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Reproduction in the diadematoid sea urchin *Centrostephanus rodgersii* in contrasting habitats along the coast of New South Wales, Australia

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Abstract Reproduction in the sea urchin *Centrostephanus rodgersii* was examined in two types of habitats (''barrens'', i.e. habitats characterised by the high crustose coralline algal cover typical of urchin-barren grounds, and by the absence of macroalgae; and ''fringe'', i.e. habitats characterised by a high macroalgal biomass and few *C. rodgersii*) at four locations in New South Wales. The four locations: the Solitary Islands, Sydney, Ulladulla and Eden, span the distribution of *C. rodgersii* from the subtropics at its northern limit to temperate waters near its southern limit. Histology and estimates of gonad retrieval rate (GRR) from January 1994 to October 1995 indicated that reproduction was synchronous at all locations. An increase in the tempo of gametogenesis in May and onset of spawning in June at all locations is consistent with entrainment in response to exogenous factors. Over the range studied, *C. rodgersii* experienced relatively similar daylength cycles and contrasting sea-temperature cycles. Short days and lunar conditions coinciding with the solstice appear likely proximate cues for the onset of spawning. The major difference in reproduction among locations was in the duration of spawning. In the southern parts of its range breeding occurred over a 5 to 6 mo period, whereas at the Solitary Islands it lasted $\simeq$1 mo. At most locations the GRRs were significantly higher in the fringe habitat than in the barrens habitat. The lower reproductive output of urchins in the barrens habitat was attributed to the food-poor conditions typical of this habitat. The developing fishery for *C. rodgersii* is likely to be most effective from March to early May. Urchins from barrens areas may not provide sufficient yield to warrant harvesting.

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Introduction

Many marine invertebrates reproduce with a discrete and predictable annual cycle of gametogenesis and spawning (Giese and Pearse 1974). Echinoderms have been particularly useful for investigating factors controlling reproduction in the sea, because gametogenesis in this phylum is well understood and because their gonads are easily accessed for gravimetric and histological analyses (Byrne 1998). Echinoid reproduction is controlled by a suite of endogenous and environmental factors, which appear to interact in a complex synergistic fashion (Kennedy and Pearse 1975; Pearse et al. 1986; Bay-Schmith and Pearse 1987; Pearse and Cameron 1991; Guillou and Michel 1993). Depending on the species, various seasonally-variable environmental factors such as photoperiod, temperature and food availability play an important role in regulating the different stages of gametogenesis (proliferation, growth and maturation) and breeding (Kennedy and Pearse 1975; Pearse and Cameron 1991).

Sea urchins in the family Diadematoida, particularly *Diadema* species are among the most readily recognised and ecologically important echinoids in the tropical regions of the world's oceans. Less familiar are the temperate and subtropical members of this family in the genus *Centrostephanus*. In southeastern Australia, *C. rodgersii* is an abundant herbivore in subtidal systems, and grazing by this species plays a major role in structuring benthic communities (Fletcher 1987; Andrew and Underwood 1989, 1993; Andrew 1991, 1993). *C. rodgersii* is found from the subtropical region of northern New South Wales (28°37′S; 153°38′E) to the cool temperate regions in eastern Victoria and northern

Tasmania (41°52′S; 148°18′E). Investigations of reproduction in *C. rodgersii* indicate that this species has a short, intensive breeding season near its northern limit and prolonged breeding in the middle of its range (O'Connor et al. 1978; King et al. 1994). In the present study, the influence of photoperiod and temperature on reproduction is examined in the contrasting environmental conditions found in the subtropical and temperate waters of New South Wales.

At each location we quantified differences in reproduction between contrasting barrens and fringe habitat-types. In New South Wales, the barrens habitat is found in areas subject to intense grazing by *Centrostephanus rodgersii*. This habitat is defined in part by the high crustose coralline algal cover typical of urchin-barren grounds and by the absence of macroalgae (Andrew and Underwood 1989, 1993; Andrew 1991, 1993; Underwood et al. 1991). In contrast, the fringe habitat has a high biomass of macroalgae and, although *C. rodgersii* may be present, they are not sufficiently abundant to remove all the macroalgae and create a barrens habitat (Andrew and Underwood 1989, 1993; Andrew 1991; Underwood et al. 1991). No attempt was made to quantify the biomass of algae in the fringe habitats sampled. The comparisons made are therefore between areas with no macroalgae (barrens) and areas with large but variable standing crops of laminarian and fucoid algae (fringe). The gonads are the main nutrient storage organ in sea urchins, and in food-poor barrens conditions a lower gonad yield would be expected (Pearse 1981; Lawrence and Lane 1982; Andrew 1986; Byrne 1990).

A developing commercial fishery for *Centrostephanus rodgersii* exists in New South Wales. Previous studies in the Sydney region indicated that a spring/summer harvest is required to obtain roe with the firm texture preferred by the market (King et al. 1994). This texture is characteristic of gonads dominated by nutritive cells rather than gametes. We assessed the generality of this result at major fishing ports spread across a wide geographic range to provide advice on times of year in which the yield and quality of roe per urchin can be maximised.

Materials and methods

Reproduction of *Centrostephanus rodgersii* in barrens and fringe habitats was investigated at Sydney (33°54′S; 151°17′E), Ulladulla (35°23′S; 150°29′E) and Eden (37°06′S; 149°55′E) (Fig. 1). Collections from Eden and Sydney started in January and February 1994, respectively and those from Ulladulla started in July 1994. Twenty to thirty urchins (66 to 120 mm test diam) were collected at approximately bimonthly intervals from each location until May 1995, and thereafter at monthly intervals from June to October 1995. *C. rodgersii* was also collected from barrens and fringe habitats from May to August 1995 and in June 1997 at the Solitary Islands (30°08′S; 153°14′E) near the northern limit of its range.

Each urchin was weighed and the weight of gonad per urchin was estimated by either weighing the whole gonad or scaling up the weight of one randomly selected, undamaged element. Although the gonad index (GI: gonad weight as a fraction of body weight) is typically used in studies of urchin reproduction, it is inappropriate for studies such as this, where the GI does not provide a clear indication of the reproductive cycle (King et al. 1994) and where a wide range of sizes of urchins are sampled (Gonor 1972; Grant and Taylor 1983). We used the gonad retrieval rate (GRR) method, which is calculated as the slope of a regression of gonad weight against total weight. Regressions were fitted separately for each sample using a common non-zero intercept. When different intercepts were fitted among samples they were not significantly different.

For each location, the maximum GRR recorded for the barrens and fringe habitats in 1994/1995 were compared by a two-factor orthogonal analysis of variance. The factors analysed were location (Solitary Islands, Sydney, Ulladulla, Eden) and habitat (barrens, fringe). For this analysis, 20 urchins were randomly selected from each sample. For the sample of urchins from the Solitary Islands collected in June 1997, a Student's *t*-test was used to compare the urchins from and barrens and fringe habitats. The influence of test diameter on GRR was examined by linear regression.

For histology, one gonad from each urchin was fixed in Bouin's fluid. The gonads were dehydrated in ethanol, embedded in paraffin and sectioned. Sections (7 μm thick) were stained with haematoxylin and eosin. The gametogenic condition was categorised into five maturity stages based on the morphological criteria used by King et al. (1994) . The criteria for four of the stages: spent, recovery, growing and partly-spawned stages are as detailed by King et al. The mature stage used here combines the premature and mature stages defined by King et al. Although these broad categories assist in presenting the overall pattern of gonad development, among-location differences in the details of gametogenesis during the breeding season were not well presented by this method. For the among-location comparison during breeding, the gametogenic status of the ovaries was examined in detail and recorded photographically.

Sea-surface temperatures for the four study locations were obtained from the CSIRO, Hobart. Temperature was estimated by satellite, using a grid of nine points around the coordinates for each site. Mean monthly temperature was calculated from mean temperature across 10 d which was recorded every 5 d. Times of sunrise and sunset, obtained from the Sydney Observatory, were used to estimate day length.

Results

Gonad growth and histology of gametogenesis

Seasonal patterns in the GRR and gametogenesis in *Centrostephanus rodgersii* were similar at the four locations (Figs. 1 to 3). Across all locations the reproductive cycle was divided into four main phases, which were most easily discerned in the fringe habitat. In both males and females these phases were: (1) a major spawning period in winter starting in June; (2) a period of post-spawning recovery; (3) a period of gonad weight increase between August and April due to enlargement of the nutritive phagocytes; (4) a period of intense gametogenesis in May when the gonads contain rapidly developing gametes in preparation for spawning (Fig. 3). Within these broad phases there were differences in the gametogenic state of the gonads at the four locations, as detailed below (Figs. 3, 4). During the breeding season these differences were most apparent in the ovaries (Fig. 4).

Solitary Islands

Gonad development of *Centrostephanus rodgersii* at the Solitary Islands was highly synchronous, with little or no

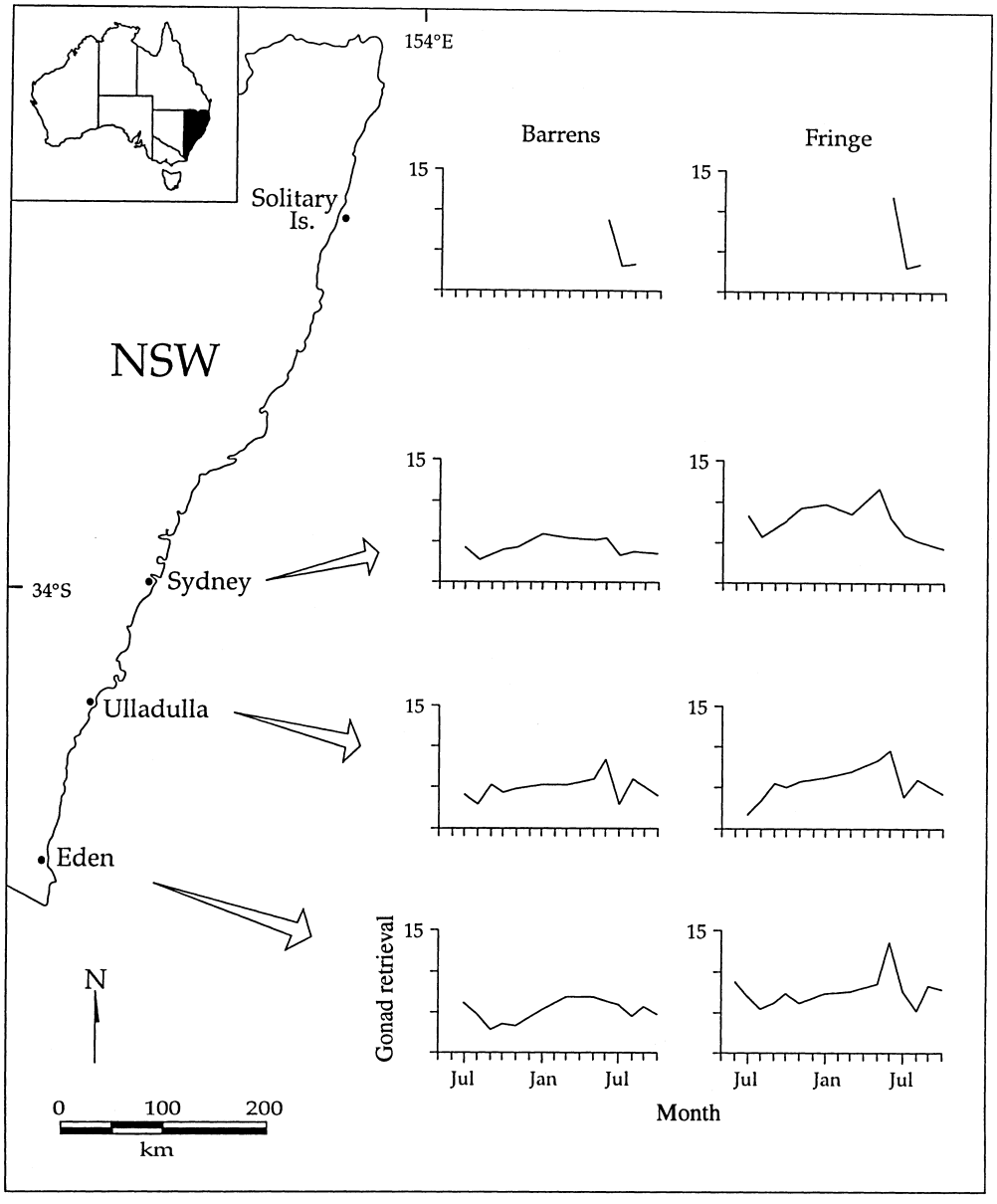
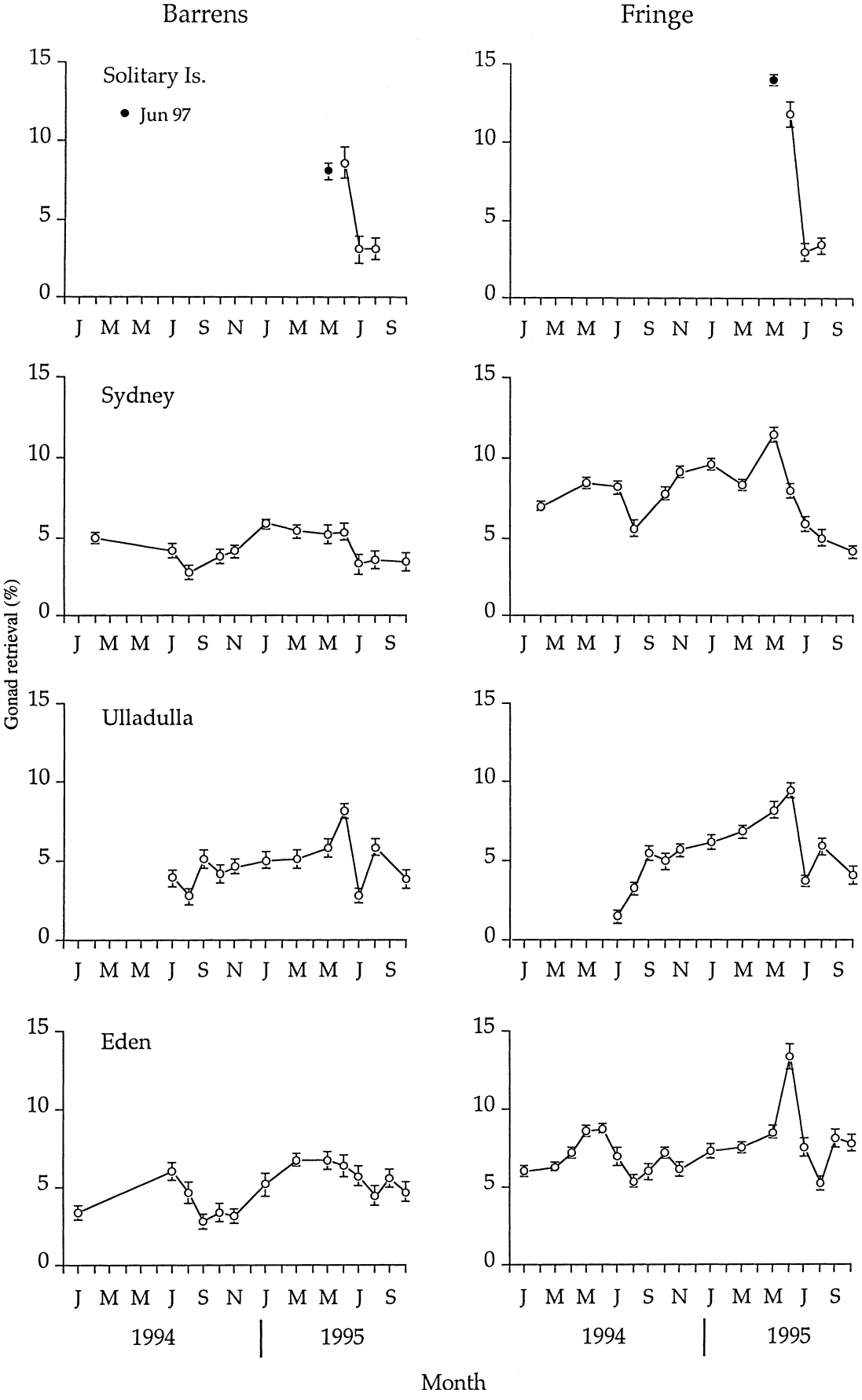


Fig. 1 *Centrostephanus rodgersii*. Sampling locations along coast of New South Wales and trends in gonad retrieval rates recorded for each site and habitat

variability in gametogenic condition among urchins and habitats (Fig. 3). All urchins collected on 11 May 1995 had growing gonads at an early stage of gametogenesis (Fig. 4a). In both males and females they were strongly eosinophilic due to the abundance of nutritive phagocytes which filled the lumen. The ovaries were lined with pre- and early-vitellogenic oocytes, and the testes had a layer of developing sperm in short spermatocyte columns. When the next sample was collected on 27 June, spawning was under way (Fig. 4c). The ovaries contained an abundance of ova (100 to 110 μm diam), and the testes had a large store of spermatozoa. The period between 11 May and 27 June was characterised by synchronous and rapid gametogenesis. The 10 June 1997 sample illustrated the gametogenic condition and GRR shortly before spawning (Figs. 2, 4b). At this time the females contained late-vitellogenic oocytes and a few ova.

Synchronous development of the entire annual cohort of gametes resulted in exhaustion of the nutritive tissue. Vitellogenesis was completed within 1 mo. The absence of developing gametes on 27 June indicated that gametogenesis was completed for the 1995 breeding season (Fig. 4c). By July the GRR was at its lowest, and the gonad condition indicated that the urchins had finished spawning for some time (Figs. 2, 4d). The absence of gametes in most urchins collected in July and August made it difficult to identify the sex of the urchins (Fig. 4d).

In 1995, spawning at the Solitary Islands occurred between 11 May and 27 June (Figs. 2, 3, 4b, d). The 1997 sample indicated that the gonads would have still been in a pre-spawning condition on 10 June (Fig. 4c). Spawning at the Solitary Islands most probably occurs in late June as a complete and potentially short-lived


Barrens
Fringe
Solitary Is.
Jun 97
Sydney
Ulladulla
Eden
Gonad retrieval (%)
15
10
5
0
J M M J S N J M M J S
1994
1995
Month

event. The mean GRR recorded in June 1995 for the barrens and fringe (8.8% and 12.0%, respectively: Table 1), underestimated the maximum gonad output at the Solitary Islands because spawning had started (Fig. 4c). Gonad weights were not recorded for the pre-spawning May 1995 sample. The GRR measured on 10 June 1997 for the barrens and fringe sites, 8.0 and 14.0%, respectively (Table 1), provided an indication of the maximum gonad output for *C. rodgersii* at the Solitary Islands.

Sydney

There was little change over time in the GRR in the Sydney barrens habitat except for a slight rise between the end of spawning in August 1994 and the beginning of spawning in June 1995 (Fig. 2). This was followed by a slight decrease in the GRR due to spawning in July. In contrast, gonad growth of the urchins in the fringe habitat exhibited greater seasonal change, resulting in a pre-spawning peak in the GRR in May followed by a sharp decrease due to spawning (Figs. 1, 2).

Despite the difference in the GRR between the barrens and fringe sites, histology revealed that gonad condition was similar at both sites (Figs. 3, 4e–g). Gametogenic synchrony was most evident shortly before and during the early part of breeding. All urchins collected on 26 May 1995 had growing or mature gonads and the nutritive tissue was reduced (Figs. 3, 4e). The ovaries contained an abundance of mid- and late-vitellogenic oocytes which were beginning to take up a central position, and ova were present (Fig. 4e). Vitellogenic oocytes continued to develop in the germinal layer. The testes had well-developed spermatocyte columns giving rise to spermatozoa. On 22 June, the gonads were filled with mature gametes and spawning had begun (Figs. 3, 4f). In some gonads the germinal layer contained developing gametes which would be spawned later in the season. In July, the gonads of urchins from the barrens and fringe sites differed markedly (Fig. 3). By the end of July most urchins from the barrens habitat had finished spawning and it was difficult to discern their sex. In contrast, those in the fringe habitat had a considerable store of mature gametes present, and this population continued to spawn through October (Figs. 3, 4g). The germinal layer of the fringe urchins was inactive from July onwards, indicating that gametogenesis was finished for the season (Fig. 4g).

Data from histology indicated that spawning by *Centrostephanus rodgersii* in Sydney started in mid to late June (Figs. 2 to 4e–g). During the first weeks of the breeding season, spawned gametes were replaced in the lumen due to ongoing gametogenesis. The GRR dropped sharply between June and July. This was due to a complete spawn-out at the barrens site, possibly limited to a single episode. In contrast, urchins in the fringe habitat spawned through October in both years due to prolonged gamete storage and episodic release. The barrens urchins spawned for ≃2mo, while those at the fringe site spawned for ≃4 mo. The maximum GRR recorded for the Sydney barrens and fringe habitats were, 6.0 and 11.6%, respectively (Table 1).

Ulladulla

The pattern of gonad growth at Ulladulla was similar in the barrens and fringe habitats (Fig. 2). After the 1994 spawning period, the GRR increased from August 1994 to a maximum in June 1995, followed by a sharp drop due to spawning. All urchins collected from Ulladulla on 16 May 1995 were in pre-spawning condition, with gonads at an advanced stage of gametogenesis (Figs. 3, 4h). The ovaries contained mid- and late-vitellogenic oocytes, and a few ova were present (Fig. 4h). The testes contained well-developed spermatocyte columns and were accumulating spermatozoa. This gametogenic activity was accompanied by a reduction in the nutritive tissue. On 14 June, the gonads were filled with mature gametes and some urchins had spawned (Figs. 3, 4i). The germinal layer contained late-stage developing gametes (Fig. 4i).

In July 1994 and 1995, *Centrostephanus rodgersii* from the barrens and fringe sites contained partially spawned or spent gonads (Fig. 3). The germinal layer did not contain developing gametes, indicating that gametogenesis was finished for the season (Fig. 4g). As a result, subsequent spawning was due to storage of mature gametes. In August 1994, most of the urchins were spent, whereas in 1995 gametes were still present in the gonads at both sites. The rise in the GRR between July and August (Fig. 2) was not due to renewed gametogenesis and may reflect an increase in nutritive tissue. The final decline in the GRR between August and October was due to final gamete release. By October all the urchins were spent (Fig. 3).

In 1995, *Centrostephanus rodgersii* from Ulladulla initiated spawning between the May and June sampling dates, with major activity between June and July and a final period of gamete release between August and September. Urchins from both the barrens and fringe sites had a 4 mo breeding period. The maximum GRR recorded for these sites were, 8.3 and 9.5%, respectively (Table 1).

Eden

At Eden, the pattern of gonad growth was similar in the barrens and fringe habitats (Fig. 2). The cycle of change in the GRR was, however, less pronounced for the

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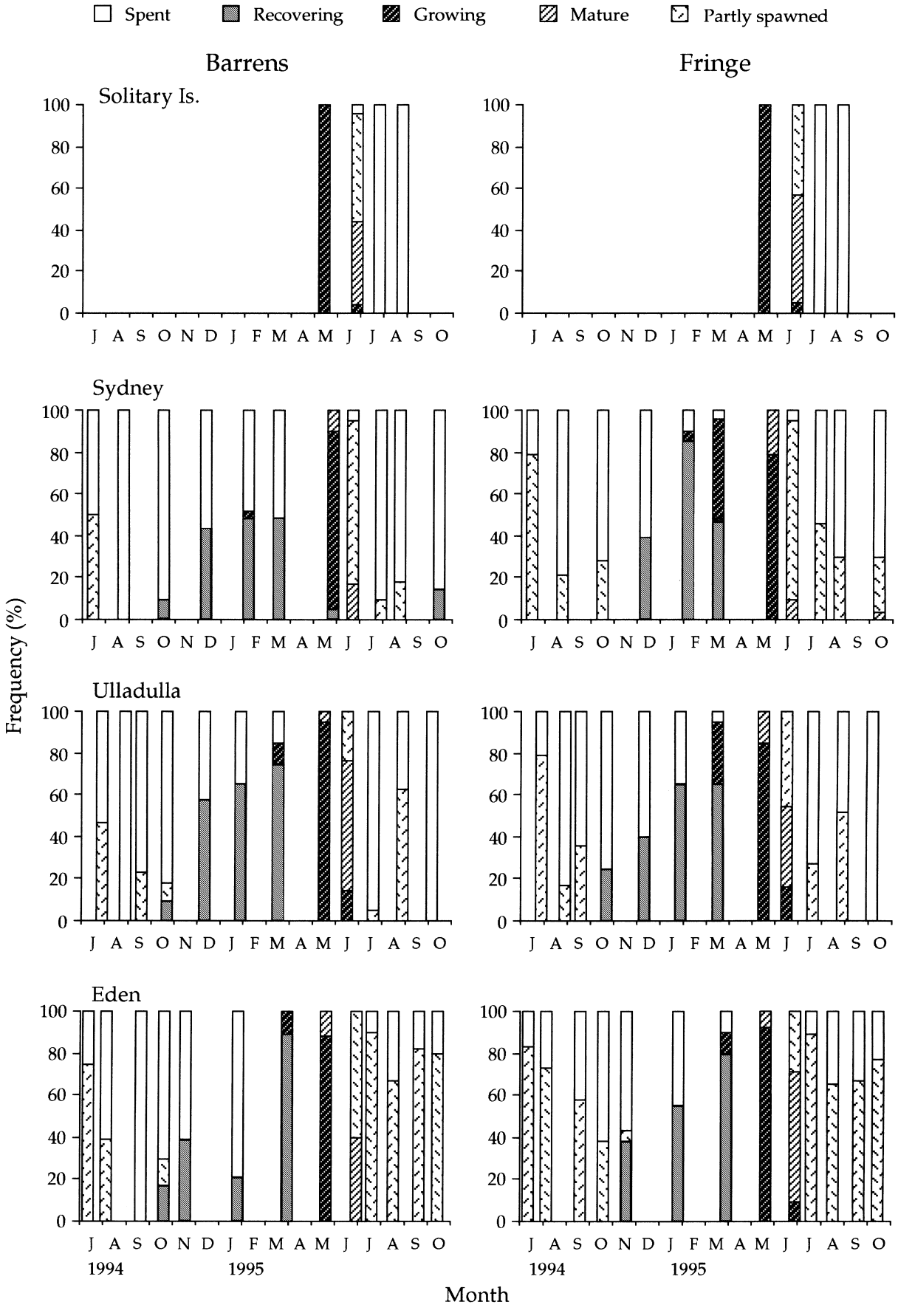
Fig. 2 *Centrostephanus rodgersii*. Gonad retrieval rate (mean + SE, $n = 20–30$) in barrens and fringe habitats at Solitary Islands, Sydney, Ulladulla and Eden. Rate recorded for Solitary Islands in June 1997 is also shown


Spent
Recovering
Growing
Mature
Partly spawned
Barrens
Fringe
Solitary Is.
Sydney
Ulladulla
Eden
Frequency (%)
0
20
40
60
80
100
J A S O N D J F M A M J J A S O
1994
1995
Month

barrens urchins. From the end of breeding in November 1994 to March 1995, the GRR increased through expansion of the nutritive phagocytes (Figs. 2, 3). This was followed by gametogenic growth in May and June (Fig. 4k, l). The GRR was greatest in late June 1994 and 1995, followed by a decrease due to spawning (Fig. 2).

All the urchins collected from Eden on 18 May 1995 had growing or mature gonads, and most had a substantial store of nutritive tissue (Figs. 3, 4k). The ovaries contained mid- and late-vitellogenic oocytes, but ova were not present (Fig. 4k). The testes had well-developed spermatocyte columns and were accumulating spermatozoa. By 28 June, the gonads were packed with mature gametes and spawning had started (Figs. 3, 4l). Mid- and late-vitellogenic oocytes continued to develop in preparation for release, and some nutritive tissue remained at the periphery (Fig. 4l). In July and August 1994 and 1995, most urchins had partly spawned gonads. During these months a conspicuous store of gametes was present and the germinal layer was largely inactive (Fig. 4m). Stored gametes were present in the gonads of the fringe urchins through October of both years and at the barrens in 1995. In both years there was little change in gonad condition from July to October at the fringe site. The rise in GRR between August and September may reflect an increase in nutritive tissue (Fig. 2).

In 1994 and 1995, gamete release by *Centrostephanus rodgersii* at Eden started between the May and June sampling dates, with the major period of gamete release between late June and August. This was followed by prolonged gamete storage and episodic spawning through October at both sites in 1995, while in 1994 spawning at the barrens site was finished by September. At Eden, *C. rodgersii* had a 5 to 6 mo breeding season between June and October. The maximum GRR recorded for the Eden barrens and fringe sites were 6.9 and 13.5%, respectively (Table 1).

Influence of habitat on reproductive output and breeding

Although the timing of gametogenesis was similar in the barrens and fringe habitats at all locations, reproductive output differed markedly between locations and habitats (Table 1). The effect of habitat was dependent on location (significant habitat location effect, $F_{(3,152)} = 8.03$, $p < 0.001$). Analysis of the GRR data recorded just prior to initiation of spawning at Sydney and Eden revealed that the fringe urchins had significantly larger gonads than their barrens conspecifics (a posteriori Ryan's test). At Ulladulla, the pre-spawning GRR did not differ between the barrens and fringe sites (Ryan's test). A similar result was obtained for the Solitary Islands on 27 June 1995. Spawning however, had already begun. Comparison of the pre-spawning GRR obtained for the Solitary Island on 10 June 1997 provided a better indication of the maximum gonad output at this location, and showed that the fringe urchins had significantly larger gonads than barrens urchins (student's $t_{(48)} = 6.74$, $p < 0.001$) at that time.

At Sydney and Eden, the reproductive output of urchins in the barrens habitat was particularly low; the maximum GRR was approximately half that recorded for the fringe urchins (Table 1). The smaller gonads of barrens urchins correlated with their shorter breeding period compared with the fringe urchins at Sydney (Figs. 2, 3). At Sydney and Eden, the urchins from the fringe habitat had a greater store of nutrients in their gonads at the beginning of the May gametogenic period, and this resulted in a greater production of gametes compared with their conspecifics at the barrens. This enhanced condition at the onset of breeding supported prolonged gamete storage and extended the spawning period of the fringe urchins at Sydney in both years and at Eden in 1994 (Figs. 2, 3). Ulladulla differed from the other locations in having a similar breeding period at the barrens and fringe in both years (Fig. 3).

Morphometry of gonad growth

The relationship between test diameter and reproductive output by *Centrostephanus rodgersii*, assessed when the gonads were at their heaviest, shows that gonad weight increased with increasing diameter (Fig. 5). There was considerable variation in gonad weight, with the r^2 values for the barrens and fringe data sets being 0.63 and 0.39, respectively.

There was no significant relationship between size and relative yield in urchins from either the barrens ($r^2 = 0.005$, NS) or fringe habitats ($r^2 = 0.004$, NS). At maximum gonad output, the GRR of the urchins from the barrens habitat were on average $< 10\%$, while that of urchins from the fringe habitat was $> 10\%$ (Fig. 6a, b, Table 1).

Differences in gametogenesis and spawning among locations

At all four locations, the increase in GRR in May was due to an accumulation of nutritive tissue followed by mobilisation of stored nutrients for gametogenesis. The marked inverse relationship between nutritive tissue and gamete development was particularly clear at the Solitary Islands, where the gonads exhibited sharply synchronous development of a single cohort of gametes (Fig. 4a–d). In contrast, stored nutrients were utilised over a longer time frame at the southern locations in association with ongoing gametogenesis. At the Solitary

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Fig. 3 *Centrostephanus rodgersii.* Gametogenic cycle. Histograms show relative frequencies of gonad stages from May to August 1995 at Solitary Islands and from July 1994 to October 1995 at Sydney, Ulladulla and Eden ($n = 20$ to 30)

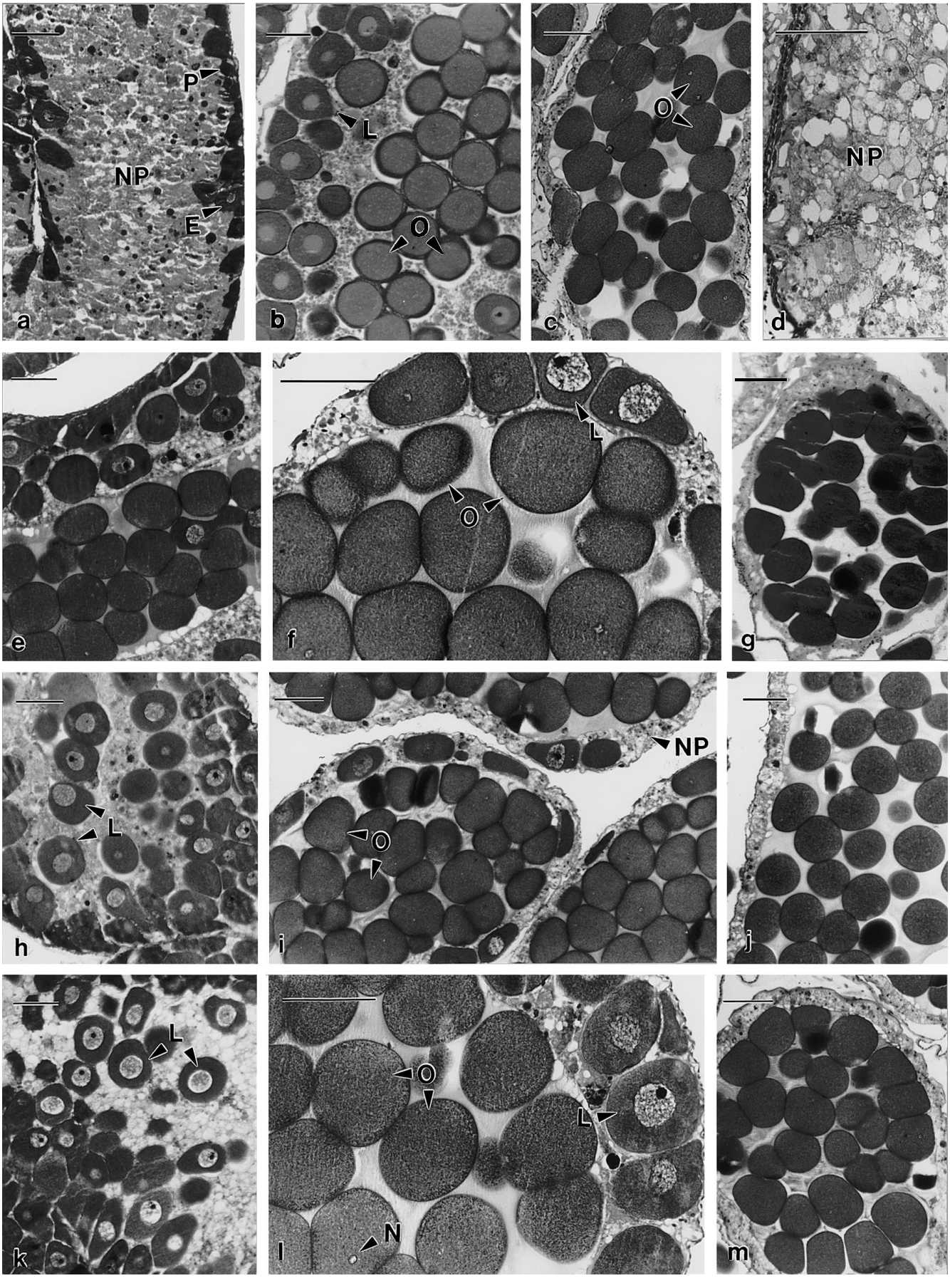
a
P
NP
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Table 1 *Centrostephanus rodgersii*. Maximum gonad retrieval rates (*GRR*). Standard errors and sample size in parentheses

Location	Maximum GRR	
	barrens	fringe
Solitary Islands 1995	8.77 (1.0, 22)	11.98 (0.84, 22)
Solitary Islands 1997	8.01 (0.53, 25)	14.02 (0.34, 25))
Sydney 1995	5.98 (0.31, 22)	11.63 (0.45, 20)
Ulladulla 1995	8.25 (0.47, 22)	9.54 (0.45, 22)
Eden 1995	6.89 (0.4, 24)	13.47 (0.81, 21)

Islands, gamete development was completed by mid-June in 1995 followed by complete spawn-out (Fig. 4b–d). In contrast, at Sydney, Ulladulla and Eden, mature gametes were provided by the germinal epithelium in late June and early July (Fig. 4f, i, l)

The onset of spawning occurred over a remarkably similar time frame at the four locations (Figs. 1–3). At all sites, *Centrostephanus rodgersii* had mature gametes by early June, followed by the onset of spawning in mid- to late-June (Figs. 2–4). At the northern end of its range, *C. rodgersii* had a short 1 mo breeding period, while at the southern end of its range there was an extended 5 to 6 mo breeding period (Fig. 3). The presence of mature gametes from August onwards at the southern sites was due to storage.

Photoperiod was similar across all locations with a 35 min difference in day length between the most northern and southern sites on the shortest day of the year (Fig. 7). On 21 June, day lengths at the Solitary Islands, Sydney, Ulladulla and Eden were 612, 594, 586 and 577 min, respectively. The increased tempo of gametogenesis in May occurred after the inflection point in April, when day length became shorter than night length. At all locations, *Centrostephanus rodgersii* came into breeding condition near the winter solstice and spawning coincided with increasing day length.

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Fig. 4 *Centrostephanus rodgersii*. Histology of ovaries shortly before and at beginning of spawning in May (*left column*: **a, e, h, k**), June (*middle column*: **b, c, f, i, l**), and July (*right column*: **d, g, j, m**). **a–d** Solitary Islands: **a** 10 May 1995, pre-spawning ovary filled with nutritive phagocytes and lined with small oocytes; **b** 10 June 1997, pre-spawning ovary with late vitellogenic oocytes and ova; **c** 27 June 1995, partly spawned ovary, germinal layer lacks developing gametes, **d** 25 July 1995, spent ovary, nutritive phagocytes have started to recover. **e–f** Sydney: **e** 26 May 1995, pre-spawning ovary filled with ova and with developing oocytes at periphery; **f** 22 June 1995, partly spawned ovary with developing oocytes; **g** 22 July 1995, partly spawned ovary, germinal layer lacks developing gametes. **h–j** Ulladulla, **h** 16 May 1995, pre-spawning ovary with late-vitellogenic oocytes: **i** 14 June 1995, partly spawned ovary with ova and developing oocytes; **j** 17 July 1995, partly spawned ovary, germinal layer lacks developing gametes. **k–m** Eden: **k** 18 May 1995, pre-spawning gonad filled with late vitellogenic oocytes; **l** 28 June 1995, partly spawned ovary with ova and developing oocytes; **m** 18 July 1995, partly spawned ovary, germinal layer lacks developing gametes (*E* early-vitellogenic oocytes; *L* late-vitellogenic oocytes; *N* nucleus; *NP* nutritive phagocytes; *O* ova; *P* pre-vitellogenic oocytes; scale bar = 100 μm)

Changes in sea temperature in 1994 and 1995 were smallest at the Solitary Islands and greatest at the most temperate location at Eden (Fig. 8). At the Solitary Islands, Sydney, Ulladulla and Eden, annual sea temperatures ranged from 19.4 to 27.3 °C, 15.9 to 25.8 °C, 14.3 to 25.6 °C and 12.3 to 23.7 °C, respectively (Table 2). The biggest difference was in minimum sea temperature, with a 7C° difference between the Solitary Islands and Eden (Table 2). Maximum temperature at these locations differed by 3.6C°. Rapid oocyte growth in May coincided with decreasing temperatures, and spawning in June and July occurred during the winter, as the sea temperature was approaching its annual minimum (Fig. 8). In 1995, spawning at the Solitary Islands was bracketed by temperatures of 20.5 and 20.8 °C. The major June–July spawning period at Sydney coincided with temperatures ranging from 16.4 to 18.7 °C. At Ulladulla and Eden this spawning period coincided with temperatures ranging from 14.6 to 18.2 °C and, 13.3 to 17.5 °C, respectively. Across all locations, initiation of spawning coincided with temperatures between 13.3 and 20.8 °C (Table 2).

Discussion

Gametogenesis in *Centrostephanus rodgersii* was typical of diadematoids, with a marked temporal separation of gonad growth due to enlargement of the nutritive phagocytes followed by mobilisation of the reserves during an intense period of relatively synchronous gametogenesis prior to spawning (O'Connor et al. 1978; Pearse and Cameron 1991; King et al. 1994). The onset of vitellogenesis in May was well-illustrated by the appearance of a rapidly growing cohort of oocytes in the ovaries of urchins from the Solitary Islands. Vitellogenesis in *C. rodgersii* takes ≃1 mo, similar to that reported for other echinoids (Gonor 1973; Byrne 1990). At the Solitary Islands, the pre-spawning gametogenic period involved the entire cohort of gametes and marked the end of gametogenesis for the season. Gametogenesis was less synchronous at Sydney, Ulladulla and Eden, where gamete development continued through late June and early July.

The major difference in reproduction by *Centrostephanus rodgersii* along the coast of New South Wales was in the duration of spawning. A rapid increase in gonad weight followed by complete spawn-out over a few weeks is characteristic of reproduction by *C. rodgersii* at the Solitary Islands (O'Connor et al. 1978). Spawning at this most northern site in 1995 was finished by July. In contrast, spawning by *C. rodgersii* at Sydney, Ulladulla and Eden in June and July 1994 and 1995 was partial. At these sites gamete storage, particularly by the fringe urchins, ensured that spawning continued for several months. The longest breeding period was recorded at the most southern location at Eden.

An increase in the tempo of gametogenesis in May and onset of breeding in June–July occurred in parallel

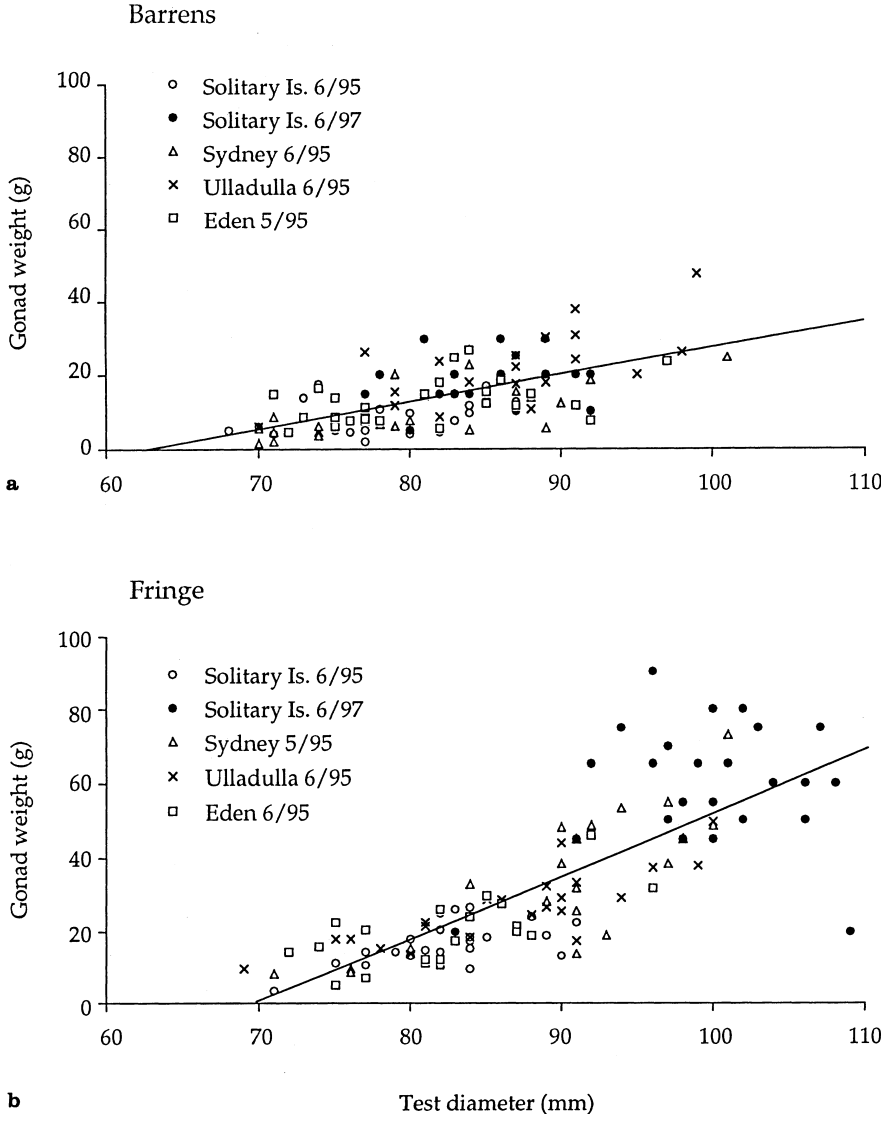

Fig. 5 *Centrostephanus rodgersii*. Relationship between maximum gonad weight and test diameter across all locations at barrens and fringe habitats. **a** $R^2 = 0.39$; **b** $R^2 = 0.63$

at all locations. This reproductive synchrony in *Centrostephanus rodgersii* is consistent with gametogenesis and spawning being cued by exogenous factors operating across all the populations studied. At all locations, spread over nine degrees of latitude, the most consistent and most likely factor to entrain these reproductive events is photoperiod. Initiation of gametogenesis appears to be triggered by decreasing day length, and probably occurs in April when the days becomes shorter than nights. The gonads reached their maximum development just prior to the winter solstice, and spawning occurred shortly thereafter. For *C. rodgersii*, short days and lunar conditions coinciding with the solstice appear likely proximate factors which might cue the onset of spawning across its range. A similar reproductive pattern occurs in widely separated populations of *Strongylocentrotus purpuratus* along the west coast of North America (Pearse 1981). Detailed field and laboratory studies demonstrate that gametogenesis in *S. purpuratus* is controlled by seasonally changing photoperiod, with little or no influence by temperature (Gonor 1973; Pearse et al. 1986; Bay-Schmith and Pearse 1987).

Although gametogenesis and spawning coincided with decreasing sea temperature, this factor would not provide a uniform cue to promote reproductive synchrony at all locations. In the light of the contrasting winter temperatures experienced by northern and southern populations, it is unlikely that *Centrostephanus rodgersii* has a critical temperature for initiation of breeding, as suggested for other sea urchins (Fenaux 1968; Byrne 1990). Temperature however, may influence gamete storage and duration of spawning. The differences observed among locations in the present study suggest a latitudinal trend in breeding by *C. rodgersii*, with a 1 mo spawning period at its sub-tropical northern limit and a 5 to 6 mo spawning period at its temperate southern limit. Cool temperature has been suggested to play a role in extending gamete storage and spawning by deep-water populations of *Strongylocentrotus purpuratus* (Leahy et al. 1981).

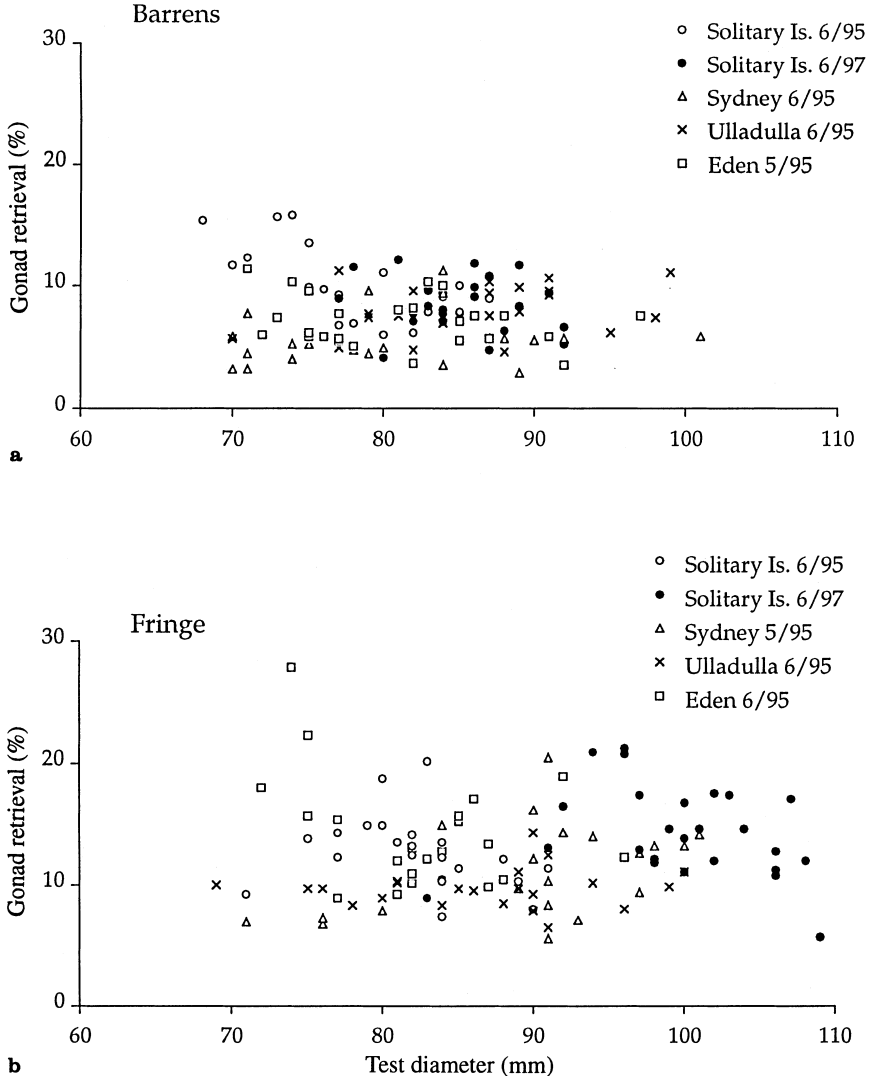

Fig. 6 *Centrostephanus rodgersii.* Relationship between maximum gonad retrieval rate and test diameter across all locations at barrens and fringe habitats. **a** $R^2 = 0.005$; **b** $R^2 = 0.004$

Many diadematoids reproduce with a monthly pattern of gametogenesis and spawning which are under lunar control (Pearse 1970; Kennedy and Pearse 1975; Lawrence and Lane 1982; Lessios 1984). For *Centrostephanus rodgersii*, synchronous growth of the cohort of gametes in urchins from the Solitary Islands reflects the diadematoid pattern. The possibility that gametogenesis at this location is influenced by the lunar cycle would have to be assessed by weekly examination of the gonads with respect to the lunar phases in May and June. If reproduction at Sydney, Ulladulla and Eden is influenced by the lunar cycle, the prolonged pattern of gametogenesis at these sites would make this difficult to discern. Within the annual breeding period of its congener, *C. coronatus*, gametogenesis and spawning occur with a monthly pattern (Kennedy and Pearse 1975). Extended spawning by *C. rodgersii,* however, was due to prolonged gamete storage and not to a monthly renewal of gametogenesis.

Growth of sea urchin gonads is highly sensitive to food quantity and quality (Ebert 1968; Vadas 1977; Pearse 1981; Andrew 1986; Byrne 1990; Pearse and Cameron 1991). As seen here for *Centrostephanus rodgersii*, inhabiting food-poor barrens areas has a negative influence on reproduction. At the Solitary Islands, Sydney and Eden, the barrens urchins had a lower reproductive output than their fringe conspecifics. The underlying cause of the lower GRR and shorter breeding period of *C. rodgersii* at the barrens was most probably the low abundance of macroalgal food, which resulted in the urchins having a smaller store of nutrients at the onset of gametogenesis. The property of the gonads as the major nutrient storage organ in sea urchins and the ability of the nutritive phagocytes to respond to food of differing quality is utilised by fisheries and aquaculturalists to enhance gonad output through control of diet (de Jong-Westman et al. 1995; Lawrence et al. 1997; Goebel and Barker 1998). This has prompted research to identify optimal natural diets and formulation of artificial diets for sea urchins with the aim to achieve maximum yield of high-quality gonads with the yellow-orange colour preferred by the market (de Jong-Westman et al. 1995; Lawrence et al. 1997; Goebel and Barker 1998). For aquaculture, the potential for

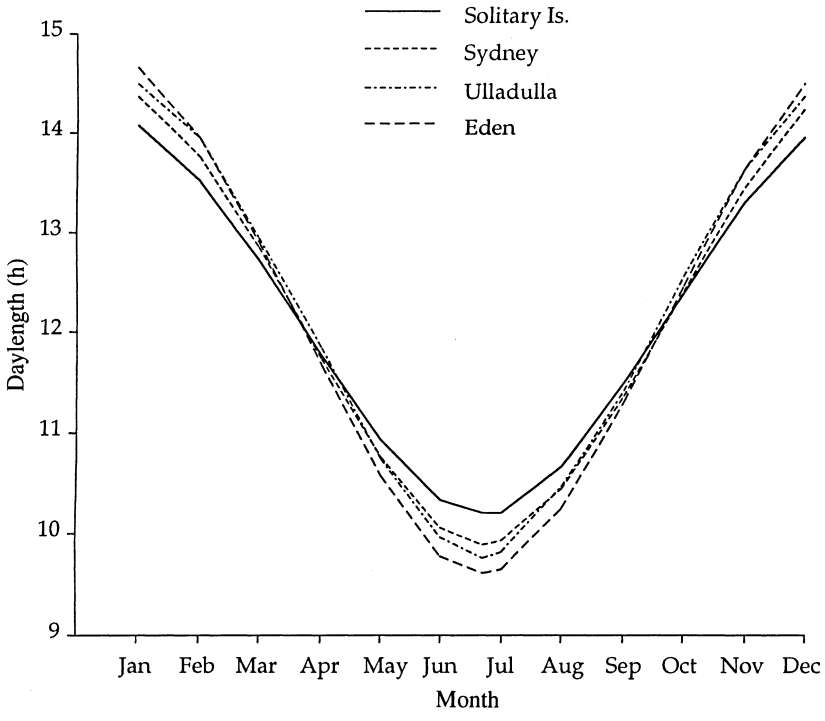

Fig. 7 Annual day-length cycles at the Solitary Islands, Sydney, Ulladulla and Eden

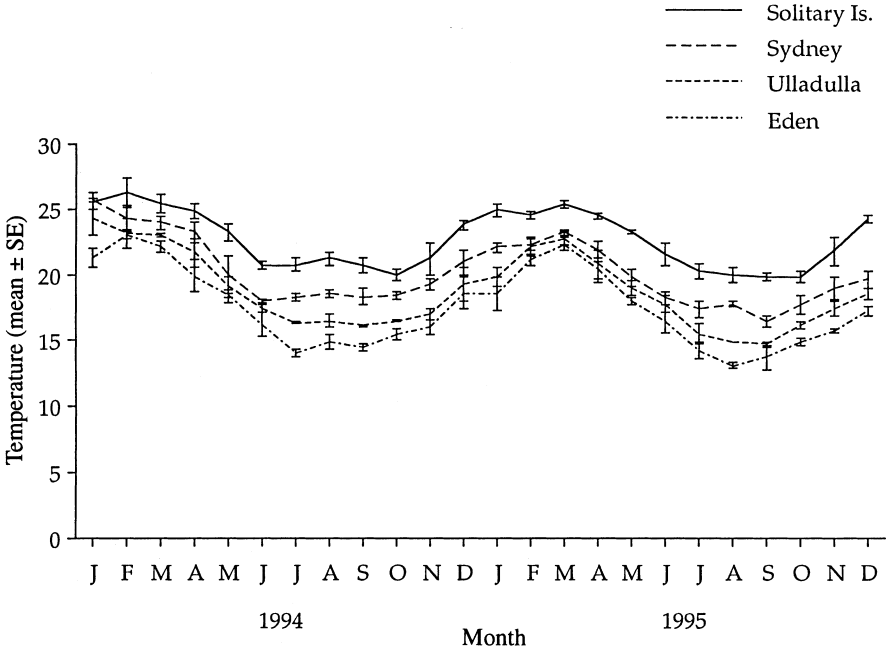

Fig. 8 Mean sea temperatures at Solitary Islands, Sydney, Ulladulla and Eden from January 1994 to December 1995

Table 2 *Centrostephanus rodgersii*. Sea temperature range (annual and during the June/July spawning period) and breeding patterns at four locations along New South Wales coast

Location	Latitude (°S)	Sea temperature range (°C)			Breeding period
		Annual	June/July		
			1994	1995	
Solitary Islands	30	19.4–27.3	20.4–21.2	20.5–20.8	June–July
Sydney	33	15.9–25.8	17.8–18.7	16.4–18.7	June–Sep./Oct.
Ulladulla	35	14.3–25.6	16.2–17.8	14.6–18.2	June–Sep.
Eden	37	12.3–23.7	13.5–17.0	13.3–17.5	June–Oct./Nov.

Table 3 *Centrostephanus rodgersii*. Seasonal trends in gonad maturity (stages detailed in King et al. 1994), GRR and expected commercial value of roe in urchins from fringe habitats in Sydney, Ulladulla and Eden

Gonad maturity stage	Months	GRR (%)			Commercial quality
		Sydney	Ulladulla	Eden	
Partly spawned/spent	Oct.–Dec.	4.1–9.2	4.1–5.7	6.2–7.8	low
Spent/recovery, growing	Jan.–May	7.0–11.5	6.1–8.2	6.1–8.6	medium to high
Mature/partly spawned	June–Sep.	5.0–8.2	1.5–9.4	5.2–13.4	medium to low

re-programming reproduction in urchins through alteration of photoperiod creates the potential to produce out-of season crops of gonads (Pearse et al. 1986; Bay-Schmith and Pearse 1987). For *C. rodgersii*, it appears that manipulation of summer photoperiod may enhance gonad growth out of season (see also *Strongylocentrotus purpuratus*: Pearse et al. 1986). With the current interest in echinoculture and desire to produce market-quality gonads year round, control of reproduction in sea urchins will continue to attract research emphasis.

The suitability of *Centrostephanus rodgersii* for commercial harvest in New South Wales depends on the reproductive cycle (Table 3). The roe are optimal for harvest when they have a firm texture during the recovery and growing stages. *C. rodgersii* with recovering and growing-stage gonads were abundant at Sydney, Ulladulla and Eden from January to May. Within this period, yields would be greatest in late March to early May prior to the mobilisation of nutrient stores for gamete production. During May, the nutritive cells shrink and the gonads soften as the number of gametes increase. Although the short, synchronous reproduction of *C. rodgersii* at the Solitary Islands means that they have marketable gonads for 2 to 3 mo longer, it is unlikely that a commercial fishery could be sustained here, because of comparatively low densities of urchins and the high conservation status of these reefs.

With respect to the importance of obtaining a high yield of gonad per urchin, it is clear that harvesting of *Centrostephanus rodgersii* in fringe habitats would maximise the return to the fishery. Although there was considerable variation among urchins, the GRR in the fringe habitat was ≥10%. In contrast, the retrieval rates obtained for urchins from the barrens habitat was generally < 10%, indicating that this habitats may not yield sufficient roe to warrant harvesting.

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