar are shown

*Dunaliella tertiolecta* (Fig. 2c). These differences were also statistically significant ( $p < 0.05$ ). Despite the lack of increase in the size of larval structures, echinus rudiments of all groups continued to increase dramatically in size from 15 through 22 d. By Day 22, food effects on rudiment size were not significant ( $p > 0.05$ ): rudiments of all treatment groups were large (mean diam. 100 to 150  $\mu\text{m}$ ).

Survival of plutei through 22 d ranged from 0.244 to 0.571. Mean survival of larvae fed *Dunaliella tertiolecta* ( $0.352 \pm 0.059$ ) and those fed *Chaetoceros gracilis* ( $0.466 \pm 0.065$ ) was broadly similar. However, contingency table analysis of survival pooled across replicates suggested that more larvae survived when fed *C. gracilis* (Yates' corrected  $X^2 = 13.667$ ,  $p < 0.001$ ).

Few of the 22-d-old larvae in either treatment were competent to settle: three larvae in each treatment (out of a total of 430 survivors) settled. These numbers were deemed too small to justify statistical treatment.

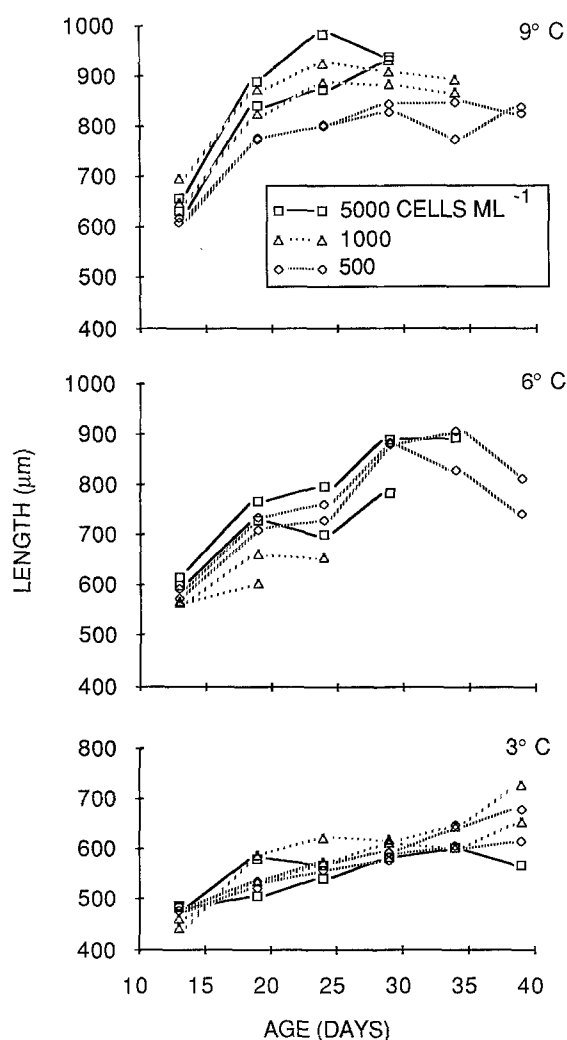


Fig. 3. *Strongylocentrotus droebachiensis*. Changes in length of larvae reared at three different temperatures (3°, 6° and 9°C), fed three different algal food ratios (500, 1 000, 5 000 cells  $\text{ml}^{-1}$ , during development. Sample sizes as in Fig. 2

#### Combined effect of food abundance and temperature

Larval length and total arm length of *Strongylocentrotus droebachiensis* plutei were strongly affected by temperature, and to a much smaller degree by food abundance. The interaction between these factors was highly significant ( $p < 0.001$ ) for the first three sampling dates (when it could be tested). Main effects for temperature were very large and always highly significant, while food effects were smaller and often not significant. The same trend was apparent throughout the experiment: food effects were small or negligible at low temperature, and larger at high temperature.

Larvae grew quickly at 9°C, and achieved a maximum mean length of 800 to 900  $\mu\text{m}$  in 24 d (Fig. 3). Groups fed larger food ratios grew more quickly than those fed the smallest ration. At 6°C, larvae grew more slowly but reached maximum length in about 34 d. Larvae reared at 3°C grew very slowly, and were only 600 to 700  $\mu\text{m}$  in length

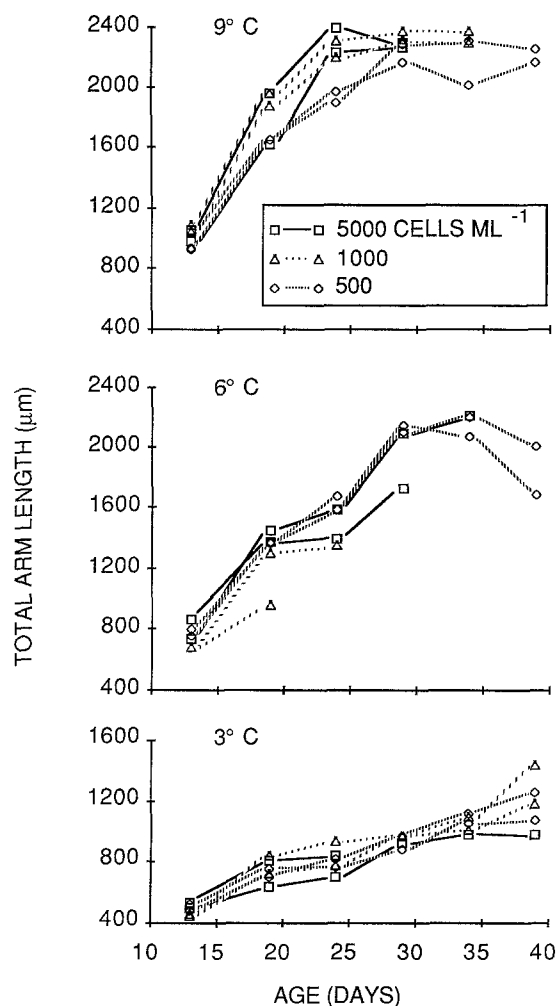


Fig. 4. *Strongylocentrotus droebachiensis*. Changes in total arm length of larvae during development. Treatments and sample sizes as in Fig. 3

at age 39 d. Because these larvae also failed to develop long posterodorsal and preoral arms, differences in total arm length (Fig. 4) were even more pronounced: most 39-d-old larvae at 3°C were only about half as large as 24-d-old larvae raised at 9°C (regardless of food ration). Effects of food ration on measures of larval size (at any age) were also generally larger at 9°C than at lower temperatures.

Larval length decreased significantly from 34 to 39 d of age for both groups of larvae at 6°C fed 500 cells ml<sup>-1</sup>, as did total arm length for one of the groups (Student's *t*-test,  $p < 0.05$ ). Other small decreases in these measures were not significant. Highsmith and Emlet (1986) found similar size decreases in competent echinoid larvae prevented from metamorphosing, as larval arms began to de-differentiate from the tips. In our study, these smaller larvae showed no evidence of extensive breakdown of arm tissues. Also, metamorphosis of these larvae probably was not delayed, because they settled in numbers comparable to or less than larvae that continued to grow until settlement (see below).

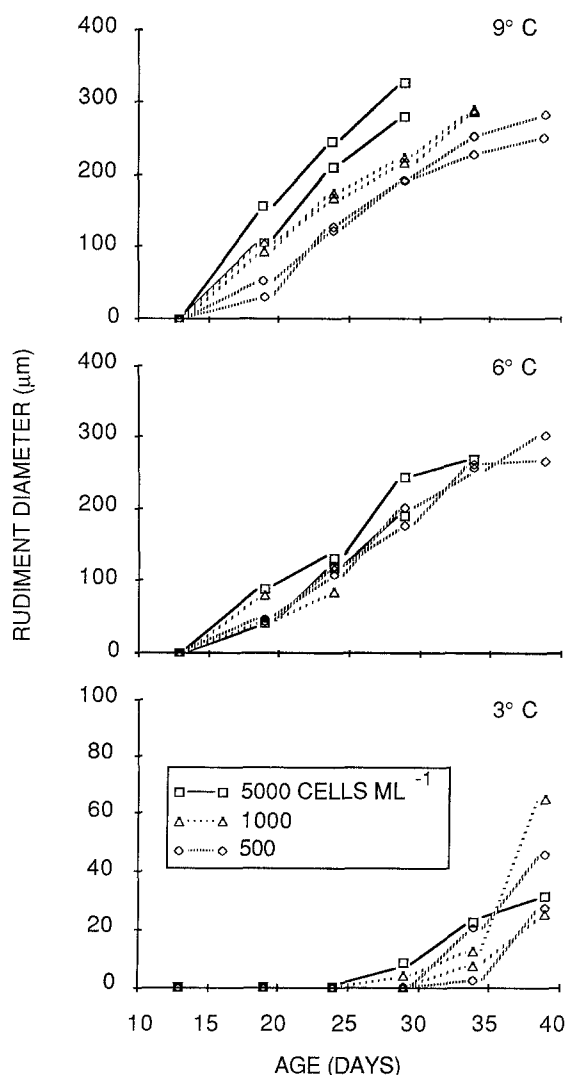


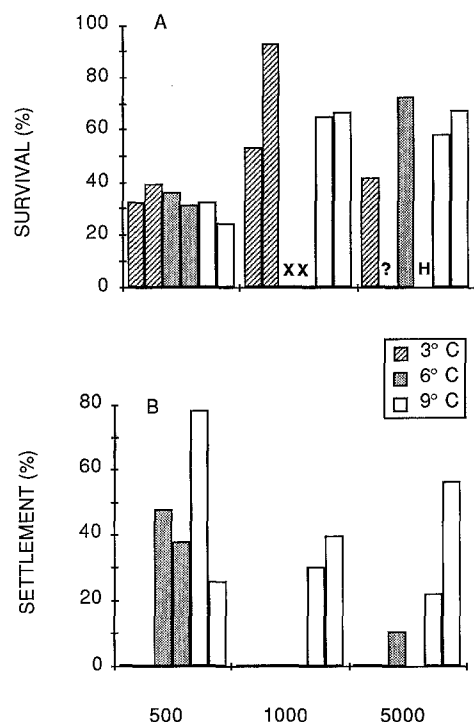
Fig. 5. *Strongylocentrotus droebachiensis*. Changes in echinus rudiment diameter of larvae during development. Treatments and sample sizes as in Fig. 3

Poor growth of larvae at 6°C fed 1 000 cells ml<sup>-1</sup> was evident after 19 d, and in all cases these larvae were smaller than larvae fed 500 cells ml<sup>-1</sup>. This difference probably reflects the incipient effects of contaminants or other agents that eventually killed all larvae in these jars.

Echinus rudiment diameter was strongly affected by temperature, and by food abundance at high temperature. These effects (and their interaction terms for 19- and 24-d-old larvae) were all highly significant between 19 and 34 d. Rudiments developed quickly at temperatures above 3°C, and moreso when larvae were fed larger rations (Fig. 5). Interestingly, rudiment diameter was the only measure of growth for which increased food abundance could compensate for the effects of lower temperature. Plutei reared at 6°C and fed 5 000 cells ml<sup>-1</sup> developed rudiments as large or larger than larvae at 9°C fed 500 cells ml<sup>-1</sup>.

Rudiment development at 3°C was extremely slow, regardless of food ration. Most 39-d-old larvae developed rudiments less than 1/4 the maximum diameter observed at





**Fig. 6.** *Strongylocentrotus droebachiensis*. A. Percent survival, and B. percent settlement of survivors, of larvae. Treatments as in Fig. 3. Survival and settlement of larvae reared at 9°C fed 5 000 algal cells ml<sup>-1</sup> were measured after 29 days; measures for larvae reared at 9°C fed 1 000 cells ml<sup>-1</sup>, and at 6°C fed 5 000 cells ml<sup>-1</sup> were made after 34 d; all other measures were for 39-d-old larvae. ?: culture lost due to unknown causes; H: culture lost due to a handling error; X: cultures lost, probably due to contaminants

higher temperatures. This result suggests a long developmental period at low temperature, probably in the range of the longest development time observed by Strathmann (1978), around 152 d (although it is difficult to extrapolate the shape of the entire growth curve from our limited data set).

Survival of plutei was extremely variable from 0.247 to 0.926 (groups that failed during the experiment were not included in this comparison, because death of larvae was probably not due to treatment effects) (Fig. 6a). Contingency table analysis suggested that survival differences among temperature treatments were small ( $X^2=0.714$ ,  $p=0.70$ ), while food ration effects were highly significant ( $X^2=296.7$ ,  $p\leq 0.001$ ). The main source of this difference was the low survival of larvae fed 500 cells ml<sup>-1</sup>.

Settlement of plutei apparently was not affected by food ration or by temperature above 3°C (no larvae developed to competency at this temperature), although settlement of larvae fed 5 000 cells ml<sup>-1</sup> at 6°C was very low. These proportions ranged from 0.107 to 0.781, with large variation within some treatment groups (Fig. 6b). No statistical treatment of these data is presented, in part because of the clear effect of low temperature, and because of the obvious large variation in settlement among groups of larvae of similar size with large echinus rudiments.

## Discussion

### Larval growth in culture

Our results show that temperature has a strong influence on the growth and development of larval and juvenile structures of *Strongylocentrotus droebachiensis*.  $Q_6$  for measures of larval length and total arm length in 29-d-old *S. droebachiensis* fed 5 000 cells ml<sup>-1</sup> *Dunaliella tertiolecta* at 3° to 9°C were 1.6 and 2.6, respectively (i.e. at 6°C difference in temperature produced about a two-fold difference in size). McEdward (1985) found a  $Q_5$  of 1.8 to 2.0 for development rates of sand dollar larvae (*Dendraster excentricus*) to the 6 arm pluteus stage between 12° and 22°C.

Effects of temperature on echinus rudiment development were even more pronounced. Rudiments of 39-d-old larvae reared at 9°C fed the smallest food ration were 4 to 8 times larger than rudiments of larvae reared at 3°C (regardless of ration). This result is especially important, because the ultimate measure of larval success is not growth or development of larval structures (although these are interesting for other reasons), but the completion of development to the juvenile stage. The faster this occurs, the more likely the developing juvenile will successfully enter the benthic stage of the sea urchin life cycle. The speed of this process largely depends on water temperature.

In contrast, larval survival and settlement apparently were not affected by temperature (except to the extent that settlement was affected by development of the echinus rudiment). Given that *Strongylocentrotus droebachiensis* occurs widely in Arctic seas (Jensen 1974), develops normally at high temperature, and grows rapidly on very small algal rations, it seems unlikely that these larvae starve or die in large numbers due to the direct effects of temperature or food abundance. Indirect effects of these factors on growth and development rates are more likely to affect larval abundance by altering time spent in the plankton (thus increasing exposure to planktonic predators, and transport away from appropriate benthic habitat).

It is evident that *Strongylocentrotus droebachiensis* larvae are capable of development at temperatures much greater than those they are likely to encounter in coastal Nova Scotia. Inshore surface temperatures on the Atlantic coast rarely exceed 10° to 12°C in early summer (Lauzier and Hull 1969). Stephens (1972) found "gross asynchrony" in larval development at 10°C, irreversible arrest of cell division at 12°C, and suggested 14° to 15°C as an upper lethal limit for *S. droebachiensis*. Stephens (1972) proposed that high temperature effects on larvae might limit the southward distribution of shallow water *S. droebachiensis* populations along the Atlantic coast of North America. Our results suggest that simple effects of high temperature on larvae are probably not an adequate explanation of this distribution. Pre-feeding development in one experiment (comparing algal food species at high temperature) occurred at 12°C, but subsequent experimental temperatures were 2° to 6°C higher.

Food ration affected growth of *Strongylocentrotus droebachiensis* plutei, but effects of food on all measures of

growth and development depended on temperature, and were generally small. This result is consistent with Roller and Stickle's (1985) observation that food ration (between 500 and 6 000 *Dunaliella tertiolecta* ml<sup>-1</sup>) did not affect the size of 30-d-old *S. droebachiensis* larvae.

Results from both of our experiments suggest that the quality and quantity of algal food may affect the larval survival of *Strongylocentrotus droebachiensis*. Larval growth on equivalent concentrations of *Dunaliella tertiolecta* and *Chaetoceros gracilis* was very similar (though nascent juvenile structures may develop more quickly on the latter diet). This result partly confirms the usefulness of *D. tertiolecta* in studies of echinoderm larval growth (Hinegardner 1969, Strathmann 1971, Lucas 1982, McEdward 1984, 1985, Rumrill and Chia 1984, Paulay et al. 1985, Roller and Stickle 1985, Rumrill et al. 1985, Emler 1986). Generalizations about the effect of food quality on pluteus growth are complicated by different algal cell sizes and compositions, and by the unknown nutritional requirements of larvae.

Plutei developed even with very small food rations in our study. Food concentrations of 500 algal cells ml<sup>-1</sup> [and as low as 100 cells ml<sup>-1</sup> (own unpublished data)] supported growth and development at high temperature (when energy should be most limiting and food limitation strongest). Given a pigment concentration for *Dunaliella tertiolecta* of about 1.38 µg chlorophyll *a* 10<sup>-6</sup> cells (Paulay et al. 1985), 500 cells ml<sup>-1</sup> represents about 0.69 µg chlorophyll *a* l<sup>-1</sup>. In coastal areas of Nova Scotia, phytoplankton are much more abundant. For example, chlorophyll *a* levels in St. Margaret's Bay are typically <1.0 µg l<sup>-1</sup> in midwinter, but rise to 15 µg l<sup>-1</sup> or more during the spring bloom in March to April (Platt and Irwin 1968, 1970).

The timing of sea urchin spawning and larval development off Nova Scotia may also affect food limitation. Sea urchin gonads mature during the winter, and spawning of urchins off Newfoundland and Nova Scotia probably occurs between late March and early May (Himmelman 1978, R. E. Scheibling unpublished data). Early in the spawning season, food abundance may fall in the range of the smallest rations employed in our study (0.5 to 1.0 µg l<sup>-1</sup>), but surface seawater temperatures are normally <4°C at this time. Development at these temperatures is very slow, regardless of food availability. Food abundance is likely to influence larval growth and development of sea urchins only in the case where both urchin spawning and the onset of the spring phytoplankton bloom are delayed sufficiently to coincide with early summer temperature increases. Although the size and onset of the spring phytoplankton bloom will certainly vary from year to year, even a "small" bloom of 5 µg chlorophyll *a* l<sup>-1</sup> represents an algal feast for sea urchin larvae, equivalent to about 3 600 *Dunaliella tertiolecta* ml<sup>-1</sup>. Relative to even small temperature changes, interannual variation around such a food ration probably means small changes in the survival and growth of echinoplutei.

#### Temperature and recruitment patterns

Ebert (1983) has reviewed the episodic nature of annual recruitment of echinoids, and summarized evidence for a

variety of planktonic and benthic effects on numbers of surviving juveniles. These effects included upwelling, planktonic and benthic predator abundance, and transport by currents. In particular, Ebert reviewed evidence for correlation between temperature and recruitment anomalies. Thorson (1950) considered that the major influence of temperature was to delay or advance the development of invertebrate larvae, thereby increasing or decreasing exposure to predators. Ebert (1983) found that this relationship may hold for some sea urchins, but that recruitment of *Strongylocentrotus purpuratus* off southern California may actually be inversely related to temperature (recruits being most abundant after coldest winters).

Foreman (1977) observed unusually large populations of *Strongylocentrotus droebachiensis* at locations in the Strait of Georgia, British Columbia. These populations consisted mainly of sea urchins from a single cohort that settled in 1969. Based on long-term surface temperature measurements for the Strait of Georgia (Hollister and Sandnes 1972), and Stephens' (1972) suggested 10°C temperature limit for larval development, Foreman (1977) suggested that spring temperatures in the Strait are normally marginal for development of *S. droebachiensis* larvae. He concluded that record low spring water temperatures in 1969 probably led to intensive recruitment that year. However, our results suggest just the opposite conclusion. Spring temperatures near Foreman's (1977) study area in the Strait of Georgia normally increase from a mean March temperature of about 7°C to a mean June temperature of 13° to 15°C (Hollister and Sandnes 1972). Our results indicate that temperatures in the Strait are normally conducive to rapid growth and development of *S. droebachiensis* larvae. It is possible, however, that genetically distinct populations of sea urchins evolve independent temperature optima for larval development.

Recruitment of *Strongylocentrotus droebachiensis* along the Atlantic coast of Nova Scotia also may be episodic (Scheibling 1986). Raymond and Scheibling (1987, and unpublished data) monitored recruitment at Mill Cove, St. Margaret's Bay, following a mass mortality of sea urchins there in 1981. They found newly-settled recruits (1 to 2 mm test diameter) in 1982 to 1984 and in 1986, but not in 1985. Also, C. R. Johnson (personal communication) was unable to find recruits at Mill Cove in early June 1981 and in late September-early November of the same year (although sea urchins were eliminated by disease at this time). Because newly-settled juveniles are highly cryptic, they cannot be counted and collected from this habitat in proportion to their true abundance. Observations on recruitment events are therefore qualitative only.

If environmental effects on larval growth and development influence recruitment, then it might be possible to explain temporal variation in recruitment in terms of large scale oceanographic events (such as temperature anomalies). Mean spring surface temperatures (March to June inclusive, 1979 to 1986) are shown in Fig. 7 for two locations, Northwest Arm and Fink Cove, within 38 and 42 km (straight line distance), respectively, of Mill Cove in St. Margaret's Bay. Generally, recruitment at Mill Cove occurred in years of

relatively warm (1982 to 1984) or moderately warm (1986) spring water temperatures, but failed in a relatively cold year (1985). No data are available for 1981, when all sea urchins were eliminated by disease in Mill Cove.

Destructive grazing of kelps by large sea urchin populations was first observed in St. Margaret's Bay in 1968 (but probably began a few years earlier) (Breen and Mann, 1976a, b). Given a growth period of 4 to 6 yr from settlement to a large (>40 mm diam.) adult sea urchin (Miller and Mann 1973, Raymond and Scheibling 1987), our hypothesis leads to the prediction that destructive grazing beginning before 1968 was presaged in the early 1960's by one or more major recruitment events associated with high temperatures (and rapid larval growth and development).

Deviations from long-term monthly mean spring temperatures (March-June inclusive) in Halifax Harbor for the period 1952 to 1986 are shown in Fig. 8 (data from Lauzier and Hull 1969, and unpublished temperature records). A single, large, positive deviation from long-term mean temperatures occurred in June 1960, resulting in average temperatures 3.5°C warmer than normal (average temperature in June 1960 was 13.7°C). Based on our laboratory culture experiments, such a temperature increase could produce planktonic periods of only 25 to 30 d. This single point was about twice as large as almost all other positive deviations for the same period, and occurred 8 yr before the first report of destructive grazing.

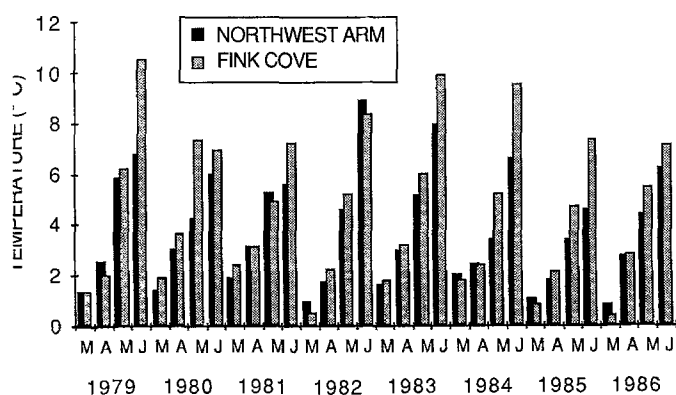
The link between high spring water temperature in 1960 and subsequent destructive grazing (a massive recruitment

event) is uncertain: no data on recruitment rates for this period are available. Nonetheless, it is tempting to suggest that this anomalous period of high temperature may have led to accelerated larval growth and an unusually large cohort of juvenile sea urchins in prelude to destructive grazing.

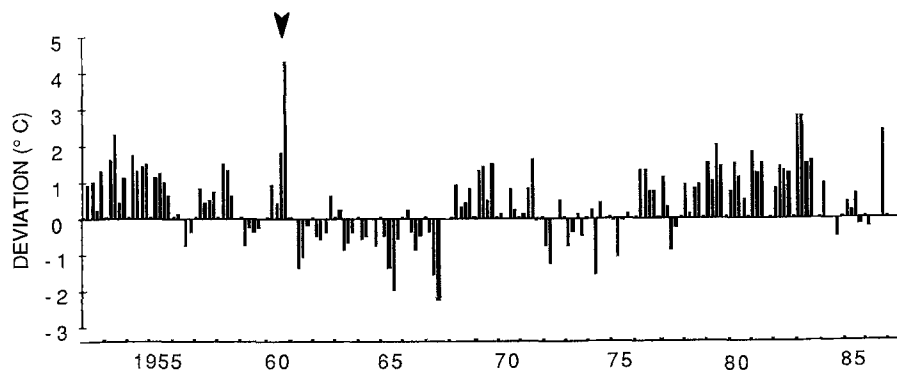
Certainly, a single cohort of sea urchins that settled in 1960 was not responsible for the continued destructive grazing observed through the 1970's. The lifespan of *Strongylocentrotus droebachiensis* off Nova Scotia is probably 7 to 10 yr (Miller and Mann 1973, Lang and Mann 1976, R. E. Scheibling unpublished data). There is evidence, though that recruitment of sea urchins is reduced in kelp beds (Tegner and Dayton 1981, Wharton and Mann 1981, Miller 1985b, Scheibling 1986), probably by hydrodynamic forces, substratum selection by larvae, or predation by fish and invertebrates associated with kelp beds. Lang and Mann (1976) suggest that recruitment at sites in St. Margaret's Bay was higher the year after destructive grazing occurred, and that juveniles continued to recruit to newly-created coralline barrens. If destructive grazing was initiated by a single cohort of sea urchins that settled in 1960, subsequent increased recruitment of urchins to newly created barren areas may have produced more large cohorts capable of continued destructive grazing.

Evidence for a mechanistic link between surface sea temperature and destructive grazing (through rapid larval development and intense recruitment at high temperature) is in itself not especially compelling. Yet destructive grazing of kelp beds by sea urchins was preceded by a large, positive temperature anomaly at a time consistent with the hypothesized influence of temperature and larval abundance on recruitment. This correspondence of events, coupled with evidence (albeit limited) of recruitment failure in a year of cool spring water temperature, and the strong effect of temperature on larval growth in laboratory culture, suggests a causal relationship worthy of further study.

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**Fig. 7.** Mean spring surface temperatures (March to June, inclusive) in Northwest Arm (15-m depth) and at Fink Cove (6 m depth), Halifax Co., Nova Scotia, 1979 to 1986



**Fig. 8.** Deviations from long-term (1926 to 1969) mean spring surface temperatures (March to June, inclusive) in Halifax Harbor, 1952 to 1986. Long-term means from Lauzier and Hull (1969); data are from Lauzier and Hull (1969) and I. Perry (St. Andrews Biological Station, unpublished data). Arrow indicates single, large, positive deviation from longterm mean temperature in June 1960



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