THE ECOLOGY AND REPRODUCTION OF THE BROODING ANTARCTIC BIVALVE *Lissarca miliaris*

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ABSTRACT. Investigation of associated fauna on the fronds of the sub-littoral macro-alga *Desmarestia anceps*, in Antarctic waters, has determined the relative importance of the Mollusca in an epifaunal habitat. Gastropods were the principal component of the fauna with 29 species present. The Pelecypoda, represented by only four species, accounted for 38 per cent by weight and 47 per cent by number of molluscs. The most important single species of mollusc, accounting for over 98 per cent of the Pelecypoda by weight and number, was the philobryid *Lissarca miliaris* (Philippi, 1845), whose iso- and allometric parameters and relationships are discussed. This bivalve occurs in a very high density on *D. anceps;* up to 232·4 g. (dry weight) and 133,755 individuals per kg. dry weight of *Desmarestia* were recorded. Rings produced by growth cessation during winter were used in an investigation of population age structure, growth, recruitment and mortality. *L. miliaris* broods its larvae within the parent mantle cavity, releasing the young as miniature adults synchronously during the austral summer. The length of the brooding period is greatly extended and öocytes and embryos are large. The arithmetic relationship of fecundity to adult length is linear with a mean brood size of 60. A slow and seasonal growth rate is established with a maximum recorded length of 5·8 mm. in an individual 7 years old.

Lissarca miliaris (Philippi, 1845) is a sub-littoral purple philobryid bivalve, less than 6·0 mm. long, usually attached to macro-algal fronds, although common on rocks and epifauna, for example sponges (Soot-Ryen, 1951). The species has been noted in many Antarctic molluscan taxonomic studies, under different specific and generic names (Dell, 1964), whilst Bergmans (1970) has discussed the relationships of the genus *Lissarca*. The Philobryidae, with the exception of *Philobrya setosa*, are confined to the Southern Hemisphere and species endemism to Antarctic and sub-Antarctic waters is high. *L. miliaris* has been recorded from the Straits of Magellan, Tierra del Fuego, the Falkland Islands, South Georgia and the island groups of the Scotia Ridge. The southernmost record is from Deception Island, South Shetland Islands (Soot-Ryen, 1951). Ice scour on Antarctic shores restricts the species to protected areas and it is absent from the intertidal and immediate sub-littoral zones. The greatest depth at which it has been found is 121 m. off Tierra del Fuego (Dell, 1964).

Despite past observations on the numerical and biomass importance of the Mollusca to Antarctic benthos (Gruzov and others, 1967; Everson and White, 1969; Rabarts, 1970, 1971; Hardy, 1972) in both infaunal and epifaunal communities, detailed studies on growth and reproduction of Pelecypoda are restricted to few investigations: Ralph and Everson, 1972 —*Kidderia bicolor;* Rabarts, 1970, 1971—*Yoldia eightsii;* Shabica, 1974—*Kidderia subquadratum*. *L. miliaris*, which shows many of the general characteristics of Antarctic pelecypods outlined by Nicol (1970) and Dell (1972), was found in great numbers sub-littorally in Borge Bay, Signy Island, South Orkney Islands.

MATERIALS AND METHODS

Whole plants of the sub-littoral brown alga *Desmarestia anceps* were collected at monthly intervals during 1972 by SCUBA diving in depths of 5–9 m. from Borge Bay, Signy Island (lat. 60°43′S., long. 45°36′W.). Nets with a mesh size of 0·3 mm. were used to collect the samples. No plants were obtained during March and April, and the sample of December 1972 was collected with a 1 m. Agassiz trawl hauled through a bed of *D. anceps* at 9 m. depth. In the laboratory, plants were divided into holdfasts and fronds. Most of the associated fauna of the fronds was extracted by immersing and strongly agitating small sections of plant in a dilute solution of formaldehyde in sea-water (0·25 per cent). Any remaining animals were extracted

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by hand. The wet weight of holdfasts and fronds was recorded and the fronds were dried at 100° C to constant weight.

Animals were collected on a 0·25 mm. sieve and preserved in 5 per cent neutralized formol saline for future identification and analysis. Molluscs were hand sorted from the samples, counted, dried at 60° C and stored under vacuum until weighed. Specimens of *Lissarca miliaris* were measured to the nearest 0·08 mm. using an eye-piece micrometer. The maximum antero-posterior length (*L*) has been used as the standard measurement and correlated with total dry weight (*W*), dorso-ventral height (*H*) and lateral breadth (*B*). The age of animals was determined by examination of periodic growth rings. Ash weights were obtained after ignition, of bulk samples of approximately 50–100 mg. dry weight, at 500° C for 5 hr.

<p align="center">RESULTS</p>

Mollusca associated with macro-algae

Ten samples of *D. anceps* were analysed. Plant weights (wet) ranged from 3·52 to 0·14 kg. ($\bar{x}=1\cdot25$ kg.) with a mean frond water content of 81·8 per cent.

The numbers and weight of total Mollusca present on *D. anceps* fronds are given in Table I and composition in terms of abundance and weight of the four major groups (Pelecypoda, Gastropoda (excluding *Nacella concinna*), Polyplacophora and *Nacella concinna*) are given in Table II. The data on the Antarctic limpet have been categorized separately due to its large weight and sporadic distribution (Walker, 1972). Most of the limpets present on *D. anceps* were small- to medium-sized individuals less than 1·0 cm. long. The species composition of the molluscan fauna comprises 29 Gastropoda, four Pelecypoda and two Polylacophora. The chitons are of rare occurence, whereas the pelecypods, although represented by few species (two *Philobrya* spp., *Mysella charcoti* and *Lissarca miliaris*), share a major role with the gastropods in the weed habitat.

All four bivalves attach themselves to a suitable substrate by byssal threads produced just after post-larval release. The pelecypods account for 47 per cent numerically and 38 per cent of the total mollusc biomass of *D. anceps* fauna. The most important element, both numerically and by weight, of the Mollusca is the gastropods, which account for 57 per cent of the total biomass and 53 per cent numerically. The most conspicuous gastropod *Laevilacunaria antarctica* represented 20·2 per cent by weight and 14·6 per cent by number of all Mollusca (Table III). The relative importance of all molluscs, which had a weight or number greater than 1 per cent, is shown in Table III. Certain species important in weight are represented by few individuals (e.g. *Margarella antarctica* and *Nacella concinna*); others whose numbers are appreciable, for example *Cyclostrema meridionale*, comprising 20·2 per cent by number of the May sample, contribute little to the population weight. Without comparative data on growth and population dynamics, an assessment of the relative importance in terms of production of each species is not possible.

The data in Table I have been arranged to present weight (*W*) and abundance (*N*) of the groups: total Mollusca, Gastropoda, Pelecypoda and *Lissarca miliaris*. Correcting *N* and *W* per kg. dry weight of *D. anceps* (*wp*), a relationship N or $W=bwp^m$ is found. Alternatively, this can be expressed as

$$\log N \text{ or } \log W = m \log wp + \log b,$$

in which the two constants *m* and *b* can be determined by the method of least squares. The relationships for the abundance and weight of various mollusc groups are presented in Table IV. In all equations excluding Equation (7) (which is not significant at $P=0\cdot05$), there is a negative relationship between the unit expression of mollusc/plant weight and the original dry weight of sample. Smaller plants have a far higher population of molluscs/weight than larger plants. The October sample (*wp*=25·3 g.) gave corrected figures for *N* and *W*/kg. *wp* of 305·5 g. and 165,810 individuals, whereas February's sample (*wp*=640·1 g.) gave corresponding figures of

TABLE I. NUMERICAL AND WEIGHT COMPOSITION OF THE MOLLUSCAN FAUNA ASSOCIATED WITH *Desmarestia anceps* FRONDS

Date 1972	Sample Plant weight (g) Wet	Dry(wp)	Total mollusca W/kg.wp	N/kg.wp	Gastropoda (excluding Nacella concinna) W	N	W/kg.wp	N/kg.wp	Pelecypoda W	N	W/kg.wp	N/kg.wp	Lissarca miliaris W	N	W/kg.wp	N/kg.wp
13 January	2,140	389·5	54·38	28,606	13·05	5,455	33·50	14,005	4·59	5,677	11·79	14,575	4·49	5,616	11·53	14,418
19 February	3,517	640·1	11·36	7,334	5·00	3,975	7·81	6,210	1·81	835	2·83	1,304	1·76	1,343	2·75	2,098
9 May	1,772	322·5	29·22	10,546	5·69	2,113	17·64	6,552	2·95	1,268	9·15	3,932	3·03	1,264	9·40	3,919
9 June	945	172·0	27·33	8,808	2·22	594	12·91	3,453	2·48	921	14·42	5,355	2·46	917	14·30	5,331
10 July	1,496	272·3	40·34	10,716	6·06	1,043	22·25	3,830	4·79	1,872	17·59	6,875	4·77	1,860	17·52	6,831
16 August	450	81·9	89·01	43,894	4·88	2,358	59·58	28,791	2·41	1,237	29·43	15,103	2·39	1,224	29·18	14,945
11 September	560	101·9	182·38	61,796	10·00	3,234	98·14	31,737	7·07	3,033	69·38	29,764	7·02	3,019	68·89	29,627
9 October	139	25·3	205·53	165,810	1·85	78·3	73·12	30,949	5·88	3,412	232·41	134,861	5·88	3,384	232·41	133,755
10 November	260	98·4	29·80	12,978	2·29	883	23·27	8,974	0·65	381	6·61	3,872	0·64	381	6·46	3,872

wp = plant weight (dry), N = abundance and W = weight (g).

TABLE II. THE PERCENTAGE COMPOSITION, BY WEIGHT (W) AND NUMBER (N) OF THE MAJOR MOLLUSC GROUPS PRESENT ON THE MACRO-ALGA *Desmarestia anceps*

Percentage weight

| | Sample date (1972) | | | | | | | | | | |
	13 Jan.	19 Feb.	9 May	9 Jun.	10 Jul.	16 Aug.	11 Sept.	9 Oct.	10 Nov.	$\bar{x}$	S.D.±
Polyplacophora	—	—	—	—	—	—	0·2	—	—	—	—
Pelecypoda	21·7	24·9	31·3	52·7	43·6	33·1	38·0	76·1	22·0	38·2	17·5
Gastropoda	61·6	68·8	60·3	47·3	55·1	66·9	53·8	23·9	77·0	57·2	15·3
N. concinna	16·7	6·0	8·3	—	1·3	—	8·0	—	—	4·5	5·8
TOTAL W (g.)	21·181	7·274	9·424	4·705	10·985	7·299	18·585	7·730	2·933		

TOTAL $W = 90·12$ g.

Percentage number

	13 Jan.	19 Feb.	9 May	9 Jun.	10 Jul.	16 Aug.	11 Sept.	9 Oct.	10 Nov.	$\bar{x}$	S.D.±
Polyplacophora	—	—	—	—	—	—	0·1	—	—	—	—
Pelecypoda	51·0	16·8	37·3	60·8	64·1	34·4	48·2	81·1	29·8	47·1	19·8
Gastropoda	49·0	82·7	62·1	39·2	35·7	65·6	51·4	18·7	69·2	52·6	19·6
N. concinna	0·1	0·3	0·6	—	0·1	—	0·4	—	0·2	0·2	0·2
TOTAL N	11,142	4,695	3,401	1,515	2,918	3,595	6,297	4,223	1,227		

TOTAL $N = 39,063$

TABLE III. SPECIES OF MOLLUSCS OCCURRING IN SAMPLES OF *Desmarestia anceps*; ONLY SPECIES PERCENTAGE FREQUENCIES >1·0 HAVE BEEN GIVEN

	Percentage numbers and weights — Sample date (1972)																			x̄		±S.D.	
	13 January		19 February		9 May		9 June		10 July		16 August		11 September		9 October		10 November					
	N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W
L. miliaris	50·40	21·18	14·63	24·24	37·17	32·10	60·53	52·28	63·74	43·43	34·05	32·79	47·94	37·77	80·67	76·08	29·84	21·68	46·55	37·95	20·04	17·62
Gastropod spp.																						
Subnoba turqueti	11·28	4·32	26·26	5·09	14·88	3·76	20·79	4·02	6·55	1·21	4·79	2·14	15·23	3·35	2·38	—	10·10	2·57	12·47	2·94	7·71	1·62
Rissoa spp. 1	—	1·32	3·71	16·49	10·20	26·51	—	1·41	6·48	12·34	10·76	37·18	3·64	7·28	1·95	15·49	7·99	20·00	4·97	15·34	4·09	11·67
Laevilacunaria antarctica	26·15	22·36	48·63	18·84	8·26	11·05	11·29	32·77	15·38	15·14	7·10	2·02	21·96	11·88	7·56	4·09	35·47	13·47	20·20	14·62	14·39	9·34
Pellilitorina setosa (rough spine)	—	—	—	6·67	—	3·70	—	—	—	4·96	—	6·59	—	3·88	—	2·09	—	—	—	3·10	—	2·72
Cyclostrema meridionale	1·71	—	—	—	1·18	—	1·98	—	1·54	—	27·08	2·41	4·13	—	5·46	—	6·19	—	5·47	—	8·36	—
Margarella antarctica	—	27·24	—	18·01	—	8·40	—	8·16	—	16·10	—	9·39	1·08	22·21	—	2·43	—	36·57	—	16·23	—	11·24
Pellilittorina setosa (fine spine)	—	—	—	—	—	2·66	—	—	—	3·23	—	—	—	3·30	—	—	—	1·15	—	1·15	—	1·49
N. concinna	—	16·70	—	5·95	—	8·34	—	—	—	1·29	—	—	—	8·01	—	—	—	—	—	4·48	—	5·80
Rissoa regularis	—	—	—	—	—	—	—	—	2·40	—	4·65	2·81	—	—	—	—	1·41	1·32	—	—	—	—
Rissoa scotiana	5·38	3·19	1·36	—	2·18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cerithiella spp. (?)	—	1·70	1·17	—	—	1·30	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rissoa spp. (?)	1·91	—	—	—	20·52	—	2·84	—	—	—	—	—	—	—	—	—	—	—	2·81	—	6·73	—

TABLE IV. REGRESSION ANALYSIS FOR THE log/log RELATIONSHIPS FOR EXPONENTS

	Equation number	r	m	$\log b$	var. $y\pm$	var. $m\pm$	P
Lissarca miliaris	1 Abundance	$-0\cdot7793$	$-1\cdot0057$	$6\cdot2224$	$0\cdot1371$	$0\cdot0934$	$0\cdot05$
	2 Weight	$-0\cdot8327$	$-1\cdot1102$	$3\cdot7154$	$0\cdot1142$	$0\cdot0778$	$0\cdot02$
Pelecypoda	3 Abundance	$-0\cdot7933$	$-1\cdot0887$	$6\cdot3850$	$0\cdot1464$	$0\cdot0998$	$0\cdot02$
	4 Weight	$-0\cdot8325$	$-1\cdot1043$	$3\cdot7072$	$0\cdot1132$	$0\cdot0771$	$0\cdot02$
Gastropoda	5 Abundance	$-0\cdot7915$	$-0\cdot8547$	$6\cdot2321$	$0\cdot0913$	$0\cdot0622$	$0\cdot05$
	6 Weight	$-0\cdot7358$	$-0\cdot6250$	$2\cdot8395$	$0\cdot0694$	$0\cdot0473$	$0\cdot10$ (ns)
Total Mollusca	7 Abundance	$-0\cdot7915$	$-0\cdot8547$	$6\cdot2321$	$0\cdot0913$	$0\cdot0622$	$0\cdot02$
	8 Weight	$-0\cdot8119$	$-0\cdot8453$	$3\cdot5872$	$0\cdot0774$	$0\cdot0527$	$0\cdot02$

Where $\log N$ or W/kg. $wp = m \log wp + \log b$.
Non-significant.
ndance (N) and weight (W) per kg. (dry weight) of plant (wp) with the original dry plant weights.

$11\cdot36$ g. and 7,334 individuals. Observations on the structural morphology of young and old *D. anceps* plants indicate that the surface area/weight of plant fronds remains nearly constant with size and cannot be attributed to the massive density increase of molluscs on smaller plants. Since the relationships with increasing weight hold for all types of mollusc, and their differing requirements, the cause is difficult to define, but it may be an increased affinity by the fauna for the smaller more protected understorey macro-algae within the weed bed. No weight change with weight of macro-algae was detected within the depth range sampled.

The most important single species of mollusc both by weight (W) and number (N) is *Lissarca miliaris* with respective percentage means (for all molluscs) of $37\cdot95$ (S.D. $\pm17\cdot62$) and $46\cdot55$ (S.D. $\pm20\cdot04$) (Table III). The October sample produced maximum figures, with a percentage composition of $76\cdot08$ per cent by weight and $80\cdot67$ per cent by number. *L. miliaris* accounts for means of $97\cdot77$ (S.D. $\pm3\cdot35$) per cent and $98\cdot81$ (S.D. $\pm0\cdot90$) per cent of the pelecypod population for abundance and weight, respectively.

Ecology of Lissarca miliaris

L. miliaris is a sessile, brooding epifaunal species living attached to macro-algae or other suitable substrates by byssus threads and having many of the features common to Antarctic pelecypods (Nicol, 1970; Dell, 1972). The species is small, reaching a maximum recorded gth of $5\cdot77$ mm. after 7 years. Growth is very slow and shows seasonal variation producing aracteristic shell growth rings.

An unusual feature of *L. miliaris*, already noted by Dell (1972), is its colour, a deep purple, colour code 12 (D-E) (3–6) (Kornerup and Wanscher, 1967). Most sub-Antarctic and Antarctic species lack shell colour (Nicol, 1970).

The maximum antero-posterior length (L) has been used as the standard measurement and Fig. 1 shows the relationships of other parameters to length. The relationships $\log$ breadth (B) against $\log$ length (L) and $\log$ height (H) against $\log$ length (L) were linear, whilst comparisons of the slopes of the regression lines to $1\cdot0$ using t-tests indicated that comparisons of breadth and length were isometric and that height and length were allometric ($t=1\cdot55$ and $6\cdot38$, respectively; $P<0\cdot05$). The various relationships between measurements of *Lissarca miliaris* are given in Table V. Regression lines were fitted by the method of least squares.

The mean percentage tissue dry weight/total dry weight is $14\cdot3$ per cent, which is similar to figures for other larger pelecypods *Mytilus edulis* ($13\cdot98$ per cent) and *Mya arenia* ($11\cdot61$ per
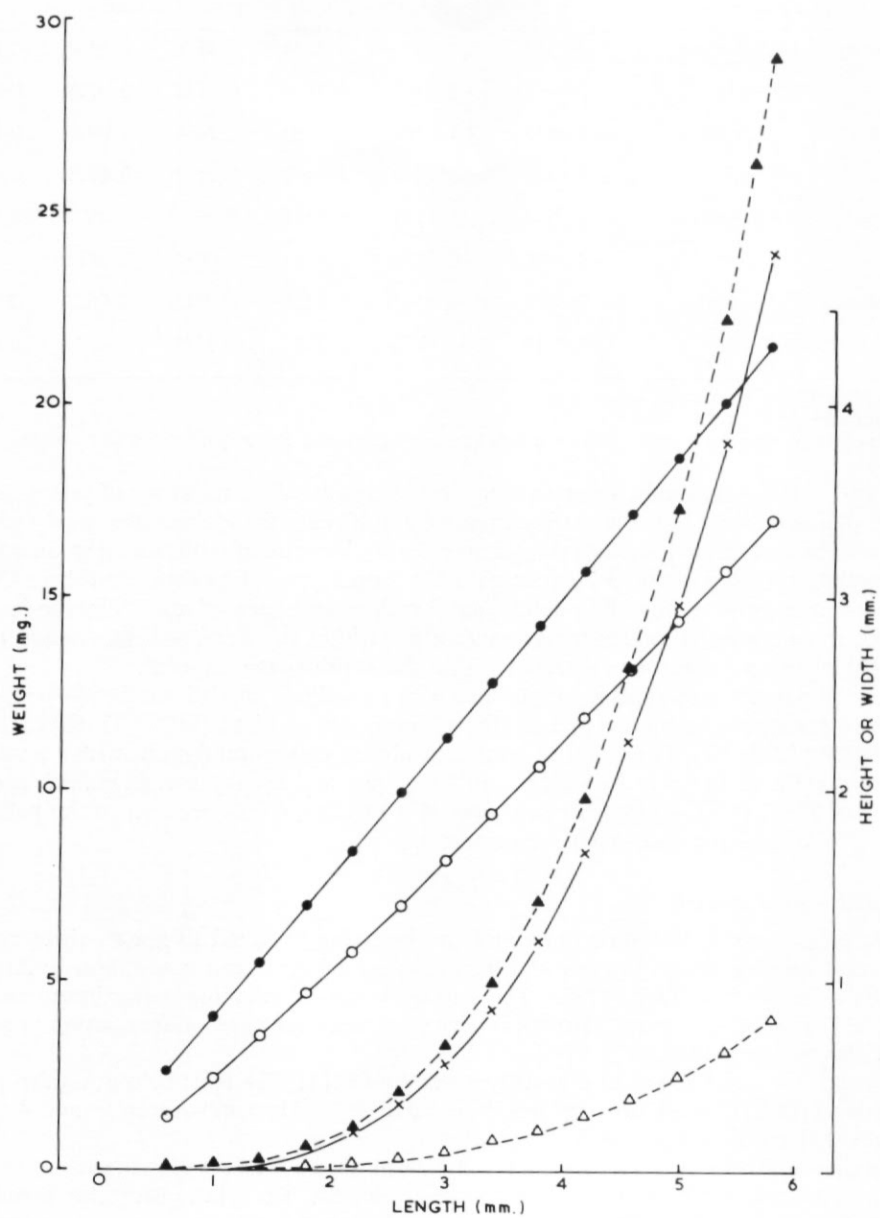
Fig. 1. Allometric parameters of *Lissarca miliaris* against length. ○──○ Breadth; ●──● Height; ▲----▲ Total weight (dry), X──X Shell weight (dry), △──△ Tissue weight (dry).

TABLE V. REGRESSION RELATIONSHIPS ($y=mx+b$) BETWEEN VARIOUS PARAMETERS TO LENGTH FOR THE BIVALVE *Lissarca miliaris*

n	y	m	x	b	var. $y \pm$	var. $m \pm$	r
64	log dry tissue weight (mg.)	3·0788	log length (mm.)	−0·7732	0·0051	0·0370	0·9719
18	log dry shell weight (mg.)	2·8130	log length (mm.)	−0·8501	0·0025	0·0186	0·9829
96	log dry total weight (mg.)	3·0993	log length (mm.)	−0·0097	0·0721	0·0358	0·9473
53	log height (mm.)	1·1103	log length (mm.)	−0·4274	0·0006	0·0003	0·9908
53	Breadth (mm.)	0·7324	Length (mm.)	+0·0678	0·0102	0·0001	0·9935

cent) (Nixon and others, 1971). The proportions of *L. miliaris* varied slightly with the size of the animal according to the relationship:

$$\frac{\text{Tissue weight}}{\text{Shell weight}} = 0 \cdot 1982 - \frac{0 \cdot 01214}{\text{Shell weight}}.$$

where $r = 0 \cdot 9505$, var. of $y \pm 0 \cdot 0386$, var. of $m \pm 0 \cdot 0003$ and $n = 18$.

The weight of older animals increased appreciably, not only through deposition of calcium carbonate in the shell but also through increased tissue weight due to structures absent in immature animals, e.g. reproductive tissues. Allometry in *L. miliaris* was apparent only in the relationship between length and height with the dorso-ventral distance showing a greater per unit increase in length in older animals.

Ash-free weights for total animals varied from 40 to 25 per cent, indicating an ash-free weight of 16–30 per cent for shell weight. The very high ash-free weights recorded are probably due to carbonate sublimation or transformation; further material was not available to repeat ignition experiments and dry-tissue weight not ash-free weight is the parameter referred to later.

Population structure

The *L. miliaris* population composition is outlined in Fig. 2 by the length–frequency histograms for the ten monthly sub-samples investigated. Size of sub-samples varied from $n = 281$ (December) to 1,781 (September). The totals for monthly samples are shown in Table I. All animals were measured and individuals greater than $2 \cdot 5$ mm. in length were examined for reproductive status and sex. The samples for December, January and February demonstrate considerable numerical recruitment of small-sized animals to the population. The population age structure of animals which confine larvae or egg release to short favourable periods of the year can often be determined by examination of histogram modal classes. In *L. miliaris*, despite the presence of a discrete cohort from recruitment, later modes were less clearly defined due to overlap of sexual, reproductive and growth variations, whilst the increased mortality leaving few individuals in older age classes further complicated interpretation. In most monthly histograms, only two or three modes were apparent and the composition of age groups could not be resolved using normal probability methods (Harding, 1949; Cassie, 1954).

Many previous workers have used ring markings produced by winter-growth checks as a means of ageing populations of bivalves. Studies include those on *Cerastoderma edule* (Walton, 1919; Orton, 1926; Boyden, 1972), *Kidderia bicolor* (Ralph and Everson, 1972), *Macoma balthica* and *Mya arenia* (Burke and Mann, 1974), *Mytilus edulis* (Seed, 1973), *Siliqua patula* (Weymouth and McMillan, 1930; Weymouth and others, 1931) and *Venerupis pullastra* (Quayle, 1951, 1952).

The validity of ring markings as indicators of seasonal growth always needs to be checked each species, since cyclical patterning can be induced by a variety of factors. Disturbance (Boyden, 1972) or tides (Evans, 1972) can add extra rings, whilst loss of growth patterns due to shell erosion and abrasion can lead to misrepresentation of the age composition of a population. Ideally, the incremental patterns observed in the field should be correlated with those of marked animals kept under observation in the same environment. Failing this, some method is required of tracing ring formation from one year to the next. Soot-Ryen (1951) concluded that ring formation in *L. miliaris* was absent but this observation may be attributed to preservation peculiarities which can cause shell discoloration and obscuring of ring morphology. Two types of ring were present: major rings, denoting growth checks in winter numbered up to seven, whilst secondary rings, possibly reproductive or induced by disturbance, were superimposed. Older animals of breeding age showed greater frequency of secondary rings. Coupled with severe pitting and abrasion, these increased the difficulty of ring interpretation. The large
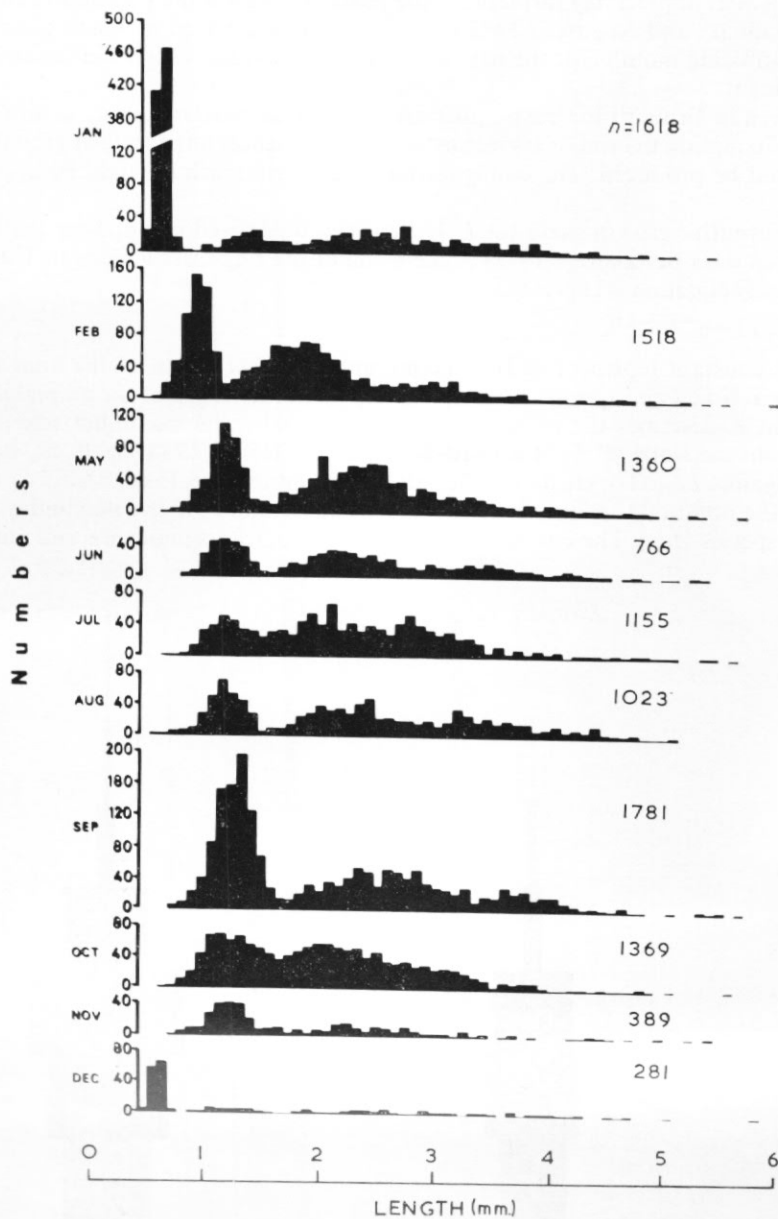
Fig. 2. Monthly population frequency histograms for the bivalve *Lissarca miliaris*.

variances about the mean of ring groups in Table VI are largely a function of the difficult task of attributing individuals to discrete groups. The inter-monthly population composition within ring classes can alter appreciably throughout the year. Fig. 3 gives the population composition, by rings, for January and August in 1972 (before and after a period in which growth ceased). These two contrasting months for the beginning and middle-year samples indicate the proportion of recruitment.

Data are given in Table VI for the number and mean with standard errors of all ring classes, by months. By coupling the ring-class means in direct sequence, a theoretical growth curve for *L. miliaris* could be produced. The configuration of the relationship would be approximately linear.

A more quantitative growth curve for *L. miliaris* can be derived by applying the Bertalanffy growth equation (von Bertalanffy, 1938) to the mean of the ring-class lengths in Table VI.

The Bertalanffy equation is expressed as:

$$L_t = L_\infty(1 - e^{-K(t-t_0)}),$$

where L_∞ is a constant representing the maximum theoretical length of the animal, $t=$time, $L_t=$the length at time t and $t_0=$the theoretical time when the length of the animal is zero.

The constant K describes the growth rate of the animal to its maximum size and can determined from the slope (e^{-K}) of a Ford-Walford plot (Ford, 1933; Walford, 1946), where L_t is plotted against L_{t+1}. To satisfy the Bertalanffy equation, the Ford-Walford plot should be linear and the point on the line where $L_t=L_{t+1}$ is an estimate of the maximum theoretical length of the species (L_∞). The constant t_0 has little biological significance and can be deter-
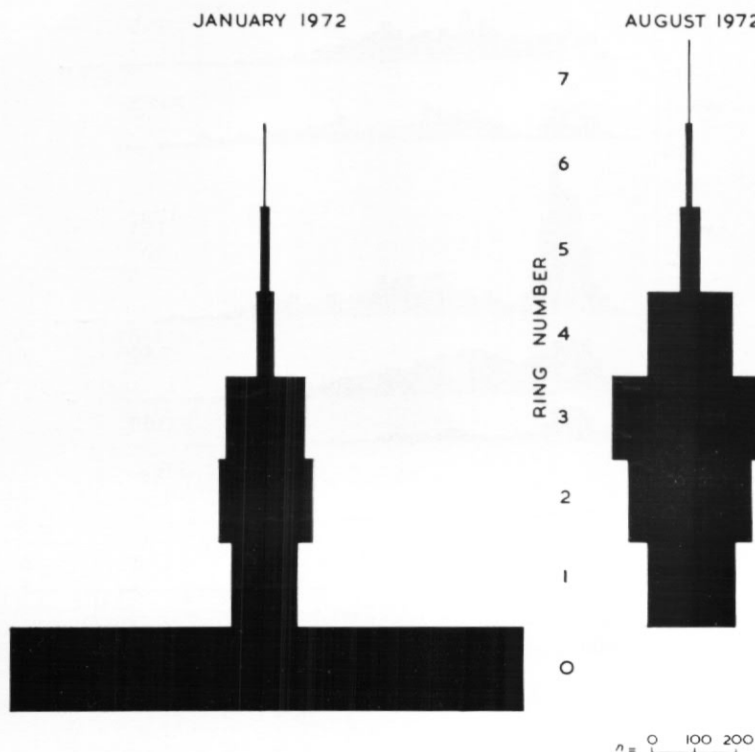

Fig. 3. Contrasting monthly population compositions for *Lissarca miliaris*.

TABLE VI. DATA OF THE AGE STRUCTURE OF THE *Lissarca miliaris* POPULATION FOR EACH MONTHLY SAMPLE, GIVING NUMBERS, MEAN LENGTHS WITH STANDARD ERRORS FOR RING CLASSES 0–7

Ring number	13 January			19 February			9 May			9 June			10 July			16 August			11 September			9 October			10 November			29 December		
	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.
0	1,012	0·73	0·0016	515	1·01	0·0049	436	1·25	0·0072	235	1·29	0·0099	213	1·26	0·0110	312	1·29	0·0100	904	1·36	0·0058	633	1·47	0·0122	197	1·46	0·0120	130	0·73	0·0047
1	156	1·50	0·0215	239	1·54	0·0113	435	2·18	0·0109	249	2·18	0·0157	301	1·96	0·0162	270	2·19	0·0152	337	2·33	0·0159	501	2·39	0·0150	65	2·15	0·0342	41	1·37	0·0292
2	217	2·42	0·0229	440	1·99	0·0093	355	2·83	0·0165	152	2·90	0·0273	369	2·62	0·0174	224	2·88	0·0247	325	2·89	0·0181	196	3·15	0·0289	83	2·84	0·0321	40	2·31	0·0389
3	185	3·21	0·0304	211	2·80	0·0200	99	3·75	0·0361	83	3·55	0·0273	212	3·33	0·0242	129	3·52	0·0268	171	3·71	0·0233	34	3·81	0·0907	23	3·55	0·0626	36	3·09	0·0450
4	39	4·05	0·0466	75	3·49	0·0406	26	4·40	0·0698	39	4·22	0·0484	44	4·29	0·0713	60	4·04	0·0473	33	4·30	0·0658	4	4·53	0·1040	8	4·63	0·1120	23	3·90	0·0676
5	6	4·51	0·1502	24	4·29	0·0861	9	4·86	0·1280	8	4·89	0·1370	14	4·91	0·1040	25	4·42	0·0510	11	4·97	0·1410	1	5·45	—	5	4·94	0·1650	8	4·21	0·1170
6	3	5·03	0·1484	13	4·74	0·0982	2	5·41	0·2450	—	—	—	2	5·12	0·2800	3	4·76	0·2150	—	—	—	—	—	—	—	—	—	3	4·72	0·1470
7	—	—	—	1	5·77	—																								
TOTALS	1,618			1,518			1,360			766			1,155			1,023			1,781			1,369			381			281		

TOTAL n = 11,252

TABLE VI. DATA OF THE AGE STRUCTURE OF THE *Lissarca miliaris* POPULATION FOR EACH MONTHLY SAMPLE, GIVING NUMBERS, MEAN LENGTHS WITH STANDARD ERRORS FOR RING CLASSES 0–7

			Sample																										
...ary		19 February			9 May			9 June			10 July			16 August			11 September			9 October			10 November			29 December		
S.E.	n	$\bar{x}$	S.E	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.
0·0016	515	1·01	0·0049																						130	0·73	0·0047
0·0215	239	1·54	0·0113	436	1·25	0·0072	235	1·29	0·0099	213	1·26	0·0110	312	1·29	0·0100	904	1·36	0·0058	633	1·47	0·0122	197	1·46	0·0120	41	1·37	0·0292
0·0229	440	1·99	0·0093	435	2·18	0·0109	249	2·18	0·0157	301	1·96	0·0162	270	2·19	0·0152	337	2·33	0·0159	501	2·39	0·0150	65	2·15	0·0342	40	2·31	0·0389
0·0304	211	2·80	0·0200	355	2·83	0·0165	152	2·90	0·0273	369	2·62	0·0174	224	2·88	0·0247	325	2·89	0·0181	196	3·15	0·0289	83	2·84	0·0321	36	3·09	0·0450
0·0466	75	3·49	0·0406	99	3·75	0·0361	83	3·55	0·0273	212	3·33	0·0242	129	3·52	0·0268	171	3·71	0·0233	34	3·81	0·0907	23	3·55	0·0626	23	3·90	0·0676
0·1502	24	4·29	0·0861	26	4·40	0·0698	39	4·22	0·0484	44	4·29	0·0713	60	4·04	0·0473	33	4·30	0·0658	4	4·53	0·1040	8	4·63	0·1120	8	4·21	0·1170
0·1484	13	4·74	0·0982	9	4·86	0·1280	8	4·89	0·1370	14	4·91	0·1040	25	4·42	0·0510	11	4·97	0·1410	1	5·45	—	8	4·94	0·1650	5	4·72	0·1470
—	1	5·77	—	2	5·41	0·2450	—	—	—	2	5·12	0·2800	3	4·76	0·2150	—	—	—	—	—	—	—	—	—	—	—	—
	1,518			1,360			766			1,155			1,023			1,781			1,369			381			281		

TOTAL n = 11,252

mined by plotting $\log_e (L-L_t)$ against t. The results from the Bertalanffy equation fit the data for *L. miliaris* and are shown in Fig. 4 and Table VII.

The yearly percentage incremental increase shows the typical decreased relative growth with age by a factor of $\times 7$ (Fig. 5).

Fig. 6 shows the lengths of animals from the smallest modes of Fig. 2 plotted against time. At the point when primary mode animals (bearing one ring) reach 1 year $+1$, their mean length corresponds to that of animals previously identified as ring 2 class animals. The implication is that animals possessing 1 ring are 3–15 months old, 2 rings 15–27 months, etc. The first indication of ring formation takes place just after onset of the winter period, when current-year juveniles are 3–6 months old. A similar seasonal growth pattern is shown in the horse clam *Tresus capax* (Bourne and Smith, 1972)
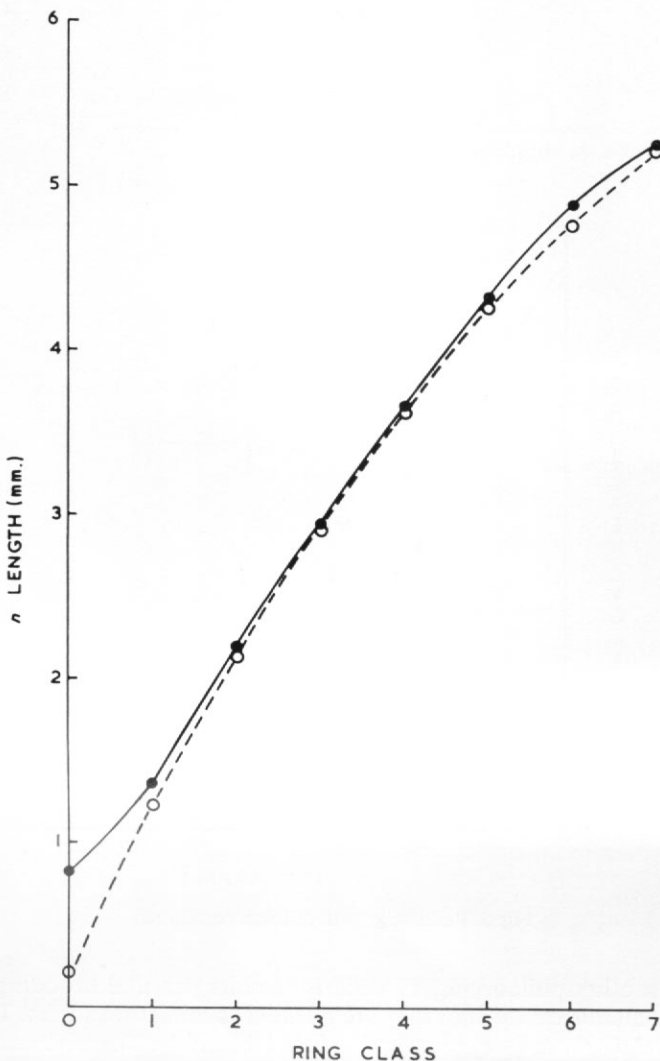
Fig. 4. Growth curve of *Lissarca miliaris* from observed data ●——●, and from estimates derived from the Bertalanffy equation ○——○. ($K=0\cdot1304, L_\infty = 8\cdot61$ mm.).

TABLE VII. OBSERVED AND CALCULATED LENGTHS, USING THE BERTALANFFY EQUATION $L_t = L_\infty (1 - e^{-K(t-t_0)})$, FOR EACH RING CLASS OF THE BIVALVE *Lissarca miliaris*

Ring number	Observed length (mm.)	Calculated length (mm.)
0	0·82	0·20
1	1·38	1·23
2	2·21	2·13
3	2·91	2·92
4	3·67	3·62
5	4·34	4·23
6	4·89	4·76
7	5·27	5·23

$L_\infty = 8·61$ mm., $K = 0·1304$, $t_0 = 0·8212$.
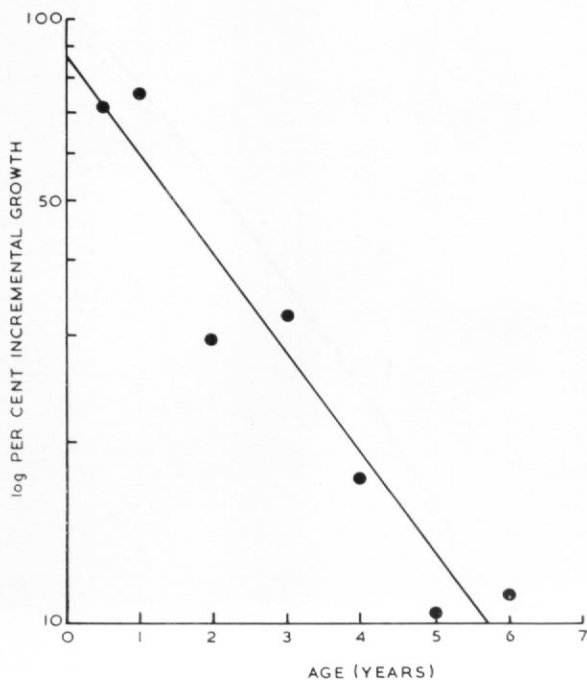
Fig. 5. Relative growth of *Lissarca miliaris*.

Reproduction

In common with other philobryids, *L. miliaris* exhibits parental brooding. The larvae are retained within the mantle cavity until they are released as miniature adults. This phenomenon is associated with relatively large egg size and reduced fecundity. The high mortality associated with planktonic larval existence is thus avoided. The occurrence of ovovivipary appears more commonly in species which have to withstand harsh environmental conditions. Brooding by
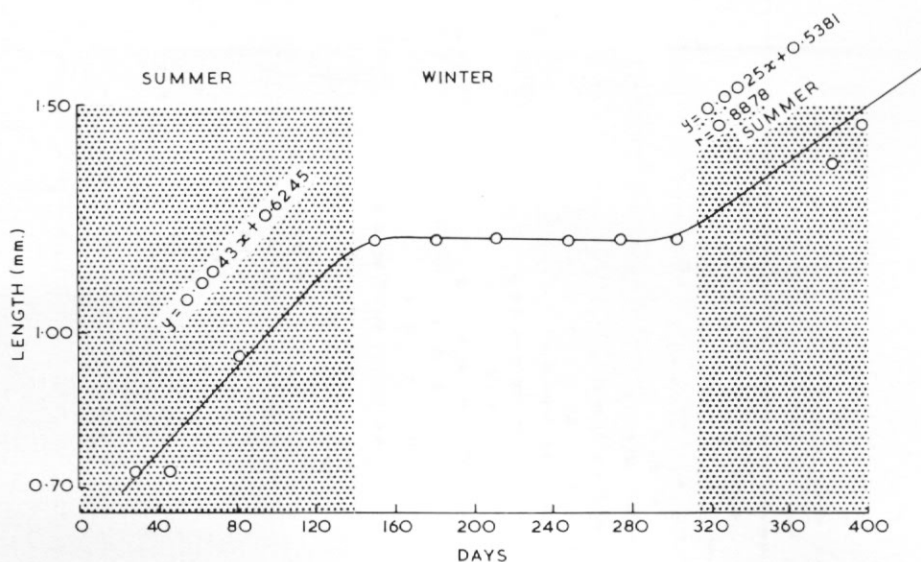
Fig. 6. Seasonal growth rates of the first year post-hatching in *Lissarca miliaris*. Data obtained from the primary modes of Table II.

benthic invertebrates in the Antarctic has been reviewed by Dell (1972). Young stages may be retained within the parent for as long as a year (Shabica, 1974).

Fecundity

The number of larvae that can be produced and carried by any female is related to the development of ovarian tissue and the available internal space of the female, and is thus a function of parental age and size. The size of larvae was independent of the parental length. The mean number of larvae per female remained constant throughout the year (range 54·3–70·0; Table X), whilst regressions of the numbers of larvae to the length of brooding female demonstrated linear relationships. Δt tests for variation in slopes of regression lines between monthly samples proved non-significant, indicating that there was minimum growth of brooding females during the period of retention and also that mortality of larvae during brooding was negligible. All monthly data were therefore grouped together (Fig. 7) to give a fecundity relationship of:

$$y = 53 \cdot 6869x - 160 \cdot 1688$$

where y=the numbers of brooded larvae per female, x=the length of brooding female (mm.) ($r = 0 \cdot 8636$ and $n = 152$).

The minimum observed size of a brooding female was 3·09 mm. (12 larvae), whilst the theoretical minimum length for this species is 3·02 mm. as derived by extrapolation from the above fecundity/size formula.

Reproductive cycle

Investigation of shells greater than 2·5 mm. long enabled sex ratios and periodicity of reproduction to be established. *L. miliaris* is dioecious with size ranges of males and females similar. The sex ratio of adult bivalves was significantly weighted towards females (Table VIII) with a mean ratio of 1·54 females to 1·0 male. Histological investigation of gametogenesis

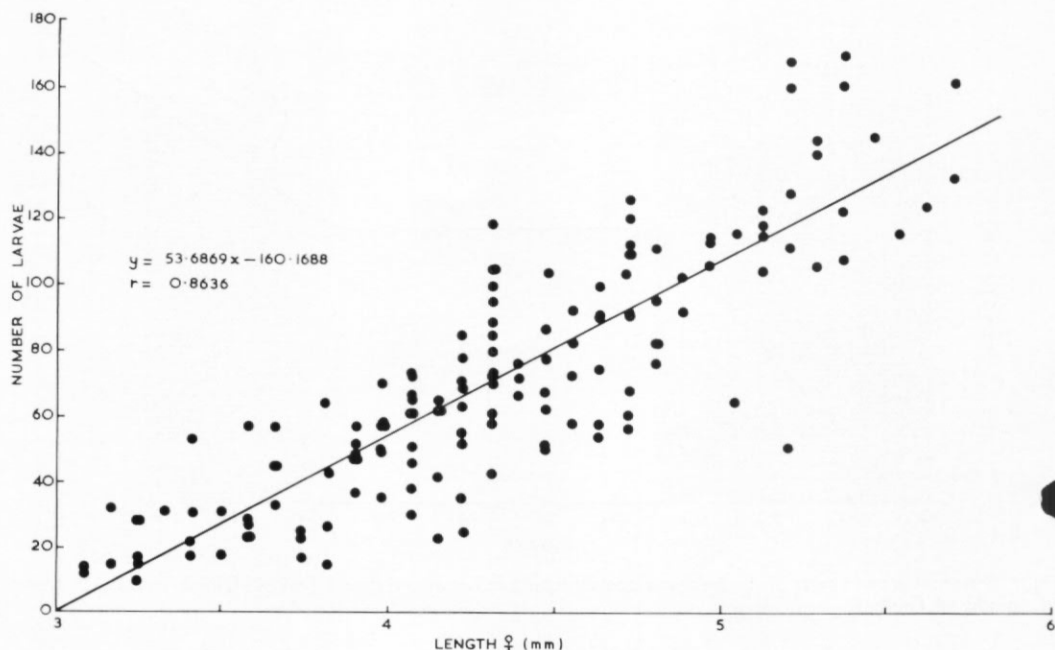$$y = 53 \cdot 6869x - 160 \cdot 1688$$
$$r = 0 \cdot 8636$$

Fig. 7. Fecundity in *Lissarca miliaris*. The relationship between the number of larvae and the length of brooding females, $n = 152$,

TABLE VIII. SEX RATIOS OF *Lissarca miliaris* (FOR ALL ANIMALS WITH A LENGTH $> 2 \cdot 5$ mm.)

Sample	January	February	May	July	August	September	November	December
♀	66	52	65	45	56	78	20	21
♂	34	37	65	31	36	63	10	12
Totals	100	89	110	76	92	141	30	33
Ratio ♀/♂	1·94	1·41	1·00	1·45	1·56	1·24	2·00	1·75

χ^2 significant $(12 \cdot 72, P > 0 \cdot 05)$

was not conducted but the onset of öogenesis in female bivalves was readily discernible. Female *L. miliaris* greater than $3 \cdot 0$ mm. long were placed in four arbitrary reproductive classes:

    A.   Ovarian tissue undergoing öogenesis, öogonia present in ovaries.
    B.   Larvae brooding in mantle cavity.
    C.   States A and B both present.
    D.   States A and B both absent.

In the majority of examples, categories A and B represent females breeding for the first time, whilst older females were identifiable as category C. Females in group D represent spent, infertile or non-breeding individuals and the percentage of bivalves in this group is low, remaining constant throughout the year and never rising above $11 \cdot 5$ per cent. The percentage composition of group A females declines rapidly from $94 \cdot 0$ per cent in January to $8 \cdot 6$ per cent

in August followed by a steady increase in öogenic females during spring. Conversely, the proportion of females brooding larvae in the mantle cavity is very low at the beginning of the year, 1·5 per cent, but it rapidly rises to peak at 72·2 per cent by May, whilst the optimum for category C females at 65·5 per cent occurs in August. The results for the monthly composition of females, of breeding size, is outlined in Fig. 8b and adjacent is the size frequency and breeding status plotted against time for all females (Fig. 8a). The cycle illustrated is, however, an over-simplification of the field situation but, from interpretation of these two sets of data, Fig. 9 (depicting reproductive cycling) has been derived.

Overlapping generations of developing young within the parent were apparent and from Fig.
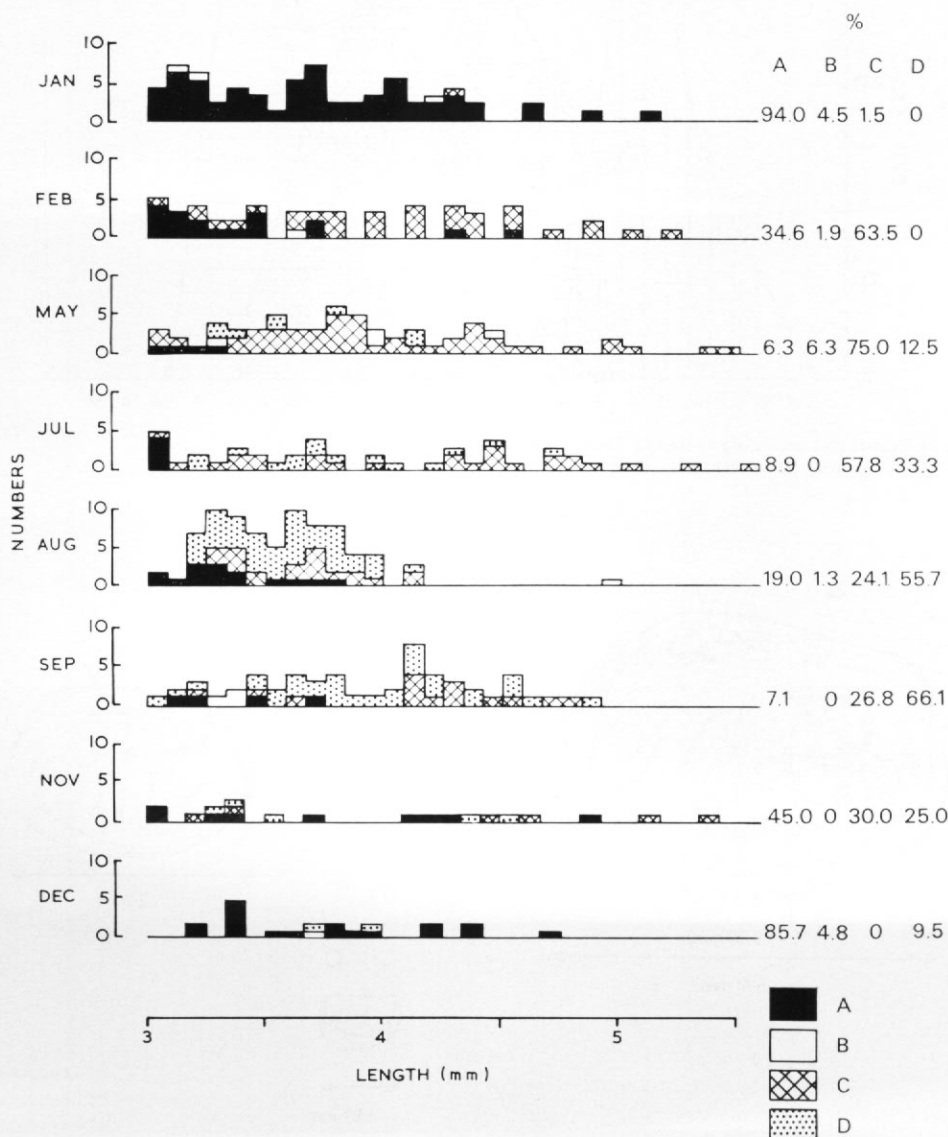
Fig. 8. Frequency histograms for size with time of the four breeding conditions of *Lissarca miliaris*. Percentage composition of each breeding condition/brooding population is shown on the right.
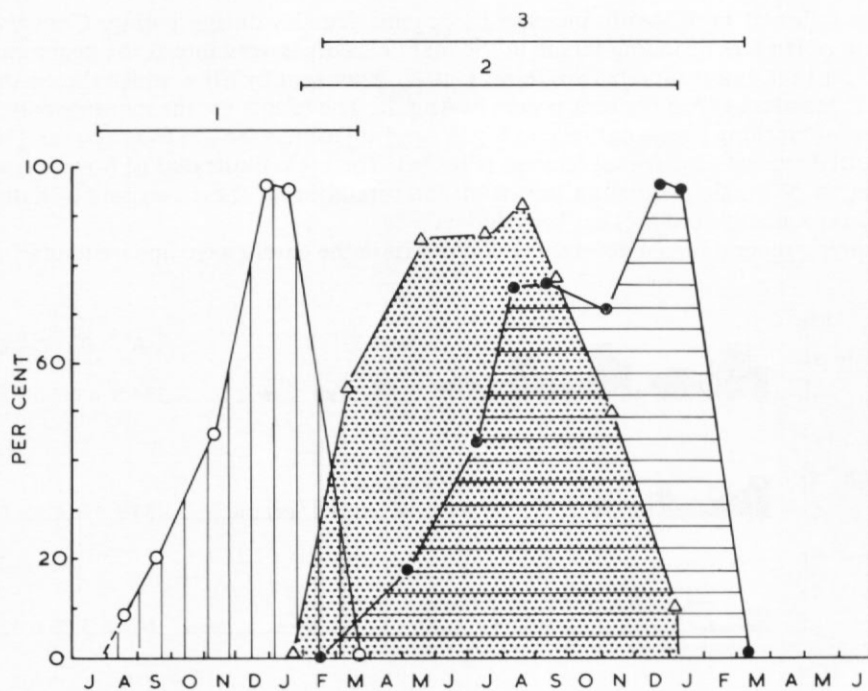
Fig. 9. Öogonic and brooding cycles of *Lissarca miliaris*.
1. Öogenesis (generation 1); 2. Brooding; 3. Öogenesis (generation 2).
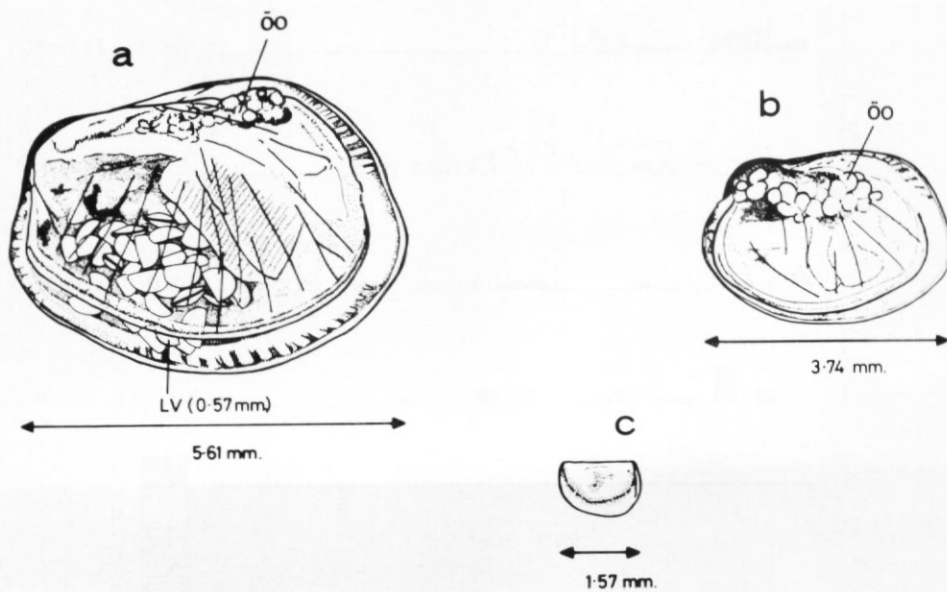
Fig. 10. The brooding bivalve *Lissarca miliaris;* a. Mature female carrying öogonia (öo) and well-developed larvae (LV); b. Immature female with öogonia (öo); c. Post-release hatchling.

8 a chronology of events can be established. The reproductive cycle for immature *L. miliaris* is initiated in September (Fig. 9) when öogenesis begins in the ovaries of individuals over 3·0 mm. long. The percentage of females in this reproductive state increases until by the beginning of the year most individuals greater than 3·0 mm. long are carrying primary öocytes. During February, primary öocytes are released into the anterior section of the mantle cavity, fertilization presumably occurring at this time. Brooding within the mantle cavity continues through until the following December. Meanwhile, a second generation of öogonia is developing from March onwards within the ovaries.

Embryos within the anterior mantle cavity are held in two clusters, one in each of the valves. Each cluster is surrounded by a thin transparent membrane whose function is presumably to prevent premature ejection. Sketches of the appearance of group A and C females plus the typical D-shaped straight-hinged protoconch are shown in Fig. 10.

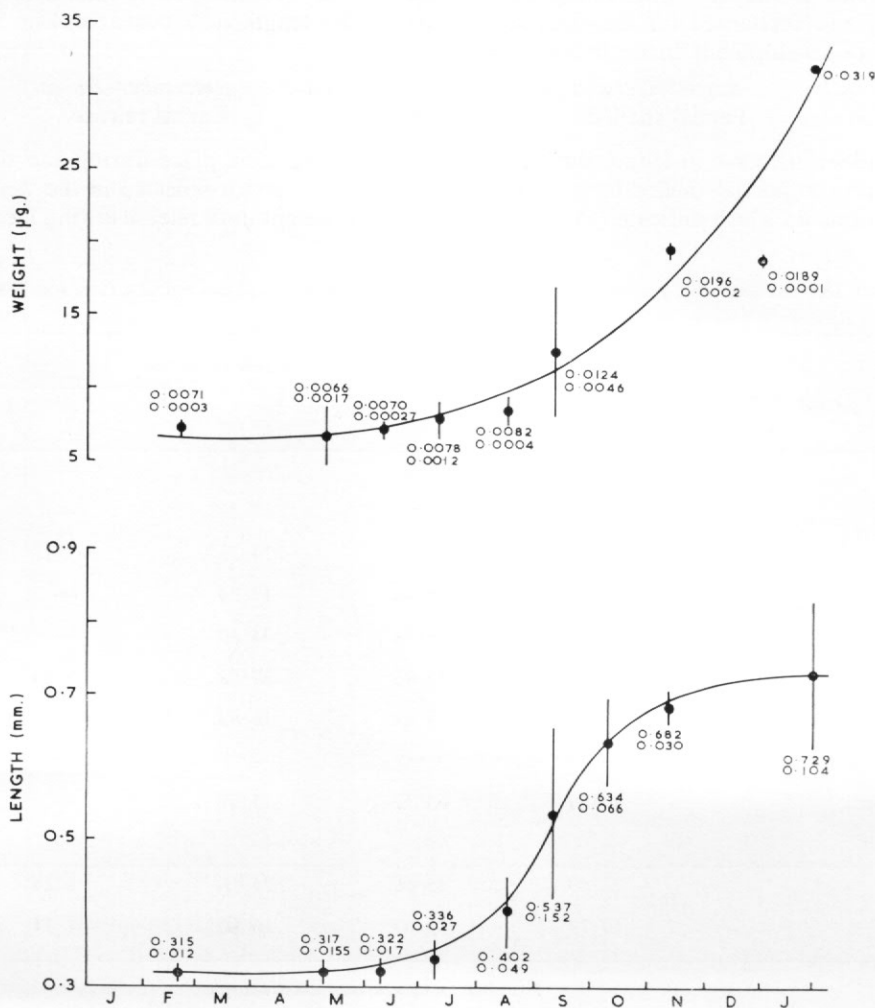The complete cycle of egg maturation through the öogonium, öocyte to the immediate pre-

Fig. 11. Weight and length changes during brooded development of *Lissarca miliaris*.

release larva takes 17–18 months, during which time a second generation of öogonia, still bound within the ovary, is apparent (Fig. 9).

Larval development

The öocytes and larvae of *L. miliaris* are relatively massive compared to those of other bivalves but of comparable size to larvae brooded by non-polar pelecypods. The growth of larvae within the adult females during the extended retention period was determined by inspecting the broods of up to 20 females per month and measuring and weighing a random sample of ten individuals from each brood. Larvae were dried at 60° C and stored under vacuum to obtain weights. Re-location of öocytes into the suprabranchial chamber of the mantle cavity occurred in mid-summer. Males at this time had active gonads and fertilization probably occurred within the female mantle cavity. Initial embryos are spherical with a diameter of 0·317 mm. (S.D.±0·014) and a mean weight of 7·14 μg. Growth during brooding was very slow and partial-shelled individuals were not apparent until August. Development to the characteristic D-shaped straight-hinged protoconch larvae occurred in the final 2 months of brooding and accounted for the sigmoidal shape of the length/time curve of Fig. 11. The sequence of development during brooding was as follows:

February–July	*August–October*	*November–December*	*December–January*
Pre-shelled	Partial shelled	Fully shelled	Larval release

The sudden increase in length during early austral spring took place during the development of pre- to partial-shelled larvae. Growth configuration is not reflected in the weight per time relationship which indicated exponential increase of weight until release during December.

TABLE IX. THE RELATIVE IMPORTANCE OF RING CLASSES TO THE POPULATION PRODUCTION FOR TEN MONTHLY SAMPLES OF *Lissarca miliaris*

Month	Percentage production of larvae			
	Ring number			
	4	5	6	7
January	—	—	—	—
February	19·67	43·05	37·28	—
May	44·64	33·89	14·28	7·18
June	25·04	55·72	19·24	—
July	9·03	56·38	34·59	—
August	9·97	46·96	37·78	5·29
September	63·20	19·82	16·98	—
October	—	—	—	—
November	20·26	63·77	15·97	—
December	—	—	—	—
$\bar{x}$	27·40	45·66	25·16	6·24
S.D.±	19·73	15·05	10·80	1·34

$$\text{Percentage production} = \frac{\text{Number of larvae/ring class/sample}}{\text{Total larvae/sample}} \times 100.$$

TABLE X. DATA FOR THE FECUNDITY AND POTENTIAL PRODUCTION OF *Lissarca miliaris*

Sample date	Sample population number	Percentage brooding	Number of larvae	$\frac{P}{N}$	Percentage tissue recruitment	$\bar{x}$ larvae/ ♀
February	1,518	2·24	2,288	1·507	5·97	67·29
May	1,360	4·41	3,564	2·620	6·67	59·40
June	766	7·31	3,123	4·070	10·10	55·77
July	1,155	3·98	3,111	2·693	6·01	67·63
August	1,023	5·18	3,269	3·196	9·02	61·68
September	1,781	4·83	4,671	2·623	6·92	54·31
November	381	2·89	770	2·020	6·88	70·00
			$\bar{x}$	2·676	7·37	62·30

$\frac{P}{N}$ = potential recruitment of the sample population;

Percentage tissue recruitment = $\dfrac{\text{larval tissue weight/sample } (W_{Lt})}{\text{total sample population tissue weight} - W_{Lt}}.$

Population structure, recruitment and mortality

Brooded embryos are apparent in females of ring classes 4, 5, 6 and 7 with repeated annual breeding in *L. miliaris*, resulting in production of three or four generations per female. Nearly half of the young produced each year are accounted for by the year 5 generation (45·7 per cent). Females of the 4 year old group may be immature, undergoing öogenesis or carrying brooded larvae. Though the numbers of group 4 brooders may be high, these bivalves were breeding for the first time and so produced relatively few young; thus the importance of this year group as contributors to the annual population recruitment is small (27·4 per cent). Similarly, though the numbers of larvae produced per individual in the older age classes are large, the number of specimens/ring class has diminished, again reducing the overall production/year group. Data for the percentage composition of relative year groups are given in Table IX.

The number of the population brooding at any one time was small and remained low (Table X), never rising above 7·31 per cent.

Length–frequency histograms (Fig. 2) for the monthly sub-samples showed the large recruitment of small individuals during the months of December, January and February. Designating observed recruitment as the ratio of 0 class bivalves to the remainder of the population

$$\text{Observed recruitment} = \frac{0 \text{ class animals}}{\text{Total population} - 0 \text{ class}},$$

gave results for these 3 months as the following ratios:

December $\quad \dfrac{130}{153} = 0·850$

January $\quad \dfrac{1,012}{606} = 1·670,$

February $\quad \dfrac{516}{1,001} = 0·516.$

These data of post-release recruitment are lower than nearly all potential production (P_N) figures determined from analyses of brooding females (Table X) where numerical potential recruitment is expressed as

$$P_N = \frac{\text{Number of larvae brooded/sample}}{\text{Total sample population} - \text{larvae}}$$

with a mean ratio of 2·64.

Differences between observed recruitment and P_N are possibly caused by pre- or post-larval mortality, migration of recently released young or sampling inefficiency. Migration is presumed to be of a steady-state nature with emigration (if present) equal to immigration. *t*-tests on regression analyses of monthly fecundity demonstrated negligible brooding mortality of embryos, and so only error in sampling or appreciable juvenile mortality could account for these discrepancies. The sampling technique used would certainly have collected and extracted representatives of the small animals if they were attached to macro-algae, and subsequent hand sorting under a ×50 dissecting microscope validated the methods. Although the byssus of *L. miliaris* is secreted shortly after release, ejection of young during storm conditions could result in immediate post-release juveniles being swept away from suitable anchorage into unfavourable habitats. If the mortality suggested by the data above is added to that caused by differences in the population structure between first- and second-year individuals (Fig. 2; Table VI), net mortality for this small bivalve during its initial year is in the region of 60–70 per cent. The weight involved in this loss from the population is of little significance, since
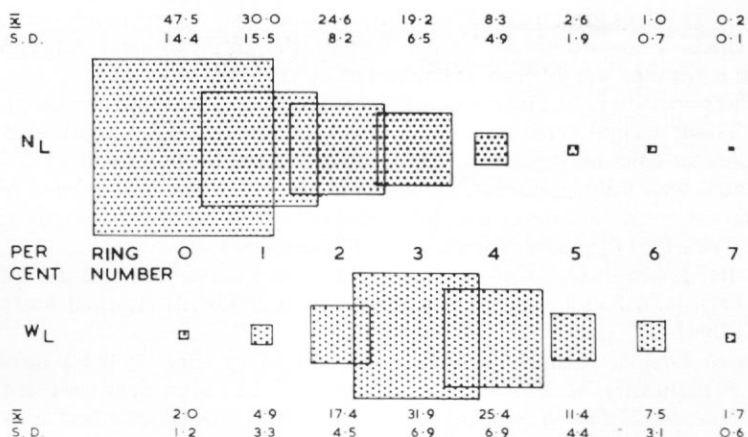
Fig. 12. Population structure of *Lissarca miliaris*. Mean percentage values of biomass and numerical abundance by ring classes.

potential production in terms of dry tissue weight (larvae) over the total dry tissue weight of the population minus larvae had a mean value of $7 \cdot 4$ per cent (range $5 \cdot 97$–$10 \cdot 10$ per cent). The relative proportion of first-year animals to the total population can be obtained by summing the 0 and 1 ring classes (Fig. 12) where, despite over 70 per cent numerical dominance of first-year individuals in the population, the weight of the year group contributes only $6 \cdot 9$ per cent. Decline in numerical status of ascending ring classes (Fig. 12) was assumed to be a direct measure of population mortality. Less than 10 per cent of bivalves reach the breeding age of 4 years, whilst the proportion of animals gaining 6 or more years was only $1 \cdot 2$ per cent. The maximum ring class observed was 7, whilst ring classes 2, 3 and 4 are the main contributors to population weight ($74 \cdot 7$ per cent). A similar weight relationship to population structure was apparent in Baltic populations of *Mytilus edulis* (Bergh, 1974).

DISCUSSION

The anomalous situation of plant-weight dependent mollusc density producing negative log–log linear relationships (Table IV) is difficult to attribute to specific causes. Density factors associated with time rather than sample weights may produce some fluctuations. Such effects should be minimized by the non-synchronized reproductive strategies of different mollusc species.

The biomass and abundance of Antarctic epifaunal molluscs/area are less than comparable faunal figures where densities and numbers may apparently be considerable, for example Pelecypoda $636 \cdot 2$ g./m.^{2}, Gastropoda $38 \cdot 4$ g./m.^{2} (Hardy, 1972), *Yoldia eightsii* 1,545/m.^{2} (Rabarts, 1971) and *Laternula elliptica* up to 2,000 g./m.^{2} (Hardy, 1972).

Corresponding figures for the mean and maximum recorded biomass of epiphytic molluscs are $47 \cdot 9$ g./m.^{2} and $25 \cdot 8$ g./m.^{2}, or numerically 62,540 individuals/m.^{2} and 20,830/m.^{2}. These figures are derived using the mean weight of macro-algae of 178 g. *wp*/m.^{2} (980 g. wet weight) with a maximum of 374 g. *wp*/m.^{2} (2,050 g. wet weight) (Richardson, 1979).

Net dry tissue weights/area for the molluscan epifauna are small with a maximum of $7 \cdot 2$ g./m.^{2} ($\bar{x}=3 \cdot 9$ g./m.^{2} where

$$\frac{\text{dry tissue weight}}{\text{total dry weight}} \times 100 = 14 \cdot 3).$$

Nicol (1966), examining 36 shallow-water Antarctic species, concluded that the tendency towards reduced size was strongly characteristic of the Antarctic marine pelecypod fauna.

Some Antarctic bivalves, infaunal in habitat, can achieve appreciable sizes; for instance, *L. elliptica*, which is the dominant component of the shallow-water infauna, reaches wet weights of 300 g. Similar weights are not achieved by epifaunal species.

Measurement parameters of *Lissarca miliaris* generally follow those of other mollusc species (Seed, 1973). Tissue weight remained a constant function of total weight with the increased weight attributed to calcium deposition being offset by the development of soft reproductive tissue. Allometry was only apparent, to a small extent in the inter-umbo distance (H), a condition different from that described by Seed (1973) for *Mytilus*. Comparative figures for *Venerupis* (Quayle, 1951) showed isometry in all dimensions measured.

Growth studies on molluscs using check rings have been reviewed and discussed by Wilbur and Owen (1964), whilst more specific studies using individually marked animals have been followed by Gilbert (1973).

The growth of *Lissarca miliaris* follows a sigmoid curve (Fig. 4) (or a double sigmoid if larval growth is included). Molluscan sigmoidal growth has been demonstrated in the Pacific razor clam, *Siliqua patula*, by Weymouth and others (1931), who described such growth using the Gomperz (1825) equation where:

$$\log lt = \log L_\infty (1 - e^{-k(t - t_1)}),$$

where $t_1 =$ time and $lt = 1$.

Thiesen (1973), working on *Mytilus edulis* from Arctic waters, also demonstrated sigmoidal growth with the curve best evaluated using both the Gomperz and Bertalanffy equations. The Gomperz equation was found to fit growth of the animal up to half its maximum length, whilst the Bertalanffy equation gave a better fit when the observed length data related to a size above one-third of the maximum length, but proved unsuitable for the smaller individuals in the size range.

The estimates derived from the Bertalanffy equation gave a good fit for the observed values of *L. miliaris* above the year 1 class. The value of K (0·1304) indicates the slow nature of growth towards maximum size and the L_∞ estimate for the species $= 8·61$ mm., higher than the observed value of 5·8 mm. length. Relative incremental growth diminished with age by a factor of 7, from 71·6 per cent in length from first-year animals to 11·2 per cent for 6 year olds. Corresponding values for temperate species indicate faster initial growth: *Mytilus edulis*, 190–300 per cent for 2–4 year olds (Seed, 1973) or *Pecten maximus*, 200–300 per cent in 2 year olds (Gibson, 1956).

Growth data for southern cold-water species are extremely sparse. The small gaimaridan *Kidderia bicolor* showed more constant growth with relative incremental increases of 43·6 during second-year growth, diminishing to 11·0 per cent by the fifth (Ralph and Everson, 1972). Similarly, the infaunal pelecypod *Yoldia eightsii* produced a diminishing relative growth from 100 per cent for second-year animals, 9 per cent at 12 years to less than 5 per cent at 17 years (Rabarts, 1971).

Thorson (1936, 1946, 1950) and Ockelmann (1965) have reviewed relationships between environmental conditions, brooding tendency and the reproductive variations that increased parenthood involves. Most marine pelecypods shed eggs directly into the sea, where the larvae undergo planktotrophic development. Increased parental protection in bivalves has been observed only in the fresh-water Sphaeriidae (Foster, 1932; Zumoff, 1973) and Unionidae (Wiles, 1975), the marine Erycinidae (Howard, 1953; Oldfield, 1963) and Montacutidae (Oldfield, 1963), whilst in Antarctic bivalves the Cyamidae (Ralph and Everson, 1972; Shabica, 1974), Philobryidae (Howard 1953; Dell, 1964) and Laternulidae (Burne, 1920) brood their young (the last record for *Laternula elliptica* has not been substantiated by more recent workers). Brooding may be ovoviviparous or larviparous and Thorson (1950) correlated the incidence of brooding with severe environmental conditions. The common occurrence of brooding in Antarctic invertebrates (Dell, 1972) and pelecypods (Soot-Ryen, 1951) adds support to this statement. Planktotrophism in Antarctic waters could only be of selective advantage to

TABLE XI. THE INCIDENCE OF BROODING IN ANTARCTIC PELECYPODA

Species	References
Pseudokellya cardiformis	Pelseneer, 1903
Mysella arthuri	Dell, 1964
Kidderia bicolor	Soot-Ryen, 1951; Ralph and Everson, 1972
Kidderia subquadratum	Shabica, 1974
Gaimardia trapesina	Pelseneer, 1903; Ralph and Maxwell, 1977
Laternula elliptica	Burne, 1920
Lasaea rubra	Pelseneer, 1903
Adacnarca nitens	Burne, 1920; Soot-Ryen, 1951; Dell, 1964; Nicol, 1966
Cyamiocardium crassilabrum	Dell, 1964
Lissarca miliaris	Soot-Ryen, 1951; Richardson, this study
Lissarca notocadensis	Dell, 1964
Philobrya sublaevis	Soot-Ryen, 1951; Dell, 1964
Philobrya capillata	Dell, 1964
Bathyarca sinuata	Pelseneer, 1903 (probably a brooding species)

young stages if a high degree of synchronization of larval release to maximum primary productivity could be satisfactorily achieved and maintained throughout different climatic years (White, 1977). Brooding within Antarctic species is outlined in Table XI.

Fecundity of Antarctic species has only been established in a few examples (Soot-Ryen, 1951; Dell, 1964). The degree of fecundity is normally dependent on the size of the parent, though Ralph and Everson (1972) found no such correlation in *K. bicolor* at South Georgia. The linear relationship of brood numbers to female lengths in *L. miliaris* was similar to the situation expressed for *K. subquadratum* (Shabica, 1974). However, in the latter example the variance about the slope for this relationship was considerably increased. Shabica (1974) discussed the degree of fatality throughout brooding in *Kidderia*. However, no such larval mortality could be discerned in *Lissarca* and the relative öocyte or embryo size/clutch number to female length remained constant.

The size disparity of eggs and embryos of molluscs with different reproductive strategies has been widely discussed (Thorson, 1936, 1946, 1950; Ockelmann, 1965; van Oertzen, 1972). Thorson (1952) determined the critical transitional egg size for bivalves undergoing pelagic or brooding developments at 100–200 μm. diameter. The relatively large egg size (350 μm.) of *L. miliaris* compares with the size range of other brooding species. Franz (1973) speculated on the comments of Sellmer (1967) that brood protection amongst bivalves was most prevalent in smaller species, with very small animals perhaps lacking sufficient energy reserves to create vast numbers of planktotrophic larvae. Work on the necessary energy required to produce independent young of ovoviviparous, larviparous and planktotrophic organisms is needed to clarify this hypothesis. Assuming equal energy expenditure/volume of egg production, figures of decreased reproductive output (as egg volume) can be derived:

L. miliaris (ovoviviparous $6 \cdot 6963 \times 10^8$ μm.^{3}),
M. planulata (larviparous $1 \cdot 4367 \times 10^9$ μm.^{3}),
C. islandica (planktotrophic $5 \cdot 3878 \times 10^{10}$ μm.^{3}).

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However, if increased egg volume tends to proportionally increased lipid content (Thorson, 1936), energy expenditure between the different reproductive categories may be closer than the above indicates.

Most brooding species produce more than one clutch; *Sphaerium* broods twice per year (Foster, 1932), though *Gemma gemma* apparently broods only once in a lifetime (Sellmer, 1967). The repetition of brooding by individuals at different ages of the population may allow greater stability in populations undergoing severe pressures (Murphy, 1968).

REFERENCES

BERGH, G. 1974. Biomass of the bottom fauna in Tvaren Bay in the Baltic. *Zoon*, **2**, No. 1, 57–66.
BERGMANS, W. 1970. The validity of the genera *Lissarca, Austrosarepta, Cratis* and *Denticosa* with notes on some Australian species (Bivalvia, Philobryidae). *J. malac. Soc. Aust.*, **2**, No. 1, 35–38.
BOURNE, N. *and* D. W. SMITH. 1972. Breeding and growth of the horse clam, *Tresus capax* (Gould), in southern British Columbia. *Proc. natn. Shellfish. Ass.*, **62**, No. 1, 38–44.
BOYDEN, C. R. 1972. Relationship of size to age in the cockles *Cerastoderma edule* and *C. glaucum* from the River Crouch estuary, Essex. *J. Conch., Lond.*, **27**, No. 7, 475–89.
BURKE, M. V. *and* K. H. MANN. 1974. Productivity and production: biomass ratios of bivalve and gastropod populations in an eastern Canadian estuary. *J. Fish. Res. Bd. Can.*, **31**, No. 2, 167–77.
BURNE, R. H. 1920. Mollusca. Part IV—Anatomy of Pelecypoda. *Br. Antarct. Terra Nova Exped. 1910*, Natural History Reports, Zoology, **2**, Pt. 10, 233–56.
CASSIE, R. M. 1954. Some uses of probability paper in the analysis of size frequency distributions. *Aust. J. mar. Freshwat. Res.*, **5**, 513–22.
DELL, R. K. 1964. Antarctic and subantarctic Mollusca: Amphineura, Scaphopoda and Bivalvia. '*Discovery*' *Rep.*, **33**, 93–250.
———. 1972. Antarctic benthos. *Adv. mar. Biol.*, **10**, 1–216.
EVANS, J. W. 1972. Tidal growth increments in the cockle *Clinocardium nuttalli*. *Science, N.Y.*, **176**, No. 4033, 416–17.
EVERSON, I. *and* M. G. WHITE. 1969. Antarctic marine biological research methods involving diving. *Rep. Underwat. Ass.*, **4**, 91–95.
FORD, E. 1933. An account of the herring investigations conducted at Plymouth during the years from 1924–1933. *J. mar. biol. Ass. U.K.*, **19**, No. 2, 305–84.
FOSTER, T. D. 1932. Observations of the life history of a fingernail shell of the genus *Sphaerium*. *J. Morph.*, **53**, No. 3, 473–97.
FRANZ, D. R. 1973. The ecology and reproduction of a marine bivalve, *Mysella plantulata* (Erycinacea). *Biol. Bull. mar. biol. Lab.*, Woods Hole, **144**, No. 1, 93–106.
GIBSON, F. A. 1956. Escallops (*Pecten maximus* L.) in Irish waters. *Scient. Proc. R. Dubl. Soc.*, **27**, 253–70.
GILBERT, M. A. 1973. Growth rate, longevity and maximum size of *Macoma balthica* (L.). *Biol. Bull. mar. biol. Lab.*, Woods Hole, **145**, No. 1, 119–26.
GOMPERZ, B. 1825. On the nature of the function expression of the law of human mortality, and on a new mode of determining the value of life contingencies. *Phil. Trans. R. Soc.*, **115**, 513–85.
GRUZOV, YE. N., PROPP, M. V. *and* A. F. PUSHKIN. 1967. Biologicheskie soobshchestva pribrezhnykh rayonov morya Deyvisa (po rezul'tatam vodolazynykh nablyudeniy) [Biological communities of the inshore areas of the Davis Sea (from data of diving observations]. *Inf. Byull. sov. antarkt. Eksped.*, No. 65, 124–41. [English translation: Vol. 6, No. 6 (1967), 523–33.]
HARDING, J. P. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. mar. biol. Ass. U.K.*, **28**, No. 1, 141–53.
HARDY, P. 1972. Biomass estimates for some shallow-water infaunal communities at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, No. 31, 93–106.
HOWARD, J. 1953. Some viviparous pelecypod mollusks. *Wasman J. Biol.*, **11**, No. 2, 233–40.
KORNERUP, A. *and* J. H. WANSCHER. 1967. *The Methuen handbook of colour*. 2nd edition. London, Methuen and Co. Ltd.
MURPHY, G. 1968. Pattern in life history and the environment. *Am. Nat.*, **102**, No. 927, 391–403.
NICOL, D. 1966. Size of pelecypods in recent marine faunas. *Nautilus*, **79**, No. 4, 109–13.
———. 1970. Antarctic pelecypod faunal peculiarities. *Science, N.Y.*, **168**, No. 3936, 1248–49.

NIXON, S. W., OVIATT, C. A., ROGERS, C. *and* K. TAYLOR. 1971. Mass and metabolism of a mussel bed. *Oecologia*, **8**, No. 1, 21–30.

OCKELMANN, W. K. 1965. Developmental types in marine bivalves and their distribution along the Atlantic coast of Europe. *Proceedings, First European Malacological Congress, London, 1962*, 25–35.

OLDFIELD, E. 1963. The reproduction and development of some members of the Erycinidae and Montacutidae (Mollusca, Eulamellibranchiata). *Proc. malac. Soc. Lond.*, **36**, No. 2, 79–120.

ORTON, J. H. 1926. On the rate of growth of *Cardium edule*. Part 1. Experimental observations. *J. mar. biol. Ass. U.K.*, **14**, No. 1, 239–79.

PELSENEER, P. 1903. II. Mollusques (Amphineura, Gastropodes et Lamellibranches). *Résult. Voyage S.Y. Belgica*, Zoologie, **10**, 1–87.

PHILIPPI, R. A. 1845. Diagnosen einiger neuen Conchylien. *Arch. Naturgesch.*, **2**, 50–71.

QUAYLE, D. B. 1951. The rate of growth of *Venerupis pullastra* (Montagu) at Millport, Scotland. *Proc. R. Soc. Edinb.*, Sec. B, **64**, No. 4, 384–406.

———. 1952. Structure and biology of the larva and spat of *Venerupis pullastra* (Montagu). *Trans. R. Soc. Edinb.*, **62**, Pt. 1, No. 8, 255–97.

RABARTS, I. W. 1970. Physiological aspects of the ecology of some Antarctic lamellibranchs (B.A.S. No. N9/1970/H), 10 pp. [Unpublished.]

———. 1971. Physiological aspects of the ecology of some Antarctic lamellibranchs (B.A.S. No. N9/1971/H), 11 pp. [Unpublished.]

RALPH, R. *and* I. EVERSON. 1972. Some observations on the growth of *Kidderia bicolor* (Martens) (Mollusca : Lamellibranchiata) at South Georgia. *British Antarctic Survey Bulletin*, No. 31, 51–54.

———. *and* J. G. H. MAXWELL. 1977. The oxygen consumption of the Antarctic lamellibranch *Gaimardia trapesina trapesina* in relation to cold adaptation in polar invertebrates. *British Antarctic Survey Bulletin*, No. 45, 41–46.

RICHARDSON, M. G. 1979. The distribution of Antarctic marine macro-algae related to depth and substrate. *British Antarctic Survey Bulletin*, No. 49, 1–13.

SEED, R. 1973. Absolute and relative growth in the mussel, *Mytilus edulis* (L.) (Mollusca, Bivalvia). *Proc. malac. Soc. Lond.*, **40**, No. 5, 343–57.

SELLMER, G. P. 1967. Functional morphology and ecological life history of the gem clam *Gemma gemma* (Eulamellibranchiata : Veneridae). *Malacologia*, **5**, No. 2, 137–223.

SHABICA, S. V. 1974. *Reproductive biology of the brooding Antarctic lamellibranch Kidderia subquadratum Pelseneer.* M.S. thesis, Department of Oceanography, Oregon State University. [Unpublished.]

SOOT-RYEN, T. 1951. Antarctic pelecypods. *Scient. Results Norw. Antarct. Exped.*, No. 32, 46 pp.

THEISEN, B. F. 1973. The growth of *Mytilus edulis* L. (Bivalvia) from Disko and Thule District, Greenland. *Ophelia*, **12**, No. 1, 59–77.

THORSEN, G. 1936. The larval development, growth and metabolism of arctic marine bottom invertebrates compared with those of other seas. *Meddr Grønland*, **100**, No. 6, 155 pp.

———. 1946. Reproduction and larval development of Danish marine bottom invertebrates. *Meddr Danm. Fisk.-og Havunders.*, Ser Plankton, **4**, 1–523.

———. 1950. Reproduction and larval ecology of marine bottom invertebrates. *Biol. Rev.*, **25**, No. 1, 1–45.

———. 1952. Zur jetzigen Lage der marinen Bodentier-Ökologie. *Verh. dt. zool. Ges.*, **34**, 279–327.

VAN OERTZEN, J. A. 1972. Cycles and rates of reproduction of six Baltic Sea bivalves of different zoogeographical origin. *Mar. Biol.*, **14**, No. 2, 143–49.

VON BERTALANFFY, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). *Hum. Biol.*, **10**, No. 2, 181–213.

WALFORD, L. A. 1946. A new graphic method of describing the growth of animals. *Biol. Bull. mar. biol. Lab. Woods Hole*, **90**, No. 2, 141–47.

WALKER, A. J. M. 1972. Introduction to the ecology of the Antarctic limpet *Patinigera polaris* (Hombron and Jacquinot) at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, No. 28, 49–69.

WALTON, C. L. 1919. Notes on the shell of *Cardium edule*. *Proc. Trans. Lpool biol. Soc.*, **34**, 134–36.

WEYMOUTH, F. W. *and* H. C. MCMILLIN. 1930. Relative growth and mortality of the Pacific razor clam (*Siliqua patula* Dixon) and their bearing on the commercial fishery. *Bull. Bur. Fish., Wash.*, **46**, 543–67.

———., ———. *and* W. H. RICH. 1931. Latitude and relative growth of the razor clam *Siliqua patula* Dixon. *J. exp. Biol.*, **8**, No. 3, 228–49.

WHITE, M. G. 1977. Ecological adaptations by Antarctic poikilotherms to the polar marine environment. (*In* LLANO, G. A., *ed. Adaptations within Antarctic ecosystems*. Houston, Texas, Gulf Publishing Co., 197–208.)

WILBUR, K. M. *and* G. OWEN. 1964. Growth. (*In* WILBUR, K. M. *and* C. M. YONGE, *ed. Physiology of Mollusca*. New York and London, Academic Press, **1**, 211–42.)

WILES, M. 1975. The glochidia of certain Unionidae (Mollusca), in Nova Scotia, and their fish hosts. *Can. J. Zool.*, **53**, No. 1, 33–41.

ZUMOFF, C. H. 1973. The reproductive cycle of *Sphaerium simile*. *Biol. Bull. mar. biol. Lab., Woods Hole*, **144**, No. 1, 212–28.