ON THE BIOLOGY OF *ANTARCTOMYSIS OHLINI* (CRUSTACEA: MYSIDACEA) AT SOUTH GEORGIA

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ABSTRACT. Aspects of the biology of *Antarctomysis ohlini* from two interconnected fjord systems at South Georgia are compared. In Moraine Fjord, an enclosed 'poll' system, growth was slower, maturity deferred (generation time egg-to-egg 5 years) and adults and larvae were generally larger. In Cumberland East Bay, which opens directly to the sea, the initial growth rate of juvenile mysids was higher, maturity achieved earlier (generation time egg-to-egg 3 years) and adults and larvae were generally smaller. Possible reasons for these differences are discussed in the context of the effect that fjord morphology may have on production levels.

INTRODUCTION

The two commonest species of mysid in the seas immediately surrounding South Georgia are from the genus *Antarctomysis*. The most widespread is *A. maxima*, which is found over the shallower (< 250 m) areas of the continental shelf where it is an important prey for a number of different fish species (Ward, 1984). In contrast *A. ohlini*, although locally abundant, appears to be restricted in distribution to the near coastal and fjord zone (Ward, unpubl.), where its role as a prey resource is less clear. Recent zooplankton collections made at South Georgia in the Cumberland Bay area as part of the BAS Offshore Biological Programme (OBP) as well as material from the Discovery collection have provided specimens of *A. ohlini*, and certain aspects of its biology have been investigated.

MATERIALS AND METHODS

Moraine Fjord, an embayment within Cumberland East Bay, is situated midway along the north-east coast of South Georgia. Cumberland East Bay shares a common entrance with Cumberland West Bay and is some 14 km long and 3–7 km wide. The maximum recorded depth is *c.* 275 m, with a sill at approximately 200 m depth occurring at the seaward end. Another sill, 2–7 m deep, separates it from Moraine Fjord, a smaller basin, some 5 km long and 200 m deep. Both areas are fed by glaciers and in summer experience considerable freshwater runoff from the land.

Samples were obtained from Cumberland East Bay during January 1982 and July and September 1983 using an RMT 1+8M net (Roe and Shale, 1979). Additional samples were obtained in March using a 3-m Agassiz trawl in 1972 and either N4-T or N7-T nets in 1926 (Discovery Collection). Samples from adjoining Moraine Fjord were obtained during October 1981 and January, February and March 1982 using a 1-m ring net of 0.35 mm mesh size. Mysids were preserved in 4% neutralized formalin made up with seawater. In the UK, total length (apex of rostrum to posterior end of telson) was measured and individuals assigned to maturity stages based on those of Mauchline (1980) (see Ward, 1984). Length–frequency histograms based on the monthly grouping of samples were compiled and the mean length of modal classes determined, overlapping classes being separated by probability paper (Cassie, 1954). Separate dry-weight determinations were made on formalin-preserved, ovigerous, female mysids and their broods. Samples were dried to constant weight in a vacuum desiccator at 60 °C. Adult female and larval ash weights were determined by ignition at 550°C in a muffle furnace of 12 pooled batches ($n = 4$ adult females) of brooding females, and between 2 and 10 pooled batches ($n = 50$–100 larvae) for each of the three larval stages recognized. Embryos were counted and measured under a stereomicroscope following removal from those brood pouches adjudged to be full.

Results

Gravimetric analysis

Statistics of the regression, fitted by the method of least squares, of $\log_{10}$ ash-free dry weight (AFDW) on $\log_{10}$ length for formalin-preserved mysids from Cumberland East Bay and Moraine Fjord are given in Table I. Analysis of variance indicated that,

Table I. *Antarctomysis ohlini*. Relationship between ash-free dry weight (AFDW) (mg) and length (mm) for formalin-preserved brooding female mysids from Moraine Fjord and Cumberland East Bay. Body ash content as % of body dry weight 14.62% ±1.948% ($n = 12$ pooled batches of 4 females each) at both locations.

	Regression of $\log_{10}$ AFDW (mg) on $\log_{10}$ length (mm)					
	Regression coefficient b	*Standard error of b*	*Intercept*	r^2	*F*	*n*
Moraine Fjord (October)	3.191	0.312	−3.409	0.68	104.62	52
Cumberland East Bay (January)	3.528	0.202	−3.918	0.94	337.84	22

Table II. *Antarctomysis ohlini*. Mean ash free dry weight (AFDW) (mg) of larval stages from Moraine Fjord and Cumberland East Bay. (n) refers to pooled batches of 50–100 larvae.

	Larval stage		
Location	*I*	*II (mid)*	*III (mid-late)*
Moraine Fjord	1.414 ±0.094 (7)	0.937 ±0.040 (2)	0.981 ±0.118 (10)
Cumberland East Bay	1.071 ±0.156 (7)	0.930 ±0.054 (5)	0.855 ±0.069 (5)

although there was no significant difference between the slopes of the regression lines ($F = 0.103$, 1, 70 d.f.), there was a significant difference between their elevations ($F = 20.090$, 1, 71 d.f.). For Moraine Fjord, the relationship between dry weight and length did not differ significantly from the anticipated cubic function (t test $P > 0.10$) but for Cumberland Bay it was significantly greater (t test $P < 0.025$). Information is presented in Table II on the mean AFDW of formalin-preserved larval stages from both sites. Larval Stages I and III from Moraine Fjord were significantly heavier than their counterparts from Cumberland East Bay (t test $P < 0.05$), whereas larval Stage II, although slightly heavier, were not.

Reproduction

The relationship between 'egg' numbers and female AFDW for both Cumberland East Bay and Moraine Fjord is illustrated in Fig. 1. ('Egg' refers to the sub-spheroid stage I embryo.) Significant relationships exist at both localities ($P < 0.001$). Least squares data are summarized in Table III. Analysis of variance showed that the slope of the two regression lines did not differ significantly ($F = 0.72$, 1, 70 d.f.) but that

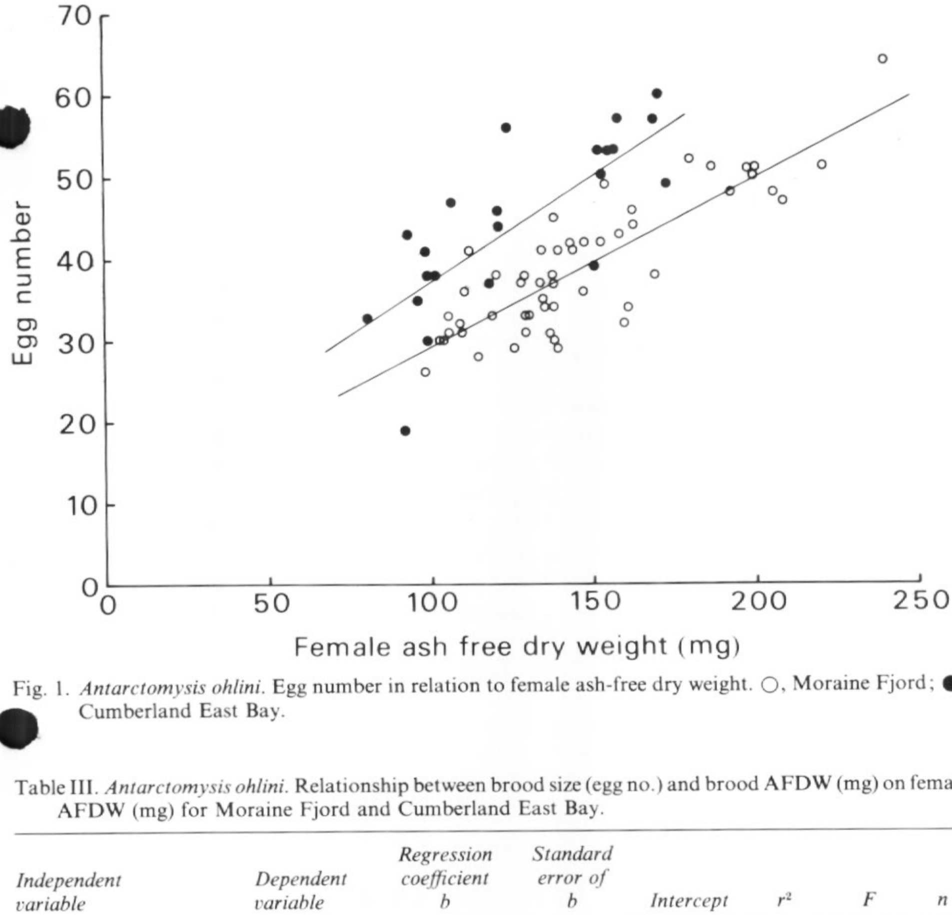

Fig. 1. *Antarctomysis ohlini*. Egg number in relation to female ash-free dry weight. ○, Moraine Fjord; ●, Cumberland East Bay.

Table III. *Antarctomysis ohlini*. Relationship between brood size (egg no.) and brood AFDW (mg) on female AFDW (mg) for Moraine Fjord and Cumberland East Bay.

Independent variable	*Dependent variable*	*Regression coefficient b*	*Standard error of b*	*Intercept*	*r^2*	*F*	*n*
Moraine Fjord							
Female AFDW	Egg no.	0.205	0.018	8.818	0.713	124.18	52
Cumberland East Bay							
Female AFDW	Egg no.	0.261	0.030	11.311	0.597	29.68	22
Data pooled from both sites							
Female AFDW	Brood AFDW	0.293	0.022	11.483	0.703	171.09	74

there was a significant difference between intercepts ($F = 53.04$, 1, 71 d.f.). Egg production for a female of given mass is greater in Cumberland East Bay than in Moraine Fjord. A comparison of the relationship of brood AFDW on female AFDW, however, indicated that by virtue of a larger 'egg', brood production by females from Moraine Fjord is equivalent to that of those in Cumberland East Bay. Least squares data are summarized in Table III.

Population structure

Population histograms compiled from data pooled on a monthly basis for both sites are presented in Fig. 2. Data for Moraine Fjord span the summer months of 1981/82 whereas data for Cumberland East Bay are drawn from a number of years, although the July and September samples were taken during winter 1983. Samples from both sites had a characteristic pattern of clearly defined modal classes. Evidence that these may be interpreted as year classes can be seen by reference to data on the occurrence of brooding females in the samples taken (Table IV). Females brooding Stage I ('eggs') embryos during spring and early summer were present at both sites. In Cumberland East Bay, July samples contained females that were carrying Stage II larvae exclusively and in September a greater proportion of the 69 females examined were carrying Stage III larvae. The implication is that 'eggs' are laid in summer, larval development takes place in the brood pouch over winter and young are released during spring. In Moraine Fjord the situation appears more complex, since females brooding larvae of all stages were present during the spring and summer months. A greater proportion of females, however, were carrying 'eggs' during October and January, whereas in February there was an increase in the proportion of females carrying Stage II larvae. Mature Stage III larvae on the point of parental release were present in October. Given the slow growth rates prevailing in Moraine Fjord (Table V) and the presence in February and March (Fig. 2) of a juvenile cohort according with a spring release of young, it is extremely likely that here too only one generation per year is produced. Despite the persistence into the summer months of females brooding Stage II larvae, the presence of discrete cohorts indicates that the production and release of young is fairly well, but not completely, synchronized. There may, however, be differences in the period of larval incubation between the two sites, young being brooded for up to one year in Moraine Fjord and for perhaps somewhat less in Cumberland East Bay, although data for spring at the latter site are lacking.

Moraine Fjord samples from October and February are sufficiently large and the year classes sufficiently pronounced to allow estimates of growth to be made over the $3\frac{1}{2}$-month period (Table V). Growth of about 1.00–1.50 mm per month is apparent for juvenile and immature classes I–III but is somewhat less, approximately 0.50 mm per month, for Class IV. This latter estimate is made largely for mature or maturing males and females, which are probably using energy to synthesize reproductive material, and is in any case biased by the presence of brooding females, which do not moult. The mean growth rate during the year for classes I–III is 1.00 mm per month. Sexual differentiation of juvenile *A. ohlini* appears to take 1–2 yr in Moraine Fjord with the attainment of sexual maturity taking a further 2 yr. Exceptionally, sexual maturity appears to be possible as early as Class III (one female of 40 mm was found brooding young in October) but for the majority of both males and females it was confined to Class IV. Sexual maturation in the majority of females takes place some time between March and October. The build-up of ovigerous material may take place over winter but it is likely that it accelerates during the later stages and final maturation takes place in early spring. Males may mature in advance of females during the

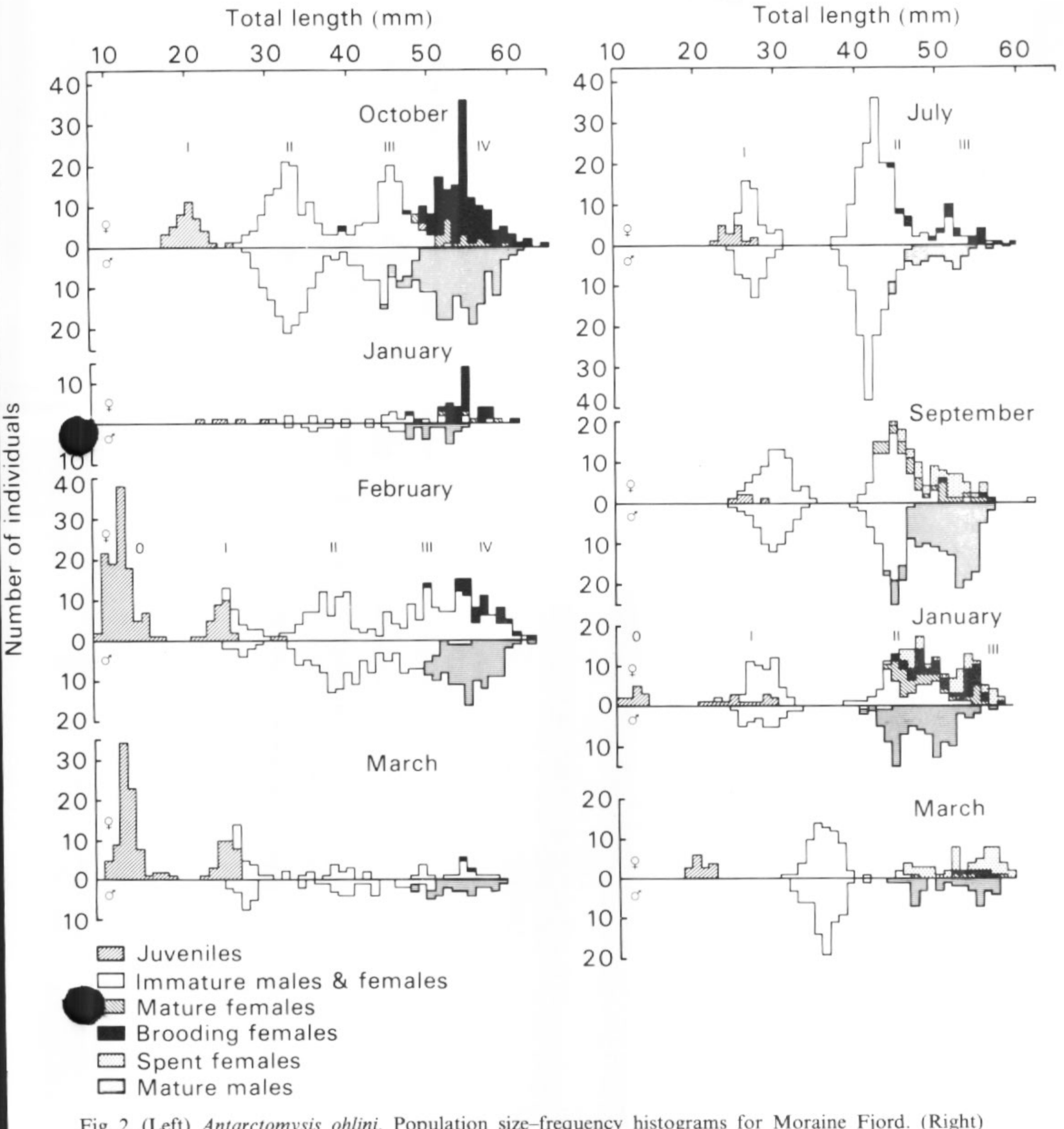

Fig. 2. (Left) *Antarctomysis ohlini*. Population size–frequency histograms for Moraine Fjord. (Right) *Antarctomysis ohlini*. Population size–frequency histograms for Cumberland East Bay.

preceding summer period but data are limited. Thus the generation time egg-to-egg for *A. ohlini* from Moraine Fjord is about 5 yr.

Size–frequency analysis does not clearly indicate whether females are able to breed for a second time (Fig. 3). Only one size class of females is clearly indicated, although with smaller growth increments anticipated in older females it is unlikely that the size class of females breeding for a second time will be distinguishable by this method.

In Cumberland East Bay only three size classes (I–III) are apparent during July and

Table IV. *Antarctomysis ohlini*. Comparison of the larval stage of broods retrieved from females on a monthly basis for Moraine Fjord and Cumberland East Bay.

Location	*Month of capture*	*Larval stages of broods examined (%)* I	II	III	*Total no. of brooding females examined*
Moraine Fjord	October	73	3	24	116
	January	52	32	16	31
	February	47	47	6	30
	March	0	100	0	2
Cumberland East Bay	January	97	3	0	32
	March	0	100	0	8
	July	0	100	0	45
	September	1	35	64	69

Table V. *Antarctomysis ohlini*. Monthly mean size (mm) $\pm$ SD of modal classes at Moraine Fjord and Cumberland East Bay.

	Juvenile 0	*Juvenile I*		*II°*	*II°*	*III°*	*III°*	*IV°*	*IV°*
Moraine Fjord	—	20.77		33.26	33.34	45.70	44.80	54.20	53.80
October	—	$\pm$1.49		$\pm$2.74	$\pm$2.43	$\pm$2.70	$\pm$2.50	$\pm$3.55	$\pm$2.90
	—	(39)		(119)	(124)	(106)	(71)	(130)	(146)
February	11.92	25.61		37.58	38.80	49.00	48.40	56.00	55.30
	$\pm$1.53	$\pm$1.89		$\pm$2.76	$\pm$2.85	$\pm$3.20	$\pm$2.45	$\pm$2.70	$\pm$2.60
	(113)	(59)		(76)	(87)	(60)	(51)	(73)	(87)
Cumberland East Bay		I°	I°						
July	—	27.27	27.80	43.05	42.45	52.80	51.03		
	—	$\pm$1.86	$\pm$1.35	$\pm$1.98	$\pm$1.81	$\pm$2.72	$\pm$2.56		
	—	(59)	(41)	(151)	(135)	(35)	(32)		
September	—	30.14	29.93	44.80	45.20	52.10	52.80		
	—	$\pm$2.18	$\pm$1.94	$\pm$1.80	$\pm$2.20	$\pm$2.50	$\pm$1.50		
	—	(70)	(56)	(100)	(116)	(47)	(95)		
January	12.75	28.05	28.57	46.60	44.30	54.10	50.30		
	$\pm$1.05	$\pm$2.38	$\pm$2.08	$\pm$2.85	$\pm$1.65	$\pm$1.70	$\pm$2.30		
	(12)	(60)	(28)	(112)	(42)	(48)	(55)		
March	20.50	35.79	35.72						
	$\pm$1.09	$\pm$1.82	$\pm$1.77						
	(16)	(67)	(70)						

September. The first, arising from the previous year's release of larvae, has largely differentiated into males and females. The second, whilst largely immature in July (although including a few brooding females and mature males), has started to mature by September, and by January comprises mature males and females and includes a number of females brooding Stage I embryos. Class III in July consists of mature males and females brooding Stage II larvae (Table IV) as well as a number of immature females. By September the majority of brooding females were carrying Stage III larvae and a number of spent females were also present. This category may arise either by females having recently liberated young or by having lost them at the time of capture (Mauchline, 1980). In January and March a small juvenile cohort is present which, as in the Moraine Fjord samples, accords with a spring release of young. Growth estimates for *A. ohlini* in Cumberland East Bay between July and September (Table V) vary from 0.88 to 1.38 mm per month for classes I and II and over the year vary

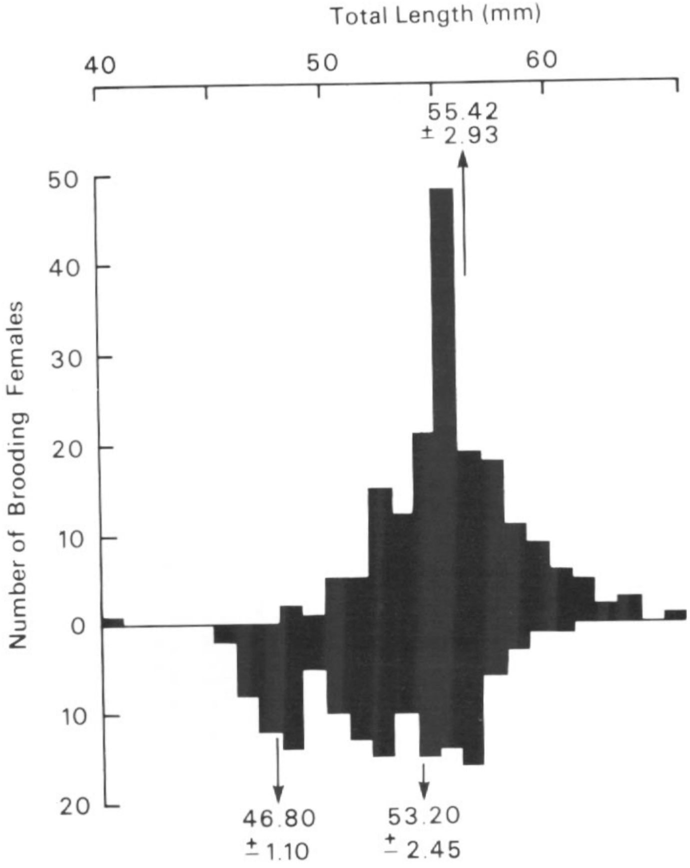

Fig. 3. *Antarctomysis ohlini*. Size–frequency distribution and mean size ± SD for modal classes of brooding females from Moraine Fjord (upper histogram) and Cumberland East Bay (lower histogram). Data pooled to include females brooding larval stages I–III.

between 1.22 and 1.55 mm per month – somewhat higher than the rates in Moraine Fjord. Sexual maturation of males (Class II) proceeds during the summer months (September–January) and it is possible that this is also the case for females, although we lack data between September and January. The generation time egg-to-egg for *A. ohlini* from Cumberland East Bay is 3 yr. The presence in January of two year-classes of females carrying Stage I larvae suggests that rematuration can occur and that there *A. ohlini* may breed twice (see also Fig. 3).

A proportion of the females may, however, defer maturity for a year, as witnessed by the presence in July of a proportion of immature females in year class III.

Discussion

Previous investigations in the South Georgia area provide little information on the biology of this species. Tattersall (1955) records *A. ohlini* from nine stations worked by Discovery Investigations around South Georgia, eight of which were worked in, or close to Cumberland Bay in water up to 275 m deep. The one exception to this was Station WS 32 at the mouth of Drygalski Fjord. At all stations it was taken in company with *A. maxima*. Tattersall (1923) noted that its distribution extended as far south as the Ross Sea and that there was an increase in adult size (up to 70 mm in the Ross Sea) with increasing latitude.

In this investigation pronounced differences occur in many of the biological characteristics of *A. ohlini* investigated at the two sites. Females taken from Cumberland East Bay in January were proportionately heavier than those taken from Moraine Fjord during October. This is interpreted as a real difference and not an artifact of preservation. Although it is anticipated that formalin preservation will lead to loss in both weight and volume (Steedman, 1976) the time elapsed between preservation and processing (*c.* 1 year) is comparable, and rapid weight losses associated with the early stages of preservation can be disregarded. By January females in Cumberland East Bay may benefit from higher summer production levels that allow them to increase stored reserves, whereas in Moraine Fjord during October, female reserves may be relatively depleted following winter and subsequent spawning in early spring.

The faster growth rate exhibited by *A. ohlini* in Cumberland East Bay is especially pronounced during the first year as a free-swimming mysid. Assuming that larval release takes place during September/October at both sites and that the length of newly released and newly moulted young exceeds by no more than 25% the length of Stage III larvae contained in the marsupium (Mauchline, 1980) (a figure equivalent to approximately 10 mm) then growth (in length) during the first year in Cumberland East Bay is approximately twice that of mysids from Moraine Fjord (Table V). After this initial year growth rates are more comparable, averaging 1.00 to 1.50 mm/month over the year up to the time that individuals start to mature and breed, although it is likely that, at both sites, growth is seasonal and will accelerate during the summer months. Thus juveniles in Cumberland East Bay clearly gain an initial trophic advantage that allows them to mature and reproduce earlier. The extent to which *A. ohlini* is directly dependent on elevated summer production levels is, however, unclear. Gut content analysis indicates that they are omnivorous feeders (Ward, unpubl.), but the release of young coinciding with increased primary production indicates that juveniles may be initially phytophagous.

In terms of reproduction, egg production is greater in Cumberland East Bay (Fig. 1), although the 'egg' and subsequent larval stages are generally larger in Moraine Fjord (Table II). Brood production in terms of AFDW relative to female AFDW is the same at both sites, being described by a common regression equation (Table III), although in overall terms the reproductive effort may well be higher in Cumberland East Bay where females are clearly iteroparous.

These differences between the two sites, *A. ohlini* in Moraine Fjord exhibiting relatively slower growth (at least initially), deferred maturity and larger adult and offspring size, are summarized in Table VI. They mirror to some extent differences noted for other Antarctic marine invertebrates, where comparisons have been made between animals from study areas that are latitudinally considerable distances apart. Thus, *A. maxima* for example at the South Orkney Islands (60° 35′ S, 45° 30′ W) has been shown to grow more slowly, take longer to reach maturity and to produce larger but fewer eggs than at South Georgia (54° 15′ S, 36° 45′ W) (Ward, 1984). Makarov (1970, 1973) has also demonstrated similar differences for the burrowing crangonid shrimp *Notocrangon antarcticus* from the same two localities. The reasons for such differences are not altogether clear but are likely to be related to the marked effects that increasing latitude has on environmental temperature, and more importantly on the seasonality of food supply. Whether the timing and levels of production differ

Table VI. *Antarctomysis ohlini*. A summary of the main differences found in the life cycle between Moraine Fjord and Cumberland East Bay.

	Moraine Fjord	*Cumberland East Bay*
Juvenile growth	Slow Animal 20 mm in length approximately one year after liberation	Fast Animal 30 mm in length approximately one year after liberation
Sexual differentiation	1–2 years following liberation	9 months to 1 year following liberation
Generation time (egg–egg)	5 years	3 years
Iteroparous	?	Yes
Mean size (mm) of brooding females	55.42 ± 2.93	46.10 ± 1.10 53.20 ± 2.45
Mean brood size	38.11	35.93 50.00
Mean AFDW (mg), stage I larvae	1.414 ± 0.094	1.071 ± 0.156

markedly between Cumberland East Bay and Moraine Fjord is unknown; however, fjord systems are known to be complex, and Matthews and Heimdal (1980) consider that their physical characteristics may have a marked influence on production levels. Matthews and Heimdal distinguish between fjords *sensu stricto*, where sills occur at 100 m depth or more, and smaller more enclosed systems known as 'polls', where a shallow sill may be at only a few metres depth. In the former, to which Cumberland East Bay may be compared, upwelling areas, generally considered to provide good conditions of nutrient supply and vertical water movement, are often present and production is often high. In the 'poll' systems, to which Moraine Fjord corresponds morphologically, the opportunities for water exchange are limited and production is generally lower. Evidence to support this hypothesis from the two sites is inconclusive. Hart (1934), in a summer survey of Cumberland East Bay, found low levels of phytoplankton (cell counts) compared with open ocean values throughout his study period. He attributed this to local instability brought about by wind-driven mass movement of water and to the presence of inorganic particulate material, derived from land runoff, inhibiting photosynthesis. In contrast, higher integrated chlorophyll *a* values were found during September 1983 at the seaward end of Cumberland East Bay (up to 80 mg m^{-2}) than were found at an offshore station (53° 17′ 40 S, 35° 31′ 50 W) worked on 20 August (35 mg m^{-2}) and on 3 October 1983 (33 mg m^{-2}) (Priddle, pers. comm.). Further, Hart (1934) implied that the relatively stable waters of Moraine Fjord could allow the development of a richer phytoplankton, although cell counts on the only occasion he sampled it still compared unfavourably with open ocean values and were no higher than the maximum values recorded from Cumberland East Bay. Pearson (1980), on the other hand, indicates that the presence of brackish ice-melt water at the surface of enclosed basins (a normal summer phenomenon in Moraine Fjord) often leads to the creation of stable density gradients that inhibit the vertical circulation of nutrients and result in lower rates of primary production. Thus no clear pattern concerning production levels emerges. Other biotic and abiotic factors may also be implicated as causes for the observed differences between the two sites and further comparative data are needed.The fjord and 'poll' systems of South Georgia and their relationship to the open ocean are poorly understood at present but it is clear that it is unwise to characterize growth rates and other biological processes, occurring at specific sites, as being typical of a general area.

Both *A. ohlini* and *A. maxima* exhibit many of the lifecycle features commonly seen as responses to cold, highly seasonal environments. These include slow and seasonal growth rates, longevity, seasonal breeding and an extended brooding period. They may differ, however, in some aspects of their local distribution. Although often taken in association with *A. maxima* from inshore waters around South Georgia, OBP investigations have so far failed to locate *A. ohlini* in surrounding shelf waters. Thus, although there is some overlap in general distribution, the two species may be segregated to some extent. This may account for the apparent lack of importance of *A. ohlini* in studies of the diet of Antarctic fish species. Although many of these studies fail consistently to discriminate between mysid species, some identify *A. maxima* as forming the larger part of the 'mysid' grouping (Targett, 1981; Kock, 1981). Many of these investigations have, however, either been carried out over coastal continental shelf areas (e.g. Targett, 1981; Permitin and Tarverdiyeva, 1972) or in nearshore sites (Burchett and others, 1983) and have not extensively sampled the deeper fjord areas that appear to be favoured by *A. ohlini*. Thus it may be that, in these areas, *A. ohlini* will form a significant part of the diet of fish species that inhabit the fjord ecosystem for all or part of the year.

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