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Effects of food ration and feeding regime on growth and reproduction of the sea urchin *Strongylocentrotus droebachiensis*

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Abstract To determine the effects food ration and feeding regime on growth and reproduction of *Strongylocentrotus droebachiensis* (Müller), sea urchins in laboratory aquaria were fed kelp (*Laminaria longicruris*) supplied at either a high (H, ad libidum daily) or a low (L, ad libidum 1 d wk^{-1}) ration in two successive 12-wk intervals during the reproductive period. After 24 wk, urchins fed the high ration continuously (HH) or for the last 12 wk only (LH) had a significantly greater mean gonad index [(gonad weight/total body weight) × 100] and body weight than urchins fed the low ration continuously (LL) or for the last 12 wk only (HL). Urchins in the HL treatment had a significantly greater gonad index than those in the LL treatment; there was no significant difference in gonad index between the LH and HH treatments. Females had a greater gonad index than males in the low ration (LL and HL) treatments at the end of the experiment; there was no significant difference between sexes in the high ration (LH, HH) treatments. Gametogenesis proceeded to maturation in all treatments and some individuals spawned at the end of the experiment. Females in the high ration (HH and LH) treatments had a greater proportion of nutritive phagocytes in their ovaries than females in the low ration treatments, but there was no effect of feeding treatment on oocyte or ovum size. Feeding treatment had no effect on the relative abundance of nutritive phagocytes in the testes, although the proportion of spermatocytes was higher (and that of spermatozoa lower) in the high ration than in the low ration treatments. Urchins in the high ration treatments had a lower mean jaw height index [(jaw height/test diameter) × 100] and greater mean test diameter than those in the low ration treatments at the end of the experiment, although these differences were not statistically significant. Feeding rate on kelp at the end of the experiment was significantly greater for urchins in the low ration than in the high ration treatments. Our experimental results show that even relatively low rations of kelp support somatic and gonadal growth in *S. droebachiensis*. Increasing the supply of kelp, particularly during the period of active gametogenesis, results in maximal rates of growth and reproduction. These results suggest that populations of *S. droebachiensis* in barrens may derive a substantial proportion of their nutrition from drift kelp, which may contribute to their persistence in these habitats. They also explain the large body size, high reproductive effort and fecundity of urchins grazing on kelp beds. These findings have important implications for understanding the dynamics of natural populations of *S. droebachiensis* and for development of effective aquacultural practices.

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Introduction

Numerous field and laboratory studies have demonstrated that growth and reproduction in strongylocentrotid sea urchins are directly related to the quantity and quality of available food (e.g., Ebert 1968; Himmelman and Steele 1971; Vadas 1977; Larson et al. 1980; Thompson 1983, 1984; Briscoe and Sebens 1988). Temporal variation in food supply over the reproductive cycle may influence the allocation of resources to somatic and gonadal growth, although this has received little attention (Thompson 1984; Munk 1992). Food availability also may affect gametogenesis and maturation, accounting for differences in spawning times between sites and years (Fuji 1960a,b; Chatlynne 1969; Gonor 1973a,b; Himmelman 1978; Falk-Petersen and Lonning 1983). Gametogenesis may be arrested under poor nutritional conditions and gametes resorbed (Bernard 1977), although increased feeding after a period of starvation can enable completion of gametogenic development (Bishop and Watts 1993).

The allocation of resources to different components of somatic growth also may vary with the level of food availability (Ebert 1988). Various studies have indicated an inverse relationship between the relative size of Aristotle's lantern (the jaw-like feeding apparatus) and food availability among populations of strongylocentrotid and other species of regular sea urchins (Ebert 1980; Black et al. 1982, 1984; Edwards and Ebert 1991; Levitan 1991). Ebert (1980) proposed a functional role for such morphological plasticity: a larger relative jaw size should enhance an urchin's foraging ability when food is in low abundance. Black et al. (1984) provided support for this hypothesis by showing a direct relationship between feeding rate and jaw size in *Echinometra mathaei*. Levitan (1991) found that differences in relative jaw size (compared to test size) of *Diadema antillarum* under different feeding conditions are mainly due to differences in the growth rate of the test.

Strongylocentrotus droebachiensis is the dominant grazer in rocky subtidal communities in eastern Canada. Large-scale fluctuations in the abundance of this species result in major transitions in community structure from kelp beds to barren grounds (Mann 1977; Miller 1985; Scheibling 1986). During population outbreaks, the urchins form dense aggregations along the margins of kelp beds, destructively grazing kelps and other macroalgae and forming barren grounds (Breen and Mann 1976). After the kelps are consumed, urchins will persist indefinitely on these barrens by grazing microalgae and coralline algal crusts and capturing drift algae (Johnson and Mann 1982). However, the growth and reproductive rate of sea urchins in barrens decrease over time after the destruction of kelp beds (Lang and Mann 1976).

The physiological response of *Strongylocentrotus droebachiensis* to changes in food availability may help to explain the population dynamics of sea urchins during outbreaks, or their persistence in habitats with little kelp or other high-quality foods. Moreover, understanding the relationship of food supply to growth and reproduction is crucial to the development of effective aquacultural and harvesting practices for sea urchins. In this study, we examine the effect of food (kelp) ration and feeding regime on somatic and gonadal growth and gametogenesis of *S. droebachiensis* in a laboratory experiment.

Materials and methods

Experimental design

Strongylocentrotus droebachiensis (Müller) were hand-collected using SCUBA from urchin-dominated barren grounds off Little Duck Island, Nova Scotia (44°22′N; 64°11′W) and transported to flowing sea water tanks at Dalhousie University in September 1994. Only sexually mature individuals, 38 to 52 mm horizontal test diameter, were selected for experimental use. Prior to the experiment, the sea urchins were starved for 2 wk to standardize their nutritional condition.

To examine the effects of food ration and feeding regime on growth and reproduction, we maintained sea urchins on 4 feeding treatments in a 24 wk (18 October 1994 to 1 April 1995) experiment: (1) continuous high ration (HH) in which urchins were fed kelp ad libidum for 24 wk; (2) continuous low ration (LL), fed kelp ad libidum for 1 d wk^{-1} for 24 wk; (3) high-to-low ration (HL), fed the high ration for the first 12 wk and the low ration for the last 12 wk; and (4) low-to-high ration (LH), fed the low ration for the first 12 wk and the high ration for the last 12 wk. Twenty sea urchins were randomly allocated to each of 24 aquaria containing 47 litres of flowing sea water (0.625 liter min^{-1}) arranged in 3 tiers of 8 aquaria per tier. Within each tier, 2 replicates of each of the 4 treatments were randomly assigned to aquaria. Sea water temperature was measured daily and ranged from 15 °C at the start of the experiment to 2 °C at the end. Temperature differences among aquaria on any day never exceeded 2 °C and were usually < 1 °C. Lighting was from windows adjacent to the aquaria, providing a natural photoperiod. Kelp (*Laminaria longicruris*) was freshly collected from nearby areas by divers and maintained in flowing sea water tanks for no more than 2 wk before use in the experiment. Previous studies have demonstrated that *Laminaria* spp. are a preferred algal food which yields high rates of growth and reproduction in *S. droebachiensis* (Vadas 1977; Larson et al. 1980). Fecal matter was removed from aquaria by aspiration at least once per week.

At the start of the experiment, all experimental urchins were measured and weighed and an additional random sample of 38 urchins was dissected to determine initial gonad and jaw height indices, and for histological analysis. All urchins were measured and weighed again at the middle (12 wk) and end (24 wk) of the experiment; 10 randomly selected urchins from each aquarium were dissected at the middle and the remaining urchins (5 to 10) were dissected at the end of the experiment. Horizontal test diameter (HTD) and jaw height (the length of the demipyramid from the oral tip to the rotule) were measured with vernier calipers (0.05 mm accuracy). Jaw height index was calculated as the ratio of jaw height to HTD, expressed as a percentage. Total body wet weight (after allowing superficial water to drain from the urchin for 10 s) and gonad wet weight were measured on an electronic balance (0.01 g accuracy). Gonad index was calculated as the ratio of gonad weight to total wet weight, expressed as a percentage. Sex was determined by examining gonadal smears with a compound microscope.

For histological analysis, ovaries from 2 females and testes from 2 males from each aquarium were fixed separately in 10% formalin for 4 to 6 wk. Samples from the center of each gonad were embedded in paraffin, cut into 7 μm sections with a microtome, and stained with haematoxylin and eosin. For each specimen of each sex, cross sections of 8 (6 in 4 cases) randomly selected gonadal lobes were examined using light microscopy and a computerized image analysis system (Bioscan Optimus Analysis System). Only cross sections of lobes which fit within the image analysis frame (0.917 mm^2) were sampled. For females, the relative area (expressed as a percentage) of nutritive phagocytes was measured for each ovarian lobe, and the absolute areas of oocytes and ova were measured for 4 randomly selected lobes. Only germinal cells sectioned through the nucleus (for an ovum) or nucleolus (for an oocyte) were measured. Cells surrounding the germinal cells, excluding oogonia, were identified as nutritive phagocytes. For males, the relative areas of nutritive phagocytes, spermatocytes and spermatozoa were measured for each testicular lobe.

In the last week of the experiment, the feeding rate of urchins in each treatment was measured. A known fresh weight of kelp (0.01 g accuracy) was added to each aquarium and the remainder was removed and weighed after 24 h. Feeding rate was expressed as the weight of kelp consumed per urchin per aquarium.

Statistical analysis

Experimental results were analyzed by nested analysis of variance (ANOVA). At the middle of the experiment, the HH and HL treatments were combined, as were the LL and LH treatments, to compare groups with the same feeding regime during the first 12 wk

of the experiment: high ration (H) or low ration (L). Differences in sea urchin wet weight and test diameter at the start and middle of the experiment were analyzed using a three-factor nested ANOVA with the factors: (1) Treatment (HH, HL, LH, and LL; or H and L), (2) Tier (3 levels), and (3) Aquarium nested within each combination of Treatment and Tier (2 or 4 aquaria). Treatment was a fixed factor; Tier and Aquarium were random factors. There were 15 to 20 replicate urchins per aquarium. The ANOVA model is given by:

$$X_{ijkl} = \mu + \text{Treatment}_i + \text{Tier}_j + \text{Treatment} \times \text{Tier}_{ij} + \text{Aquarium (Treatment} \times \text{Tier)}_{k(ij)} + e_{ijkl} \ ,$$

where X_{ijkl} is the measure of the dependent variable for the lth replicate of the ith level of Treatment, jth level of Tier, and kth level of Aquarium; e_{ijkl} is the error term associated with that replicate; and μ is the parametric grand mean.

The same three-factor model was used to analyze differences in the relative area of female or male nutritive phagocytes, and of male spermatocytes and spermatozoa, at the middle and end of the experiment. Individuals were pooled for each sex within aquaria (1 to 3 females/males per aquarium) giving 8 to 24 replicate measures per aquarium.

Differences in wet weight and test diameter at end of the experiment, and in the gonad index and jaw height index at both the middle and the end, were analyzed using a four-factor nested ANOVA with the factors: (1) Treatment (H and L; or HH, HL, LH, and LL); (2) Tier (3 levels); (3) Aquarium nested with each combination of Treatment and Tier (4 or 2 aquaria); and (4) Sex (female and male), a fixed factor. There were 1 to 9 replicate urchins of each sex per aquarium. The ANOVA model is given by:

$$X_{ijklm} = \mu + \text{Treatment}_i + \text{Tier}_j + \text{Treatment} \times \text{Tier}_{ij} + \text{Aquarium (Treatment} \times \text{Tier)}_{k(ij)} + \text{Sex}_l + \text{Sex} \times \text{Treatment}_{li} + \text{Sex} \times \text{Tier}_{lj} + \text{Sex} \times \text{Treatment} \times \text{Tier}_{lij} + \text{Sex} \times \text{Aquarium (Treatment} \times \text{Tier)}_{lk(ij)} + e_{ijklm} \ ,$$

where X_{ijklm} is the measure of the dependent variable for the mth replicate of the ith level of Treatment, jth level of Tier, and kth level of Aquarium, and lth level of Sex; e_{ijklm} is the error term associated with that replicate; and μ is the parametric grand mean.

At the middle and end of the experiment, differences between feeding treatments in median oocyte/ova size (area) were analyzed using a Kruskal–Wallis test. Measurements of oocyte/ova area were pooled across ovaries and individuals within treatments.

Some mortality of urchins occurred during the experiment (see "Results") resulting in unequal numbers of observations in different treatment combinations. Also, in analyses with Sex as a factor, there were usually unequal numbers of males and females, since there are no secondary sexual characteristics which would permit equal allocation of each sex to experimental treatments as part of the design. Consequently, we used ANOVA procedures for unbalanced data. In an unbalanced analysis of a factorial design, different methods of partitioning variance (i.e. computing sums of squares, SS) yield different results, the SS corresponding to each of the factors and their interactions are not necessarily independent, and the ratio of mean squares is not exactly distributed according to the F-distribution (Shaw and Mitchell-Olds 1993). Computational methods designed specifically for analysis of unbalanced data are generally available on statistical computing packages (e.g. SAS, SPSS, BMDP). We have used the SAS General Linear Models procedure (SAS Institute Inc. 1990) based on models given in Searle (1971, 1987) and Milliken and Johnson (1984). Despite the inherent ambiguities in the estimation of effects and testing of hypotheses, we consider an unbalanced analysis of the data preferable to methods of imposing balance, such as deleting observations (which reduces power) or imputing missing values (which can bias tests).

We computed Type III SS (as designated by SAS) because the Type III method (cf. Type I and II) provides the most readily interpretable tests of the main effects (Shaw and Mitchell-Olds 1993). The Type III SS for each factor is the sum of the squared differences of the unweighted marginal means (i.e. the least square means). Type III SS measures the effect of a particular factor adjusted for all other factors in the model, but is independent of the ordering of the factors in the model (unlike Type I and II SS). We used the method of moments (Milliken and Johnson 1984) to estimate the variance components for each of the terms in our mixed effects models. This method provides good unbiased estimators, particularly for models that are not too unbalanced. Because the SS in an unbalanced model are not necessarily independent, the denominator mean square of the test statistic (F-ratio) generally is constructed from a linear combination of mean squares, based on the variance components. The degrees of freedom for the divisor are estimated using the Satterthwaite approximation, and the test statistic is referred to an F-distribution. For a detailed treatment of parametric statistical procedures used for analysis of unbalanced data, see textbooks by Searle (1971, 1987), Milliken and Johnson (1984), and Maxwell and Delaney (1990).

Prior to ANOVA, the raw data were tested for homogeneity of variance using Cochran's test ($\alpha < 0.05$). In a few cases for the gonad index and jaw height index, the data were arcsin-transformed to meet this assumption. A posteriori comparisons of least square means for Treatment and Sex were done using a t-test procedure ($\alpha < 0.05$) based on estimates of marginal means expected for a balanced design (Searle et al. 1980; Milliken and Johnson 1984).

Results

At the start of the experiment, a three-factor nested ANOVA confirmed random allocation of sea urchins to Treatments, Tiers, and Aquarium: there were no significant effects of any of these factors ($P > 0.40$) on test diameter or wet weight. A total of 27 moribund urchins were removed from the experiment during the first 5 wk. These individuals were distributed across all treatments and no more than five were removed from any one aquarium.

By the middle of the experiment, urchins fed the high ration diet (H) had a significantly greater mean gonad index than urchins fed the low ration diet (L) (Fig. 1a; Table 1). There were no significant differences in wet weight, jaw height index, or test diameter (Fig. 1b, c, d; Table 1) at this stage in the experiment.

At the end of the experiment, urchins fed the high ration diet throughout the 24 wk (HH) or for the last 12 wk (LH) had a significantly ($P < 0.05$) greater mean gonad index and wet weight than urchins fed the low ration diet throughout the 24 wk (LL) or for the last 12 wk (HL) (Table 1 and least square mean comparisons). Urchins in the HL treatment had a significantly greater mean gonad index than those in the LL treatment, but there was no significant difference in gonad index between the LH and HH treatments (Fig. 1a). Wet weight did not differ significantly between HH and LH treatments or between HL and LL treatments (Fig. 1b). Urchins in the HH and LH treatments had a greater mean test diameter than those in the LL and HL treatments (Fig. 1d), although these differences among treatments were marginally nonsignificant ($P = 0.059$, Table 1). Differences in mean jaw height index among treatments at the end of the experiment (Fig. 1c) were

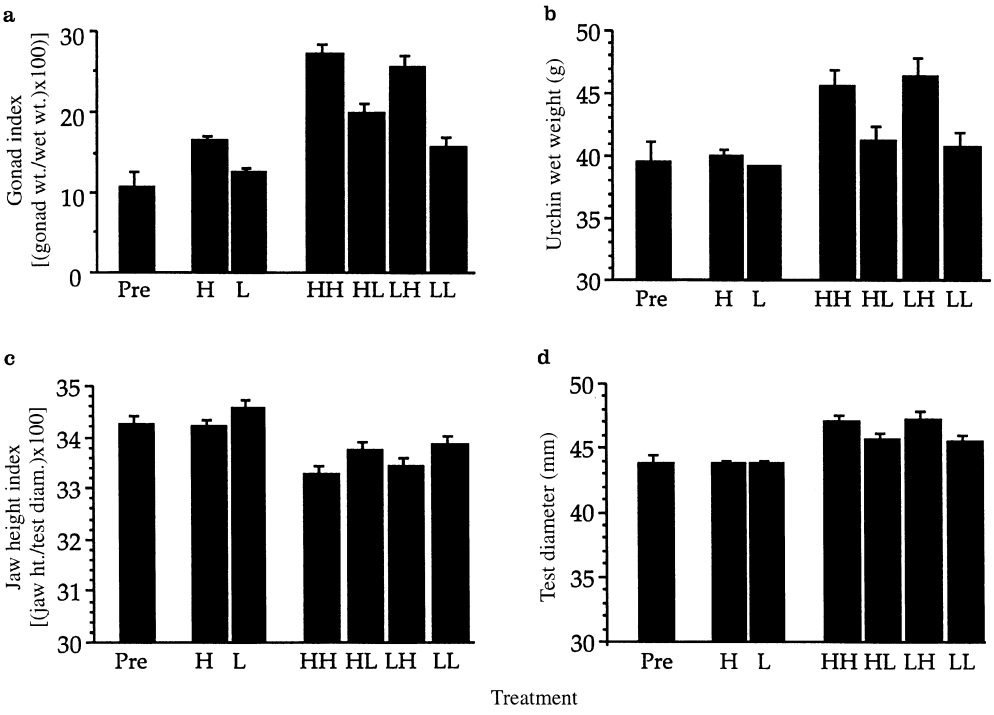

Fig. 1 *Strongylocentrotus droebachiensis*. Mean (±SE) of **a** gonad index, **b** wet weight, **c** jaw height index, and **d** test diameter for different feeding treatments at three times during the 24-wk experiment: pre-experiment (*Pre*); middle (*H*, high ration; *L*, low ration); and end (*HH*, continuous high ration; *HL*, high-to-low ration; *LH*, low-to-high ration; *LL*, continuous low ration). Means are based on raw data pooled over all levels of Tier, Aquarium, and Sex (end only). Sample sizes are: pre-experiment, 38 (gonad index, jaw height index) and 478 (wet weight, test diameter); middle, 106 to 108 (gonad index, jaw height index) and 225 to 228 (wet weight, test diameter); end, 58 to 60

not statistically significant ($P = 0.10$, Table 1) but reflected differences in mean test diameter: further analysis of absolute jaw height showed no effect of feeding treatment (or any other factor) at either the middle ($P > 0.20$) or end ($P > 0.35$) of the experiment.

There was no significant difference between sexes in gonad index or jaw height index by the middle of the experiment (Table 1). However, by the end of the experiment, females had a significantly greater gonad index than males (pooled mean ± SE: females, 22.7 ± 0.06; males, 21.2 ± 0.05) and males had a significantly greater jaw height index than females (females: 33.5 ± 0.02; males: 33.6 ± 0.01) (Table 1). Further analysis of mean gonad index within feeding treatments indicated that this sexual difference occurred only in the low ration treatments (LL: females, 17.3 ± 0.73; males, 13.8 ± 0.82; HL: females, 21.2 ± 0.69; males, 18.4 ± 0.78). There was no significant difference in gonad index between sexes in the high ration treatments (HH: females, 27.5 ± 0.75; males,

Table 1 *Strongylocentrotus droebachiensis*. Nested analysis of variance of gonad index, wet weight, jaw height index, and test diameter at the mid point and end of a 24-wk experiment. Data are degrees of freedom (*df*), *F*-ratio and *P*-value (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$) for Feeding Treatment (*T*), Tier (*L*), Aquarium (*A*, nested in Treatment × Tier), Sex (*S*), and all interaction terms

Source	Period	*df*	Gonad index		Wet weight		Jaw height index		Test diameter	
			F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
T	mid	1	41.05	0.023*	1.38	0.361	4.19	0.177	0.01	0.952
	end	3	19.15	0.002**	5.88	0.030*	3.27	0.098	4.25	0.059
L	mid	2	0.43	0.737	3.46	0.224	0.30	0.076	6.19	0.139
	end	2	0.15	0.866	0.93	0.628	5.89	0.143	2.17	0.448
T × L	mid	2	4.73	0.531	1.45	0.261	15.67	0.816	0.62	0.551
	end	6	0.45	0.833	1.11	0.481	5.64	0.588	1.47	0.420
A(T × L)	mid	18	0.90	0.591	0.61	0.896	1.01	0.493	0.66	0.849
	end	12	12.62	<0.001***	1.14	0.414	0.71	0.716	0.82	0.630
S	mid	1	6.93	0.071	–	–	0.20	0.696	–	–
	end	1	262.19	<0.001***	6.69	0.116	19.88	0.009**	3.00	0.219
S × T	mid	1	3.46	0.200	–	–	8.77	0.084	–	–
	end	3	3.10	0.107	0.47	0.714	1.85	0.230	0.66	0.607
S × L	mid	2	0.06	0.946	–	–	26.26	0.037*	–	–
	end	2	0.02	0.982	0.36	0.715	0.04	0.962	0.43	0.668
S × T × L	mid	2	0.33	0.724	–	–	0.07	0.932	–	–
	end	6	1.14	0.393	1.14	0.393	0.51	0.793	1.12	0.405
S × A × (T × L)	mid	18	1.39	0.145	–	–	1.02	0.440	–	–
	end	12	1.07	0.389	0.80	0.646	0.96	0.485	0.74	0.709

26.7 ± 0.80; LH: females, 25.0 ± 1.10; males, 26.1 ± 0.64). Differences between sexes in the mean jaw height index within treatments were considered too small (< 0.06) to be biologically meaningful.

There were no significant effects of Tier or Aquarium, except for a significant effect of Aquarium on gonad index at the end of the experiment ($P < 0.001$, Table 1) which we attribute to spawning in some of the aquaria. Dissections at the end of the experiment indicated that 3 males (from HL and LH treatments) and 14 females (all treatments) had partially or completely spawned. Their gonads did not ooze gametes upon dissection and, in those considered completely spent (1 male from HL treatment; 6 females from HH, HL, and LH treatments), were small and lacked ova or sperm. Urchins which appeared to be partially or completely spawned were excluded from all statistical analyses of reproductive measures.

The sequential reduction in nutritive cells and proliferation of germinal cells which characterizes the gametogenic process in both sexes was evident in all treatments during the experiment. There were no significant differences between H and L treatments in the proportion (by cross-sectional area of gonadal lobe) of spermatocytes, spermatozoa, or nutritive phagocytes in the testes by the middle of the experiment (Fig. 2a, b, c; Table 2). By the end of the experiment, however, males in the HH and LH treatments had significantly smaller proportions of spermatozoa in their testes, and significantly greater proportions of spermatocytes, than males in the LL and HL treatments (Fig. 3a, b; Table 2). There were no significant differences among feeding treatments in the proportion of nutritive phagocytes in testes at the end of the experiment (Fig. 3c; Table 2). Females in the H treatment had a greater proportion of nutritive phagocytes in their ovaries by the middle of the experiment than females in the L treatment (Fig. 2d; Table 2). This trend was still evident at the end of the experiment: females in the HH and LH treatments had significantly greater proportions of nutritive phagocytes in their ovaries than females in the LL and HL treatments (Fig. 2d; Table 2). Oocyte size (by cross-sectional area) increased in all feeding treatments as oocytes matured into ova (Fig. 3). Kruskal–Wallis tests showed no effect of treatment on median oocyte or ovum size at either the middle (oocytes: $\chi^2 = 0.001$, $df = 1$, $P = 0.988$) or the end (oocytes: $\chi^2 = 1.119$, $df = 3$, $P = 0.773$; ova: $\chi^2 = 0.291$, $df = 3$, $P = 0.962$) of the experiment. There were no significant effects of Tier or Aquarium on any histological measurement (Table 2).

Mean feeding rate on kelp supplied ad libitum at the end of the experiment was significantly greater for urchins from the HL and LL treatments than for those in the HH and LH treatments (one-way ANOVA: $df = 3, 20$; $F = 8.85$; $P < 0.001$; Student–Newman–Keuls multiple comparisons of means test: $P < 0.05$) (Fig. 4).

Discussion

Strongylocentrotus droebachiensis continuously fed kelp (*Laminaria longicruris*) to satiation, either throughout or during the latter part of the reproductive cycle, had a

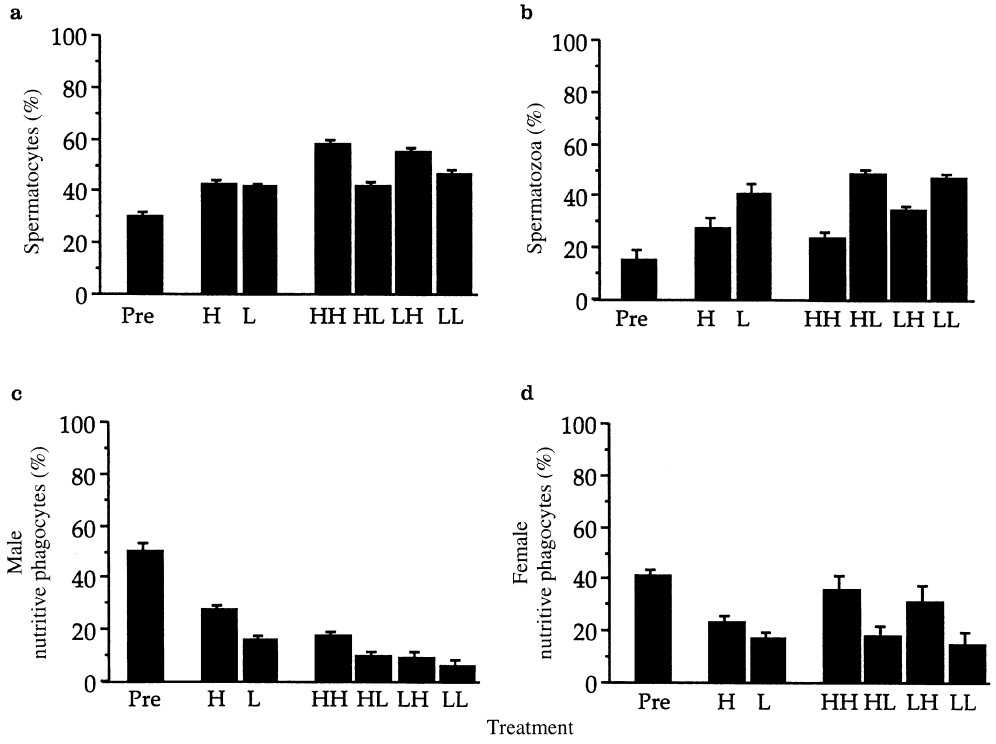

Fig. 2 *Strongylocentrotus droebachiensis*. Mean (±SE) relative abundance (percentage of gonadal lobe cross-sectional area) of **a** spermatocytes, **b** spermatozoa, **c** male nutritive phagocytes, and **d** female nutritive phagocytes for different feeding treatments (see Fig. 1 for abbreviations) at three times during the 24-wk experiment: pre-experiment (Pre), middle (H and L), and end (HH, HL, LH, and LL). Means are based on raw data pooled over individuals of each sex within aquaria and over all levels of Tier and Aquarium. Sample sizes for males (**a**, **b**, **c**) are: pre-experiment, 22; middle, 22 to 23; end, 9 to 13. Sample sizes for females (**d**) are: pre-experiment, 15; middle, 19 to 21; end, 6 to 12

Table 2 *Strongylocentrotus droebachiensis*. Nested analysis of variance of the relative abundance (percentage of gonadal lobe cross-sectional area) of spermatocytes, spermatozoa, and male and female nutritive phagocytes at the mid point and end of a 24-wk experiment. Data are degrees of freedom (*df*), *F*-ratio and *P*-value (*$P < 0.05$) for Feeding Treatment (*T*), Tier (*L*), Aquarium (*A*, nested in Treatment × Tier), and the interaction of Feeding Treatment and Tier

Source	Period	*df*	Spermatocytes		Spermatozoa		Male nutritive phagocytes		Female nutritive phagocytes	
			F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
T	mid	1	0.71	0.487	6.99	0.117	7.28	0.113	2.21	0.275
	end	3	5.19	0.039*	8.92	0.011*	1.39	0.332	6.18	0.029*
L	mid	2	6.41	0.135	2.37	0.297	0.41	0.707	0.64	0.610
	end	2	2.16	0.193	1.58	0.277	0.32	0.739	1.64	0.271
T × L	mid	2	0.28	0.760	0.49	0.622	0.71	0.508	1.45	0.261
	end	6	1.08	0.423	0.54	0.768	1.71	0.192	1.66	0.215
A(T × L)	mid	18	1.08	0.429	1.42	0.220	0.90	0.592	1.57	0.144
	end	12	0.99	0.488	1.22	0.332	0.78	0.676	1.09	0.417

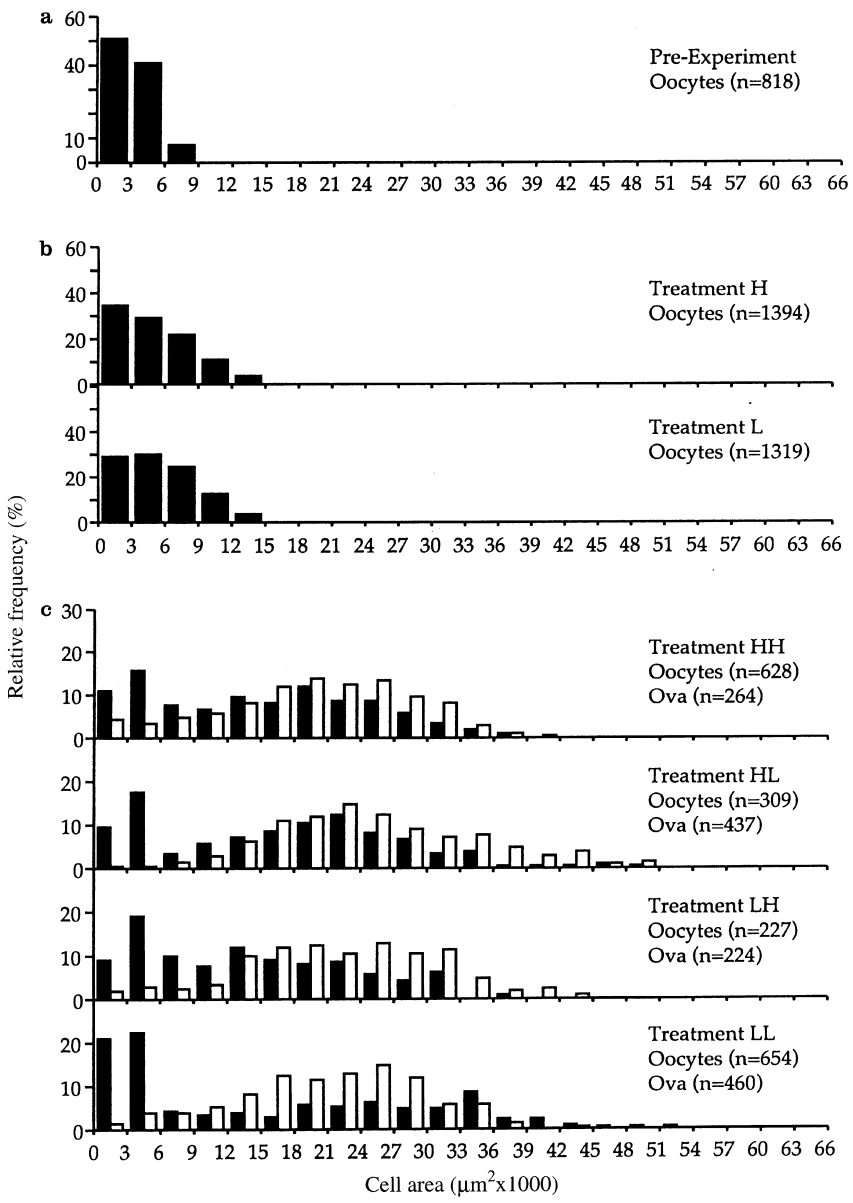

Fig. 3 *Strongylocentrotus droebachiensis*. Size–frequency distributions of oocytes (*shaded bars*) and ova (*open bars*) for different feeding treatments (see Fig. 1 for abbreviations, *n* is sample size) at three times during the 24-wk experiment: **a** pre-experiment, **b** middle (H and L), and **c** end (HH, HL, LH, and LL)

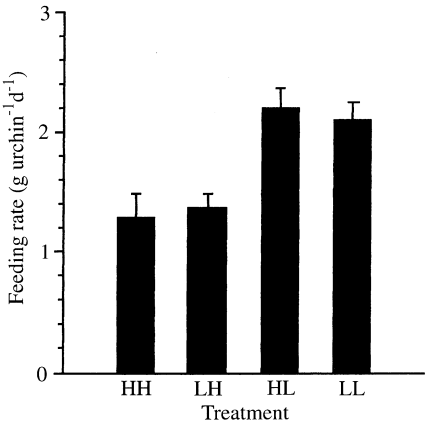

Fig. 4 *Strongylocentrotus droebachiensis*. Mean (±SE, $n = 6$) feeding rate (g kelp urchin^{-1} d^{-1}) for different feeding treatments (see Fig. 1 for abbreviations) at the end of the 24-wk experiment

significantly greater gonad index and wet weight than urchins fed a smaller ration (kelp once a week). These results are consistent with previous laboratory and field studies demonstrating that a diet of laminarian kelp, a preferred food of *S. droebachiensis*, markedly enhances urchin growth and reproduction (Himmelman and Steele 1971; Vadas 1977; Himmelman 1978; Larson et al. 1980; Thompson 1983; Briscoe and Sebens 1988; Munk 1992). They also show that both the ration and the feeding regime (timing of provision of a given ration) relative to the reproductive cycle are important determinants of somatic and gonadal growth. Urchins switched from the low to the high ration for the latter part of the reproductive cycle had a greater gonad index and body size than those switched from the high to the low ration.

Despite a large effect on gonadal size, food ration had relatively little effect on gametogenesis and maturation. The progression of nutritive and germinal cells in both sexes was similar among all feeding treatments and consistent with previous descriptions of gametogenesis in *Strongylocentrotus* spp. (Chatlynne 1969; Gonor 1973a, b; Bernard 1977; Himmelman 1978; Falk-Petersen and Lonning 1983). Nutritive phagocytes (storage cells rich in glycogen) were generally more abundant in the gonads of urchins fed continuously, either throughout or in the latter part of the reproductive cycle, suggesting that the higher ration provided additional reserves for gametogenesis. Our different feeding treatments had no effect on egg size distributions in females. However, measures of egg size give no indication of potential differences in egg quality which may influence larval development and survival (George et al. 1990). Thompson (1983) showed that female *S. droebachiensis* fed a low ration released eggs of similar size but with a lower lipid and energy content than those fed higher rations. Similarly, de Jong-Westman et al. (1995b) found that *S. droebachiensis* fed different artificial diets produced eggs that were of similar size but which differed in energy and organic content, and produced larvae that differed in morphology and developmental rate.

Male *Strongylocentrotus droebachiensis* fed the low ration in the latter part of the reproductive cycle had proportionally more spermatozoa and less spermatocytes in testes than males fed the high ration. This may reflect a sampling artifact: males in the high ration treatments probably lost more sperm during dissection and histological preparation than those in the low ration treatments. Males in general matured earlier than females, which is consistent with previous studies of *S. droebachiensis* (Stephens 1972; Munk 1992) and other congeneric species (Lasker and Giese 1954; Bennett and Giese 1955; Fuji 1960a, b).

A significant effect of the nested factor Aquarium on final gonad index is attributed to variable spawning of some urchins (mainly females), which we were unable to detect. Since spawning of *Strongylocentrotus droebachiensis* is relatively synchronous (Himmelman 1978), we probably terminated our experiment at the onset of the spawning period. The concurrence of spawning among our different feeding treatments suggests that factors other than adult nutritional condition (e.g. temperature, photoperiod, or spring phytoplankton levels) may cause the interannual and regional differences in spawning time observed in field studies (Stephens 1972; Himmelman 1978; Munk 1992). Females had a higher gonad index than males at the end of the experiment but only in the low ration treatments. Partial spawning of some females in the high ration treatments may have resulted in underestimation of female gonad index. Previous studies also have recorded higher female than male gonad indices at the peak of the reproductive period of *S. droebachiensis* (Munk 1992; de Jong-Westman et al. 1995a) but not other congeneric species (Bennett and Giese 1955; Bernard 1977; Fuji 1960b).

Jaw height index was greater in urchins fed the low ration throughout or during the latter half of the experiment, although differences between feeding treatments were not statistically significant. These differences are due to differences in test diameter, which varies inversely with the jaw height index, rather than differences in absolute jaw size (see also Levitan 1991). Our results do not support Ebert's (1968) contention that sea urchins allocate energy to increase jaw size when food is scarce. As pointed out by Levitan (1991), the degree of deviation from the jaw height index for well-fed urchins can be used as an index of food limitation for a species. Thus our index for the HH treatment (33.3) may be used as a benchmark to assess the nutritional condition of similar sized *Strongylocentrotus droebachiensis* in natural habitats.

Urchins fed the low ration had a higher feeding rate than continuously fed urchins when provided with kelp at the end of the experiment. Increased feeding activity during periods of high food availability may increase the rate of nutrient acquisition in urchins which are otherwise food limited. Increased gut passage time and absorption efficiency are other mechanisms which may

enhance nutrition under low food conditions (Lawrence et al. 1989; Lares and McClintock 1991), although these were not measured in our study.

Our experimental results show that even relatively low rations of kelp (ad libitum once per week) support gonadal and somatic growth in *Strongylocentrotus droebachiensis*. The mean gonad index of urchins in the continuous low ration (LL) treatment at the end of the experiment (15.5, sexes pooled) was lower than that concurrently recorded at Little Duck Island for urchins in the kelp bed (16.9 ± 3.4 SD) or along the grazing front (16.8 ± 3.6 SD), but higher than that recorded for urchins (from the same source population) in the barrens (12.2 ± 3.0 SD) (S. K. Meidel unpublished data). Sea urchins in barrens may derive a substantial proportion of their nutrition from drift algae, particularly kelps. The distribution of this resource is patchy in time and space; however, it is rapidly located and consumed by urchins in barrens. The availability of drift algae may increase towards the latter part of the urchin's reproductive cycle as plants are more likely to be dislodged and fragmented by winter storms. Our experimental results suggest that increased supply of drift kelp, particularly during winter, could markedly increase gonadal growth and contribute to the persistence of sea urchins in these habitats. Our results also show that a diet of unlimited kelp results in high rates of gonadal and somatic growth. The mean gonad index of urchins in the continuous high ration (HH) treatment at the end of the experiment (27.0) markedly exceeded that of urchins within the kelp bed or along the grazing front at Little Duck Island, presumably due to lower foraging costs and higher per capita food availability in laboratory aquaria. The increase in body size, reproductive effort and fecundity of sea urchins which occurs during destructive grazing of kelp beds presumably results in increased larval production, which may perpetuate or accelerate an urchin outbreak through increased recruitment.

With the expansion of the roe fishery for *Strongylocentrotus* spp. on both coasts of North America (Kato and Schroeter 1985; Sloan 1985; Scheibling and Hatcher 1994), there is increasing interest in sea urchin ranching and aquaculture (Tegner 1989). Our experimental results demonstrate that a diet of laminarian kelp can markedly increase roe yield over intervals of 12 to 24 weeks. In addition, we have shown that urchins need only be fed a high ration in the latter part of the reproductive cycle to maximize roe yield. This finding should improve the cost effectiveness of culturing *S. droebachiensis* and other commercially important sea urchins.

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