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Annual reproductive cycle of the green sea urchin, *Strongylocentrotus droebachiensis*, in differing habitats in Nova Scotia, Canada

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Abstract We monitored the reproductive cycle of *Strongylocentrotus droebachiensis* (OF Müller) between April 1993 and August 1995 in kelp beds, barren grounds and grazing fronts at both a wave-exposed and a sheltered site along the Atlantic coast of Nova Scotia. Gonad index and histological analyses showed that *S. droebachiensis* has an annual reproductive cycle that is synchronous across sites and habitats, and between females and males. Spawning occurs in March/April of each year but a small proportion of sea urchins in the study populations also spawned in fall 1995. During most of the year, sea urchins in kelp beds and grazing fronts have a higher gonad index than those in barren grounds. Gonad indices also tended to be higher at the wave-exposed than the sheltered site. Interannual variability in peak gonad index was significant in the barren grounds at the wave-exposed site and in the grazing front at the sheltered site. The gametogenic cycle is characterized by six stages based on the abundance of nutritive and germinal/gametic cells. Nutritive phagocytes are abundant after spawning and replaced by increasing numbers of germinal and gametic cells as the gametogenic cycle progresses. The temporal patterns of abundance of each cell type were similar among habitats indicating that the gonads were qualitatively similar despite large differences in gonadal mass. The quantity of gut contents (ratio of food volume to body volume) was similar among habitats, but the quality (percentage of organic material) tended to be higher in kelp beds and grazing fronts than in barren grounds suggesting that differences in gonad index of *S. droebachiensis* in different habitats are related to differences in diet. The high density of sea urchins in grazing fronts combined with their high fecundity suggests that they make the greatest contribution, per unit area, to the overall larval pool.

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Introduction

The green sea urchin, *Strongylocentrotus droebachiensis*, is the dominant herbivore in the shallow, rocky, subtidal zone in eastern Canada (Miller and Mann 1973; Mann 1977). Along the Atlantic coast of Nova Scotia, large-scale fluctuations in population size of *S. droebachiensis* cause dramatic changes in the state of the shallow subtidal ecosystem (Mann 1977; Wharton and Mann 1981; Miller 1985; Scheibling 1986). When sea urchins are in low abundance, kelp beds (mainly *Laminaria longicruris* and *L. digitata* and various understorey algae) flourish in the rocky subtidal zone. Sea urchins in kelp beds are usually cryptic and sparsely distributed. They function mainly as detritivores consuming drift algae in crevices and under boulders (Mann 1985). As sea urchins increase in number, they begin to aggregate along the edge of kelp beds forming "fronts" which destructively graze the kelp (Breen and Mann 1976; Lang and Mann 1976; Wharton 1980). These grazing fronts can advance at rates of 1 to 4 m per month creating extensive barren grounds denuded of fleshy macroalgae (Breen and Mann 1976; Scheibling et al. 1994).

The mechanisms leading to sea urchin population increases are poorly understood, but may include sporadic recruitment events (Hart and Scheibling 1988; Scheibling 1996) and/or migration (Foreman 1977; Scheibling et al. in preparation). The formation of dense grazing fronts may initiate positive feedback mechanisms that drive a population outbreak. For example, increased fecundity due to consumption of kelp (Vadas 1977; Larson et al. 1980), or increased fertilization rate due to the proximity of spawning individuals (Pennington 1985), may result in increased larval production. If the advance of the fronts is uninterrupted (e.g. by mass mortality because of disease or harvesting), the subtidal ecosystem will shift from the kelp bed to the barren

ground state over several years (Breen and Mann 1976; Mann 1977). Sea urchins may persist long after the disappearance of kelp beds but rates of growth and reproduction decrease as they adjust to lower food availability (Lang and Mann 1976; Wharton and Mann 1981; Johnson and Mann 1982; Chapman and Johnson 1990).

Strongylocentrotus droebachiensis has an annual reproductive cycle with a major spawning period (as evidenced by a decline in gonad index) in late winter or early spring (Cocanour and Allen 1967; Himmelman 1978; Falk-Petersen and Lønning 1983; Keats et al. 1984; Munk 1992). Some spawning also has been observed in summer and fall off Newfoundland (Keats et al. 1987). Numerous studies have shown that food quantity and quality strongly influence reproduction of *S. droebachiensis* and other sea urchins (e.g. Lasker and Giese 1954; Ebert 1968; Lawrence 1975; Vadas 1977; Larson et al. 1980). The greater gonad index of *S. droebachiensis* in kelp beds than barren grounds (Lang and Mann 1976; Wharton 1980; Johnson and Mann 1982; Keats et al. 1984; Sivertsen and Hopkins 1995) is generally attributed to differences in food availability between these two habitats (Lang and Mann 1976; Sivertsen and Hopkins 1995). However, few investigators have included gut content analysis in their studies, and usually only the occurrence of particular food items is recorded (Himmelman and Steele 1971; Chapman 1981; Himmelman and Nédélec 1990). Consequently, there is little quantitative information to compare the amounts and type of food consumed by sea urchins in kelp beds versus barren grounds.

Wave exposure is another factor that may directly or indirectly influence the reproduction of sea urchins at a site. For example, the supply of drift algae may be greater at wave-exposed sites due to increased wave action which dislodges and transports plants (Rogers-Bennett et al. 1995). However, Ebert (1968) and Gonor (1973a) found that *Strongylocentrotus purpuratus* at exposed sites had reduced gonad indices compared to those at sheltered sites. Ebert (1968) attributed this difference to a higher cost of repair for broken spines at the exposed site, leaving less energy available for reproduction.

In the present study, we compare the reproduction of subpopulations of *Strongylocentrotus droebachiensis* in kelp beds and barren grounds, and in grazing fronts at the ecotone between these two habitats, at both a wave-exposed and a sheltered site in Nova Scotia. We use both gonad index and histological methods to quantify the reproductive cycle and to examine the effects of habitat and site on maturation and spawning. Also, we compare gut contents of sea urchins in the different habitats and sites to relate differences in reproductive patterns to quantity and quality of consumed food. Finally, we combine data on reproduction with other population characteristics to examine the relative contribution of sea urchins in kelp beds, grazing fronts, and barren grounds to the overall larval pool.

Materials and methods

Study sites and sea urchin subpopulations

We studied the reproductive cycle of *Strongylocentrotus droebachiensis* (OF Müller) at two sites along the southwestern shore of Nova Scotia: Little Duck Island (44°22′N; 64°11′W), a wave-exposed island at the mouth of Mahone Bay, and Mill Cove (44°35′N; 64°3′W), a sheltered cove in St. Margaret's Bay. At Little Duck Island, the substratum consisted of basaltic bedrock intersected by ridges and grooves. At Mill Cove, the underlying granitic bedrock was covered with rocks and boulders. At both sites, the study areas were at a depth of 6 to 9 m.

We compared sea urchins from kelp beds and adjacent barren grounds, and from grazing fronts at the interface between the two habitats. Kelp beds at both sites consisted of a dense canopy of *Laminaria longicruris* with an understorey of branching (e.g. *Ceramium rubrum*, *Plumaria plumosa*) and foliose algae (e.g. *Chondrus crispus*, *Palmaria palmata*), and articulated coralline algae (*Corallina officinalis*). At Little Duck Island, kelp plants were relatively short with narrow and ruffled blades, a morphology associated with high wave exposure (Gerard and Mann 1979). At Mill Cove, kelp density was lower and the plants were longer, wider, and thinner. Barren grounds at both sites were dominated by encrusting coralline algae (mainly *Phymatolithon laevigatum*, *Lithothamnion glaciale*) with scattered patches of ephemeral filamentous algae (mainly *Desmarestia viridis*) appearing in summer/fall. Barren grounds also received input of drift algae (mainly kelp) from the adjacent kelp beds. The grazing front at the interface of the kelp bed and barren grounds was characterized by kelp stipes (stripped of blades) and articulated corallines, which were the last erect macroalgae to be consumed by the sea urchins.

At both sites, sea urchin density and mean size differed in space and time. In the kelp beds at both sites, sea urchins were sparsely distributed throughout the study period (mean density: <20 urchins m^{-2}; Scheibling unpublished data). Sea urchin density was greater in the barren grounds (mean density: $\sim$120 and $\sim$40 urchins m^{-2} at Little Duck Island and Mill Cove, respectively) and highest in the grazing fronts (up to 400 and up to 160 urchins m^{-2}, respectively; Scheibling and Hennigar 1997; Scheibling unpublished data). In October 1993, an outbreak of disease reduced the sea urchin population at Little Duck Island by 87%, but by summer 1995 sea urchin densities had returned to pre-disease levels (Scheibling and Hennigar 1997; Scheibling unpublished data). Throughout the study period, sea urchins in grazing fronts were much larger (mean test diameter: $\sim$50 and $\sim$30 mm at Little Duck Island and Mill Cove, respectively) than those in barren grounds ($\sim$17 and $\sim$12 mm, respectively) and kelp beds ($\sim$20 and $\sim$16 mm, respectively; Scheibling unpublished data).

Analysis of gonad index

We sampled *Strongylocentrotus droebachiensis* at approximately 1-month intervals in each habitat at each site between March/April 1994 and August 1995. Additional monthly samples were collected from April 1993 to March 1994 in the barren grounds and grazing front at Little Duck Island. At each sampling date (except March/April 1995, see below), we collected 8 to 25 urchins of 35 to 50 mm test diameter in 10 (grazing front and barren grounds) or 20 (kelp bed) 0.25-m^2 quadrats. The quadrats were haphazardly placed within a 4×40 m transect in both the kelp bed ($\sim$5 m from the offshore edge of the kelp bed) and barren grounds (10 to 15 m from the edge), and along 40 m of the approximately 2-m-wide grazing front. Sea urchins collected between April 1993 and March 1994 at Little Duck Island were frozen upon return to the laboratory and processed 6 to 15 months later. Sea urchins collected between March/April 1994 and August 1995 at both sites were kept individually in perforated plastic containers (to enable collection of faeces) in flow-through aquaria at ambient water temperatures. These sea urchins were processed live within 24 to 72 h of collec-

tion. Total body wet weight and gonad wet weight were measured with an electronic balance (0.01 g accuracy). Gonad index was calculated [(gonad wet weight/total body wet weight) × 100] to give a percentage. Sex was determined by examining a gonad smear under a compound microscope. Horizontal test diameter was measured with vernier calipers (0.05 mm accuracy).

Temporal patterns in gonad index of female and male sea urchins were compared across habitats (kelp bed, grazing front, barren grounds) using three-way analysis of variance (ANOVA) with Date (March 1994 to August 1995, when sea urchins were sampled concurrently in all three habitats), Habitat, and Sex as fixed factors. Gonad indices for each sex at the peak of the reproductive cycle were compared between years using one-way ANOVA (grazing front and barren grounds at Little Duck Island, 1993 to 1995) or *t*-tests (kelp bed at Little Duck Island, grazing front and barren grounds at Mill Cove, 1994 and 1995; a missed sampling interval for the kelp bed at Mill Cove at the peak of the reproductive cycle in 1994 precluded statistical analysis in this habitat). Gonad index at the peak of the reproductive cycle (March/April 1995) and after spawning was completed (June 1995) was compared between sites and sexes, and among habitats (all classified as fixed factors) by three-way ANOVA. We classified Site as a fixed factor because the two study sites were chosen to represent different degrees of exposure to wave action. Raw data were arcsine transformed to remove heterogeneity of variance as indicated by Cochran's *C*-test ($p < 0.05$). Because sample sizes varied between sites, dates, habitats and sexes, we used Type III sums of squares, and carried out post-hoc comparisons using the GT2-method (Sokal and Rohlf 1995).

To examine changes in gonad index with body size in *Strongylocentrotus droebachiensis* and to confirm that the gonad index of adult sea urchins within the size range used in our study was independent of test diameter, we sampled 66 to 75 sea urchins between 14.3 and 74.9 mm in each habitat at the peak of the reproductive season in 1995 (late March/early April). In *S. droebachiensis*, the development of gonad index with increasing test diameter can be described with a logistic growth model (Munk 1992). We related gonad index to size using the following function:

$$Y = \frac{Y_0 M}{Y_0 + (M - Y_0)\mathrm{e}^{-kM(d-15)}} \quad , \qquad (1)$$

where Y is gonad index, Y_0 is gonad index in immature sea urchins (given a small positive value, 0.1), M is the asymptotic gonad index, k is a constant, and d is test diameter. In all cases the logistic model provided a better fit to our data than a straight-line regression. We used linear regression techniques to analyse the relationship between gonad index (arcsine transformed) and adult body size (35 to 50 mm) in *S. droebachiensis* at the peak of the reproductive cycle. In ~50% of samples collected at the peak of the reproductive cycle, a few individuals (usually <4 per sex) appeared to have already started to release gametes (i.e. had partly spawned). These sea urchins were excluded from statistical and graphical analysis.

Histological analysis

At each sampling date between June 1994 and May 1995, gonads of 2 to 12 female and 3 to 8 (1 in a single case) male sea urchins were prepared using standard histological techniques. Serial cross sections (7 μm) were cut through the centre of a gonad and stained with haematoxylin and eosin. For analysis of reproductive maturation, histological sections were classified according to the six maturity stages used by Byrne (1990) and King et al. (1994): Stage I, recovering; Stage II, growing; Stage III, premature; Stage IV, mature; Stage V, partly spawned; and Stage VI, spent. This classification scheme is based on changes in the relative abundance of different cell types present in gonads during the maturation process. In samples from February/March and March/April 1995, the ripe gonads of 58 mature sea urchins (27 females, 31 males) disintegrated upon processing and could not be preserved for histological analysis. These sea urchins were classified as mature and included in the analysis of reproductive maturation.

For quantitative analysis of reproductive maturation, histological sections from selected dates from both sites (June, October and December 1994, and February/March, March/April and May 1995) were analysed using light microscopy and a computerised image analysis system (NIH *Image*, Version 1.59; National Institutes of Health, Bethesda, Maryland, USA). Only gonadal acini that fit within the frame size of the image analysis system (719 μm^2) were analysed. For ovaries, the relative areas (expressed as a percentage of total acinal area) of nutritive phagocytes, oocytes, and unoccupied lumen were measured in eight acini, and the absolute areas of oocytes and ova were measured in four acini. Only oocytes sectioned through the nucleolus and ova sectioned through the nucleus were measured. All cells surrounding the germinal cells were classified as nutritive phagocytes. For testes, the relative areas of nutritive phagocytes, spermatocytes, spermatozoa, and unoccupied lumen were measured in eight acini. These measurements were used to quantify the different maturity stages.

The relative areas of nutritive phagocytes (females and males), spermatocytes and spermatozoa, and the absolute areas of oocytes and ova, were compared at each site by two-way ANOVA with Date (June 1994 to May 1995, except for ova: February/March to May 1995 only), and Habitat as fixed factors. For each sea urchin, the relative or absolute area of a cell type was averaged over measurements for all acini and used as a replicate. Relative areas were arcsine transformed to remove heterogeneity of variance as indicated by Cochran's *C*-test ($p < 0.05$). Because sample sizes varied between dates and habitats, we used Type III sums of squares, and carried out post-hoc comparisons using the *T′*-method, which in this case was more conservative than the GT2-method (Sokal and Rohlf 1995).

Analysis of diet

To compare the quality and quantity of food consumed by *Strongylocentrotus droebachiensis* in the different habitats, we analysed the gut contents and faeces of all sea urchins dissected for gonad index analysis at approximately 1-month intervals between April/May 1994 and August 1995. Food particles were removed from the entire digestive system (pharynx to anus) and added to the faeces collected in the plastic containers prior to dissection. Particles were examined under a dissecting microscope and divided into organic and inorganic material. Organic material consisted of remains of fleshy, filamentous or branching macroalgae, mainly of the genera *Laminaria*, *Chondrus*, *Palmaria*, and *Desmarestia*. Non-organic material consisted of remains of articulated coralline algae, pellets consisting of sediment and scrapings of encrusting coralline algae. On a few dates, empty zoaria of an epiphytic bryozoan (*Membranipora membranacea*) were present on some kelp particles in gut contents. No other animal remains were observed. The number of food particles in each category, organic or inorganic material, was counted and converted to a percentage. All food particles were then placed in a calibrated vial and allowed to settle for ~1 h, when the total food volume was measured. An index of food quality was calculated as the percentage of the total gut content (plus faeces) that was organic material. An index of food quantity was calculated as the ratio of total food volume to total body volume. Total body volume was estimated from test diameter based on a sample of 96 sea urchins (13 to 69 mm) collected in March/April 1995 in all habitats and at both sites. Volume (V) was measured by placing an urchin in a water-filled container and weighing the amount of water displaced. The measurement was repeated, and the average of the two measurements was log transformed and related to log test diameter (TD) by linear regression ($r^2 = 0.998$):

$$\ln(V) = -7.235 + 2.820 \times \ln(TD) \quad . \qquad (2)$$

Food quantity and quality were compared by two-way ANOVA with Date (food quantity: June 1994 to August 1995; food quality: April/May 1994 to August 1995) and Habitat as fixed factors. The same sums of squares and post-hoc comparisons were used as for gonad indices.

Results

Spatial and temporal patterns in gonad index

Strongylocentrotus droebachiensis displays a distinct annual cycle of reproduction as indicated by temporal changes in gonad index between 1993 and 1995 (Fig. 1). Most spawning occurred in March/April of each year, resulting in a sharp drop in gonad index. In the kelp bed and the grazing front at Mill Cove in 1995, the peak gonad index declined more slowly and spawning may have extended into May. The overall cycle is relatively synchronous across sites and habitats, and also between females and males. At each site, there was a significant

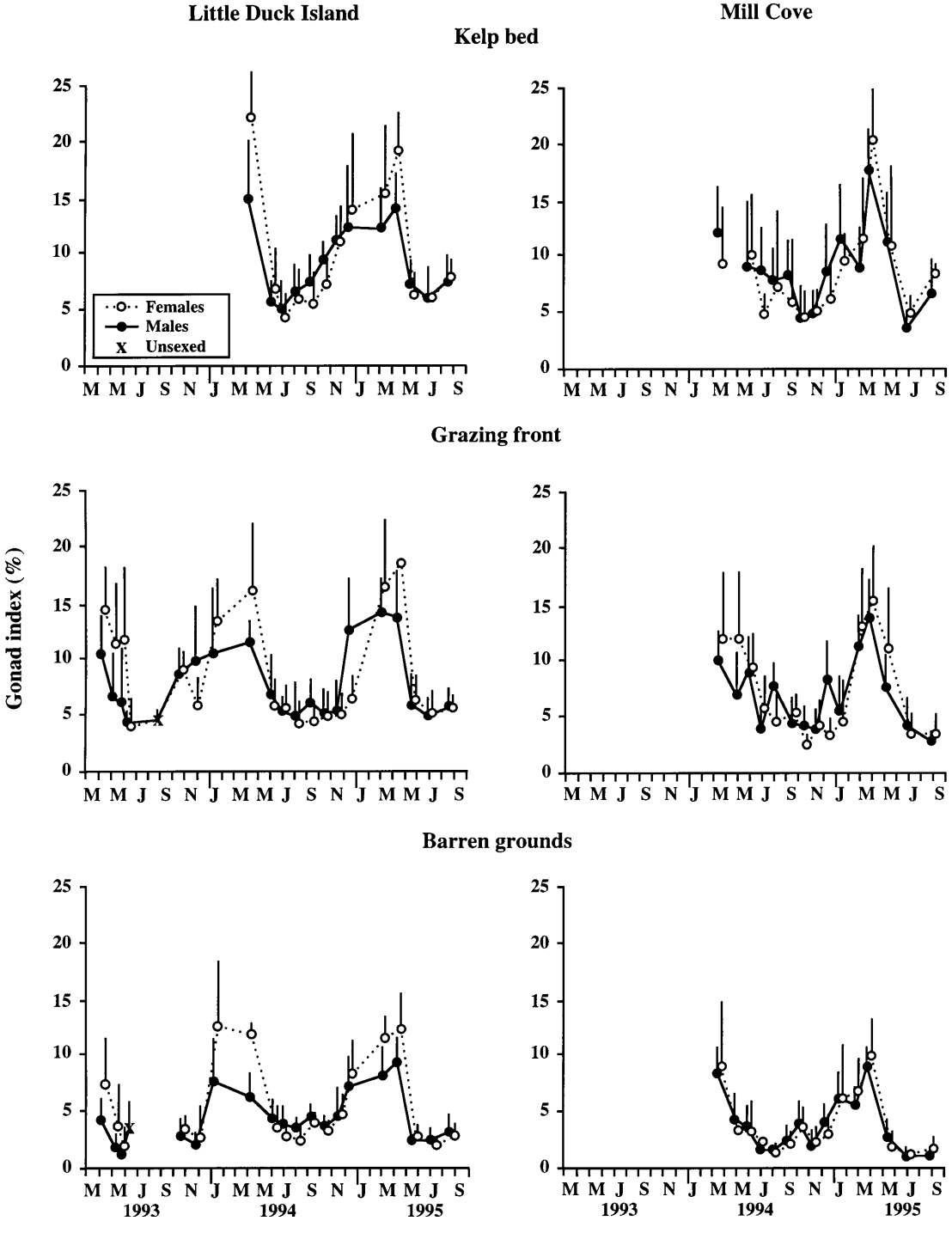


Fig. 1 *Strongylocentrotus droebachiensis*. Mean gonad index (percentage of total body wet weight, ±SD) for female, male or unsexed sea urchins (35 to 50 mm test diameter) at Little Duck Island and Mill Cove between April 1993 and August 1995 in the kelp bed, the grazing front and the barren grounds. Means are based on 2 to 17 sea urchins

Table 1 *Strongylocentrotus droebachiensis*. Three-way ANOVA of the effects of Date, Habitat, and Sex on gonad index (arcsine transformed) and GT2 post-hoc comparisons of the simple effects of Habitat (sexes pooled) and Sex (habitats pooled) at each date at Little Duck Island and Mill Cove [*Date*: Mar/Apr 1994 to Aug 1995; *Habitat*: kelp bed (*KB*), grazing front (*GF*), barren grounds (*BG*); *Sex*: female (*f*), male (*m*); *NS* not significant; $*p < 0.05$; $**p < 0.01$; $***p < 0.001$; *nd* no data]

Test	Little Duck Island				Mill Cove			
ANOVA	*df*	MS	*F*	*p*	*df*	MS	*F*	*p*
Date	12	609.46	76.66	<0.001***	14	542.42	45.61	<0.001***
Habitat	2	1069.63	134.55	<0.001***	2	1314.60	110.53	<0.001***
Sex	1	17.06	2.15	0.144 NS	1	0.52	0.04	0.834 NS
Date × Habitat	24	29.73	3.74	<0.001***	28	49.22	4.14	<0.001***
Date × Sex	12	34.27	4.31	<0.001***	14	21.09	1.77	0.039*
Habitat × Sex	2	2.66	0.33	0.716 NS	2	4.59	0.39	0.680 NS
Date × Habitat × Sex	24	7.43	0.94	0.553 NS	28	14.42	1.21	0.209 NS
Error	571	7.95			646	11.89		
GT2-test	Habitat		Sex		Habitat		Sex	
Mar 1994	nd		nd		NS		NS	
Apr 1994	KB > GF > BG		f > m		GF > BG		f > m	
May 1994	KB, GF > BG		NS		KB, GF > BG		NS	
Jun 1994	GF > BG		NS		KB > GF > BG		NS	
Jul/Aug 1994	KB > BG		NS		KB, GF > BG		NS	
Sep 1994	NS		f < m		KB, GF > BG		NS	
Oct 1994	KB > GF, BG		NS		NS		NS	
Nov 1994	KB > GF, BG		NS		KB, GF > BG		NS	
Dec 1994	KB > GF, BG		NS		KB, GF > BG		f < m	
Jan 1995	nd		nd		KB > GF, BG		NS	
Feb/Mar 1995	KB, GF > BG		f > m		KB, GF > BG		NS	
Mar/Apr 1995	KB, GF > BG		NS		KB > GF > BG		NS	
May 1995	KB, GF > BG		NS		KB, GF > BG		NS	
Jun 1995	KB, GF > BG		NS		KB, GF > BG		NS	
Aug 1995	KB, GF > BG		NS		KB > GF > BG		NS	

interaction between the effects of sampling date and habitat on gonad index (Table 1). Post-hoc comparisons (GT2-test) showed that the gonad index in the barrens was significantly lower than in the kelp bed and/or the grazing front on all dates except September 1994 at Little Duck Island, and on all dates except in March and October 1994 at Mill Cove. There also was a significant interaction between the effects of sampling date and sex on gonad index (Table 1). At Little Duck Island, females had a significantly higher gonad index than males at the peak of the gonad index cycle in April 1994 and March 1995, and males had a significantly higher index than females in September 1994. At Mill Cove, females also had a higher gonad index than males in April 1994, and males had a higher index than females in December 1994.

At Little Duck Island, the peak gonad index in the barren grounds increased significantly from 1993 to 1995 for each sex (females: $F_{2,14} = 5.87$, $p = 0.014$; males: $F_{2,11} = 11.39$, $p = 0.002$), but there were no significant interannual differences in peak gonad index in either the grazing front (females: $F_{2,19} = 0.90$, $p = 0.422$; males: $F_{2,21} = 1.33$, $p = 0.285$) or the kelp bed (females: $t_9 = 1.57$, $p = 0.150$; males: $t_{22} = 1.90$, $p = 0.071$). At Mill Cove, peak gonad index in the barren grounds did not differ significantly between 1994 and 1995 (females: $t_{11} = 0.41$, $p = 0.692$; males: $t_6 = 0.98$, $p = 0.365$), but the gonad index in the grazing front was significantly higher in 1995 than in 1994 (females: $t_{25} = 2.28$, $p = 0.031$; males: $t_{19} = 2.90$, $p = 0.009$). The peak gonad index immediately prior to spawning in 1995 did not differ significantly between sites ($F_{1,105} = 1.60$, $p = 0.209$) but differed consistently between habitats at both sites (i.e. mean gonad index was highest in the kelp bed, lowest in the barren grounds; $F_{2,105} = 33.34$, $p < 0.001$). Gonad index also was consistently higher for females than males ($F_{1,105} = 10.91$, $p = 0.001$): there was no significant interaction between site, habitat and sex. The post-spawning gonad index (June 1995) was significantly higher at Little Duck Island than at Mill Cove ($F_{1,84} = 18.06$, $p < 0.001$). It was consistently higher in the kelp bed and grazing front than in the barren grounds at both sites ($F_{2,84} = 41.33$, $p < 0.001$), and did not differ significantly between females and males ($F_{1,84} = 1.74$, $p = 0.190$): there was no significant interaction between site, habitat and sex.

The relationship between the gonad index and test diameter of *Strongylocentrotus droebachiensis* just before spawning (Fig. 2) indicates that the development of macroscopic gonads begins at a size of ~15 mm in all habitats at both sites. Gonad index increases rapidly between 25 and 35 mm and then tends towards an asymptote that is determined by habitat. Linear regression confirmed that there was no relationship between gonad index and test diameter over the size range that we used to monitor the reproductive cycle (35 to 50 mm) (Table 2). There were no signs of reproductive senescence in large individuals up to 75 mm.

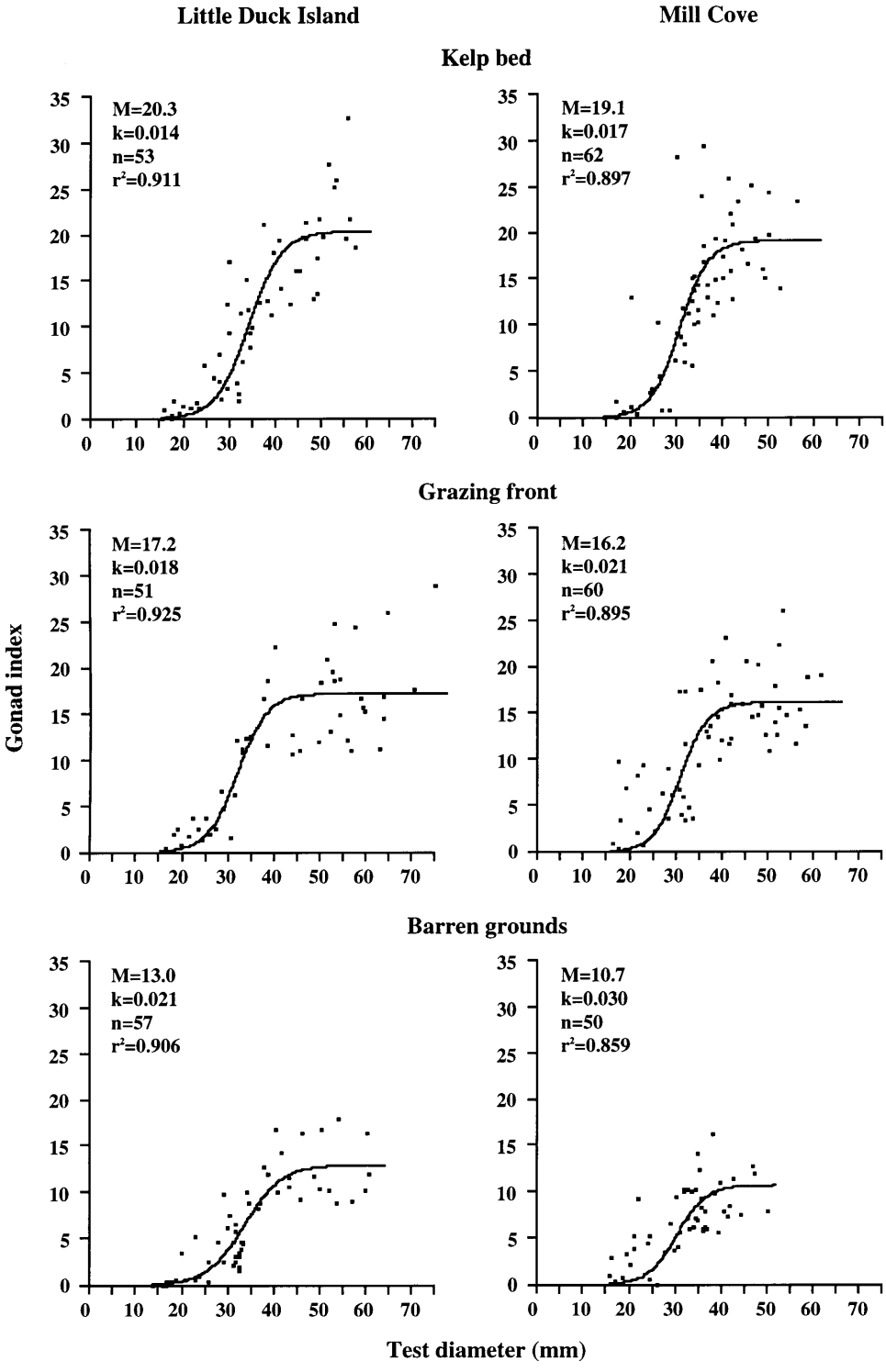


Fig. 2 *Strongylocentrotus droebachiensis*. Relationship between gonad index and test diameter (14.3 to 74.9 mm) in March (Mill Cove) and April (Little Duck Island) 1995 in the kelp bed, the grazing front, and the barren grounds. The plotted line represents the fit of Eq. 1 to each set. Parameter values for M (asymptotic gonad index), and k (a constant) are given for each relationship. Y_0 (gonad index in juveniles) equals 0.1 in all cases (n sample size; r^2 coefficient of determination)

Gametogenic cycle

The gametogenic cycles of female and male *Strongylocentrotus droebachiensis* were characterized by six maturity stages as illustrated by representative micrographs (Fig. 3). In Stage I (recovering) gonadal acini are filled with storage cells (nutritive phagocytes), and small numbers of germinal cells (oocytes in females, spermatocytes in males) are present along the acinal walls (Fig. 3a, g). In Stage II (growing), nutritive phagocytes decrease in abundance and are replaced by increasing numbers of oocytes or spermatocytes (Fig. 3b, h). In Stage III (premature), nutritive phagocytes further decrease in abundance and the first mature gametes (ova

Table 2 *Strongylocentrotus droebachiensis*. Results of linear regression analysis of gonad index (arcsine transformed) on test diameter (34.5 to 52.2 mm) (n sample size; r^2 coefficient of determination; p probability)

Site, habitat	Size range (mm)	n	r^2	p
Little Duck Island				
Kelp bed	35.2–49.8	17	0.152	0.122
Grazing front	34.5–50.9	13	0.035	0.541
Barren grounds	35.0–50.2	15	0.104	0.240
Mill Cove				
Kelp bed	34.7–52.2	28	0.033	0.650
Grazing front	35.0–50.3	24	0.008	0.685
Barren grounds	34.7–50.0	20	0.057	0.310

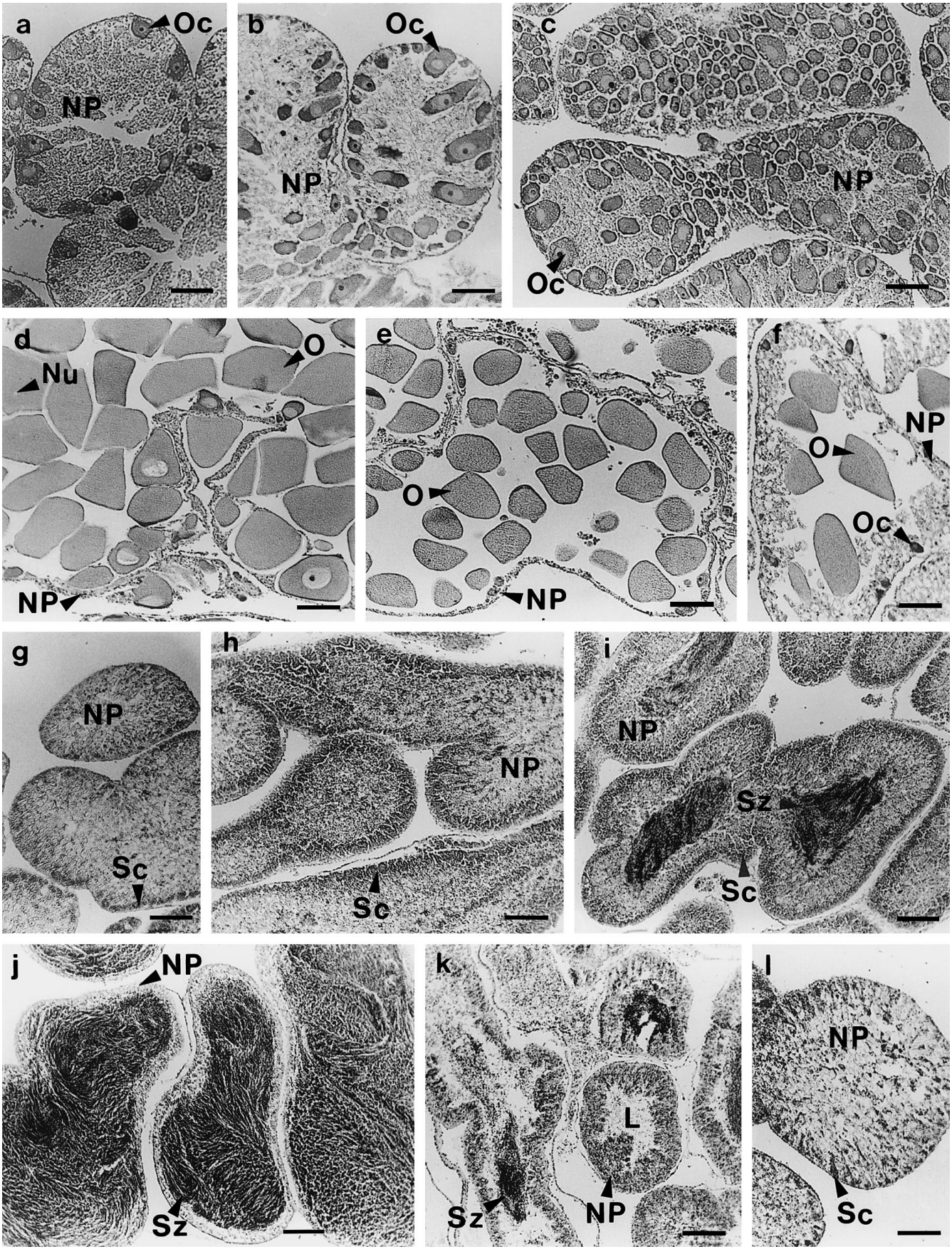
or spermatozoa) begin to accumulate in the lumen (Fig. 3c, i). In Stage IV (mature), most of the lumen is occupied by mature gametes, and nutritive phagocytes are reduced to a thin layer along the acinal wall (Fig. 3d, j). In Stage V (partly spawned), the lumen is emptied as mature gametes are shed but not yet replaced to any great extent by nutritive phagocytes (Fig. 3e, k). In Stage VI (spent), some relict oocytes/ova or spermatozoa may be present in the lumen, which is accumulating a growing layer of nutritive phagocytes (Fig. 3f, l).

The gametogenic cycle of *Strongylocentrotus droebachiensis* was approximately synchronous between sites and across habitats for both males and females, although individuals could be found in two or three different maturity stages on most dates (Figs. 4, 5). After spawning in spring, females remained in the recovering stage (Stage I) for 2 to 4 months before moving into the growing stage (Stage II) during the summer (Fig. 4). By late summer or early fall, most females had entered the premature stage (Stage III) where they remained until late winter or early spring when they became fully mature (Stage IV). Females proceeded rapidly through the partly spawned (Stage V) and spent stages (Stage VI) and started a new gametogenic cycle a few weeks after spawning. At Mill Cove, one partly spawned female was found in September in the kelp bed (Fig. 3e). Males of *S. droebachiensis* showed a similar pattern of maturation as females, although the periodicity was less pronounced (Fig. 5). After spawning, most males entered the recovering and growing stages in early or mid-summer, although up to 30% of males in some habitats (Little Duck Island, barren grounds; Mill Cove, kelp bed) remained in the spent stage until late summer. At Little Duck Island, most males entered the premature stage in late fall while at Mill Cove ~25% of males were still in the growing stage in February. Most males were fully mature in late winter or early spring, and proceeded through the partly spawned and spent stages within 1 to 2 months of spawning before starting a new gametogenic cycle. At Mill Cove, one mature male was found in October in both the grazing front and the barren grounds (Fig. 3j), and one partly spawned male was found in November in the grazing front (Fig. 3k).

Changes in gonadal microstructure during maturation

The proportion (by cross-sectional area of a gonadal acinus) of nutritive phagocytes in ovaries of females of *Strongylocentrotus droebachiensis* showed a distinct annual cycle that was synchronous across sites and habitats (Fig. 6). After the major spawning period in March/April, the proportion of nutritive phagocytes increased rapidly within 2 months. As gametogenesis proceeded, the proportion of nutritive phagocytes progressively decreased to a minimum just prior to the next major spawning period. The proportion of nutritive phagocytes in the ovaries differed significantly between dates at both sites (Table 3), and it was significantly lower in the kelp bed than in the grazing front at Little Duck Island (T'-test). Mean oocyte area increased throughout the maturation cycle and reached a maximum just prior to spawning, when it decreased sharply as large oocytes matured into ova and newly produced oocytes were small (Fig. 6). At Little Duck Island, mean oocyte area differed significantly between dates but not between habitats (Table 3). At Mill Cove, there was a significant interaction between date and habitat: mean oocyte area was significantly lower in the grazing front than in the barren grounds in February and the kelp bed in March. While oocytes were present at all times, ova first appeared in late winter and were lost at spawning (Fig. 6). There were no significant differences in mean ova area between months or habitats at either site (Table 3). The relative abundance of ova, and the proportions of oocytes, nutritive phagocytes, and unoccupied lumen were used to quantify the maturity stages of females (Table 4).

Males of *Strongylocentrotus droebachiensis* showed the same temporal pattern in the proportion of nutritive phagocytes in the gonads as females (Fig. 7). The proportion of nutritive phagocytes increased rapidly after spawning and then progressively decreased until the next major spawning period. The proportions of spermatocytes and spermatozoa (Fig. 7) showed a reciprocal pattern of abundance relative to nutritive phagocytes. After spawning, the proportion of spermatocytes increased to a maximum in early winter and remained at that level until the next spawning. The proportion of spermatozoa dropped sharply after spawning and remained low during the summer, increasing in fall and winter to a maximum at the peak of the reproductive cycle. At Little Duck Island, there was a significant interaction between the effects of date and habitat on the proportions of all three cell types in the testes (Table 5). The proportion of nutritive phagocytes was significantly higher and the proportion of spermatozoa significantly lower in the barren grounds than in the kelp bed and/or grazing front in October 1994 and May 1995. The proportion of spermatocytes also was significantly lower in the barren grounds than in the kelp bed and grazing front in May 1995. At Mill Cove, there was a significant effect of date on the proportions of both nutritive phagocytes and spermatocytes but no significant effect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of habitat (Table 5). Also at Mill Cove, there was a significant interaction between the effects of date and habitat on the proportion of spermatozoa which was significantly higher in the barren grounds than in the grazing front in February 1995. The proportions of spermatocytes, spermatozoa, nutritive phagocytes, and unoccupied lumen were used to quantify the maturity stages of males (Table 6).

Sex ratio

Sex ratios of *Strongylocentrotus droebachiensis* did not deviate significantly from 1:1 (χ^2-test, $p > 0.05$) in any habitat at either site with the exception of the kelp bed at Little Duck Island, where males were more abundant than females (148 males, 115 females; $\chi^2 = 4.141$, $p < 0.05$). Samples in which >10% of urchins could not be sexed were excluded from analysis. Three hermaphrodites were observed at Mill Cove (one from each habitat), which represented 0.35% of sea urchins sampled at that site ($n = 862$) and 0.15% of the total sampled at both sites ($n = 1968$).

Gut content analysis

The food quantity index of *Strongylocentrotus droebachiensis* was temporally variable in all habitats at both sites but tended to be lowest in late summer and early fall (Fig. 8). At Little Duck Island the index increased in the kelp bed and grazing front after spawning (March/April) in 1995. At both sites, there was a significant interaction between the effects of date and habitat on the food quantity index (Table 7). At Little Duck Island, the index was significantly lower in the barren grounds than in the kelp bed and/or the grazing front in fall 1994 and spring 1995 (5 out of 11 dates; GT2-test) and significantly lower in the kelp bed than in the grazing front and/or barren grounds in late summer and fall 1994 and June 1995 (6 out of 11 dates). At Mill Cove, the food quantity index was significantly lower in the barren grounds than in the kelp bed and/or grazing front in June and December 1994, and in late winter/early spring 1995 (5 out of 12 dates).

The food quality index of *Strongylocentrotus droebachiensis* (Fig. 8) was consistently high in the kelp bed and grazing front and more variable but generally lower in the barren grounds at both sites. As with the food quantity index, there also was a significant interaction between the effects of date and habitat on the food quality index (Table 7). At Little Duck Island, the food quality index was significantly lower in the barren grounds than in the kelp bed and/or grazing front in spring and fall 1994, and spring and summer 1995 (8 out of 13 dates). At Mill Cove, this was the case in summer and winter 1994 and throughout 1995 (9 out of 13 dates).

◀

Fig. 3 *Strongylocentrotus droebachiensis*. Histology of ovaries (**a–f**) and testes (**g–l**). (**a**) Stage I: recovering ovary with nutritive phagocytes (*NP*) filling lumen; few small oocytes (*Oc*) along acinal wall. (**b**) Stage II: growing ovary with more abundant and larger oocytes along acinal wall. (**c**) Stage III: premature ovary with many oocytes accumulating in lumen; nutritive phagocyte layer reduced. (**d**) Stage IV: mature ovary filled with ova (*O*); nutritive phagocytes are reduced to thin layer along acinal wall (*Nu* nucleus). (**e**) Stage V: partly spawned ovary with spaces vacated by spawned ova. (**f**) Stage VI: spent ovary with relict ova and few new oocytes; nutritive phagocyte layer increasing in thickness. (**g**) Stage I: recovering testes with nutritive phagocytes (*NP*) filling lumen; thin layer of spermatocytes (*Sc*) along acinal wall. (**h**) Stage II: growing testes with spermatocyte layer increasing in thickness. (**i**) Stage III: premature testes with spermatozoa (*Sz*) accumulating in lumen; nutritive phagocyte layer reduced. (**j**) Stage IV: mature testes filled with spermatozoa; nutritive phagocytes are reduced to thin layer along acinal wall. (**k**) Stage V: partly spawned testes with spaces vacated by spawned spermatozoa (*L* lumen). (**l**) Stage VI: spent testes with nutritive phagocytes almost filling lumen; scattered spermatocytes along acinal wall (Scale bars: 100 μm)

Discussion

Reproductive cycle

Strongylocentrotus droebachiensis on the Atlantic coast of Nova Scotia exhibits a distinct annual reproductive cycle with a major spawning period in early spring. The cycle was relatively synchronous between habitats differing in food quality and quantity, and between sites differing in wave exposure. Previous studies have shown a similar cycle of gonad index for *S. droebachiensis* in Maine (Cocanour and Allen 1967), Newfoundland (Himmelman 1978; Keats et al. 1984), and Norway (Falk-Petersen and Lønning 1983). Histological analysis also indicated a similar progression of non-gametic and gametic cells as previously described for females of *S. droebachiensis* (Falk-Petersen and Lønning 1983) and for both sexes of other strongylocentrotids (e.g. Fuji 1960; Chatlynne 1969; Gonor 1973a, b). Nutritive phagocytes were most abundant at the beginning of the reproductive cycle and were subsequently replaced by increasing numbers of germinal and gametic cells (oocytes and ova in females, spermatocytes and spermatozoa in males).

The general synchrony of reproduction in all habitats suggests that the annual reproductive cycle is controlled by factors other than food, possibly temperature and/or photoperiod (e.g. Gonor 1973a). Individual sea urchins, however, usually occurred in two or three gametogenic stages at any one time, with the greatest variability present during the spawning period. Such variation, which also has been documented in other sea urchins (Crapp and Willis 1975; Bernard 1977; Byrne 1990; King et al. 1994), is likely related to individual differences in the acquisition and allocation of energy reserves to gametogenesis. To our knowledge, our study is the first to quantitatively document changes in cell type abundance

in the gonads of *Strongylocentrotus droebachiensis*, and thus serves as a benchmark for future histological studies of the reproductive cycle of this species.

A more gradual decline in gonad index during the spring spawning period at Mill Cove compared to Little Duck Island suggests that spawning was more protracted or occurred somewhat later at the former site. In the northwestern Atlantic, spawning of *Strongylocentrotus droebachiensis* is triggered by phytoplankton blooms (Himmelman 1975; Starr et al. 1990, 1992, 1993) which vary in space and time. Differences in temperature or hydrodynamic regimes between our sites may have influenced the occurrence of phytoplankton blooms and hence the timing of sea urchin spawning.

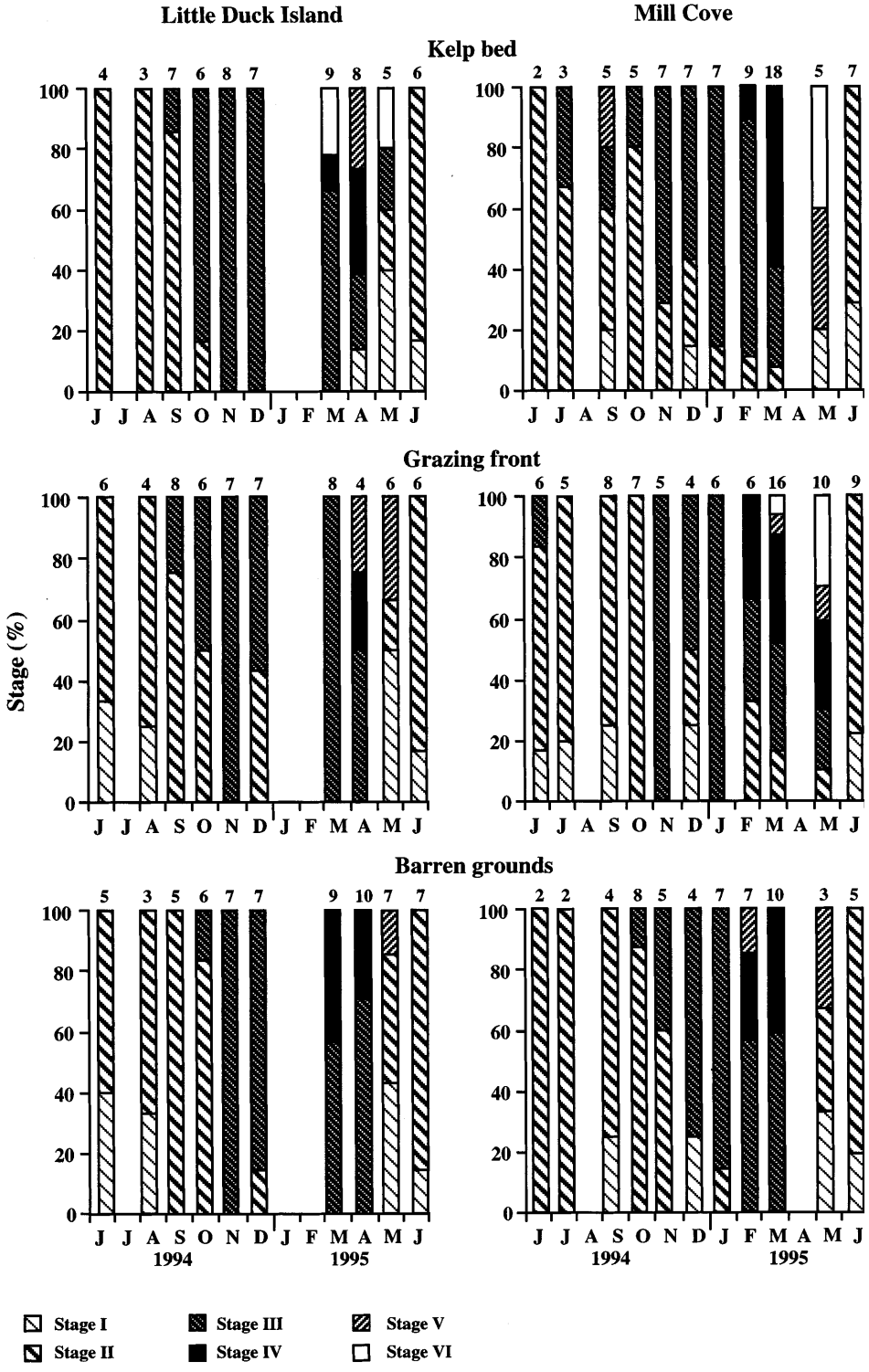

Fig. 4 *Strongylocentrotus droebachiensis*. Frequencies (%) of females in Stages I to VI of the reproductive cycle at Little Duck Island and Mill Cove between June 1994 and June 1995 in the kelp bed, the grazing front, and the barren grounds. Stage I: recovering, Stage II: growing, Stage III: premature, Stage IV: mature, Stage V: partly spawned, and Stage VI: spent. Numbers above bars indicate sample size

Histological analysis revealed that a small proportion of the population of *Strongylocentrotus droebachiensis* at Mill Cove spawned in fall. Although the incidence of summer and fall spawning is low, it corroborates observations by Keats et al. (1987) of spawning of *S. droebachiensis* in June, July and September in barren grounds in Newfoundland. Because of the low number of sea urchins that may spawn in the summer or fall, it is unlikely that these events would contribute much to the overall pool of larvae produced each year.

Spatial and interannual variation in gonad index

Gonad indices of *Strongylocentrotus droebachiensis* generally were higher in the kelp bed and grazing front

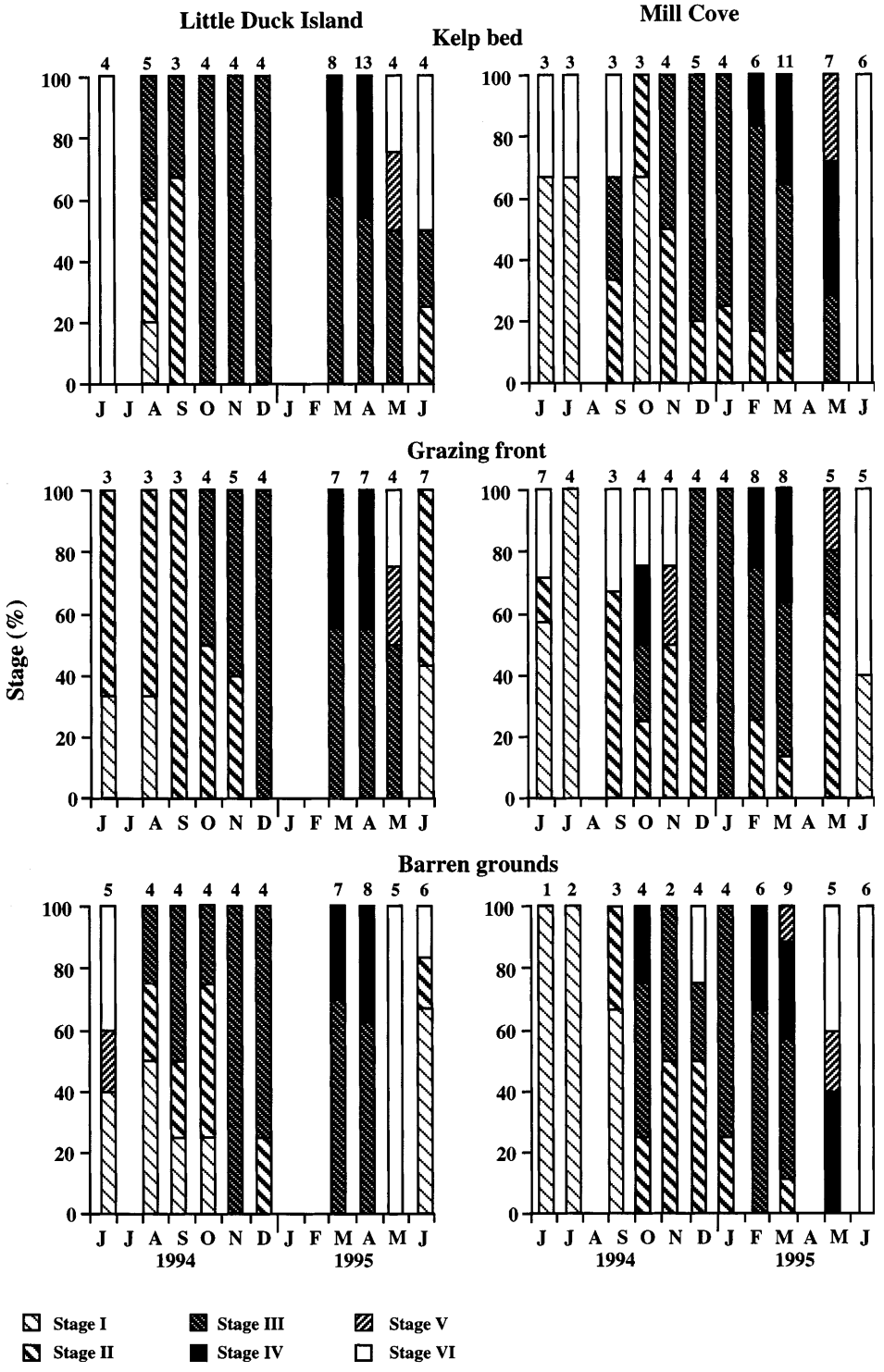

Fig. 5 *Strongylocentrotus droebachiensis*. Frequencies (%) of males in Stages I to VI of the reproductive cycle at Little Duck Island and Mill Cove between June 1994 and June 1995 in the kelp bed, the grazing front, and the barren grounds. For stage description see Fig. 4. Numbers above bars indicate sample size

than in the barren grounds. This pattern is consistent with previous studies contrasting the gonad index of this species (Lang and Mann 1976; Keats et al. 1984; Scheibling and Stephenson 1984; Sivertsen and Hopkins 1995) or other strongylocentrotids (Gonor 1973a; Pearse 1980) between kelp beds and barren grounds, and presumably is related to differences in food availability (see "Between habitat variation in food consumption", below). Several studies have shown that laminarian kelps are a preferred food of *S. droebachiensis* which supports high rates of growth and reproduction (Vadas 1977; Keats et al. 1984; Lemire and Himmelman 1996; Minor and Scheibling 1997). Our histological analysis indicated that the gonads were qualitatively similar between habitats (in terms of the proportions of different cell types) despite large differences in gonadal mass. In contrast, Minor and Scheibling (1997) found that females of *S. droebachiensis* fed kelp (*Laminaria longicruris*) ad libitum in the laboratory had significantly more nutritive phagocytes in their gonads than those fed kelp only one day per week, and suggested that the higher ration provided additional reserves for gametogenesis. How-

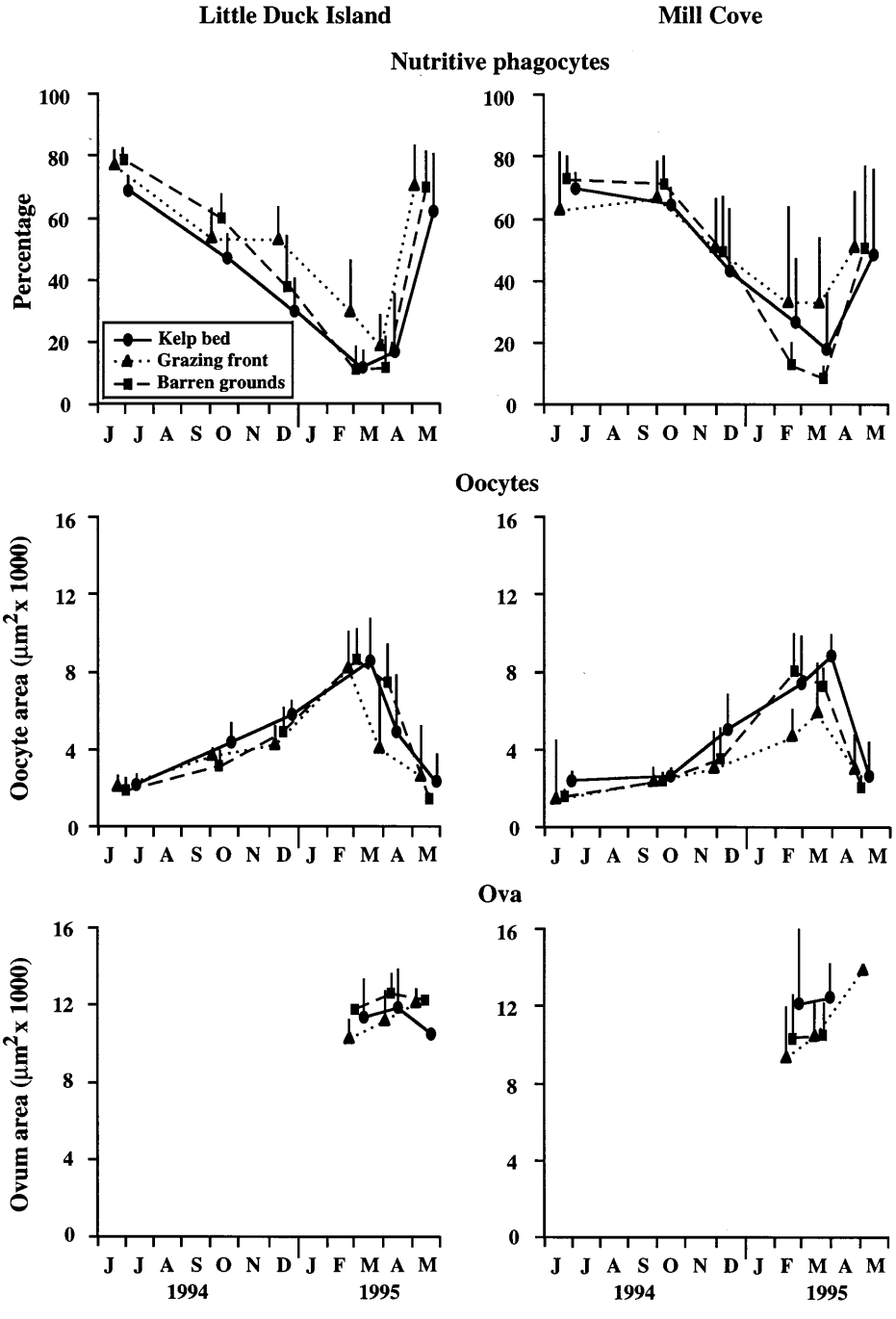

Fig. 6 *Strongylocentrotus droebachiensis*. Mean (±SD) relative area (percentage of cross-sectional area of gonadal acini) of nutritive phagocytes, and mean (±SD) absolute areas of oocytes and ova of female sea urchins in the kelp bed, grazing front and barren grounds at Little Duck Island and Mill Cove between June 1994 and May 1995. Means are based on 2 to 12 sea urchins

Table 3 *Strongylocentrotus droebachiensis*. Two-way ANOVA of the effects of Date and Habitat on proportions of nutritive phagocytes, and absolute areas of oocytes and ova of females at Little Duck Island and Mill Cove (*Date*: Jun, Oct, Dec 1994, and Feb/Mar, Mar/Apr and May 1995; *Habitat*: kelp bed, grazing front, barren grounds; *NS* not significant; $*p < 0.05$; $**p < 0.01$; $***p < 0.001$)

Source	Little Duck Island				Mill Cove			
	df	MS	*F*	*p*	*df*	MS	*F*	*p*
Nutritive phagocytes								
Date	5	3895.49	78.63	<0.001***	5	3155.45	26.43	<0.001***
Habitat	2	359.02	7.25	0.001***	2	103.97	0.87	0.422 NS
Date × Habitat	10	87.17	1.76	0.081 NS	10	139.61	1.17	0.323 NS
Error	84	49.54			85	119.37		
Oocytes								
Date	5	111 021 228	57.02	<0.001***	5	88 994 232	36.29	<0.001***
Habitat	2	317 298	0.16	0.850 NS	2	10 172 671	4.15	0.019*
Date × Habitat	10	2 319 244	1.19	0.309 NS	10	5 103 536	2.08	0.035*
Error	83	1 946 993			85	2 452 460		
Ova								
Date	2	3 703 055	2.38	0.123 NS	1	1 916 321	0.45	0.510 NS
Habitat	2	5 563 400	3.57	0.051 NS	2	11 946 850	2.78	0.081 NS
Date × Habitat	3	1 980 219	1.27	0.316 NS	2	519 675	0.12	0.887 NS
Error	17	1 559 115			25	4 295 489		

ever, greater between-diet differences in gonad production in the laboratory study may account for this disparity.

The peak gonad index increased between 1993 and 1995 in the barren grounds at Little Duck Island, which may reflect a reduction in intraspecific competition for food after the mass mortality in October 1993 (Scheibling and Hennigar 1997). There were no interannual differences in peak gonad index in the kelp bed or grazing front during this period, suggesting that food supply (mainly kelp) was not limiting reproduction in either of these two habitats. Other studies comparing gonad indices over several years also have shown interannual differences in peak gonad index (Himmelman 1978; Keats et al. 1984; Munk 1992) which in some cases were related to differences in food supply (Keats et al. 1984).

Gonad indices usually were higher at the wave-exposed site, Little Duck Island, than at the sheltered site, Mill Cove. In contrast, Ebert (1968) and Gonor (1973a) found that *Strongylocentrotus purpuratus* had lower gonad indices at exposed sites than at sheltered sites, which Ebert attributed to greater energy allocation to spine repair at exposed sites. In both studies, however, differences in wave exposure were confounded with differences in food abundance, which was lower (Ebert 1968) or higher (Gonor 1973a) at the sheltered site.

Table 4 *Strongylocentrotus droebachiensis*. Stages of the ovarian cycle. Data are qualitative records of abundance of ova, and relative areas (as the percentage of the cross-sectional area of ovarian acini) of oocytes, nutritive phagocytes, and unoccupied lumen. Note: because large numbers of ova oozed from ripe gonads upon processing, it was not possible to measure their proportion in histological sections; their relative abundance was approximated instead

Stage	Ova abundance	Oocytes (%)	Nutritive phagocytes (%)	Lumen (%)
I. Recovering	none	<15	>75	<15
II. Growing	none	15–40	40–75	<5
III. Premature	few	>40	10–40	<5
IV. Mature	very many	<5	<10	<5
V. Partly spawned	some	<5	10–30	40–70
VI. Spent	few relict	<5	>30	<40

Between habitat variation in food consumption

At both sites, the quantity of the gut contents of *Strongylocentrotus droebachiensis* was lowest in late summer and early fall when gonad indices also were low. This suggests a decrease in feeding rate at this time which is consistent with observations of sea urchin behaviour at Little Duck Island and Mill Cove during the period of study: sea urchins in the grazing front became less aggregated and grazed less actively on kelp in the late summer and fall (Scheibling unpublished data). Gut contents at Little Duck Island also were relatively low at the peak of the reproductive cycle but increased after spawning. Previous studies of *S. droebachiensis* (Vadas 1977; Himmelman 1980; Keats et al. 1983; Himmelman and Nédélec 1990) and congeneric species (Lawrence et al. 1965; Ebert 1968; Vadas 1977) also have shown a decline in feeding rate in late summer/early fall with a minimum around the peak of the reproductive cycle. The large differences in the abundance of macroalgal food resources between kelp beds and barren grounds were not reflected in large differences in the quantity of gut contents of sea urchins from these habitats. However, as sea urchins decrease gut evacuation rate when food is scarce (Lasker and Giese 1954; Propp 1977), the quantity of gut contents in barren grounds may not adequately reflect the level of food consumption or

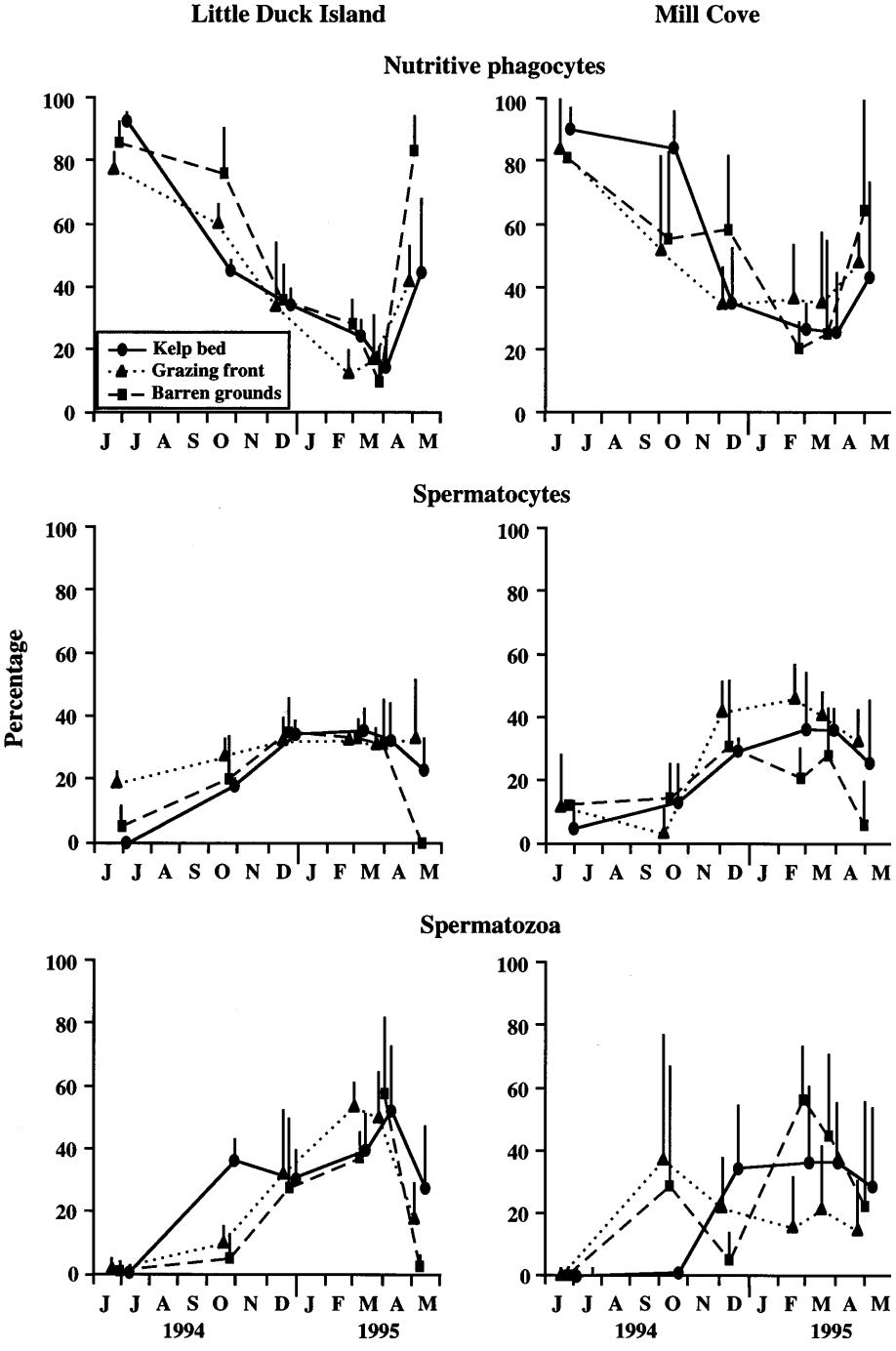

Fig. 7 *Strongylocentrotus droebachiensis*. Mean (±SD) relative abundance (percentage of cross-sectional area of gonadal acini) of nutritive phagocytes, spermatocytes, and spermatozoa of male sea urchins in the kelp bed, grazing front and barren grounds at Little Duck Island and Mill Cove between June 1994 and May 1995. Means are based on 3 to 8 sea urchins

availability. Therefore, a significant difference may exist in the quantity of food consumed between barren grounds and kelp beds which we were unable to detect.

At both sites, food quality in terms of organic material tended to be lower in the barren grounds than in the kelp bed or at the grazing front. Vadas (1977) found that food quality is more important than quantity for reproduction in *Strongylocentrotus droebachiensis*, which may explain the lower gonad index of urchins in barren grounds. Nevertheless, sea urchins in barren grounds are able to obtain sufficient nutrients for growth and reproduction owing to their generalist diet and ability to locate and consume drift algae such as kelps (Himmelman and Steele 1971; Lawrence 1975; Vadas 1977; Mann et al. 1984; Keats et al. 1984). Meidel and Scheibling (1998) found that the growth rate of adult sea urchins did not differ significantly among habitats at Little Duck Island, although it was somewhat slower in the barren grounds than in the kelp bed or grazing front at Mill Cove. If sea urchins channel a similar proportion of energy into growth in all habitats, reduced energy intake in barren grounds should result in reduced reproduction. Also, foraging costs may be higher in barren grounds where individuals tend to move greater dis-

Table 5 *Strongylocentrotus droebachiensis*. Two-way ANOVA of the effects of Date and Habitat on proportions of nutritive phagocytes, spermatocytes and spermatozoa of males at Little Duck Island and Mill Cove (*Date*: Jun, Oct, Dec 1994, and Feb/Mar, Mar/Apr and May 1995; *Habitat*: kelp bed, grazing front, barren grounds; *NS* not significant; $*p < 0.05$; $**p < 0.01$; $***p < 0.001$)

Source	Little Duck Island				Mill Cove			
	df	MS	*F*	*p*	*df*	MS	*F*	*p*
Nutritive phagocytes								
Date	5	4465.30	57.86	<0.001***	5	2240.41	9.45	<0.001***
Habitat	2	439.31	5.69	0.005**	2	14.40	0.06	0.941 NS
Date × Habitat	10	298.38	3.87	<0.001***	10	297.35	1.25	0.275 NS
Error	61	77.17			66	237.12		
Spermatocytes								
Date	5	1125.23	30.12	<0.001***	5	1184.90	9.21	<0.001***
Habitat	2	547.54	14.66	<0.001***	2	322.25	2.50	0.090 NS
Date × Habitat	10	341.29	9.14	<0.001***	10	227.23	1.77	0.085 NS
Error	61	37.35			66	128.69		
Spermatozoa								
Date	5	3143.93	33.98	<0.001***	5	1268.62	4.86	<0.001***
Habitat	2	468.94	5.07	0.009**	2	87.85	0.34	0.716 NS
Date × Habitat	10	220.11	2.38	0.019*	10	600.32	2.30	0.022*
Error	61	92.53			66	261.06		

Table 6 *Strongylocentrotus droebachiensis*. Stages of the testicular cycle. Data are relative areas (as the percentage of the cross-sectional area of testicular acini) of spermatocytes, spermatozoa, nutritive phagocytes, and unoccupied lumen

Stage	Spermatocytes (%)	Spermatozoa (%)	Nutritive phagocytes (%)	Lumen (%)
I. Recovering	<10	0	>80	<10
II. Growing	10–40	0	40–80	<5
III. Premature	>40	>15	10–40	<5
IV. Mature	<5	>70	<10	0
V. Partly spawned	<5	>10	10–30	>20
VI. Spent	<5	<10	>30	<20

tances than in kelp beds or grazing fronts (Mattison et al. 1977; Harrold and Reed 1985; Scheibling unpublished data), which would further reduce the amount of energy available for reproduction.

Sex ratio and sexual differences in gonad index

The sex ratio of *Strongylocentrotus droebachiensis* approximated 1:1 in all cases except for the kelp bed at Little Duck Island, where males accounted for a slightly higher proportion of the population (56%). Munk (1992) also reported a slight bias towards males in one population of *S. droebachiensis* in Alaska (59%), but a slight bias towards females in another population (56%). Biased sex ratios have also been reported for congeneric species (Gonor 1973c; Bernard 1977), although gonochoric echinoderms such as strongylocentrotids typically have a sex ratio of 1:1 (Lawrence 1987). The incidence of hermaphroditism in our study was very low and similar to that found in other gonochoric sea urchins (Bernard 1977; Lawrence 1987; Byrne 1990; King et al. 1994).

At the peak of the reproductive cycle in spring 1995, females had a higher gonad index than males at both sites, which is consistent with previous studies of *Strongylocentrotus droebachiensis* (Munk 1992; Minor and Scheibling 1997) but not other strongylocentrotids (Bennett and Giese 1955; Bernard 1977). After spawning, gonad indices of both sexes dropped to the same minimal levels, indicating that females released a larger proportion (~10.5%) of their body weight as gametes than males (~8.1%).

Spatial variation in zygote production

A number of studies have shown that fertilization rate in sea urchins and other echinoderms is positively related to fecundity (which generally increases with increasing body size) and population density (e.g. Pennington 1985; Levitan et al. 1992; Levitan 1995 and references therein). Adults of *Strongylocentrotus droebachiensis* in barren grounds have low fecundity (because of their small size and low gonad index), while those in kelp beds have a high gonad index but are sparsely distributed. In contrast, sea urchins in grazing fronts are both highly aggregated and much larger than those in barren grounds and kelp beds (Scheibling et al. 1994; Scheibling unpublished data) and therefore are expected to have the highest fertilization rate and produce the greatest number of zygotes per unit area of bottom. During our study, sea urchins at Little Duck Island had higher fecundity and occurred at higher densities than those at

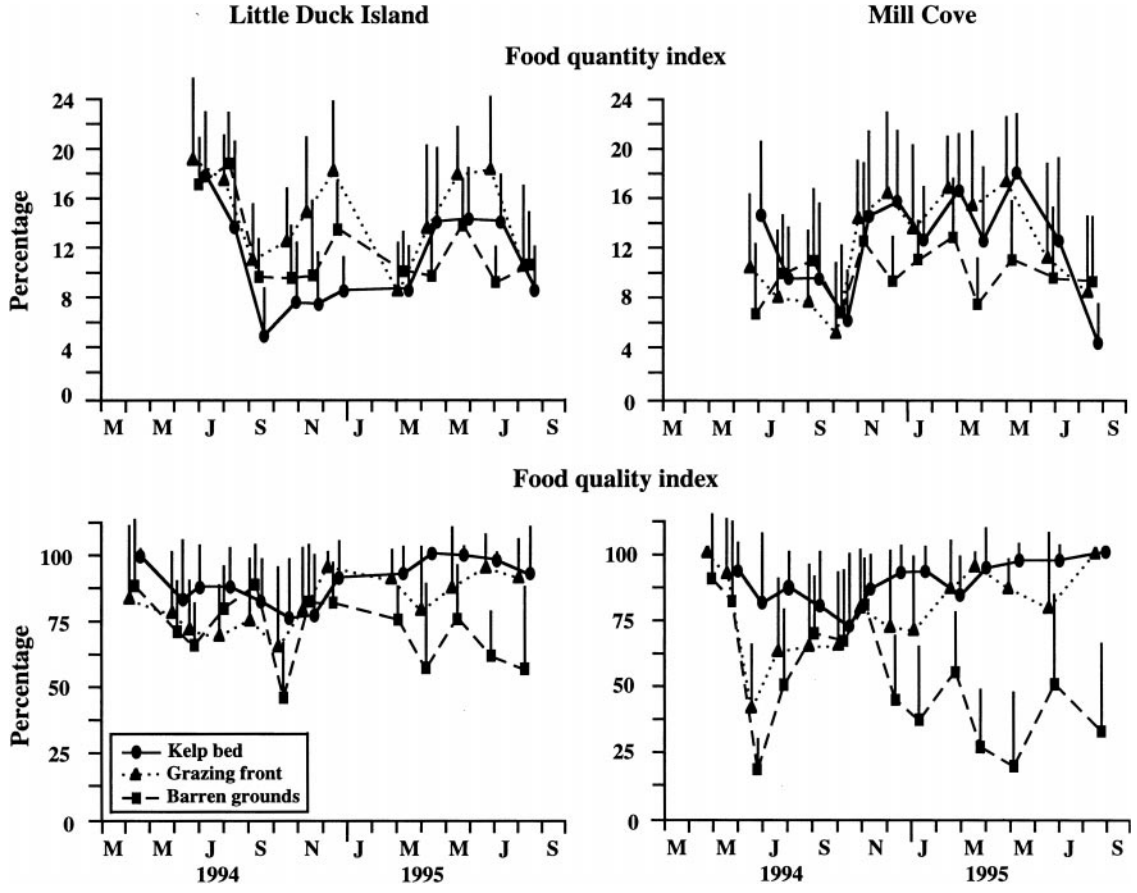

Table 7 *Strongylocentrotus droebachiensis*. Two-way ANOVA of the effects of Date and Habitat on food quantity and quality index, as well as GT2 post-hoc comparisons of the simple effects of Habitat at each date at Little Duck Island and Mill Cove [*Date*: food quantity, Jun 1994 to Aug 1995; food quality, Apr/May 1994 to Aug 1995; *Habitat*: kelp bed (*KB*), grazing front (*GF*), barren grounds (*BG*); *NS* not significant; $*p < 0.05$; $**p < 0.01$; $***p < 0.001$; *nd* no data]

Test	Little Duck Island				Mill Cove			
ANOVA	*df*	MS	*F*	*p*	*df*	MS	*F*	*p*
Food quantity index								
Date	10	601.93	29.88	<0.001***	11	1 766.08	69.86	<0.001***
Habitat	2	816.91	40.55	<0.001***	2	263.60	10.43	<0.001***
Date × Habitat	20	104.84	5.20	<0.001***	22	100.80	3.99	<0.001***
Error	596	20.15			668	25.28		
Food quality index								
Date	12	3 362.22	10.84	<0.001***	12	3 607.42	7.43	<0.001***
Habitat	2	18 332.85	59.11	<0.001***	2	85 209.63	175.55	<0.001***
Date × Habitat	24	1 734.20	5.59	<0.001***	24	4 717.86	9.72	<0.001***
Error	685	310.12			710	485.37		

GT2-test	Food quantity	Food quality	Food quantity	Food quality
Apr 1994	nd	NS	nd	nd
May 1994	nd	KB > BG	nd	NS
Jun 1994	NS	KB > GF, BG	KB > BG	KB > GF > BG
Jul/Aug 1994	GF, BG > KB	NS	NS	KB > GF, BG
Sep 1994	GF, BG > KB	BG > GF	NS	NS
Oct 1994	GF > KB	KB, GF > BG	NS	NS
Nov 1994	GF > KB, BG	NS	NS	NS
Dec 1994	GF > BG > KB	NS	KB, GF > BG	KB > GF > BG
Jan 1995	nd	nd	NS	KB > GF > BG
Feb/Mar 1995	NS	KB, GF > BG	GF > BG	KB, GF > BG
Mar/Apr 1995	KB, GF > BG	KB > GF > BG	KB, GF > BG	KB, GF > BG
May 1995	GF > BG	KB > BG	KB, GF > BG	KB, GF > BG
Jun 1995	GF > KB > BG	KB, GF > BG	NS	KB > GF > BG
Aug 1995	NS	KB, GF > BG	BG > KB	KB, GF > BG

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Fig. 8 *Strongylocentrotus droebachiensis*. Indices of food quantity and food quality (mean ± SD) at Little Duck Island and Mill Cove between April (quality) or June 1994 (quantity) and August 1995 in the kelp bed, grazing front and barren grounds. Food quantity is expressed as food volume (percentage of total body volume) and food quality as organic material (percentage of total gut content). Means are based on 5 to 34 sea urchins

Mill Cove. Consequently, sea urchins at Little Duck Island probably also experienced higher fertilization success and produced more zygotes per unit area.

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