BREEDING AND BIONOMICS OF *IDOTEA BALTICA* (PALLAS) (CRUSTACEA: ISOPODA)

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Breeding and bionomics of the valviferous isopod *Idotea baltica* were examined in 1977. This species is intertidal, an inhabitant of *Ascophyllum nodosum* and resides in this seaweed most of the year, but moves offshore to overwinter in deeper water. Adults breed only once, with peak reproductive activity between June and August. Embryonic development takes about 1.5 mo., with fecundity not strongly correlated with female body length. Extensive seasonal variations in abundance and biomass occurred which were in part related to the reproductive cycle.

Introduction

Idotea baltica (Pallas) is a member of a widely distributed genus of benthic littoral and sublittoral isopods commonly occurring on macroscopic algae, floating debris, and under rubble (Naylor 1955a, 1972). Published accounts of its ecology (Sywula 1964b), morphology and taxonomy (Naylor 1955b, Sywula 1964a), feeding (Naylor 1955c, Lukasheva 1971), and fecundity (Romanova 1974) have dealt only with populations of European coastlines, including the Baltic. Very little is apparently known about the ecology of this species in North America.

I. baltica is found intermittently in intertidal regions of the Bay of Fundy and Minas Basin, N.S., assoiiated with the alga *Ascophyllum nodosum* (L.) Le Jol., and when present usually represents a major portion of the algal epifaunal community. As a preliminary to the evaluation of an energy budget, the basic life cycle pattern had to be investigated, and collections were obtained to provide such information. This report summarizes observations on breeding and bionomics of *I. baltica* from Cape Blomidon, Minas Basin.

Materials and Methods

The intertidal population of *I. baltica* near Cape Blomidon, Minas Basin (45° 12'N, 64°20'W) was sampled from April to December of 1977 by gathering 10 to 15 kg of *A. nodosum* from the study area in plastic buckets, returning this to the laboratory, and removing the isopods by hand. A similar technique has been shown to be effective in monitoring population densities of *I. montereyensis* (Lee 1966). In addition, about 40 individuals of *I. baltica* were also collected when possible by hand picking to ensure sufficient data for fecundity measurements.

Isopods were both killed and stored at -15°C. Subsequently these animals were thawed, and length from cephalon to telson was measured to the nearest 0.1 mm with calipers. Specimens larger than 8 mm were sexed (penial papillae and rudiments of the *appendix masculinus* are discernible at this length in males), breeding condition of the female recorded, and any embryos in the brood pouch were removed, counted, and stage of embryonic development determined (see Results, for criteria). Each animal was then dried to constant weight in a vacuum oven at 70 ± 2°C and weighed to the nearest 0.01 mg on a Cahn electrobalance.

A number of embryos from different broods was measured (greatest linear dimension taken as length) with a stereomicroscope equipped with an eyepiece micrometer.

Results

Microhabit

Extensive collecting over 2 years (1976 - 1977) at Cape Blomidon indicates that *I. baltica* is associated with only one alga of the intertidal zone, *A. nodosum.* It was never found under stones and only occasionally collected from small tidal pools devoid of macroscopic seaweeds. Males were generally found in the outermost parts of an *A. nodosum* clump, whereas females, especially those with broods, tended to occupy the branches nearest the holdfast.

Not all shorelines with *A. nodosum* supported populations of *I. baltica.* Extensive sampling of selected intertidal habitats along the southern coast of the Bay of Fundy revealed only occasional specimens. The one exception was Black Rock (45°10'N, 64°48'W) where a large population inhabited *A. nodosum* on the sheltered side of a massive basalt outcrop, although it did not occur in extensive *A. nodosum* mats along the unprotected areas of the same shoreline. Thus, *I. baltica* apparently prefers intertidal habitats not exposed to wave action.

I. baltica does not inhabit the intertidal zone in winter, presumably moving offshore at low water temperature (Fig 7).

Another idoteid, *I. phosphorea* Harger was often found amongst *A. nodosum,* but never as abundantly as *I. baltica.*

Breeding Cycle

The breeding behavior of *I. baltica* was discovered to be similar to that of other species of *Idotea.* Females are held *in copula* beneath the males for 2 to 3 days prior to sperm transfer. Partial molting of the female is accompanied by fertilization; ova are thereafter extruded into the brood pouch which forms upon completion of molting. The embryo passes through 4 developmental stages, the fourth of which represents the first free living instar. These stages are separable by the following criteria:

STAGE I   Embryo spherical, yellowish, yolk centrally placed, surrounded by 2 embryonic membranes.

STAGE II   Embryo curvilinear, yolk central, segmentation complete, surrounded by 1 embryonic membrane.

STAGE III   Embryos of similar morphology to adult, abundant yolk in gut, no setae on pereiopods, not surrounded by an embryonic membrane.

STAGE IV   Synonymous with first free-living instar, no yolk in gut, setae on all appendages.

Embryos at a given developmental stage were of relatively constant length. Recently transformed Stage II embryos were smaller than their older counterparts, possibly being a function of water uptake. The mean length of each stage is included in Table 1.

I have expressed the breeding cycle in terms of degree of sexual maturity of the females and stage of embryonic development of the brood. This was necessary as very few newly released juveniles were collected by the sampling procedure I employed. Females were considered reproductively dormant if neither oöstegite

Table I. Mean length of embryonic stages of *I. baltica*

stage	mean length $(\mu m) \pm 1$ s.d.	number of measurements
I	488 ± 37	20
early II	$838 \pm 39†$	20
late II	$1133 \pm 55†$	74
III	1731 ± 68	50
IV	1944 ± 73	21

† significantly different ($t = 27.44$, 92 d.f., p. $<$ 0.001)

buds (flap-like precursors of the oöstegites) were present. Females with oöstegite buds only were considered immature, and those which had molted to acquire oöstegites (forming complete brood pouch) were therefore mature and further subdivided on the basis of stage of development of the embryos. Several females had incompletely developed brood pouches (usually only the fifth pair of oöstegite developed, the others remaining as oöstegite buds). These females have been omitted from further discussion.

The seasonal occurrence of these stages is shown in Figure 1. Females with Stage IV embryos have not been included because this stage is synonymous with the first free-living instar. Only reproductively dormant females were present in late April, but by mid-June most females brooded Stage I embryos. A period of reproductive dormancy directly followed breeding, and the last collection in November comprised many females with oöstegite buds. This suggests a winter period of reproductive activity, although it cannot be supported empirically. From Figure 1 the period of embryonic development (Stages I - III) can be estimated to be 1.5 months.

Fecundity

The correlation between the number of embryos in each brood and female body length (Fig 2) apparently could be equally well described exponentially (Daborn 1977), linearly (Jones & Naylor 1971), or logarithmically (Sheader 1977). The linear relationship, which has the highest corresponding coefficient of correlation (Table II), was accordingly chosen although it accounts for only 32.2% of the variation (P $<$ 0.01) (Fig 2, inset). The linear regression equation relating fecundity (E) to body length (L) is

$$E = 12.4 L - 35.1$$

Again, because Stage IV embryos are potentially capable of leaving the brood pouch (and hence subject to underestimation), they have been omitted. No reduction in brood size with advancing development (Stages I - III) is evident from Figure 2, suggesting little or no embryonic mortality or premature extrusion.

Sex Ratio

The sex ratio was seldom equal to unity, varying both as a function of body length and season. The seasonal sex ratio was bimodal, an early predominance of males in spring later replaced by a summer predominance of females (Fig 3). This argues for an earlier spring migration by males back to the intertidal zone, as well as death of adults of both sexes after their respective roles in the breeding cycle have been completed. On a length basis (Fig 4), females dominated the smaller length classes ($<$ 18 mm) whereas males were more abundant at lengths $>$ 18 mm.

Seasonal Changes in Abundance and Biomass

Because *I. baltica* has a relatively clumped distribution, monitoring abundance
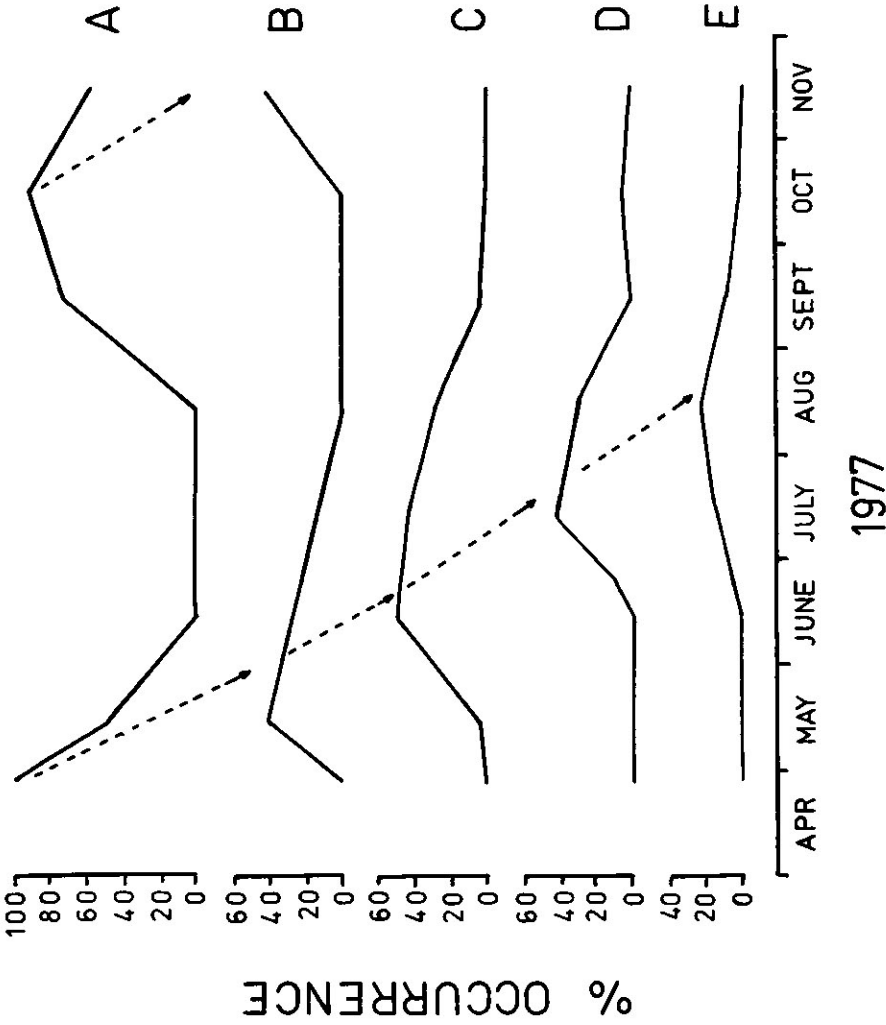
Fig 1.   Seasonal occurrence of major divisions of the breeding cycle of *I. baltica*:
A - reproductively dormant females; B - immature females; C - Stage I em-
bryos; D - Stage II embryos; E - Stage III embryos (For further explanation
of terms see text)

Table II. Correlation Coefficients (r) for different equations relating fecundity to female body length (n = 119)

type of relationship	r	% variation accounted for by relationship
logarithmic	0.564	31.8
exponential	0.555	30.8
linear	0.567	32.2
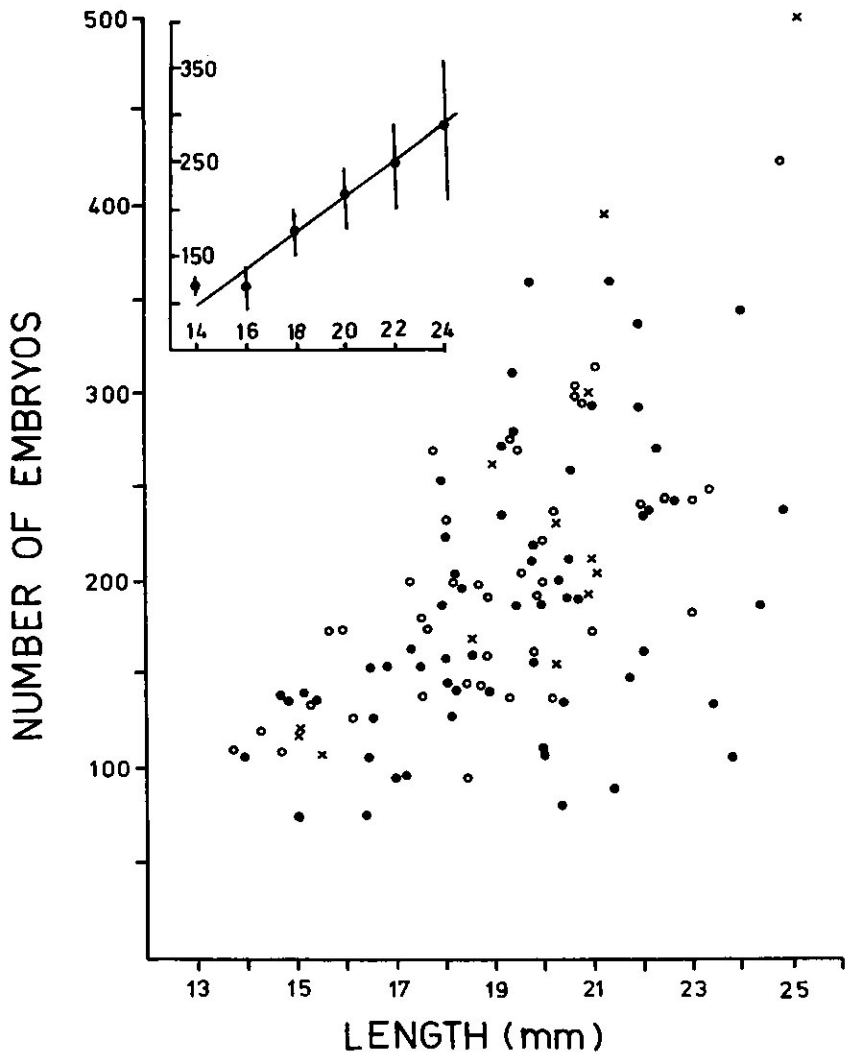
Fig. 2.   *Number of embryos per female I. baltica* as a function of body length ●- Stage I; 0 - Stage II; X - Stage III; inset - mean (± 1 s.d.) number of embryos in 2 mm increment size classes (all stages of development).

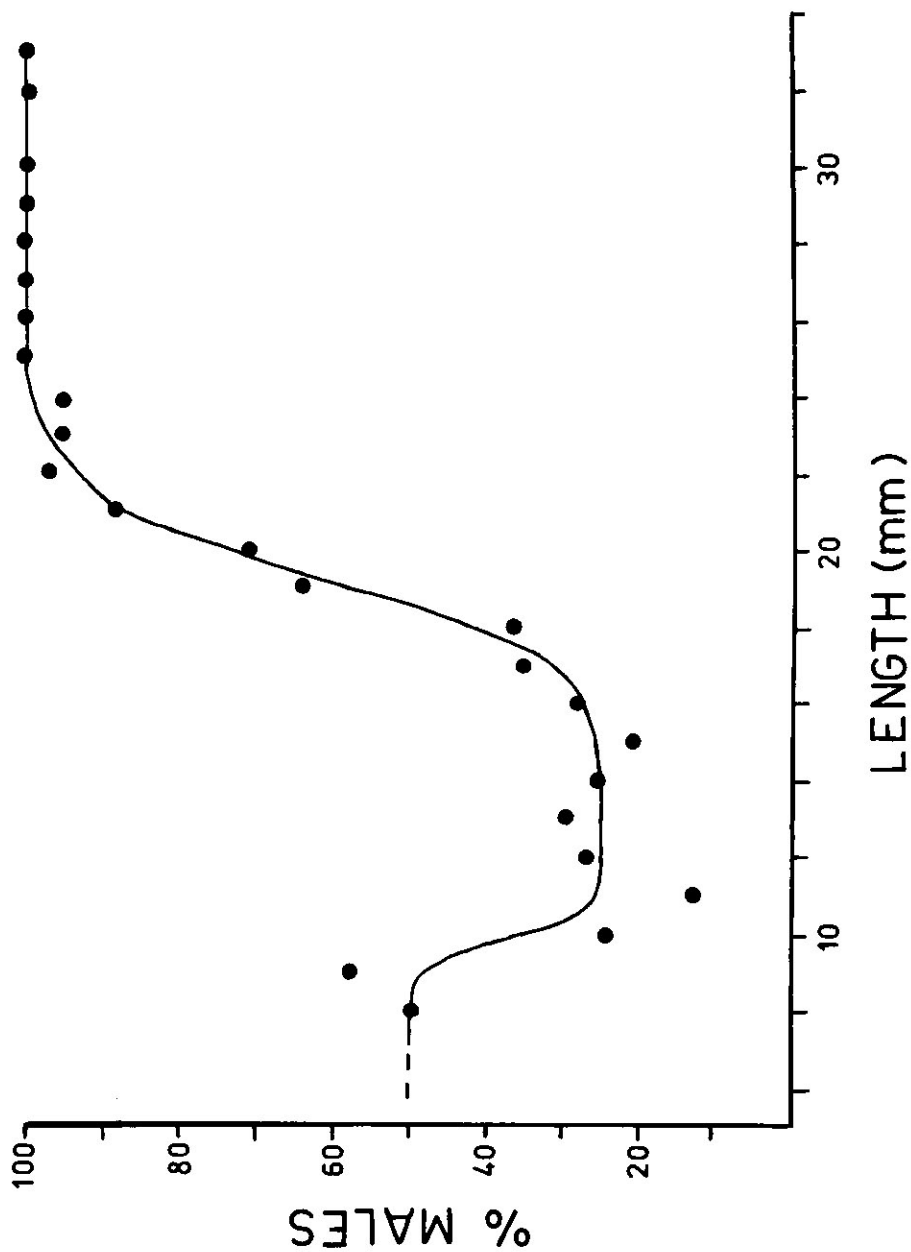Fig. 3.   Percent male *I. baltica* on each sampling date (all size ranges included).
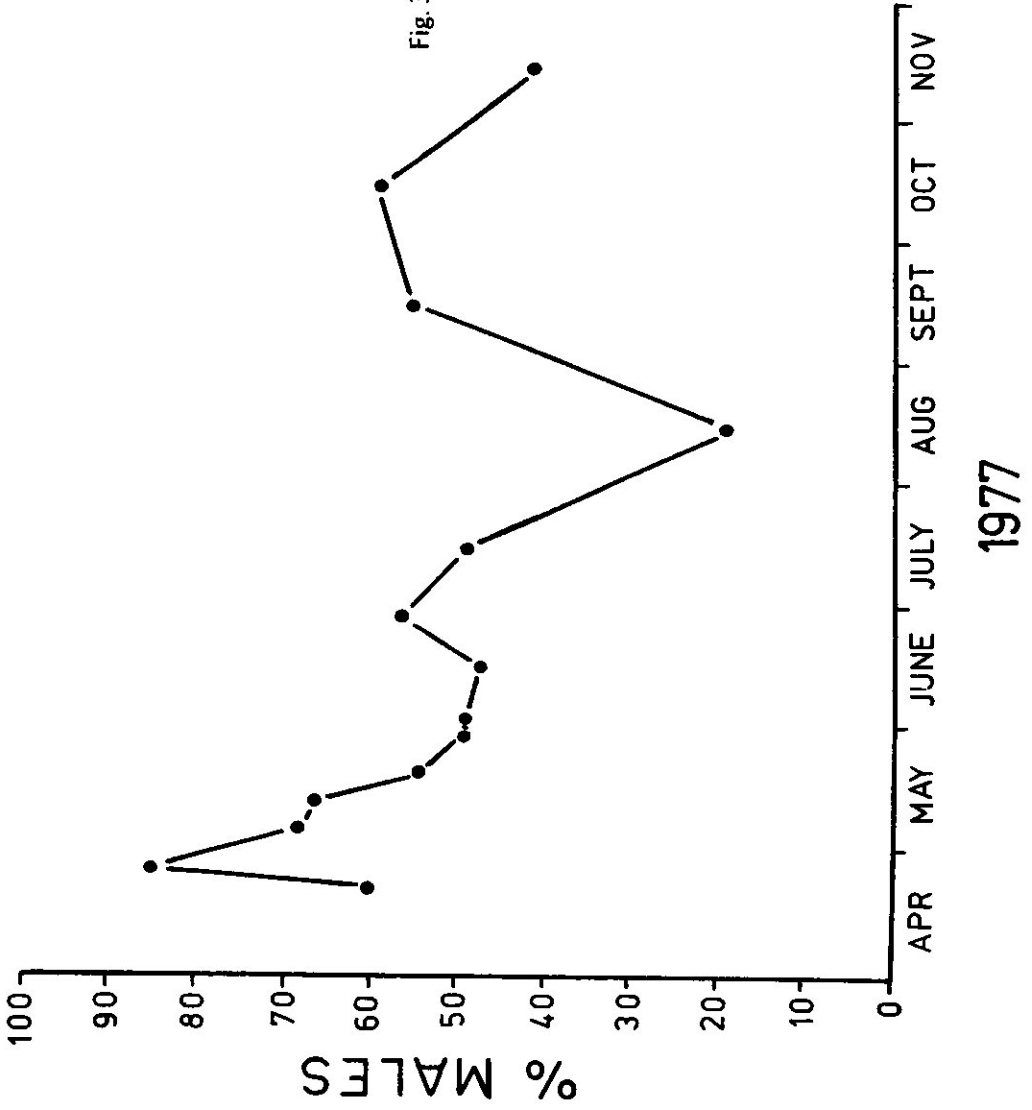
Fig 4.   Percent male *I. baltica* in successive 1 mm increment size classes (all collecting dates included).

and biomass by hand collecting for a standard length of time (e.g. Jones & Naylor 1971; Naylor & Haahtela 1966; Jones 1974) was unsuitable. Instead, A. nodosum was collected from a broad area, pooled, and the average number and biomass of I. baltica calculated for 10 kg seaweed. This was not only the most reliable way to calculate these parameters, but also provided animals of a size distribution corresponding to those in the field.

The number of animals (per 10 kg A. nodosum) dropped steadily from 42 to < 10 between mid May and mid August (Fig 5). Thereafter, as a result of recruitment, abundance increased considerably to > 90 in mid November.

Biomass (mg-dry weight per 10 kg A. nodosum) also decreased steadily from mid May to mid June. An increase in late June was evident because of the presence of mostly large adults in the population. Thereafter, trends in biomass essentially followed those of abundance.

Population Size Structure

Because the number of isopods collected (Fig 5) was too few to divide the sample adequately into small increment size classes, the mean ($\pm$ 1 s.d.) male and female length on each date was determined instead (Fig 6). A good deal of variability exists, bu he mean lengths follow a trend that can be correlated with the breeding cycle. Mean male length decreased during May (t=1.765, 22 d.f., p < 0.05), presumably resulting from death of large overwintering males. A sharp decrease in both mean length and variability occurred from June to September (t=11.363, 21 d.f., p< 0.001) as large post-reproductive males disappeared. Thereafter mean male length increased slightly (t=5.098, 56 d.f., p < 0.001). Mean female length was relatively constant most of the year (p > 0.05), but a decrease during August and September occurred (t=3.074, 32 d.f., p < 0.005) as a result of disappearance of larger post-reproductive females. On the basis of these observations and those concerning abundance and biomass, it is probable that individual I. baltica breed only once.

Discussion

Naylor (1955a) reports that I. baltica is chiefly a sublittoral species, occurring amongst attached and decaying algae, and suggests that wave action may be the limiting factor in the general inability of the sublittoral species of Idotea to colonize intertidal habitats. At Cape Blomidon, wave action is usually negligible, enabling I. baltica to colonize the intertidal seaweed A. nodosum. It is not known why this isopod is associated only with this particular alga. At Cape Blomidon other macroscopic seaweeds include Fucus edentatus Pyl., Chondrus crispus Stackh., Gigartina stellata (Stackh.) Batt. and Laminaria longicruris Pyl. The last three species may not provide a sufficiently humid atmosphere when uncovered at low tide, or perhaps do not support the proper epiphytic flora upon which I. baltica may feed. However, Fucus can almost certainly provide a humid microhabitat, but has been shown to produce phenolic compounds inimical to other organisms (e.g. Sieburth 1969). The color polymorphism of this species has been well documented (Matzdorff 1883; Pieron 1913; 1914; Peabody 1939; Suneson 1947), and it suffices here to mention that I. baltica at Cape Blomidon are mainly green (never red) and appear extremely well color matched to A. nodosum. Whether this is a cause or an effect is not known at this time.

One problem encountered during this study was difficulty in collecting juveniles (< 8 mm). Breeding presumably occurred, as females with advanced (Stage III-IV) embryos in their brood pouches were common. This indicates that adult and juvenile I. baltica do not occupy the same microhabitat. Sywula (1964b) demonstrated that juveniles display a strong positive phototaxis during the first 24 hr. following release from the brood pouch, causing them to swim at or near the surface. As a result, they might be deposited on the mud surface as the tide ebbs,
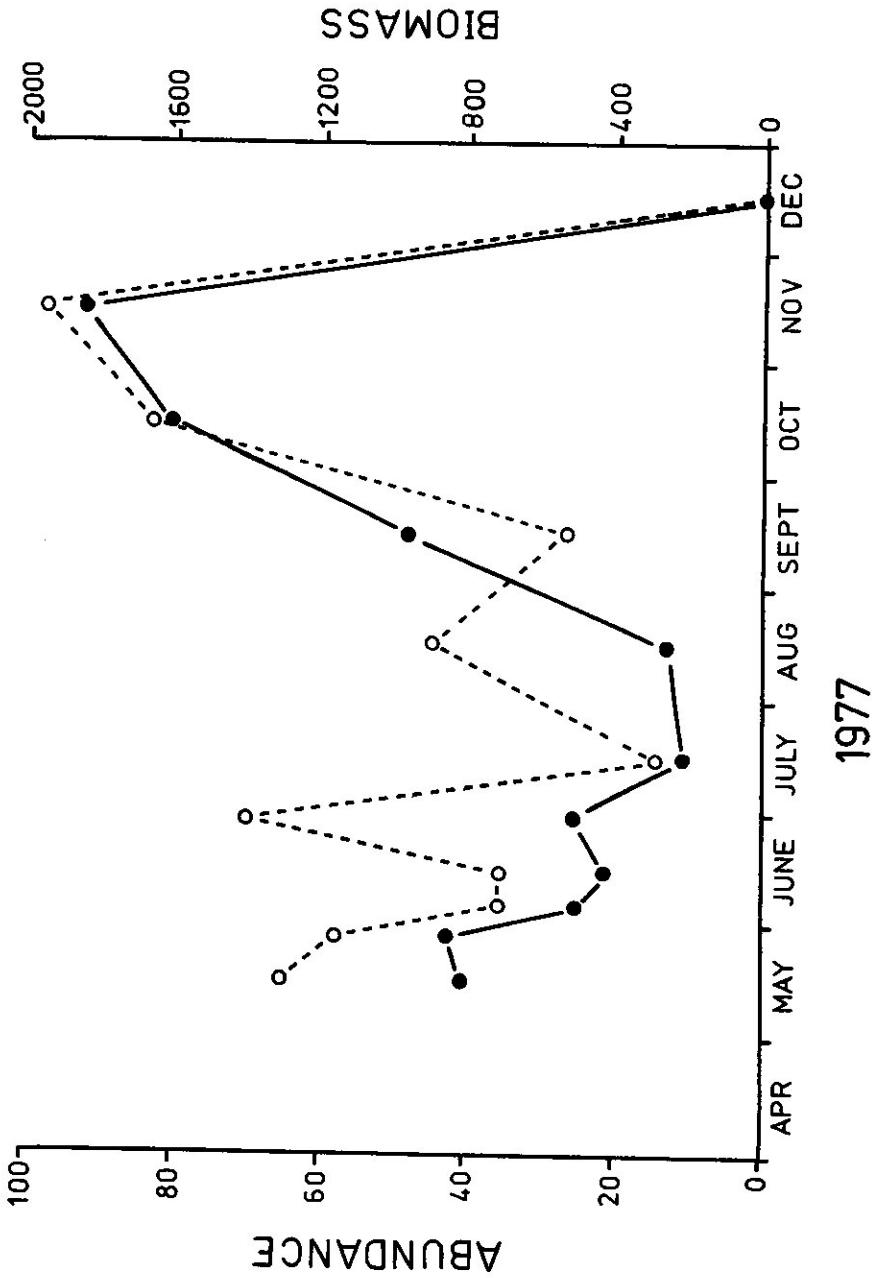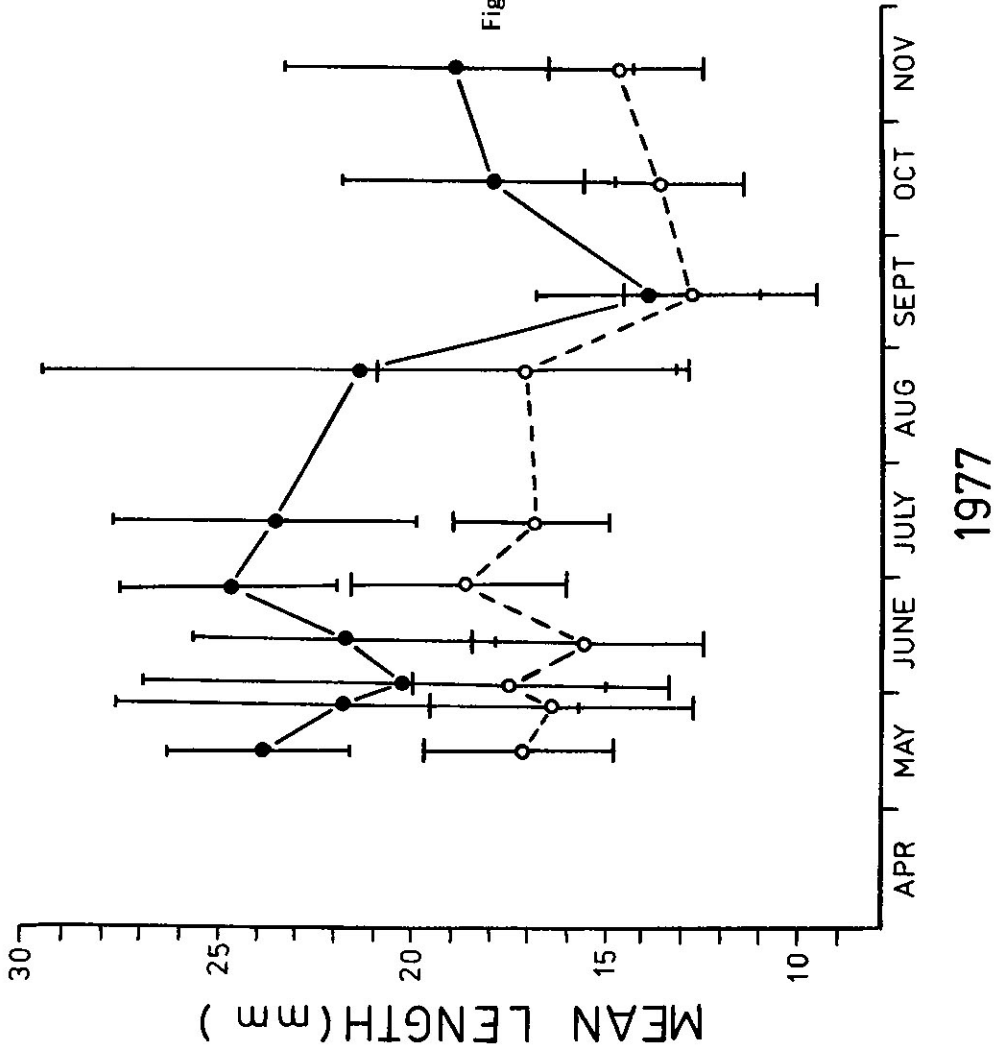
Fig. 5. Abundance (●—●-as number of animals per 10 kg of *A. nodosum*) and biomass (0—0-as mg-dry wt per 10 kg of *A. nodosum*) of *I. baltica* on each collecting date.

Fig 6. Mean length (± 1 s.d.) of male (°) and female (°) *I. baltica* on each collecting date.

particularly where the tidal amplitude is large (16 m in the Minas Basin (Bousfield & Leim 1959)). Here the juveniles could remain, feeding upon epipelic diatoms and detritus, until they are large enough to grasp the thalli of *A. nodosum*. This, if true, would allow the young to utilize a resource not available to the larger adults. It is certain that the intertidal mud flats support a flora and fauna sufficient to maintain young *I. baltica*, as other deposit feeders including *Chiridotea caeca* (Say), *Corophium volutator* (Pallas) and numerous polychaetes are abundant in the area.

The estimated period of embryonic development (1.5 mo) is slightly longer than that reported for some other members of the genus (Kjennerud 1950; Sheader 1977). Water temperature, which likely influences the duration of embryonic development (Steele & Steele 1973), was lowest during Stage I of embryonic growth (Fig 7) and might explain its extended peak of occurrence (cf Fig 1).

Fecundity was only weakly correlated with female body length, reflecting a good deal of inherent variability not uncommon among crustaceans (Daborn 1976, 1977; Hopkins 1977). This variability, which increased as body length increased, indicates that the trade-off between growth and reproduction is not constant for each member of a given population. Sheader (1977) discovered that infestation by a cryptoniscid parasite resulted in lowered numbers of Stage I embryos, particularly in larger females, but no brood pouch parasites were observed in this study.

As is general for isopods, all the embryos in a single brood were at the same stage of development. No reduction in brood size between Stage I-III was apparent, presumably because the brood pouch enlarges sufficiently in volume to permit the increase in size of the embryos. An exceptional species, *I. viridis*, broods embryos at different stages of development and undergoes brood reduction often exceeding 75% (Howes 1939).

Apparently no generalizations can be made concerning the number of broods produced by female species of *Idotea*. *Idotea emarginata* (Naylor 1955d), *I. viridis* (Howes 1939) and possibly *I. pelagica* (Sheader 1977) may produce two broods, whereas *I. neglecta* (Kjennerud 1950) and *I. baltica* (this study) produce only one. In addition, *I. baltica* apparently has the greatest fecundity of any species of *Idotea*; the maximum brood size encountered in this study was 567 embryos. Other species have relatively smaller broods (Kjennerud 1950; Howes 1939). Our laboratory recently demonstrated by the use of calorimetry that large quantities of high energy compounds (lipids) are mobilized in the formation of gametes, especially ova (Strong & Daborn, 1978) suggesting that *I. baltica* may invest suicidally in reproduction.

The length-specific sex ratio deserves some mention. Through a combination of determining the number of segments on the flagellum of the second antenna, application of the law of geometrical progression and inference from the literature (e.g. Howes 1939), I assumed that male *I. baltica* molt once or twice more often than females during the life cycle, in addition to growing to a larger length. But males and females become sexually mature at the same time of year. This means that females have a longer intermolt period than males. As a consequence, females numerically 'fill up' the smaller length classes, resulting in a sex ratio strongly in favor of females between 8 mm (acquisition of sexual characteristics) and 18 mm. At lengths greater than 18 mm, females are less common and after 25 mm only males are present. Wenner (1972), in an extensive compilation of the influence of size on crustacean sex ratios, has shown that differential molting frequencies and growth rates can often account for unequal sex ratios of the type demonstrated by *I. baltica*.

Trends in abundance and biomass were similar to those expected for a semelparous population with one truncated breeding period. Kjennerud (1950), studying the ecology of *I. neglecta*, noted similar changes in abundance, including a winter paucity of animals. Steele (1975) found much the same pattern of seasonal occurrence in *Gammarus oceanicus* Sergerstråle on Newfoundland shores. At Cape
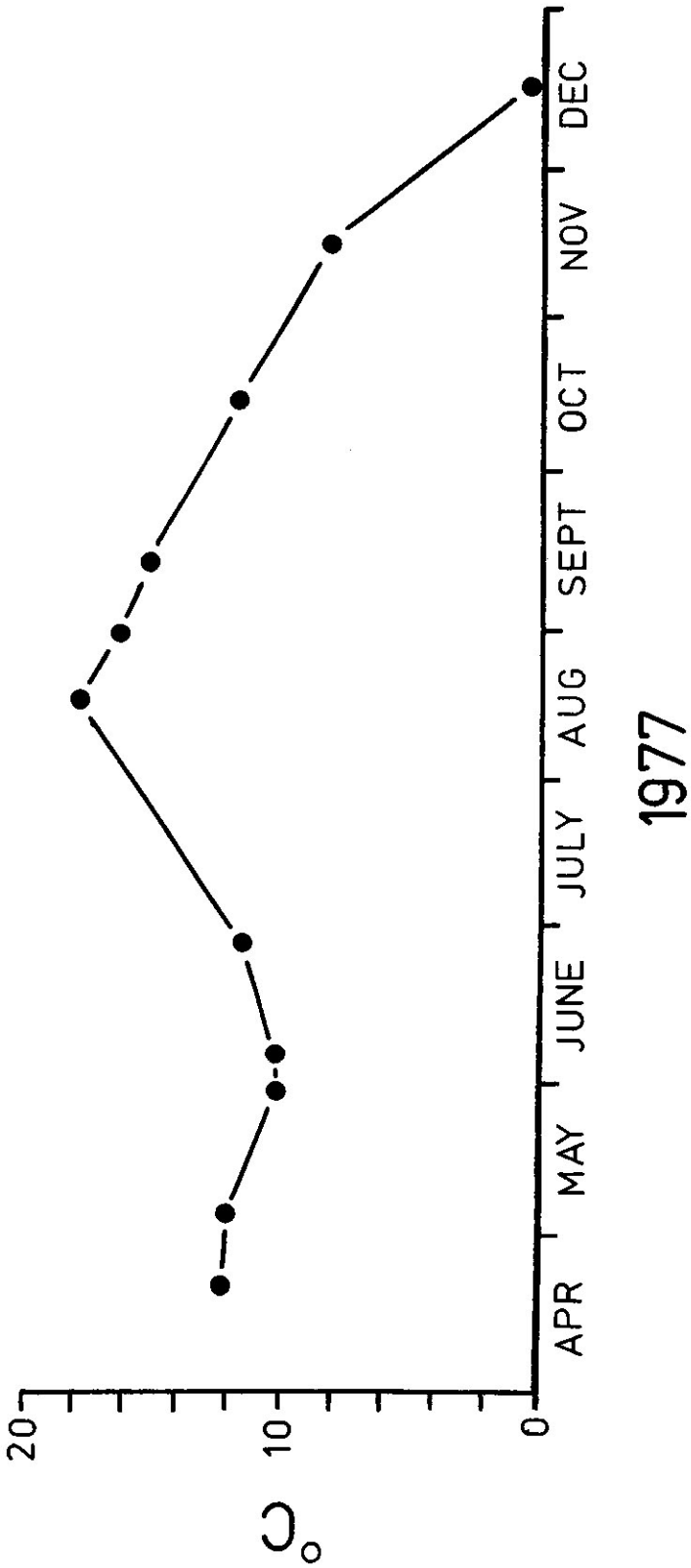
Fig 7.   Water temperature at Cape Blomidon on each collecting date.

Blomidon, movement off-shore into deeper water to overwinter is essential, as extreme tidal amplitude (16 m) and extended exposure accompanied by sub-freezing temperatures could result in high mortality (Bleakney 1972).

This migration may be passive rather than active. Horlyck (1973) showed by using photocells that *I. baltica* from Denmark is inactive from November to February; during this period daylight averaged 9.2 to 10.7 hr·d⁻¹. This photoperiod is similiar to that during Nova Scotia winters. Marsden (1976) demonstrated that the saltmarsh isopod, *Sphaeroma rugicauda* (Leach) becomes inactive below 4°C, and consequently tends to be washed out into deeper water. These observations suggest that when the water temperatures drops to a certain point, *I. baltica* is washed into deeper water, and if the photoperiod suppresses activity may not be able to move back inshore should the water temporarily warm up. This would explain the absence of even a single specimen in the *A. nodosum* in winter.

Acknowledgements

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