

# Multi-year observations on the gametogenic ecology of the Antarctic seastar *Odontaster validus*

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**Abstract** This study reports the first multi-year observations on the reproductive patterns for an Antarctic predator/scavenger, *Odontaster validus* (Koehler 1912). Seastars were collected monthly from a shallow site (15–20 m depth) near the British Antarctic Survey (BAS) Rothera Research Station (Adelaide Island, 67°34'S 68°08'W) from July 1997 to January 2001. Reproductive condition, oocyte size frequencies and spermatogenesis were examined in at least ten seastars each month using histological and image analysis techniques. Gonad indices (GI) and pyloric caeca indices (PI) were also examined in the same samples. Female and male GIs varied seasonally, in parallel with a reduction in the proportion of large oocytes and mature sperm in the gonad in August to mid-October following winter spawning. Despite there being remarkable consistency in the timing of spawning from year to year, differences in the reproductive condition of individuals were apparent. Patterns in the digestive tissues also varied with season, peaking in December and reaching a minimum in February in two of the three study years. This weaker annual pattern may partly reflect the varied diet of this

predator/scavenger species, which is not directly dependant on the timing and magnitude of the annual phytoplankton bloom. Pooled oocyte size distributions and residual analysis suggested that oogenesis progressed over 18–24 months, with the largest of the two size classes (maximum diameter = 183 µm) being spawned annually. This pattern of oocyte growth and spawning was previously reported in the early 1960s for an *O. validus* population from McMurdo Sound, which lies south of Rothera by 10° latitude. The extremely catholic diet of this predator/scavenger suggests the reproductive patterns of the seastar will be less susceptible to changes in food supply compared to polar suspension feeders or deposit feeders.

## Introduction

Multi-year evaluations of reproductive patterns of polar marine invertebrates are rare. Those that exist have reported dramatic between year variations in reproductive condition. A study of reproductive ecology of the brittle star, *Ophionotus victoriae* at Rothera Station reported nearly an order of magnitude variation in numbers of eggs spawned between some years (Grange et al. 2004). Several other studies have alluded to significant inter-annual variation in reproductive condition of abundant Antarctic taxa, including the brachiopod *Liothyrella uva* (Meidlinger et al. 1998), the scallop *Adamussium colbecki* (Chiantore et al. 2002; Tyler et al. 2003), the sea urchin *Sterechinus neumayeri* (Brockington et al. 2006) and the seastar *Odontaster validus* (Pearse 1965; Stanwell-Smith and Clarke 1998).

Reproductive success is vital for species persistence and multi-year studies provide a baseline assessment of natural variability in reproductive cycles not available from studies

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of shorter duration. Long duration investigations are particularly important in describing inter-annual variation in reproductive patterns of polar benthos, a fauna characterised by long, slow life-cycles.

Responses in many marine Antarctic organisms to climate change are expected to be larger and earlier than those of the terrestrial ecosystem and in organisms at lower latitudes (Manabe and Stouffer 1979; Clarke and Harris 2003; Peck 2005; Peck et al. 2004, 2006). Consequently, the dramatic variability described in several previous multi-year analyses of invertebrate reproductive ecology in Antarctica may provide an early insight into the effects of environmental change or form a baseline to identify such effects. However, all previous reproductive cycle studies in Antarctica have been on suspension feeders or deposit feeders (Meidlinger et al. 1998; Tyler et al. 2003; Grange et al. 2004; Brockington et al. 2006). *O. validus* is the first predator/scavenger to be evaluated.

*Odontaster validus* is a conspicuous member of the Antarctic benthos, common in shallow waters and circumpolar in distribution (Dearborn 1965; Arnaud 1974; McClintock et al. 1998). It ranges from low latitude sites in South Georgia (54°S), throughout the Southern Ocean to an extreme southerly latitude of McMurdo Sound (77°51'S) (McClintock et al. 1988), and has a depth range from the intertidal to 940 m (Dearborn 1977). *O. validus* is an opportunistic predator/scavenger, which will consume animal (small gastropods and crustaceans) and plant prey (mainly diatoms), plankton and detrital material (sponge spicules and sand grains) (Pearse 1965), including planktonic larvae (Dayton et al. 1974) and higher proportions of primary production (chlorophyll) when available (McClintock et al. 1988). Some aspects of *O. validus*' reproductive ecology are relatively well known from short-term studies at several localities, including sites in the high Antarctic at McMurdo Sound (77°51'S), Cape Evans (77°38'S) (Pearse 1965, 1969) and Terra Nova Bay (74°40'S) (Chiantore et al. 2002), and in the maritime Antarctic at Signy Island (60°43'S) (Stanwell-Smith and Clarke 1998; Stanwell-Smith and Peck 1998). All have reported 18–24 month gametogenic cycles, a winter spawning period and planktotrophic larvae (Pearse 1969, Pearse and Bosch 1986, Bosch et al. 1990). The *O. validus* population at Rothera (67°34'S) provides a basis for a wider comparison, as it lies in the middle of the latitudinal range of previous studies.

The main objectives of the present study were to: (1) describe the cycles of the gametogenic ecology of *O. validus* using histological and image analysis techniques, and to determine the extent of seasonal and inter-annual variation in several reproductive characters, (2) to compare these patterns with findings on other populations of *O. validus* and other species, and (3) to evaluate, where

possible, the differences in patterns produced by a predator/scavenger lifestyle compared to the previous Antarctic herbivores and detritivores studied.

## Materials and methods

### Seastar sampling

Monthly collections of *Odontaster validus* (Koehler 1912) were made by SCUBA divers from 15 to 20 m between July 1997 and January 2001 from a site near the British Antarctic Survey's (BAS) Rothera Research Station (67°34'S 68°08'W), where it is locally abundant (Appendix 1).

A minimum of ten individuals of a minimum "R" (radial length) of 25 mm (to ensure reproductive maturity) was randomly collected each month unless precluded by poor weather. A total of 39 months were sampled. Once collected, seastars were preserved in 4% buffered formaldehyde in seawater for transport and subsequent storage in the UK.

### Biometry and reproductive condition

Two radius measurements were recorded from fixed specimens using vernier callipers, "R" denoting radial length and "r" denoting body radius ( $\pm 0.01$  mm) (Mortensen 1927). Any excess liquid was removed by blotting each seastar on absorbent paper towel, before individuals were weighed wet ( $\pm 0.01$  g) and the internal organs dissected out.

Each seastar had a pair of gonads in each arm, which were tuft-like or digitate. All gonads were weighed wet ( $\pm 0.01$  g) from each seastar for gonad index assessment (GI):

$$GI = (GW \times 100) / BW,$$

where GW = gonad wet weight (g) and BW = total seastar wet weight (g) (Grant and Tyler 1983a).

A single pair of gonads from each seastar was placed in 70% propan-2-ol. Gonad colour ranged from white to orange, and although the testes tended to be paler than ovary tissue (Pearse 1965), sexes could only be confirmed by histology.

### Energy investment and storage

Each seastar possessed a pair of pyloric caeca in each arm. Any excess liquid was removed by blotting the pyloric caecae on absorbent paper towel. All pyloric caecae from each seastar were weighed wet ( $\pm 0.01$  g) and the pyloric caeca index (PI) calculated using total wet weight:

$$PI = (PW \times 100)/BW,$$

where PW = pyloric caeca wet weight (g) and BW = total seastar wet weight (g) (Farmanfarmaian et al. 1958; Pearse 1965; Mauzey 1966).

The PI provided a measure of changes in the allocation of resources to the pyloric caeca. Comparisons between months when the pyloric caeca were at a maximum size, and months when they were at a minimum size, provided data on storage cycles.

#### Histological preparation and image analysis

Gonad tissues were processed using the methods of Pain et al. (1982a, b) and Tyler et al. (2003). Sections (7  $\mu$ m) were stained using Haematoxylin “Z” and the counterstain Eosin (Cellpath, UK). Digital images of gonad sections were taken using Matrox Rainbow Runner software and analysed using SigmaScan Pro version 4. The feret diameter of at least 100 oocytes was measured in each female, which calculates the diameter of each oocyte assuming the best-fit spherical size of the oocyte, and the images produced used to construct pooled oocyte size distributions for each monthly sample. Males were staged on the relative amount and maturation stage of sperm in the testes according to Pearse (1965), who identified at least six gametogenic stages within the male reproductive cycle, describing the development of early spermatogonia (I) into mature, active spermatozoa (V), and finally the shedding of sperm during spawning (VI, spent).

#### Statistical analysis

Statistical techniques followed the methods of Fowler et al. (1998) and were carried out using Minitab 13.0. The majority of data were not normally distributed (Anderson-Darling Normality test) and were tested using non-parametric statistical analyses. However, parametric tests were used on any normally distributed data. An  $r \times c$  contingency table of standardised residuals was used to study the growth of oocytes, and differences in oogenic stage between monthly samples.

All experimental methods complied with the relevant legislative guidelines current in the UK.

## Results

#### Sex ratio and size characteristics

Four hundred and seven *O. validus* were sampled of which 182 (44.7%) were female and 222 (54.5%) were male, and

3 hermaphrodite (0.7%). The sex ratio of the population over the whole study was slightly biased toward males ( $\chi^2 = 3.84$ ,  $P < 0.05$ ), although this ratio varied among sampling years (Table 1).

Individual wet weight ranged from 5.92 to 37.83 g (mean = 15.92 g, SD = 5.46,  $n = 407$ ). Female and male wet weight ranged between 6.37 and 37.83 g (mean = 15.64 g, SD = 5.54,  $n = 182$ ) and 5.92 g and 34.70 g (mean = 16.19 g, SD = 5.41,  $n = 222$ ), respectively and all individuals collected were reproductively mature. Wet weight between the females and males sampled was not significantly different (Wilcoxon matched pairs test,  $W_+ = 432$   $W_- = 271$ ,  $N = 37$ ,  $P = 0.228$ ), (“ $N$ ” = number of paired observations [mean monthly female ( $x$ ) versus male ( $y$ ) wet weight] less those observations where the difference between  $x$  and  $y = 0$ ).

Radial length (“ $R$ ”) ranged from 19.00 to 47.00 mm (mean = 34.43 mm, SD = 5.54,  $n = 407$ ) and body radius (“ $r$ ”) ranged from 10.00 to 25.00 mm (mean = 16.20 mm, SD = 2.65,  $n = 407$ ). There was no significant difference in size between females and males (Wilcoxon Test for  $R$ ,  $W_+ = 420$   $W_- = 246$ ,  $N = 36$ ,  $P = 0.174$ , for  $r$ ,  $W_+ = 384.5$   $W_- = 281.5$ ,  $N = 36$ ,  $P = 0.423$ ).

#### Reproductive condition

The GI varied among years (Fig. 1). The ovary index ranged from 0.31 (October 1998) to 20.34 (April 2000) (mean = 5.5, SD = 3.28,  $n = 182$ ), whereas the testis index ranged from 0.4 (December 2000) to 19.1 (January 1999) (mean = 6.3, SD = 4.05,  $n = 222$ ).

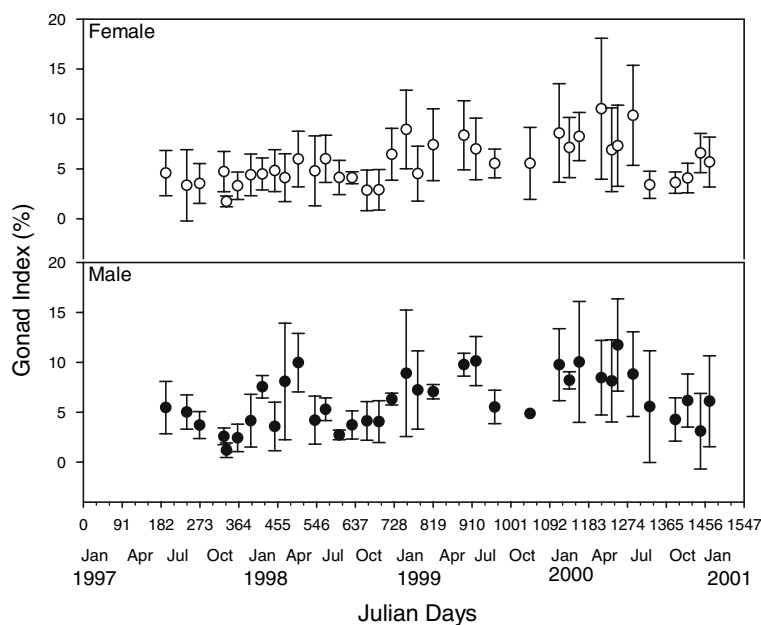
Four annual spawning events were evident from the data and occurred between August and October each year (Fig. 1 and Table 2). Dramatic differences in GI among years were not apparent, although the four spawning events varied in magnitude with the largest percentage decrease in the female gonad occurring during 1997 and 2000 (62 and 61% respectively). Relatively large reductions in testis index were observed for males during 1997 and 1998 (78 and 69% respectively) (Fig. 1). Both females and males

**Table 1** *Odontaster validus*. Sex ratio of females and males collected between July 1997 and January 2001 from Rothera Station (67°34′S 68°08′W) using a chi-square statistical test

Year	Female	Male	Chi-square test statistic
July 1997–December 1997	34	32	0.076, NS
1998	64	69	0.195, NS
1999	32	35	0.134, NS
January 2000–January 2001	52	86	8.377, $P < 0.01$

NS non significant

**Fig. 1** *Odontaster validus*. Mean female (open circle) and male (filled circle) gonad index values sampled on a monthly basis between July 1997 and January 2001 from Rothera Station (67°34'S 68°08'W). The mean male and female gonad index ( $\pm$ SD) is plotted for each month



exhibited smaller events during 1999 (34% decrease and 52% decrease, respectively) and moderate spawning episodes were recorded during the remaining years (Table 2).

Reproductive condition did not differ significantly between females and males over the sampling period (Wilcoxon Test,  $W^+ = 462$ ,  $W^- = 241$ ,  $N = 37$ ,  $P = 0.097$ ). However, there were significant differences in the magnitude of the gonad index over the 3.25-year study (Kruskal–Wallis  $H = 75.66$ ,  $P < 0.001$ ). This was also true for comparisons between years (Appendix 2), except when comparing GI between 1999 and 2000 (Mann–Whitney  $W = 6,971.5$ ,  $P = 0.861$ ).

#### Energy investment and storage

Patterns in PI varied strongly with season (Fig. 2). Minimum and maximum values of 3.25 and 32.7 were obtained

for females collected in February 1999 and December 1998, respectively. Male PI ranged from 2.6 to 36.7 in December 1997 and August 1998, respectively. Variation in PI was not as cyclical as the pattern observed in the gonad. The pyloric caeca gradually increased in size between July 1997 and January 1999. A significant reduction in mass of the pyloric caeca followed between January and July 1999. A clear annual signature, characteristic of cycles in the gonad, was not obvious in the pyloric caeca.

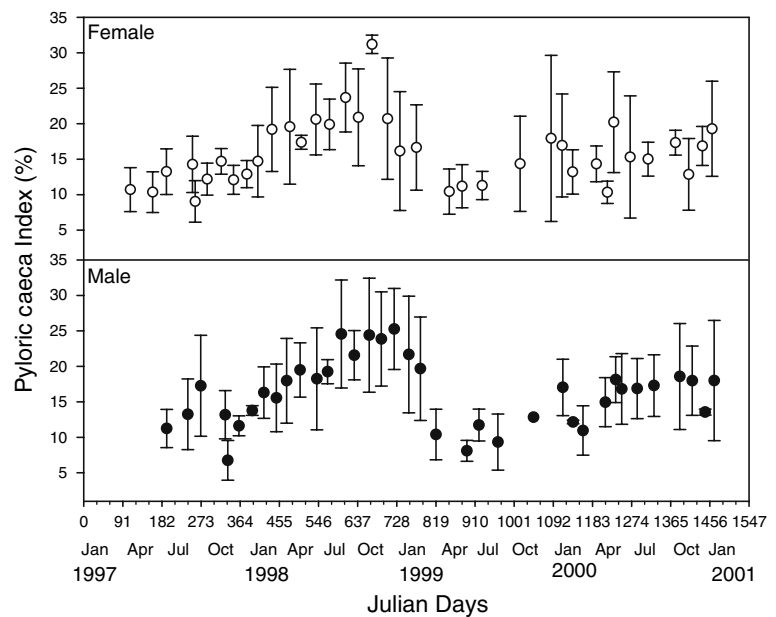
There was no significant difference between female and male PI (Wilcoxon Test,  $W^+ = 396$ ,  $W^- = 307$ ,  $N = 37$ ,  $P = 0.507$ ). However, there was significant variation in PI over the course of the study (Kruskal–Wallis  $H = 85.36$ ,  $P < 0.001$ ). This was also true when index variability between years was compared (Appendix 3), with the exception of the comparison between 1997 and 1999 (Mann–Whitney  $W = 4,055.0$ ,  $P = 0.099$ ).

**Table 2** *Odontaster validus*. Reproductive condition is presented as the percentage decrease in the female and male gonad index between July 1997 and October 2000 from Rothera Station (67°34'S 68°08'W), calculated from the average monthly gonad index before (fecund) and after spawning (spent)

$n$  number of individuals  
Values in parentheses are  $\pm$ SD

Year	Spawning	Fecund GI Mean	Spent GI Mean	%Decrease
Female				
1997	July–December	4.6 (SD = 2.6; $n = 3$ )	1.7 (SD = 0.5; $n = 6$ )	62
1998	July–November	6.0 (SD = 2.4; $n = 7$ )	2.9 (SD = 2.0; $n = 6$ )	52
1999	June–November	8.4 (SD = 3.5; $n = 6$ )	5.6 (SD = 3.6; $n = 2$ )	34
2000	July–November	10.4 (SD = 5.0; $n = 4$ )	4.1 (SD = 1.5; $n = 3$ )	61
Male				
1997	July–December	5.5 (SD = 2.6; $n = 9$ )	1.2 (SD = 0.7; $n = 6$ )	78
1998	May–August/September	10.0 (SD = 2.9; $n = 3$ )	3.1 (SD = 1.0; $n = 10$ )	69
1999	July–November	10.1 (SD = 2.5; $n = 4$ )	4.9 (SD = 0.0; $n = 1$ )	52
2000	June–October	11.7 (SD = 4.6; $n = 8$ )	4.3 (SD = 2.2; $n = 9$ )	64

**Fig. 2** *Odontaster validus*. Mean female (open circle) and male (filled circle) pyloric caeca index values sampled on a monthly basis between July 1997 and January 2001 from Rothera Station (67°34'S 68°08'W). The mean male and female pyloric caeca ( $\pm$ SD) index is plotted for each month



### Oocyte feret diameter

Monthly oocyte data were pooled and means taken. There was significant inter-annual variation in mean feret diameter for all oocytes over the year during the 3.25-year study (One Way ANOVA  $F_{3, 35} = 4.92$ ,  $P = 0.006$ ) (Fig. 3). The largest differences in mean oocyte size were recorded between 1997 and 2000, and 1998 and 2000 (Tukey's test for pairwise comparisons). The maximum oocyte size of 183  $\mu\text{m}$  was observed in one individual in July 2000. The maximum average feret diameter of 117  $\mu\text{m}$  was recorded in monthly oocyte data for May 2000.

Four spawning events were identified from the oocyte size data (Fig. 3). All occurred between August and mid-October. The observed decrease in the proportion of large oocytes in the ovary coincided with reductions in gonad index (Fig. 1) and indicated spawning periods. The details of these changes associated with spawning events are given in Table 3.

Pooled oocyte size distributions and residual analysis using a ( $r \times c$ ) contingency table (Grant and Tyler 1983b) suggest oogenesis progressed over 18–24 months and involved the development of successive annual generations of oocytes (Fig. 4 and Appendix 4). A reserve of smaller oocytes (50–100  $\mu\text{m}$ ), mainly seen in the September oocyte distributions, remained in the ovary after all the large, mature oocytes had been shed during spawning events. This successive generation of oocytes matured during the following summer ready to be spawned in the following July. The growth of each cohort of oocytes was also followed using contingency table analysis tracing the

positions of positive standardised residuals (Appendix 4). A positive residual indicates that the frequency of oocytes in that size class is greater than expected (Grant and Tyler 1983b). Positive residuals in the 50–100  $\mu\text{m}$  size classes consistently occurred during August/September each year and coincided with the transition of positive to negative residuals in the larger oocyte size classes. This pattern represents the presence of overlapping oocyte generations, where the growth and removal of the first cohort by spawning coincides with the introduction of a second cohort of smaller oocytes to the oogonial pool.

### Male maturity

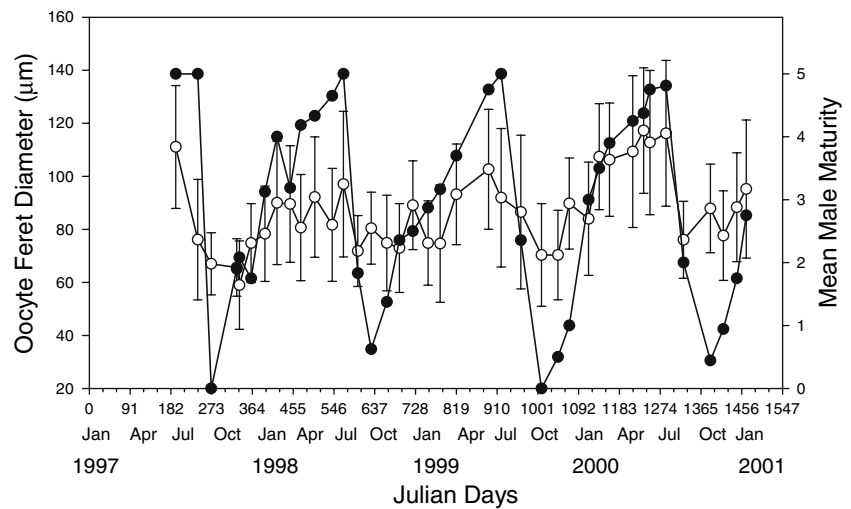
There was a clear seasonal cycle in male spawning (Fig. 3), which was consistent over the 3.25-year study and comparable with the timing of female spawning. The male maturity index ranged between being spent and being at an immature spermatogenic stage (VI and I–II) between late July and mid-October in each year. Significant amounts of active sperm (IV–V) were observed in the testes as early as February and were prevalent from May to July until spawning throughout August until mid-October.

### Discussion

The gametogenic ecology of *Odontaster validus* at Rothera had marked seasonal and inter-annual variability, but was consistent in timing of spawning between August and mid-October each year. Histological sections of both



**Fig. 3** *Odontaster validus*. Mean pooled oocyte feret diameter (*open circle*) sampled on a monthly basis between July 1997 and January 2001 from Rothera Station (67°34'S 68°08'W). The mean pooled oocyte size is plotted ( $\pm$ SD). Average male maturity stage I–V (1–5) is plotted by month (*filled circle*) according to Pearse (1965). Spent males, indicative of stage VI (Pearse 1965), are plotted as zero on the secondary “y” axis to convey the testes as “empty” and to represent the removal of reproductive material from the testes during spawning



**Table 3** *Odontaster validus*. Changes in oocyte size from maximum pre-spawning levels to minimum post-spawning sizes, with the associated reductions in gonad index (GI, %)

Year	Maximum oocyte diameter ( $\mu\text{m}$ )	Month	Minimum oocyte diameter ( $\mu\text{m}$ )	Month	Reduction in GI (%)
1997	111 (SD = 23.2; $n$ = 304)	July	59 (SD = 16.7; $n$ = 604)	December	62
1998	97 (SD = 27.5; $n$ = 734)	July	73 (SD = 16.8; $n$ = 620)	November	52
1999	103 (SD = 22.6; $n$ = 661)	July	70 (SD = 16.9; $n$ = 642)	December	34
2000	117 (SD = 27.5; $n$ = 437)	July	78 (SD = 16.9; $n$ = 349)	November	61

$n$  number of measured oocytes

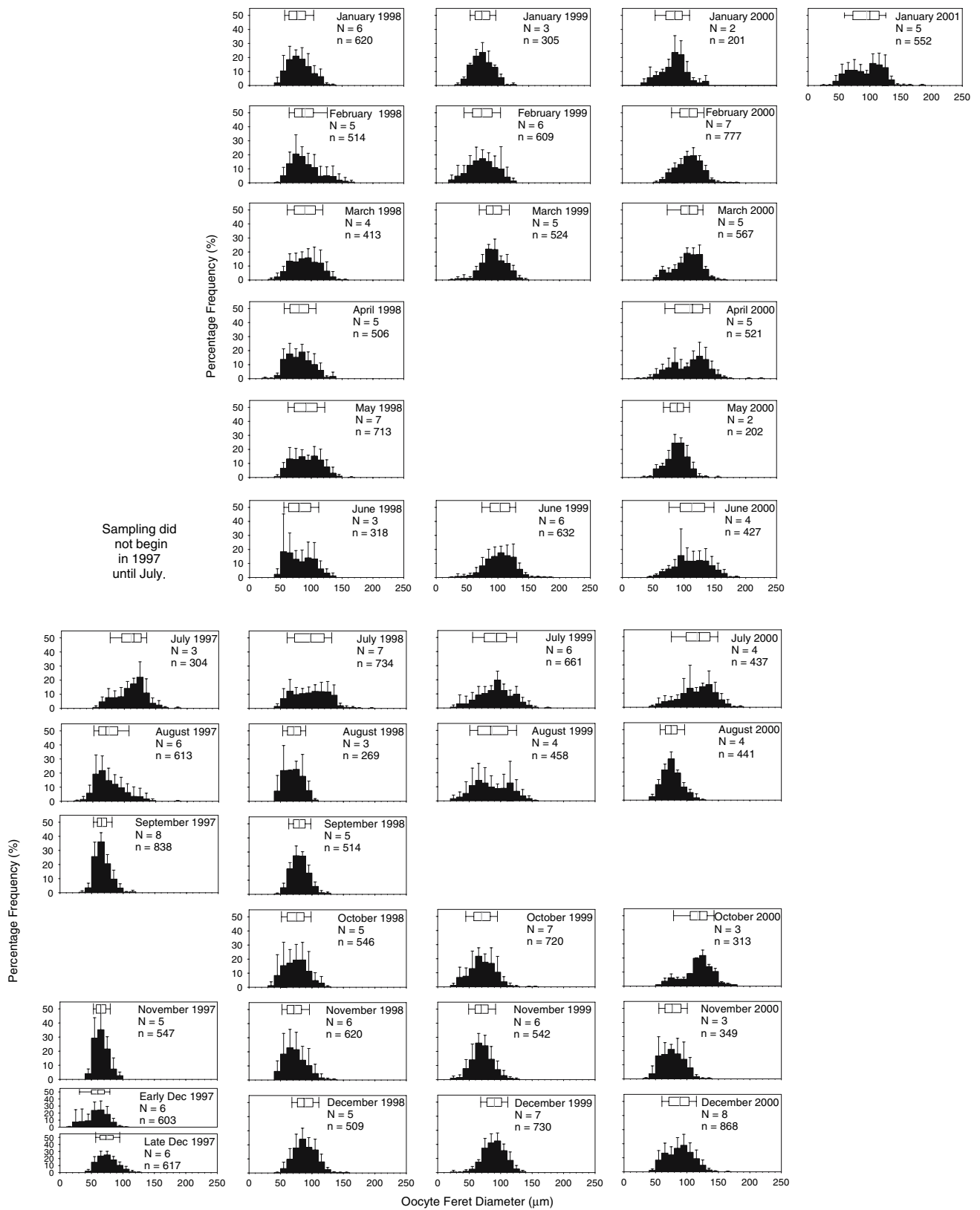
Values quoted are mean maximum oocyte feret diameters ( $\mu\text{m}$ ). Approximately 100 oocytes were measured per female sampled. Values in parentheses are  $\pm$ SD

female and male gonads indicate reproductive synchrony and an annual cycle in gonad index, where gonads increase in volume during May to August and are partially spent by September, becoming fully spent by December. The overall oocyte growth period was prolonged and progressed over 18–24 months. An annual cycle in nutrient storage was not clear from patterns in the pyloric caeca, although seasonal changes were observed. This study also noted the presence of rare (<1%) hermaphrodites amongst the studied population.

Similar findings have been reported for *O. validus* from other localities. Indeed, the same reproductive periodicity is reported in both the high and maritime Antarctic in the McMurdo Sound (77°S), Balleny Islands (67°S), Robertson Bay (71°S) (Pearse 1965, 1966, 1969), and Signy Island (60°S) (Stanwell-Smith and Clarke 1998) populations. The similarity between these studies indicates reproductive synchrony in this species over much of its circumcontinental distribution. These locations differ quite markedly in the duration of photoperiod, extent of winter fast ice and duration of winter minimum temperatures. Whereas, the onset of summer production is well defined and predictable (Peck et al. 2006) throughout Antarctic waters, it is difficult

to identify how the initiation of the bloom could synchronise reproduction towards the end of winter as seen here for *O. validus*. However, fluctuations in alternative food supplies, such as dead and detrital material, could influence aspects of reproductive cycles in scavengers such as *O. validus*. There appears to be coincidence in timing between the occurrence of ice disturbance events (Smale et al. 2007) and the settlement of asteroid larvae onto the ice-scoured bottom at Rothera (Bowden 2005). Scavengers exploit resources made available by ice disturbance, mainly dead prey, which thus increases food levels during the onset of summer and the benefit of larval settlement for scavenger species.

An annual cycle in gonad index has been described for this species across much of its latitudinal range, including Rothera and was first reported for *O. validus* from high Antarctic sites (Pearse 1965). This study represents the first multi-year evaluation of gonad index in *O. validus*, although shorter studies have also found inter-annual variation in the reproductive condition of *O. validus* at McMurdo Sound and Signy Island (Pearse 1965; Stanwell-Smith and Clarke 1998). Gonad index values have been shown to vary amongst studied populations of *O. validus*.



**Fig. 4** *Odontaster validus*. Pooled oocyte feret diameter histograms ( $\pm$ SD) constructed on a monthly basis between July 1997 and January 2001 from Rothera Station ( $67^{\circ}34'S$   $68^{\circ}08'W$ ), where *N* number of females, *n* number of eggs counted (1997–2001) and monthly box

plots covering the oocyte feret diameter range (the left and right hand limits of the boxes represent the 25th and 75th percentiles; box whiskers represent the 10th and 90th percentiles; the median (thick lines) and mean (thin lines) of each oocyte range is also shown)

Pearse (1965) observed that gonads from the Cape Evans population (77°38'S) were double the size of those from McMurdo Sound (77°51'S). He attributed these trends to a greater availability of summer phytoproduction at Cape Evans, and found large quantities of plant (diatoms) and animal food (gastropods, nauplii, ostracods and pieces of crustaceans), and small quantities of detritus (sand grains and sponge spicules) in the stomachs of the sampled seastars. Equally, differences in reproductive output between shallow versus deeper water sites at McMurdo Station, Ross Sea have been attributed to individuals utilising a higher proportion of primary production at shallower depths (McClintock et al. 1988).

Histological and gonad index data from abundant invertebrates at Rothera suggest differences in the reproductive patterns of the seastar and a common brittlestar studied over the same years (Grange et al. 2004). These studies report similar oocyte growth cycles between 18 and 24 months and isolated annual spawning events in both taxa, although the degree of inter-annual variation in gonad index at Rothera for *O. validus* is comparatively less than for the brittlestar, *Ophionotus victoriae*. Patterns in the gonad imply a magnitude difference in reproductive index between two consecutively poor years and two consecutively good years in the reproductive condition of the brittlestar, suggesting patterns in gametogenic growth to be underpinned by a two-yearly cycle. The brittlestar is a detritivore and patterns in its reproductive biology can be associated with annual sedimentation events at Rothera, which were extremely seasonal and variable during the study period (Grange et al. 2004). Magnitude differences in gonad index and multi-year (>1 year) cycles were not evident here for the predator/scavenger. In addition, Chiantore et al. (2002) described the reproductive ecology of *Odontaster validus* from Terra Nova Bay over two successive summers and compared the degree of inter-annual variation observed with the seastar and another opportunistic omnivore, the urchin *Sterechinus neumayeri*, with the suspension feeding Antarctic scallop, *Adamussium colbecki*. There were strong inter-annual differences between years in the scallop, but no comparable differences in the seastar or urchin. These patterns were attributed to the opportunistic feeding behaviour of the two echinoderms. Consequently, observations on reproductive patterns in predator/scavengers like *O. validus* are less likely to reflect variations in seasonal primary productivity as the seastar's diet is extremely catholic, and buffered by the pyloric caeca.

An 18–24 month period of oocyte growth is described for several studied populations of the seastar, probably as a result of temperature restrictions on development at polar latitudes or other seasonal factors. Pearse (1965) recorded an 18–24 month oogenic cycle in *O. validus*, with

overlapping annual generations of oocytes in both populations from McMurdo Sound and Cape Evans. Moreover, this pattern is widespread as it appears in most Antarctic annual breeders including the ophiuroid *Ophionotus victoriae* (Grange et al. 2004), the sea urchin *Sterechinus neumayeri* (Pearse and Cameron 1991; Brockington et al. 2006), the infaunal bivalve *Laternula elliptica*, the limpet *Nacella concinna* (Powell 2001), the brachiopod *Liothyrella uva* (Meidlinger et al. 1998) and the octocoral *Ainigmaptilon antarcticum* (Orejas et al. 2002).

Both parallel and reciprocal relationships have been described between the gonad and pyloric caeca indices for *Odontaster validus* from several different localities. Pearse (1965) and Stanwell-Smith and Clarke (1998) recorded an increase in size of the digestive tissues in parallel with the gonad in *O. validus* at Cape Evans (77°38'S) and Signy Island (60°43'S) and attributed this to the provision of resources to both gametogenic growth and the deposition of reserves in the pyloric caeca. Conversely, trade-offs between the gonad and the pyloric caeca would be predicted if resources were limited. Such a relationship has been described in the McMurdo Sound population of *O. validus*, which endures a nutritionally-poorer environment due to longer winters, a strongly seasonal photoperiod, a longer duration of winter fast ice and consequently, a more restricted summer bloom event (Pearse 1965). Our data indicate neither of these patterns, although seasonal changes in the pyloric caeca are apparent.

Several studies have recorded rare occurrences of hermaphrodites in *O. validus*, including individuals at Rothera (0.7% of the sampled population) (67°34'S). Pearse (1965) and Stanwell-Smith (1997) also observed some hermaphrodites from the high Antarctic at Cape Evans (77°38'S) and from Signy Island in the maritime Antarctic (60°43'S). Pearse (1965) recorded a single hermaphrodite from a population of 350 seastars (0.3% of the studied population) compared to six hermaphrodites from 230 individuals (2.6% of the studied population) at Signy Island (Stanwell-Smith 1997). These data, although not definitive suggest that there may also be a latitudinal effect on the occurrence of hermaphrodites, where hermaphroditism decreases in *O. validus* with latitude. However, more data are needed to determine if this hypothesis is correct.

This study has assessed seasonal and multi-year variability in the reproductive cycle of *O. validus* from the Antarctic Peninsula. It is the first evaluation of such patterns in a polar predator/scavenger. Multi-year studies are essential for understanding the long-term effects of environmental change, not only in the Antarctic but worldwide. Previous studies of both polar suspension and deposit feeders have revealed dramatic between year variation in reproductive condition. Observations on the gametogenic ecology of the seastar do not reveal any significant inter-



annual or multi-year cycles. These findings are attributed to a catholic diet and opportunistic feeding behaviour.

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## References

- Arnaud PM (1974) Contribution à la bionomie marine benthique des régions antarctiques et subantarctiques. *Téthys* 6:467–653
- Bosch I, Pearse JS, Basch LV (1990) Particulate food and growth of planktotrophic sea star larvae in McMurdo Sound, Antarctica. *Antarctic J US* 25:210–212
- Bowden DA (2005) Benthic assemblage development and larval ecology of marine invertebrates at Adelaide Island, Antarctica. PhD thesis, The Open University
- Brockington S, Peck LS, Tyler PA (2006) Gametogenesis and gonad mass cycles in the Antarctic echinoid *Sterechinus neumayeri*. *Polar Biol* 17:465–468
- Chiantore M, Cattaneo-Vietti R, Elia L, Guidetti M, Antonini M (2002) Reproduction and condition of the scallop *Adumessium colbecki* (Smith 1902), the sea urchin *Sterechinus neumayeri* (Meissner 1900) and the sea-star *Odontaster validus* (Koehler 1912) at Terra Nova Bay (Ross Sea): different strategies related to inter-annual variations in food availability. *Polar Biol* 25:251–255
- Clarke A, Harris CM (2003) Polar marine ecosystems: major threats and future change. *Environ Conserv* 30:1–25
- Dayton PK, Robilliard GS, Paine RT (1974) Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecol Monogr* 44:105–128
- Dearborn JH (1965) Ecological and faunistic investigations of the marine benthos at McMurdo Sound, Antarctica. PhD thesis, Stanford University
- Dearborn JH (1977) Foods and feeding characteristics of Antarctic asteroids and ophiroids. In: Llano GA (ed) Adaptations within Antarctic ecosystems. Proceedings of the third SCAR symposium on Antarctic biology. Gulf Publishing, Texas
- Farmanfarmaian A, Giese AC, Booloottian RA, Bennett J (1958) Annual reproductive cycles in four species of west coast starfish. *J Exp Zool* 138:355–367
- Fowler J, Cohen L, Jarvis P (1998) Practical statistics for field biology. Wiley, Chichester
- Grange LJ, Tyler PA, Peck LS, Cornelius N (2004) Long-term inter-annual cycles of the gametogenic ecology of the Antarctic brittle star *Ophionotus victoriae*. *Mar Ecol Prog Ser* 278:141–155
- Grant A, Tyler PA (1983a) The analysis of data in studies of invertebrate reproduction. I. Introduction and statistical analysis of gonad indices and maturity indices. *Int J Invert Reprod* 6:259–269
- Grant A, Tyler PA (1983b) The analysis of data in studies of invertebrate reproduction. II. The analysis of oocyte size/frequency data, and comparison of different types of data. *Int J Invert Reprod* 6:271–283
- Koehler R (1912) Echinoderms, report of the 11th expedition Antarct Francise. Mason et Cie, Paris
- Manabe S, Stouffer RJ (1979) A CO<sub>2</sub>- climate sensitivity study with a mathematical model of the global climate. *Nature* 282:491–493
- Mauzey K (1966) Feeding behaviour and reproductive cycles in *Pisaster ochraceus*. *Biol Bull* 131:127–144
- McClintock JB, Pearse JS, Bosch I (1988) Population structure and energetics of the shallow-water Antarctic seastar *Odontaster validus* in contrasting habitats. *Mar Biol* 99:235–246
- Meidlinger K, Tyler PA, Peck LS (1998) Reproductive patterns in the Antarctic brachiopod *Liothyrella uva*. *Mar Biol* 132:153–162
- Mortensen T (1927) Handbook of echinoderms of the British Isles. University Press, Oxford
- Orejas C, López-González PJ, Gili JM, Teixidó N, Gutt J, Arntz WE (2002) Distribution and reproductive ecology of the Antarctic octocoral *Ainigmaptilon antarcticum* in the Weddell Sea. *Mar Ecol Prog Ser* 231:101–114
- Pain SL, Tyler PA, Gage JD (1982a) The reproductive biology of the deep-sea asteroids *Benthopecten simplex* (Perrier), *Pectinaster filholi* (Perrier) and *Pontaster tenuispinus* (Düben & Koren) (Phanerozoia: Benthopectinidae) from the Rockall Trough. *J Exp Mar Biol Ecol* 65:195–211
- Pain SL, Tyler PA, Gage JD (1982b) The reproductive biology in *Hymenaster membranaceus* from the Rockall Trough, Northeast Atlantic ocean, with notes of *H. gennaueus*. *Mar Biol* 70:41–50
- Pearse JS (1965) Reproductive periodicities in several contrasting populations of *Odontaster validus* Koehler, a common Antarctic asteroid. *Antarct Res Ser* 5:39–85
- Pearse JS (1966) Antarctic asteroid *Odontaster validus*: constancy of reproductive periodicities. *Science* 152:1736–1764
- Pearse JS (1969) Slow developing demersal embryos and larvae of the Antarctic seastar *Odontaster validus*. *Mar Biol* 3:110–116
- Pearse JS, Bosch I (1986) Are the feeding larvae of the commonest Antarctic asteroid really demersal? *Bull Mar Sci* 39:477–484
- Pearse JS, Cameron RA (1991) Echinodermata: Echinoidea. In: Giese AC, Pearse JS, Pearse VB (eds) Reproduction of marine invertebrates VI echinoderms and lophophorates. The Boxwood Press, Pacific Grove, California, pp 514–662
- Peck LS (2005) Prospects for survival in the Southern Ocean: extreme temperature sensitivity of benthic species. *R Soc Spec Iss Antarct Sci* 17:497–507
- Peck LS, Webb KE, Bailey DM (2004) Extreme sensitivity of biological function to temperature in Antarctic marine species. *Funct Ecol* 18:625–630
- Peck LS, Convey P, Barnes DKA (2006) Environmental constraints on life histories in Antarctic ecosystems: tempos, timings and predictability. *Biol Rev* 81:75–109
- Powell DK (2001) The reproductive ecology of Antarctic free-spawning molluscs. PhD thesis, University of Southampton
- Smale D, Barnes DKA, Fraser KPP (2007) The influence of depth, site exposure and season on the intensity of iceberg scouring in nearshore Antarctic waters. *Polar Biol* 30(6):769
- Stanwell-Smith D (1997) Larval ecology of benthic marine invertebrates at Signy Island, Antarctica. PhD thesis, The Open University
- Stanwell-Smith D, Clarke A (1998) Seasonality of reproduction in the cushion star *Odontaster validus* at Signy Island, Antarctica. *Mar Biol* 131:479–487
- Stanwell-Smith D, Peck LS (1998) Temperature and embryonic development in relation to spawning and field occurrence of larvae of three Antarctic echinoderms. *Biol Bull* 194:44–52
- Tyler PA, Reeves S, Peck LS, Clarke A, Powell D (2003) Seasonal variation in the gametogenic ecology of the Antarctic scallop *Adumessium colbecki*. *Polar Biol* 26:727–733