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Growth, food consumption and reproductive tactics of the aquatic isopod *Idotea baltica*

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The growth and food consumption of the aquatic isopod *Idotea baltica* was studied in the laboratory. The sexual dimorphism in size developed very early during the immature stage. Males and females also showed different patterns during maturation. The relative weight gain of females was continuously higher during maturation, whereas males had higher total food consumption than females. At the beginning of maturation males allocated a larger proportion of ingested material to the production of new biomass. However this situation later changed as the production efficiency of males declined towards the breeding season. It is suggested that these differences may be consequences of different ecological selection pressures. Males are likely selected for larger size and higher activity influencing mating success, while females are selected for a higher production efficiency before breeding and for minimizing the costs of reproduction. Gravid females were observed to have a lower weight gain than non-ovigerous mature females. This may not, however, present a strict trade-off between reproduction and growth since their feeding rate was also reduced. Consequently, gravid and non-ovigerous females allocated about the same proportion of ingested material to the production of new biomass. The reduced food consumption of gravid females may be a mechanical consequence of incubation and/or it may reflect a decline in the mobility and activity of gravid females.

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1. Introduction

Females of *Idotea baltica* (Pallas) normally breed only once during their life span in the northern Baltic Sea. Maturation takes place as the oostegites forming the brood pouch develop in May and early June (Haahtela 1978; Strong & Daborn 1979). The breeding period begins with precopula as males ride on the back of females. Copulation occurs during the special moult (parturial ecdysis), at which the marsupium of mature females appears. Subsequently, females lay their eggs into brood pouches in June, and juveniles are released before the end of July (Salemaa 1979). Males die soon after copulation, so that the sex ratio gradually becomes more female biased during July, whereas mortality among females increases in August after the delivery of broods (Salemaa 1979, Tuomi et al. 1988).

Consequently, *I. baltica* males and females are subjected to partially different selection pressures. The fitness of males depends on their survival to maturity and traits improving their mating success. On the other hand, the fitness of females depends on their egg production and survival to the delivery of juveniles from brood pouches. Thus one could expect that sexes not only differ in their size (Salemaa 1979, Strong & Daborn 1979) but that this sexual dimorphism may also have other ecological consequences. Salemaa (1986), for instance, reported that immature females have a higher relative food consumption than males of *I. baltica*. Ingestion and growth rates can, however, vary during the life cycle, and sexes can behave differently during the various phases of the cycle.

In the present study, we first followed in the laboratory how the sexual dimorphism in the size of *I.*

baltica develops during the immature stages. Then we studied in several laboratory experiments whether this dimorphism leads to any differences in the food consumption and growth of *I. baltica* during maturation and breeding. In the case of females, we also followed their food consumption during and after incubation. Since these experiments cover the major parts of the life cycle, the variation in growth and food consumption may thus elucidate some basic aspects of the life-history tactics of *I. baltica.*

2. Materials and methods

The study was carried out at the Archipelago Research Institute of the University of Turku (60°14'N, 21°59'E) located in the Finnish South West Archipelago of the Baltic Sea. First we followed the growth of immature isopods produced by females that were collected during the breeding period (June 1984) and thereafter reared in the laboratory (see Tuomi et al. 1988). Juveniles were fed with filamentous algae *Cladophora sp.* and later, from September 1984 to the end of the experiment (May 1985), with the brown alga *Fucus vesiculosus* (L.). Isopods were kept individually in glass dishes (300 ml) with continuously aerated brackish water. Water and food were changed weekly, and the length (mm) of the isopods was measured 2–3 times per month. Sexes were distinguished by the male genital papillae (Naylor 1972, Haahtela 1978), and growth was analyzed separately for identified males and females.

In May and June 1985, daily weight gain and food consumption were estimated for isopods collected from samples of *F. vesiculosus* in four laboratory experiments. Separate specimens were used in each experiment. In the laboratory sexes were separated and the breeding condition of females was determined. In the first experiment, started on 15 May, females had only slightly developed oostegites. Females were classified as adult immature in the second experiment (28 May) as well, whereas in the third experiment (18 June) females had fully developed for breeding. In the field, precopula occurred during and after our third experiment, so that there were both gravid and non-ovigerous mature females in the fourth experiment (27 May). In these experiments, males were about 19–20 mm in length, whereas females were smaller, about 15 mm (for details, see Tuomi & Jormalainen 1988).

Isopods were reared separately as above, except that they were fed with the 1-year old, generative thallus parts of *F. vesiculosus*. Epiphytes were removed before the pieces of algae were used in the experiments. Isopods and their food were weighed (fresh wt, mg) at the beginning and end of the experiment. After the experiment isopods were killed by brief immersion in hot water. Then the dry weights (24 h at 60°C) of the animals and the pieces of algae were determined. The initial dry weights for isopods and the pieces of *F. vesiculosus* were calculated from their fresh weights in terms of the regression equations given in Table 1. Production efficiency was calculated (see Table 4) by relating the daily weight gain of the isopods to their food consumption. In the fourth experiment of 28 June, weight gain and food consumption were also measured for gravid females. Egg biomass in the marsupium was excluded when relative weight gain and consumption were calculated for gravid females. Since gravid females used in the above experiment were collected during the breeding period, the marsupial development of broods was at the early embryonic stages (A–B3, Holdich 1968). A further experiment was carried out (at 15°C with 12 h light and dark regimes) in order to follow the daily food consumption of gravid females at the end of the incubation period and also after the release of offspring from brood pouches. This experiment continued from 10 July 1985 until all the females had died, since we also followed female survival during the experiment (Tuomi et al. 1988). Food and water were changed weekly. The initial and final fresh weights of food were measured for estimating total food consumption. However, relative food consumption was not determined as females were not weighed, in order to avoid artificial adverse effects on their survival.

Table 1. Regression coefficients (*b*) with standard errors (*SE*), intercepts (*a*) and correlation coefficients (*r*) for fresh – dry weight (mg) relationships of isopods and their food in four experiments (1985).

	n	*b* ± *SE*	*a*	*r*	*P*
Idotea	407	0.198 ± 0.004	3.298	0.929	<0.001
Fucus	432	0.229 ± 0.002	1.769	0.977	<0.001

3. Results

3.1. Growth of immature isopods

We followed the growth of immature *I. baltica*, released on 5–12 July 1984, by rearing them first at a constant temperature of 13°C and with 12 h light and dark regimes (Fig. 1). The growth curves of males and females started to diverge relatively early, at about a size of 8–10 mm, as males grew larger than females. Growth continued in both sexes until January. When the temperature had declined to 5°C with complete darkness for 24 h, growth was suspended from January to March. A slight increase in length took place from March to April. At the end of the experiment, the mean length of males was 18.6 mm (*SD* = 1.3) and females 15.5 mm (*SD* = 1.1).

3.2. Growth and feeding rates during maturation

The growth of *I. baltica* was studied during maturation in four experiments by rearing both males and females at a constant temperature of 15°C and with 12 h dark and light regimes. Males tended to have a slightly higher total weight gain than females (Table

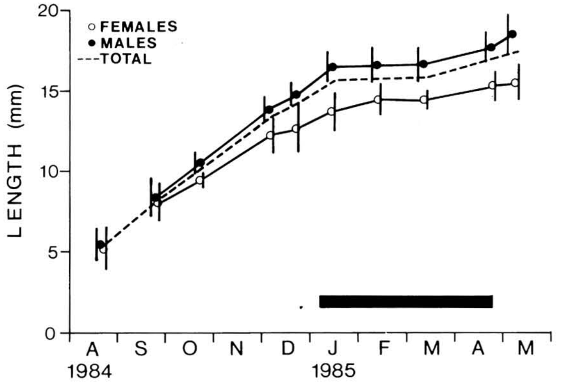

Fig. 1. Mean length and standard deviations of *I. baltica* reared in the laboratory at 13°C with 12 h light and dark regimes. From January to late April isopods were kept in complete darkness at 5°C (indicated by a black bar). Sample size for the total material was 41 (August 1984) and 15 (May 1985), for females 7 and males 8 (May 1985).

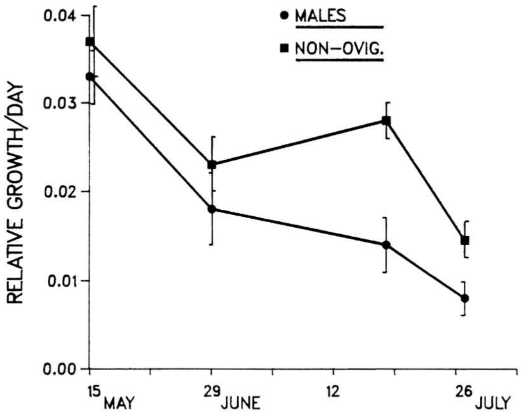

Fig. 2. Mean relative weight gain (mg/final dw/day) of *I. baltica* with standard errors in four experiments, 1985. The number of individuals in each experiment is shown in Table 4.

Table 2. Total and relative growth and food consumption of *I. baltica* in four experiments, 1985 (mean ± *SD*). The differences between the means of different sexes (*n* for males = 194, and for females *n*=196) are related to the mean values of females and shown in percentages.

	Males	Females	Diff %
Growth (mg/day)	0.565 ± 0.672	0.467 ± 0.409	–21.0
Relative growth (mg/final dw/day)	0.018 ± 0.023	0.026 ± 0.023	30.8
Food consumption (mg *Fucus*/day)	4.33 ± 2.09	2.71 ± 1.73	–59.8
Relative food consuption (mg *Fucus*/mg *Idotea*/day)	0.158 ± 0.080	0.156 ± 0.100	–1.3

2), but the difference between the sexes was statistically significant only in the first experiment (ANOVA *df* = 1, 97; *F* = 7.95, *P* <0.01). The combined tail probability for the four experiments was not statistically significant (*df* = 8, $\chi^2 = 11.57$, NS).

Females exhibited, however, a consistently higher relative weight gain than males (Table 2). This difference was most pronounced in the third experiment just before breeding (Fig. 2, ANOVA *df* = 1, 97; *F* = 17.35, *P* < 0.001), but in the other experiments the difference between females and males was statistically non-significant. When the tail probabilities of these experiments were combined, the product was statistically significant (*df* = 8, $\chi^2 = 23.22$, P < 0.001).

Growth rates declined from May to June (Fig. 2). No such tendency was found in feeding rates although there was significant variation between experiments (Table 3). As males were larger, they also had on average a higher total food consumption than females

Table 3. Two-way analyses of variance in food consumption and production efficiency of *Idotea baltica* in four experiments (Tables 2 and 4).

Variable	Source	*df*	*F*	*P*
Food consumption (logarithmic transformation)	Sex	1	93.4	<0.001
	Date	3	26.2	<0.001
	Interaction	3	2.51	0.058
	Error	373		
Relative food consumption (arcsine transformation)	Sex	1	0.39	0.534
	Date	3	18.6	<0.001
	Interaction	3	3.20	0.023
	Error	372		
Production efficiency (see Table 4)	Sex	1	1.29	0.257
	Date	3	10.2	<0.001
	Interaction	3	4.73	0.003
	Error	372		

Table 4. Production efficiency (= 100 × growth/ingestion) of *I. baltica* fed on *Fucus vesiculosus* in four experiments, 1985 (mean ± SD, (n)). Differences between the means of sexes are related to the mean values of females and shown in percentages.

	Males	Females	Diff %
May 15	25.7 ± 21.0 (47)	19.3 ± 33.6 (48)	-33.2
May 29	12.3 ± 19.2 (48)	10.5 ± 10.8 (48)	-17.1
June 18	13.3 ± 17.5 (47)	27.4 ± 17.6 (49)	51.4
June 27	7.8 ± 13.1 (46)	9.4 ± 13.1 (45)	17.0

(Table 2). When the ingested material (dry wt mg *Fucus*) was related to the final weight (dry wt mg) of isopods, the difference between the sexes in terms of relative food consumption varied according to the date, as indicated by the statistically significant interaction (Tables 2 and 3).

Differences between the sexes in terms of production efficiency also varied according to the date. The interaction between sex and date was statistically significant (Table 3). At the beginning of maturation males had, on average, a higher production efficiency than females, but the situation was reversed just before, and during, the breeding period (Table 4).

3.3. Growth and food consumption of gravid females

In the fourth experiment, started on 27 June, growth and food consumption were also measured for gravid females and compared with non-ovigerous mature females (Table 5). Gravid females tended to have both a lower weight gain and lower food consumption than non-ovigerous females. When relative weight gain and ingestion were compared, the differences between gravid and non-ovigerous females were smaller. In spite of these differences, the production efficiency of gravid females was on average 9.0% ($SD = 26.8$, $n=34$). As the production efficiency of non-ovigerous females in the same experiment was only slightly higher (i.e. 9.4%, Table 4), both gravid and non-ovigerous females allocated about the same fraction of ingested material to the production of new biomass (Mann-Whitney $U = 862$, n=79, NS).

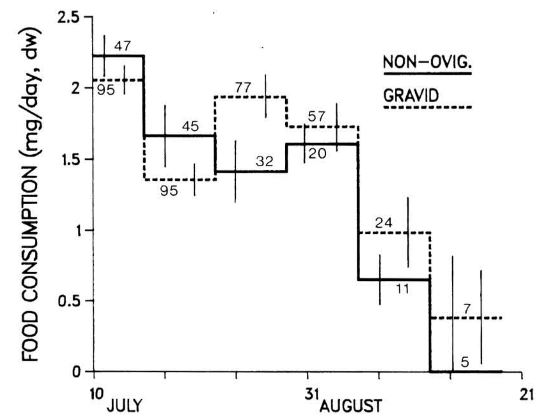

Fig. 3. Food consumption (mg *Fucus*/day) of the same specimens of gravid and non-gravid mature females of *I. baltica*. Standard errors and n's are shown in the figure.

The food consumption of the same specimens of gravid and non-ovigerous mature females was also studied during a longer time period in a temperature room (15°C) with 12 h light and dark regimes (Fig. 3). Juveniles were released from brood pouches during the second week, and during these two weeks gravid females tended to have a slightly lower food consumption than non-ovigerous females (Fig. 3, Table 6). This pattern was reversed after the release of offspring as gravid females had a higher food consumption during, and after, the third week (Fig. 3, Table 6).

Table 5. Total and relative growth and food consumption of non-ovigerous and gravid females of *I. baltica* in the fourth experiment of 27 June, 1985 (mean ± SD, (n)). Differences (%) are related to the mean values of non-gravid females and tested with the Mann-Whitney *U*-test.

Variable	Non-ovigerous	Gravid	Diff. %	U	P
Growth (mg/day)	0.294 ± 0.333 (47)	0.217 ± 0.533 (36)	–26.2	1068	<0.05
Relative growth (mg/final dw/day)	0.014 ± 0.016 (47)	0.013 ± 0.034 (36)	–7.0	1076	<0.05
Food consumption (mg *Fucus*/day)	2.63 ± 1.59 (48)	2.03 ± 1.15 (40)	–22.8	1085	<0.05
Relative food consuption (mg *Fucus*/mg *Idotea*/day)	0.145 ± 0.087 (48)	0.129 ± 0.075 (40)	–11.0	1000	NS

Table 6. Statistical differences (Mann-Whitney U-test) in daily food consumption between gravid and non-gravid females during different phases of breeding (Fig. 3). Differences (%) are related to the mean values of non-gravid females.

Period	Condition of initially gravid females	Number of gravid	Number of nongravid	Difference %	Difference U	Difference P
July 10–July 15	Incubation	95	48	–7.69	2535	NS
July 15–July 22	Delivery of juveniles	95	45	–18.63	2412	NS
July 22–August 19[1]	Post-gravid	76	31	43.70	854	0.026

[1] Mean daily food consumption of each female from 22 July to the death of each female.

4. Discussion

4.1. Ecological consequences of sexual dimorphism

Juveniles of *Idotea baltica* released in July at a length of about 2 mm first consume filamentous algae in the upper littoral zone and later, in the autumn, the brown alga *Fucus vesiculosus* (Salemaa 1979). The sexes are first distinguishable at a length of 8–10 mm (Strong & Daborn 1979). No significant growth takes place during the winter months of December–April (Salemaa 1979, Strong & Daborn 1979). Growth continues in the spring before isopods achieve sexual maturity, as the water temperature increases (Salemaa 1979). When we reared immature *I. baltica* in the laboratory, their growth showed the same pattern. However, due to the relatively low rearing temperature, their growth was slower and continued longer, up to January. The growth curves of females and males also tended to diverge very early so that sexual dimorphism obviously develops during the immature stage.

In the present material, females used in the four experiments matured gradually towards June (for details, see Tuomi & Jormalainen 1988). When males and females were compared during maturation, we found that (1) weight gain declined in both sexes from May to June, (2) relative weight gain was constantly higher for females than males, and (3) males had higher food consumption than females. However, sexual differences in relative food consumption varied during maturation (cf. Salemaa 1986). On the other hand, production efficiency relating weight gain to food consumption was first higher among males at the beginning of maturation, after which their production efficiency gradually declined below the level of females. Interestingly, the production efficiency of females was highest in the third experiment just before precopula, when the energy requirements of egg development should be highest. The assimilation efficiency of *Asellus aquaticus* is also higher among females than males, which is thus a potential mechanism for paying-off the resource expenditures of egg production without increasing food consumption (Prus 1971).

The above patterns thus seem to indicate that females and males may be under different kinds of ecological selection pressures during maturation: Males are presumably selected for such features as increase their success in precopula and copulation at the cost of their production efficiency, whereas females should be selected for traits that allow them most efficiently to transform ingested material into offspring biomass, with minimum costs for their own maintenance. Consequently, the production efficiency of males possibly declined towards the breeding point as their maintenance requirements for assimilated energy increased due to the higher activity needed for mate selection and precopula (see Jormalainen & Tuomi 1988).

This reasoning assumes that the mating success of males mainly depends on their size and activity (e.g Ridley & Thompson 1979). On the other hand, females seem to have adopted another kind of tactic during maturation. They accumulate resources for supplying egg production and ensuring their own survival over breeding and incubation periods (Tuomi & Jormalainen 1988, Tuomi et al. 1988). The higher relative growth rates of females is consistent with this hypothesis. The condition index relating body mass to length also increases among females during maturation, whereas males do not show such a pattern (Tuomi & Jormalainen 1988). Consequently, it is less likely that females are selected for a higher activity during maturation to the same extent as males. This reasoning is consistent with the fact that males tend to die earlier after copulation (Salemaa 1979), whereas mortality is very low in the laboratory among females during breeding and incubation periods (Tuomi et al. 1988).

4.2. Ecological consequences of breeding and incubation

A general assumption in life-history theory (reviewed by Stearns 1976, and Charlesworth 1980) is that reproduction decreases the parental survival or future fecundity due to the reduced amount of resources available for growth and maintenance. We have, however, proposed that *I. baltica* may at least partially avoid such direct costs of reproduction by accumulating resources for egg production during maturation (Tuomi et al. 1988, Tuomi & Jormalainen 1988). In other words, the tactics of females would be to adjust their egg production to a level which does not decrease their own survival before the release of juveniles from brood pouches.

This may not, however, completely exclude the somatic costs of reproduction. Lawlor (1976), for example, observed in the terrestrial isopod *Armadillidium vulgare* that gravid females exhibited a lower weight gain than non-ovigerous females. This was also what we observed in *I. baltica,* since the weight gain of gravid females was on average reduced by 26.2% relative to non-ovigerous mature females. However, their feeding rate was also reduced by 22.8%, so that their reduced weight gain may not indicate a reduced relative allocation to growth. This seems to be the case, as both gravid and non-ovigerous females allocated about 9% of their ingested material to the production of new biomass. Interestingly, in *A. vulgare* as well gravid females exhibit reduced feeding rates and lower mobility (Lawlor 1976).

This reduced feeding rate of gravid females differs fundamentally from mammals, in which females may increase their food intake during gestation and lactation as a positive function of brood size (Millar 1975, Randolph et al. 1977). Thus, food consumption may be adapted to the resource requirements of offspring for parental effort, which is highest during lactation in mammals (Randolph et al. 1977) and probably highest during egg growth and maturation in isopods. However, the lower food consumption of gravid isopods may also be a mechanical consequence of incubation as the egg mass in the marsupium may limit the amount of food that a female can ingest per time unit.

This reduction in the feeding rate of gravid *I. baltica* seems to be a direct consequence of incubation because their food consumption remained low until the release of the young from the brood pouches. This pattern was reversed after the delivery of offspring, as gravid females tended to have higher feeding rates than non-ovigerous mature females. Later the food consumption of gravid females gradually declined in August. This decline was also associated with a gradual decrease in survivorship, so that the average longevity of gravid females was 25 days after the delivery of juveniles (Tuomi et al. 1988). Since the same also occurred among non-ovigerous mature females, earlier reproduction does not seem to be the factor which triggers this decline in food consumption and female survival.

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