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## Seasonal variation in the gametogenic ecology of the Antarctic scallop *Adamussium colbecki*

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**Abstract** Quasi-monthly samples of the Antarctic pectinid bivalve *Adamussium colbecki* were examined to determine the gametogenic pattern and periodicity. Both female and male gametogenic patterns show a very distinct seasonal development, with the initiation of gametogenesis in October and spawning in late September and early October of the following year. The duration of the gametogenic cycle is unusually short for Antarctic benthos, being 12 months. Reproductive effort (ratio of gonad mass to total tissue mass) is significantly higher in males than females, and males are ready to spawn earlier in the austral winter than females. The digestive gland also shows a strong seasonal cycle but develops earlier than the gonad. We propose that energy from the spring bloom is stored in the digestive gland before being transferred to the gonads. Gonad size, digestive-gland size and, to a lesser extent, adductor-muscle size, are related to adult size in most samples. The length of the gametogenic cycle suggests that reproduction in *A. colbecki* is more pectinid than Antarctic.

### Introduction

The marine environment of the Antarctic represents one of the most thermally stable on earth, with an annual

temperature variation of a maximum of 3°C. The seasonal availability of food, however, represents the most important controlling factor in the physiological ecology of Antarctic marine invertebrates (Clarke 1988). This food availability is important for both filter feeders and deposit feeders, driving adult metabolism and, for some species, forms an import source of food for planktrophic larvae (Pearse et al. 1991). The extreme seasonality of the food supply (Clarke 1988) has been an important selective pressure, with the vast majority of Antarctic invertebrates having lecithotrophic development (Dell 1972; Picken 1980; Pearse et al. 1985, 1991). However, some taxa, including the bivalves and many of the most conspicuous members of the shallow-water benthic community, have a relatively high proportion of species with planktrophic development (Bosch et al. 1987; Hain and Arnaud 1992; Peck 1993).

Understanding the reproductive biology of scallops has been of interest for many years, especially in relation to fisheries (Dakin 1909; Sastry 1979 for early review). In the northern hemisphere, the general pattern of seasonality in scallop gametogenesis and fecundity was established in detail during the 1980s and early 1990s (Barber and Blake 1983; Sundet and Lee 1984; Bricelj et al. 1987; Langton et al. 1987; Barber et al. 1988; Paulet et al. 1988; MacDonald et al. 1991). These studies suggest that spawning in scallops may occur over a very short time period (Sundet and Lee 1984) or may switch annually from highly synchronous spawning to a protracted spawning period (Langton et al. 1987; Paulet et al. 1988). Fecundity in scallops may be a function of food availability (Bricelj et al. 1987) or depth (Barber et al. 1988). Many scallops are protandric hermaphrodites (Sastry 1979; Beninger and Le Pennec 1993) although some species of the genus *Chlamys* are gonochoric (Reddiah 1962; Sundet and Lee 1984).

Over the last 10 years there has been considerable interest in the Antarctic scallop *Adamussium colbecki* as a potential harvestable stock. *A. colbecki* is one of the largest megabenthic bivalves in coastal circum-Antarctic waters (Chiantore et al. 2000), living at depths from 4 to

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1,335 m (Dell 1972), and may occur in densities recorded as 100% cover (Chiantore et al. 2000). *A. colbecki* is eurytopic but is reported to prefer rocky substrata (Stockton 1984; Nigro 1993). At greater depths, it appears to prefer gravelly to silty-mud substrata. Growth rates are variable depending on site (Ralph and Maxwell 1977; Stockton 1984) and size-related (Chiantore et al. 2003). As in many pectinids, *A. colbecki* ingests detritus from the sediment surface (Berkman et al. 1991). Brey and Clarke (1993) suggested the reproductive cycle would be highly seasonal as a result of the seasonality of primary production in Antarctic waters (Clarke 1988).

The determination of the reproductive periodicity in *A. colbecki* has posed particular challenges for ecologists in Antarctica. Whereas fecundity and reproductive effort may be determined in ripe specimens from a single sample, a complete understanding of the timing and rate of gonad development requires regular sampling throughout the year. Berkman et al. (1991) determined the reproductive periodicity of *A. colbecki* from four samples from different seasons at McMurdo Sound, although three of these samples were from specimens held in aquaria during the austral winter months. They suggested spawning took place during the austral spring. More recently, Chiantore et al. (2001, 2002) suggested that spawning took place in the austral autumn, particularly February, in a population at Terra Nova Bay. With the establishment of the high-resolution long-term sampling programme close to the BAS Research Station at Rothera in northern Marguereta Bay, we have a suite of samples of *A. colbecki* taken from the wild quasi-monthly over a 12-month period, including regular

sampling through the austral winter. The aim of this paper is to determine seasonal variation in gonad index, and precise timing of spawning, and estimate reproductive effort.

## Materials and methods

Eight separate samples of *A. colbecki* were collected by scuba-diver from ~25 m depth in North Cove, Rothera over a 12-month period (Tables 1, 2). *A. colbecki* is dioecious and, wherever possible, five females and five males were sampled each month. Males ranged from 50.3 to 83.09 mm shell height, and females from 56.35 to 81.85 mm. The mantle cavity was flushed with preservative, and the shell valves kept open during fixing in 4% buffered formal saline. Environmental data, including chlorophyll *a* and temperature measurements, were taken weekly in Ryder Bay, Rothera as part of the Rothera Oceanographic Time-Series (RaTS) Programme.

Ten individuals were examined from each monthly sample. Scallop height and width were measured with callipers to 0.1 mm accuracy, and total wet weight (with and without shell) to 0.1 g. The gonad, digestive gland and muscle were dissected out, blotted dry and wet-weighed. Empty shells were reweighed. Shell weight, which is correlated with shell height, was used as an independent variable (female  $r = 0.89$ ,  $n = 42$ ;  $P < 0.001$ ; male  $r = 0.908$ ;  $n = 38$ ;  $P < 0.001$ ).

Organ indices were calculated as:

$$\text{Organ Index} = 100 * (\text{organ mass} / \text{total tissue mass})$$

A 5-mm slice of the gonad was taken and prepared for histology by standard histological methodology. Sections were prepared at 7  $\mu\text{m}$  thickness and stained with hematoxylin and eosin. Digital images of the gonad sections were taken using Matrox Rainbow Runner software and analysed using SigmaScan Pro version 4. For each female, 100 oocytes were measured. The data were used to construct oocyte size/frequency histograms for each monthly sample. Males were staged according to development: stage 0,

**Table 1** Sampling dates, number of individuals (female) examined and correlation coefficients of organs weights against shell size ( $n$  number of individuals;  $r$  correlation coefficient;  $P$  probability)

Date	No. of females $n$	Ovary		Female digestive gland		Female adductor muscle	
		$r$	$P$	$r$	$P$	$r$	$P$
5 June 1998	7	0.816	<0.02	0.902	<0.01	0.886	<0.01
8 July 1998	5	0.877	<0.02	0.595	ns	0.795	ns
7 August 1998	5	0.912	<0.02	0.516	ns	0.987	<0.001
1 September 1998	6	0.586	ns	0.668	ns	0.691	ns
1 October 1998	4	-0.75	ns	0.680	<0.01	0.545	ns
5 December 1998	5	0.868	<0.05	0.737	ns	0.981	<0.001
6 January 1998	5	0.657	ns	0.817	<0.05	0.947	<0.01
5 March 1998	5	0.985	<0.001	0.986	<0.01	0.971	<0.01

**Table 2** Sampling dates, number of individuals (males) examined and correlation coefficients of organs weights against shell size ( $n$  number of individuals;  $r$  correlation coefficient;  $P$  probability)

Date	No. of males $n$	Testis		Male digestive gland		Male adductor muscle	
		$r$	$P$	$r$	$P$	$r$	$P$
5 June 1998	3	0.994	<0.1	0.716	ns	0.948	ns
8 July 1998	5	0.779	<0.01	0.782	ns	0.766	ns
7 August 1998	5	-0.75	ns	-0.029	ns	-0.08	ns
1 September 1998	4	0.835	<0.02	0.952	<0.05	-0.480	ns
1 October 1998	6	0.615	ns	0.404	ns	0.735	ns
5 December 1998	5	0.891	<0.02	0.763	ns	0.927	<0.01
6 January 1998	5	0.879	<0.05	0.817	<0.02	0.955	<0.01
5 March 1998	5	0.885	<0.02	0.946	<0.01	0.953	<0.01

spent; stage 1, acini widely spaced, sparse and lumen empty; stage 2, acini larger and mainly filled with spermatogonia and some spermatocytes; stage 3, acini filling with spermatocytes and spermatids with some spermatozoa; stage 4, acini full of sperm packed together. A maturity index for males for each month was determined according to Yoshida (1952). All data were log-1 transformed before statistical analysis.

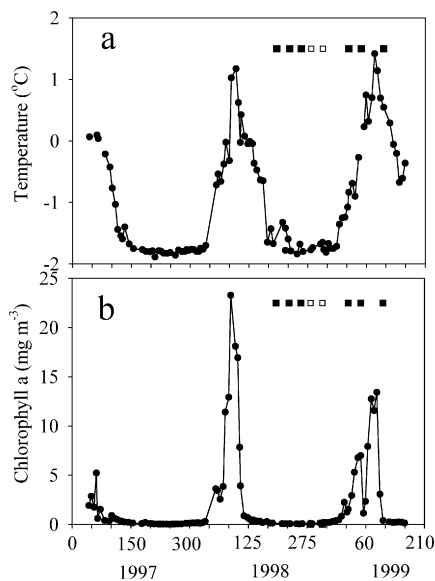
## Results

### Environmental conditions before and during sampling period

Although there is strong evidence of seasonality in primary production and temperature at the RaTS station in Ryder Bay, there is important interannual variability. In the winter prior to sampling (1997), sea ice at Rothera was heavy, whilst in winter 1998 sea ice was less extensive. This had an effect on the sea temperature, with the sea warming more quickly in austral spring of 1998 than 1997 although the maximum and minimum temperatures were very similar for both years (Fig. 1). Primary production biomass (as measured by chlorophyll *a*) occurred as a single sharp peak from mid-November 1997 to March 1998, whereas in the following year primary production was in the form of two peaks and overall production was less.

### Ovary index

There were significant differences in ovary index among monthly samples (ANOVA  $f=44.53$ ;  $P<0.0001$ ;  $df=7,34$ ). The lowest ovary index (OI) was found

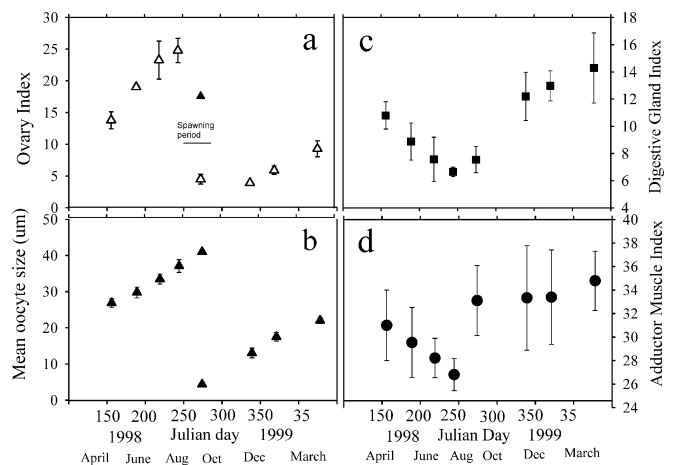


**Fig. 1a, b** RaTS time-series data for **a** temperature and **b** chlorophyll *a* before and during the sampling programme for *Adamussium colbecki*. Squares represent sampling dates and unfilled squares represent the period of spawning

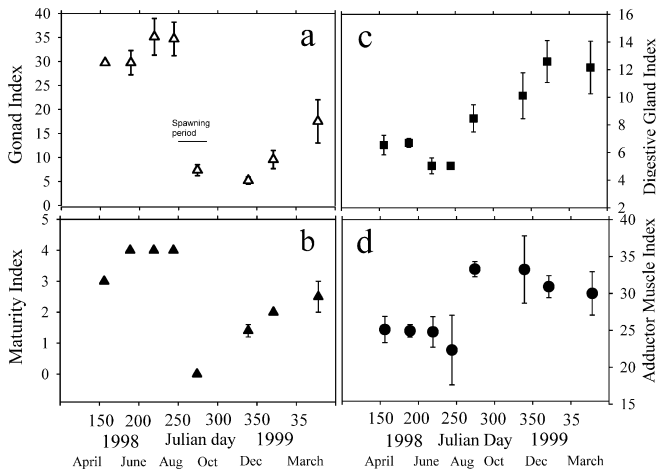
between October and December (Fig. 2a). In October, the ovary weighed between 1.4 and 2.0 g and formed 3.9% ( $\pm 0.4$ ) of tissue mass. From January, the OI started to increase, reaching a maximum in early September at which time the ovary mass varied from 5.3 to 7.0 g and formed 24.8% ( $\pm 1.9$ ) of tissue mass. By early October, the OI in all but one of the specimens examined had decreased dramatically, suggesting late September was the spawning period (Fig. 2a). Ovary mass was correlated with shell mass for all samples combined (Fig. 4a), although there was no correlation between ovary mass and shell mass for September, October and January samples, when samples were analysed separately for each month (Table 1). Thus, during the later period of ovary development, ovary mass is a function of individual shell mass.

### Testis index

The testis increased more rapidly in size than the ovary (Fig. 3a), with males also showing greater variation among individuals. There were significant differences in testis index among monthly samples (ANOVA  $f=84.45$ ;  $P<0.0001$ ;  $df=7,30$ ). The maximum testis index (TI) was found in the 1 September samples when the testis weighed between 8.6 and 12.5 g and constituted 35% ( $\pm 3.8$ ) of overall tissue mass. By 1 October there had been a sevenfold reduction in TI (testis mass was reduced to between 1.3 and 2.9 g and composed 5.2% ( $\pm 0.8$ ) of tissue mass), indicating spawning had occurred. The more subjective Maturity Index (MI) for males also shows a distinct seasonal variation from being spent in October, increasing rapidly in the austral spring, to reach maximum development between June and September (Fig. 3b), reflecting the male development evidenced by the testis index (Fig. 3a). These data



**Fig. 2a-d** Organ indices for female *Adamussium colbecki*. **a** Ovary index (unfilled triangles) (mean  $\pm$  1SD). The filled triangle represents the single female yet to spawn on 1 October. **b** Mean oocyte size for each sample (mean  $\pm$  1SD). **c** Digestive-gland index (mean  $\pm$  1SD). **d** Adductor-muscle index (mean  $\pm$  1SD)



**Fig. 3a–d** Organ indices for male *Adamussium colbecki*. **a** Testis index (mean  $\pm$  1SD). **b** Maturity index (mean  $\pm$  1SD). **c** Digestive-gland index (mean  $\pm$  1SD). **d** Adductor-muscle index (mean  $\pm$  1SD)

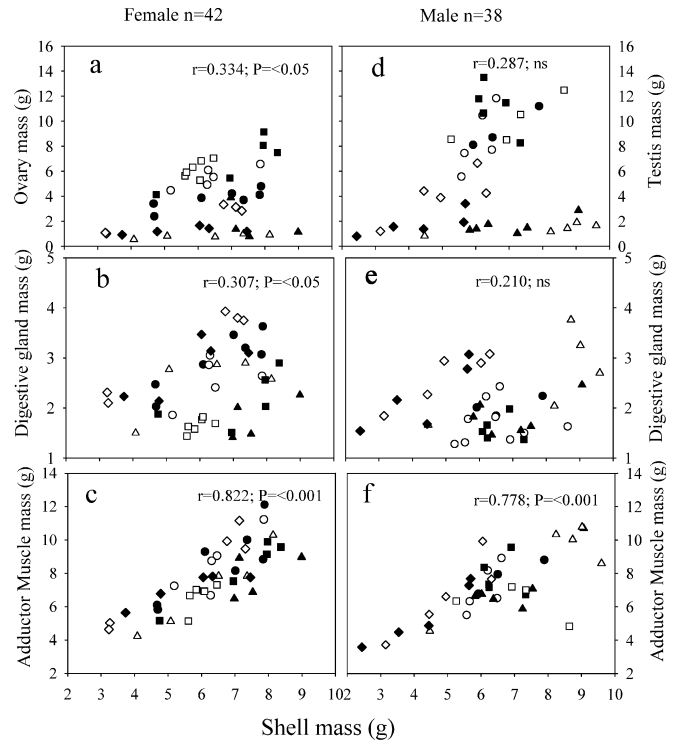
suggest that spermatogenesis is complete by June/July whereas ovary development is not complete until early September. Testis mass was not correlated with shell mass for all samples combined (Fig. 4d), although most individual monthly samples did show correlation (Table 2), and the lack of overall correlation may be a function of seasonal variation.

Comparison of the gonad indices for females and males for all samples showed that males had consistently higher gonad indices than females (ANOVA  $f=3.96$ ;  $P < 0.05$ ;  $df=1,78$ ). However, in the post-spawning month of December, gonad indices between male and female were not significantly different (ANOVA  $f=1.81$ ;  $P = ns$ ;  $df=1,8$ ), whereas in all other months the testis index was significantly greater ( $P < 0.001$ ) than the ovary index.

#### Digestive-gland index

In females, the digestive-gland index (DGI) showed significant differences among samples (ANOVA  $f=22.65$ ;  $P < 0.0001$ ;  $df=7,34$ ) with a distinct seasonal cycle. Highest values were in March (digestive-gland mass varying from 2.1 to 3.8 g, with a DGI of  $14.3\% \pm 2.6$ ), followed by a decline until spawning (Fig. 2c). Recovery started in September (digestive-gland mass 1.4–1.8 g, DGI of  $6.7\% \pm 0.3$ ) and the DGI of females increased rapidly during the austral summer. The mass of the digestive gland showed a correlation with shell mass when all the samples were combined (Fig. 4b) but there was only limited correlation between shell mass and female digestive gland when samples were analysed for individual months (Table 1).

In males, there was a significant difference among samples (ANOVA  $f=43.27$ ;  $P < 0.0001$ ;  $df=7,30$ ), with the DGI highest in the austral summer (digestive-gland mass varied from 1.5 to 3.1 g and male DGI was  $12.6\% \pm 1.5$ ) and declining rapidly in winter (September



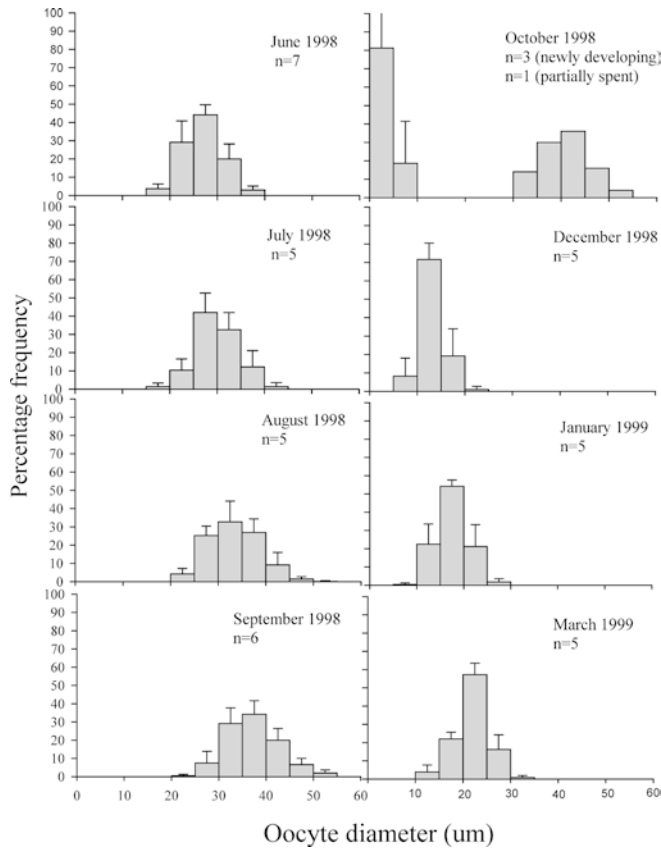
**Fig. 4a–f** Correlation of organ mass (wet weight) against empty shell weight for *Adamussium colbecki*. **a** Ovary mass. **b** Female digestive-gland mass. **c** Female adductor-muscle mass. **d** Testis mass. **e** Male digestive-gland mass. **f** Male adductor-muscle mass (● June 1998; ○ July 1998; ■ August 1998; □ September 1998; ▲ October 1998; △ December 1998; ◆ January 1999; ◇ March 1999)

digestive-gland mass from 1.3 to 1.6 g and male DGI  $5\% \pm 0.2$ ) (Fig. 3c). There was no correlation between shell mass and mass of digestive gland when combined samples were analysed (Fig. 4e) and little correlation when samples were analysed individually (Table 2) because of the seasonal differences produced by a cessation of feeding in the winter and rapid weight gain from feeding in the brief spring/summer period.

#### Adductor muscle index

The adductor-muscle index (MuI) in females was significantly different among monthly samples (ANOVA  $f=5.43$ ;  $P < 0.001$ ;  $df=7,34$ ). It was highest in March (muscle mass 4.6–11.2; MuI  $34.8\% \pm 2.5$ ), and declined in the autumn although each sample had high variance (Fig. 2d). There was a strong correlation between muscle mass and shell mass in females (Fig. 4c), suggesting that muscle mass is a strong function of individual size and shows only weak seasonal variation.

The MuI in males showed a pattern similar to females (Fig. 3d), with significant difference among monthly samples (ANOVA  $f=9.87$ ;  $P < 0.001$ ;  $df=7,30$ ). Highest muscle mass was in December (4.6–10.8 g; MuI  $33.3\% \pm 4.6$ ). Using combined samples, there was a strong correlation between muscle mass and shell mass,



**Fig. 5** Oocyte size/frequency distribution of samples of females of *Adamussium colbecki* from different months. Cohorts are sample mean  $\pm$  1SD ( $n$  is the number of females examined). The larger cohort in October 1998 is based on a single individual

but limited correlation when samples were analysed individually (Fig. 4f, Table 2)

#### Oocyte size/frequency distribution

Throughout most of the year, the sample-integrated oocyte size/frequency distribution shows a narrow single mode (Fig. 5). In the 1 October samples, there is a bimodal distribution caused by three of the four individuals having spawned, and producing oogonia for the next gametogenic season. The single individual that was partially spawned is seen as a second mode in the October oocyte size/frequency figure. In all other months, the oocytes develop as a single cohort, with the mean oocyte size for each sample increasing with month to a maximum mean oocyte size of 36  $\mu\text{m}$  in September (Fig. 2b). Maximum oocyte size observed was  $\sim$ 55  $\mu\text{m}$  diameter.

## Discussion

*A. colbecki* occupies a significant position in the benthos of circum-Antarctic shelf waters. It is the largest bivalve

(based on shell size but not mass) known from Antarctic waters (Ralph and Maxwell 1977). Most interest in its biology and ecology has arisen from studies of populations in the Pacific sector of Antarctica, and especially in the waters of the Ross Sea. In this region, reported densities reach  $\sim$ 85 individuals  $\text{m}^{-2}$  between 4 and 6 m depth, decreasing to  $<20$  ind.  $\text{m}^{-2}$  at 30 m depth (Stockton 1984). The species is recorded from a maximum depth of 1,335 m (Dell 1972). However, a considerable spatial population variability is found throughout the Ross Sea, with the depth of maximum abundance and biomass varying (Chiantore et al. 2001), partially explained by its mobility and by recruitment variability. On the other side of Antarctica, large dense populations do exist (BAS, unpublished observations). The population studied here, near the British Antarctic Survey Rothera Station was  $\sim$ 1,000 individuals, predominantly attached by byssal threads to rocks and boulders.

*A. colbecki* differs from many other Antarctic invertebrates in having planktotrophic development (Berkman et al. 1991; Chiantore et al. 2000, but see Hain and Arnaud 1992). Berkman et al. (1991) suggested that spawning occurred in the austral spring, based on gonadal sampling of specimens kept in an aquarium. More recently, Chiantore et al. (2002) suggested that spawning took place in the austral autumn, based on the observation of large oocyte diameters in January.

The establishment of a long time-series sampling programme in shallow water at the BAS station at Rothera has allowed the collection of high-resolution temporal samples of selected marine invertebrate species. Several marine invertebrate species at Rothera are being sampled on a monthly basis for analysis of reproductive cycles, together with more regular sampling of environmental factors, including temperature and chlorophyll *a* data, as part of the RaTS programme. *A. colbecki* was one of the species selected for study, but in light of its relatively low population size, regular sampling was suspended in 1999. However, in the period June 1998 to March 1999, samples of *A. colbecki* were obtained, being the first field samples of this species to be collected during the austral winter.

Detailed examination of the gametogenic pattern demonstrated that in both female and male *A. colbecki*, gametogenesis started in October, although oogonia may be present earlier. Gamete development was steady, with males reaching maturity by June of the following year but not spawning until September. Females reached maximum maturity in September. Spawning occurred between the 1 September and 1 October, with one individual still in the spawning process at the time of sampling on 1 October. Spawning was also observed in September 1998, from recently collected scallops being held in the Rothera aquarium (BAS, unpublished observations). Thus, *A. colbecki* at Rothera spawns synchronously in a very narrow window in September at the end of the austral winter. We interpret these data as showing that the gametogenic pattern of *A. colbecki* is a

12-month cycle with a high degree of synchrony between individuals of the same sex. A 12-month cycle has not previously been reported for Antarctic marine invertebrates that are known to breed seasonally. The gametogenic cycles so far reported for other Antarctic molluscs, the infaunal clam *Laternula elliptica* and limpet *Nacella concinna*, and the echinoderms *Odontaster validus*, *Sterechinus neumayeri* and *Ophionotus victoriae*, take ~18–24 months from initiation of gametogenesis to spawning (Pearse 1965; Powell 2001; L. Grange, personal communication). The seasonal pattern is even more complicated in the brachiopod *Liothyrella uva* (Meidlinger et al. 1998), where there is also considerable inter-annual variation in reproductive output.

*A. colbecki*, as with many other pectinids, is a filter feeder lying just above the seabed. The gut is known to contain sand and Foraminifera (Berkman et al. 1991), indicating that they ingest resuspended detritus from the sediment surface (Chiantore et al. 1998). They may also feed on the sinking phytoplankton bloom as it settles onto the seabed. Digestive-gland development starts immediately after spawning. The digestive gland in both sexes shows a strong seasonal cycle with the peak from December to March, presumably fuelled by the energy gained from feeding on the austral summer phytoplankton bloom. This energy is subsequently transferred to the gonad which shows a continued increase in gonad index in the austral autumn and winter coincident with a decline in the digestive-gland index. In males, the digestive gland shows no correlation with size (as shell weight), suggesting this is a function of season rather than individual size. In females, there is a significant, but weak, correlation between shell weight and digestive-gland weight, although this is seen only in three of the samples. In males, the testis weight shows no correlation with shell weight. In the females, there is a weak correlation with shell weight using combined annual data, as well as in individual monthly samples, suggesting that not only is the female showing a strong seasonal cycle but that the gonad weight in any month is size-specific (Table 1).

If spawning and fertilization take place in mid-September, and recruitment is coincident with the phytoplankton flux to the seabed (Berkman et al. 1991), *A. colbecki* might have a larval life in excess of 100 days. The embryogenesis and larval development of this species have yet to be described in full but such a larval lifespan may be considered not untypical of an Antarctic marine invertebrate. The limited data on early development of *A. colbecki* suggest 24 h to 16 cell, 43 h to 64 cell, 90 h to blastula and 177 h to trochophore (Powell 2001). The temporal development of the veliger from the trochophore has yet to be observed. Long larval development is characteristic of Antarctic species with planktonic development (Bosch et al. 1987; Peck 1993, 2002). Many of these species reach a feeding stage before the development of the phytoplankton blooms, suggesting they may utilize bacteria as an energy source (Pearse et al. 1991).

From these data, it is apparent that reproduction in *A. colbecki* is more pectinid than Antarctic. There is a single, non-overlapping, gametogenic periodicity with the production of planktonic larvae. This suggests a cold-adaptation, in that the gametogenic cycle is the same length as in those species at temperate latitudes, reinforcing the belief that, although larval-development rates appear temperature-constrained (Hoegh-Guldberg and Pearse 1995), seasonal energy availability in Antarctic ecosystems is more important than temperature for gametogenic and reproductive cycles (Clarke 1988).

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