

What do Baltic studies tell us about the isopod *Saduria entomon* (L.)?

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Saduria entomon lives all over the Baltic Sea within a salinity range of about 1 to 20‰. It occurs also in Lake Ladoga and eight lakes in Sweden. *S. entomon* is a stenothermal cold water species, but it is well able to stand temperatures of 15–20°C. The main depth of occurrence is 50–85 m or deeper. Some coastal populations live permanently at a depth of about 5 m, and the maximum depth of occurrence is determined only by the oxygen demand of at least 2 mg/l. The species lives in any substrate it can dig in, favouring ooze and fine sand. It also ascends from the bottom to swim.

The density and biomass (mean±SE) of *S. entomon* in the Bothnian Bay is 1 ind./m² and <0.1 g/m², and in the Bothnian Sea 16±10 ind./m² and 4.5±1.8 g/m². These values are higher in coastal areas, the known maximum being 180 ind./m² and 163 g/m² in the eastern Baltic proper.

The main diet of *S. entomon* is the amphipod *Pontoporeia affinis*. Also chironomid-larvae, other invertebrates, including its own kin, and all kinds of dead animals are consumed. Father lasher and young cod have *S. entomon* as their main diet. Both predation by fish on *Saduria* and of the latter on invertebrates regulates the population structure of the bottom fauna.

The sexual dimorphism is distinctive. The largest male ever recorded in the Baltic was 88 mm long, the largest female 68 mm long. The largest specimens occur in deep open sea areas. In the coastal areas of the Bothnian Bay males seldom grow longer than 50 mm, females 35 mm.

The female carries the brood in a ventral marsupium for two to four months. When released the young are 3–4 mm long, and after one year of growth about 20 mm. Sexual maturity is reached during the third year of life, females then being at least 25–32 mm, males 35–50 mm long. Reproduction takes place during the third or fourth year, after which most females die. The lifespan would thus be 3 to 4 years. In deep areas it may be much higher, and has been estimated at up to nine years. The new generation and spent females appear mainly in May and June, so that the species does not reproduce throughout the year as was earlier thought.

1. Introduction

Saduria (formerly *Mesidotea*, see Bull. Zool. Nomencl. 21:92–93, 1964) is an arctic genus of four species; *S. entomon* (L.), *S. sibirica* (Birula), *S. sabini* (Kröyer) and *S. megalura* (G. O. Sars) (Gurjanova 1933). Of these *S. megalura* lives at depths greater than 1000 m in the Norwegian Sea and Arctic Ocean, and *S. sibirica* in 15–25 ‰ water along the Siberian coast. The other two species have a circumpolar distribution, although *S. sabini* is limited to fully saline areas, whereas *S. entomon* has the widest distribution of all four, being recorded at salinities of between 0.22 and 30‰ in the sea, and furthermore in several fresh-water lakes (Jägerskiöld 1912, Gurjanova 1933, Ekman 1935:249 and 1953:172, Kussakin 1982). Each of the four species has been divided into two or more morphological forms or subspecies, those of *S. entomon* being *S. e. orientalis* Gurjanova, *S. e. glacialis* Gurjanova, *S. e. entomon* (L.) (the Baltic form, Fig. 1), *S. e. vetterensis* Ekman and *S. e. caspia* G. O. Sars (Gurjanova 1970). The relict nature of *S. entomon* has merited special attention and discussion (Segerstråle 1957).

Reviews on the biology of *S. entomon* have been published by Haahtela (1962a, b) and Gruner (1965), major Baltic studies by Kovalevskii (1864), Skorikova (1906), Apstein (1909), Ekman (1919, 1920), Bruun (1924), Gurjanova (1946), Bogucki (1948), Nikitina & Spasskii (1963), Haahtela (1975, 1978b), Kopacz & Wiktor (1986) and Leonardsson (1986). Haahtela (1978a) has described the sampling methods. Studies on the physiology and on the bottom fauna in which the biology of *S. entomon* is dealt with in detail are referred to in the text. If not stated otherwise below, *S. entomon* should be taken to mean *S. e. entomon*.

In my oral presentation I limited the subject to Fennoscandian studies on *S. entomon*, reviewing the papers at the same time. Important studies carried out in other Baltic countries were ignored. The latter have been included in the present paper, but physiological studies and papers are referred only briefly. A more complete reference list on the Fennoscandian literature can be requested from me.



Fig. 1. *Saduria entomon* from the Bothnian Sea. Larger specimens are males, smaller females of which one in the middle is showing the ventral brood pouch. Photographed by the author.

2. Distribution, salinity, temperature and oxygen tolerance, activity

S. entomon occurs in all viable parts of the Baltic, most abundantly in the Bothnian, Åland and Archipelago Seas and in the Gulf of Finland, decreasing in numbers towards the limits of the Gulfs (Haahtela 1975, Järvekülg 1979, Zmudzinski 1967, Leonardsson 1986). From the Åland Sea northwards to the end of the Bothnian Bay, it forms, together with the amphipod *Pontoporeia affinis*, the second largest bottom community of the Baltic Sea, the *Pontoporeia affinis* – *Mesidotea* community (Zenkevich 1963).

The geographical distribution of the species is limited by salinity. The Baltic form does not penetrate into fresh water, but it has been recorded in an area of 0.2‰ S (Hellen & Ehrström 1920). At

the marine border of the Baltic it has not been found at higher than 19‰ S. Only single specimens have been recorded west of the island of Hiddensee, the westernmost finds being along a line between Falsterbo and Stevnsklint (Apstein 1909, Bruun 1924, Lovén 1934, Köhn & Gosselk 1989, Köhn 1990). The optimum salinity for *S. entomon* in Estonia — in the Eastern Gulf of Finland — is 2.2–11.5‰ (Järvekülg 1979), in the southern Baltic 9–14‰ (Mulicki 1957).

The form *S. e. vetterensis* lives in fresh water only; in Mälaren, Vänern, Vettern and five smaller lakes in Västgötaland in Sweden (Letteval 1962) and in Lake Ladoga, but not in Lake Onega as sometimes reported (see Segerstråle 1956:25). *S. entomon* does not occur in any lake in Finland, although other marine glacial relicts encountered in the Baltic do so. As an explanation Segerstråle (1957) has suggested a chemical factor. A more reliable answer would appear to lie in the geological history of the distribution, discussed by Letteval (1962) (see also Croghan & Lockwood 1968). In experiments *S. e. vetterensis* has shown the widest salinity tolerance, being able to live not only in full sea water, but at even higher salinities, whereas the Baltic form could not survive in fresh water (Lockwood & Croghan 1958).

S. entomon is a stenothermic cold water species (Demel & Mulicki 1958). In the southern Baltic the optimum temperature is 2°C (Mulicki 1957). In the northern Baltic area, the temperature in the main area of occurrence (see Andersin & al. 1978) is permanently close to or less than 5°C. It is thus curious that the species is frequently recorded at 15°C (Haahtela 1962a, b) and occurs even in water warmer than 20°C (Apstein 1909, Lovén 1934, Järvekülg 1979). Experiments by Kivivuori & Lagerspetz (1990) showed that for *S. entomon* the critical thermal maximum (CTMAX) was 26°C and specimens from 4°C selected a temperature of 15–17°C, coming to rest at about 15°C.

The lowest oxygen content of the water where Mulicki (1957) has found *S. entomon* in the southern Baltic was 2.1 mg/l. Kangas & Lappalainen (1978) found that the oxygen consumption (MO_2) of *S. entomon* was independent of the oxygen tension of the water (P_wO_2), down to a P_wO_2 of 2 mg/l, and even at a P_wO_2 of less than 0.5 mg/l it survived for several hours. Kristoffersson and

Kuosa (1990) have shown a P_wO_2 of 2 mg/l to be sufficient at the natural salinity (6.8‰) of animals tested, but clearly insufficient at 1.7‰ salinity. Hagerman and Oksama (1985) confirmed that *S. entomon* could survive at a P_wO_2 of 10 Torr for at least 96 h and sustain long periods at a P_wO_2 of about 30–35 Torr. Below this point compensatory mechanisms begin: biosynthesis of hemocyanin increases the amount of oxygen that can be carried in the blood. A respiratory alkalosis also takes place. These results explain how *S. entomon* is capable of keeping up with severe oxygen conditions, common in many parts of the Baltic. The typical behaviour in decreasing oxygen tension is the raising of the abdomen, on the ventral side of which lie the gills (pleopods), above the surface of the substrate in which it is buried (Hagerman & Oksama 1985). Hagerman & Szaniawska (1988) have shown that only when P_wO_2 was lowered to 5 Torr *Saduria* emerged totally. Besides this behaviour, the respiratory independence is governed by changes in ventilatory pump flow.

Haahtela (1978a) has stated that *S. entomon* is a dark-active species which avoids strong illumination. In experiments carried out by Westin & Aneer (1987) the locomotory rhythm of the species proved to be clearly nocturnal throughout the year.

3. Depth and bottom material

Temperature — but also salinity, bottom material and profile — determines the depth at which *S. entomon* occurs. The main depth of occurrence is 50–85 m (Demel & Mulicki 1958, Nikitina & Spasski 1963). This is in agreement with Haahtela (1975), but large populations have also been found in areas deeper than 100 m in the Bothnian Sea (Haahtela 1975) and as deep as 290 m in the Åland Sea (Haahtela unpubl.). Populations of *S. entomon* also occur in shallow coastal areas of the Bothnian Bay at a depth of a few metres, single specimens being found at depths of as little as 1 m (Haahtela 1975, Kangas 1976, Leonardsson 1986).

Defining the depth of occurrence is complicated by the fact that the coastal *S. entomon* migrate into shallow water during the winter and then back to deeper areas in the summer, the migrants belonging to the younger fraction of the

population (Nikitina & Spasskii 1963, Żmudziński 1966). Whether migration is determined by seasonal changes in temperature and illumination, or whether there are other reasons as well, remains to be seen.

S. entomon lives in all kind of bottoms that are not too hard for it to dig into. In the southern Baltic, but also in the Bothnian Bay and the eastern Gulf of Finland, the species is very common in sandy mud and fine sand (Bruun 1924, Mulicki 1957, Järvekülg 1979, Leonardsson 1986). Elsewhere in the Baltic soft bottoms of mud or ooze on clay, often also with rich concentrations of iron-manganese concretions, are preferred (Haahtela 1975, Järvekülg 1979). The species is common in *Zostera*-beds (Lappalainen, Hällfors & Kangas 1977), as well as in ooze among loose-lying red algae (Seegerstråle 1933, Haahtela unpubl.). In the Bothnian Bay *S. entomon* also lives in stony bottoms, digging in the sandy spaces between and under the boulders (Kangas pers. comm. and 1976).

Although *Saduria* mainly lives at the bottom, it can swim effectively by beating with the pleopods in an upside down position. Such specimens are frequently seen in the surface waters and many have been captured in mid-water trawls in the open sea (Haahtela 1978a).

4. Density, biomass and population dynamics

Space here permits the inclusion of only a fraction of the extensive data on the density and biomass of *S. entomon*. Unless otherwise stated, biomasses are given in terms of formalin wet weight.

In most areas of the southern Baltic the biomass is $<5 \text{ g/m}^2$ (Mulicki 1957), in the Gulf of Gdańsk 10–60 g and the density 20–60 ind./m² (Żmudziński 1967). In the central Baltic (95 stations) and Gulf of Finland (260 stations) the highest densities and biomasses were recorded at depths of 30–70 m (8–24 ind. and 1.67–5.67 g/m²), whereas both in shallower and deeper water the respective numbers were <1 –10 and 0.05–2.15. In the Gulf of Riga — Sea of Dvina area (340 stations) the densities were of the same order of magnitude, but the biomasses were about five-

fold. The maximum values in these areas were very high: 180 ind. and 163 g/m² (Järvekülg 1973, 1979:314).

In the Tvärminne archipelago, in the western Gulf of Finland, Sarvala (1985) has recorded the biomasses of *S. entomon* at different depth zones, the maximum being 1.20 g AFDW/m², which was also the largest estimated annual production.

The same trend as above in the open sea areas is obvious in the Bothnian Sea and Bothnian Bay. At a depth of 0–25 m and 25+ m the biomasses were 1.1 and 6.1 g/m² respectively in the former area, and $<0.1 \text{ g/m}^2$ at 0–25 m (no data from 25+ m) in the latter. The mean \pm SE abundance and biomass for the entire Bothnian Sea were 16 ± 10 ind. and $4.5 \pm 1.8 \text{ g/m}^2$, and for the Bothnian Bay 1 ± 1 ind. and $<0.1 \text{ g/m}^2$ (Elmgren et al. 1984). In certain coastal areas of the Bothnian Bay the respective numbers resemble those given above: in the Luleå archipelago usually <1 ind. and $<0.1 \text{ g/m}^2$ (Samberg & Sövlén 1976), but sometimes as high as 30–40 ind./m² (Norrby, S of Umeå, depth 5 m) (Leonardsson 1986).

Much less is known about the population dynamics of *S. entomon*. At Tvärminne, in the north-western Gulf of Finland, the bottom fauna has been monitored for more than 50 years. Seasonal fluctuations in abundance of *S. entomon*, probably due to migration (see p. 272), are generally known. Seegerstråle (1933) mentioned that long term fluctuations also occur. Karjala & Lassig (1985) do not say anything of these in relation to *Saduria*, although they point out the fluctuation cycle of its co-dweller, *Pontoporeia affinis*. In the Airisto Sound, in the Archipelago Sea, *S. entomon* was very abundant: 25–30 ind., maximum 121 ind./m² at the end of the 1950s and beginning of the 1960s (Tulkki 1960, Haahtela 1962a, b), but it declined during the 1960s. No recovery, or at most a slow recovery, has been observed (Haahtela unpubl.). These changes do not seem to fit in with any of the known biological cycles.

Possible changes in the abundance and biomass of *S. entomon* due to eutrophication or other human impact will not be dealt with here. For these, see e.g. Andersin et al. (1978) and Cederwall & Elmgren (1980).

5. Size and growth

As a rule the maximum mean size of a population and individual body length of *S. entomon* have been registered in areas with the lowest mean temperature, or in other words with the greatest depths (Haahtela 1975).

Males attain a larger size than females. In the Baltic *S. entomon* grows largest of all in the Bothnian Sea. In the central basin of this sea, at depths greater than 100 m, the mean body length of mature males was >75 mm, of mature females >50 mm. The largest male measured was 88 mm long and weighed 10 g, the largest female 68 mm and 5 g respectively. A population composed of the smallest *S. entomon* has been reported from Norrbyn, south of Umeå in the Bothnian Bay. The mean body length of mature males was 36.0 mm, that of mature females 29.1 mm, the maximum sizes being 48 and 36 mm respectively (Leonardsson 1986). The maximum body length of *S. entomon* in different parts of the Baltic is given in Table 1.

The growth of *S. entomon* has been studied both in aquaria and in the sea. When newly released *S. entomon*, of body length 3–4 mm, were kept in aquaria at a temperature close to that in the locality of sampling in southwestern Finland, the mean growth in the first year was 11 mm for the females and 14 mm for the males, in the second year 20 mm and 25 mm. The mean body length after two years of growth was 35 mm and 43 mm, respectively, and some mature males occurred. Growth was retarded during the first winter, but

not during the second (Haahtela 1977). Another experiment showed that growth was directly proportional to test temperatures of 5°, 10° and 15°C (Haahtela 1977). In the northern Bothnian Bay the annual growth of *S. entomon* was about 8–9 mm (Leonardsson 1986). *S. entomon* can be sexed according to morphological characteristics after it reaches a body length of 17–18 mm (Haahtela 1978b, Leonardsson 1986).

The length/weight ratio for *S. entomon* in the Gdańsk Bay has been determined by Kopacz & Wiktor (1986) by functions $W = 0.0158 L^{3.18}$ for females; $W = 0.223 L^{2.87}$ for males. Females longer than 30 mm are thus heavier than males of the same body length. The length/weight ratio for the *S. entomon* of the Bothnian Sea, quoted by Haahtela (1975), is only roughly in agreement to that shown above and is the same for each sex.

6. Age and life cycle

How long does *S. entomon* live is one of the most frequently posed questions. It is not easy to give a stock answer to this. Only a few studies have dealt specifically with the subject. As Nikitina & Spasskii (1963) have pointed out, there is no accurate method for determining the age of higher Crustacea. To obtain a reasonably reliable picture of the age structure of a population one must measure the body length or some other dimension of the individuals in it, so that age classes can be distinguished. Gurjanova (1946) and Kopacz & Wiktor (1986) are sceptical about this.

Table 1. Maximum body length in mm of *S. entomon* in different parts of the Baltic Sea.

Area	Male	Female	Reference
Bothnian Bay, central	87	65	Haahtela (1975)
Bothnian Bay, coastal E	57	51	Haahtela (1975)
Bothnian Bay, coastal W	48	36	Leonardsson (1986)
Bothnian Sea, central	88	68	Haahtela (1975)
Åland Sea	81	61	Haahtela (1975)
Archipelago Sea	71	56	Haahtela (1975)
Gulf of Finland	78	54	Haahtela (1975)
Central Baltic, Klaipėdė	77	–	Nikitina & Spasskii (1963)
Gdansk (Danzig) Bay	84	63	Apstein (1909)
Gdansk Bay	79	59	Bogucki (1948)
Gdansk Bay	79	56	Kopacz & Wiktor (1986)

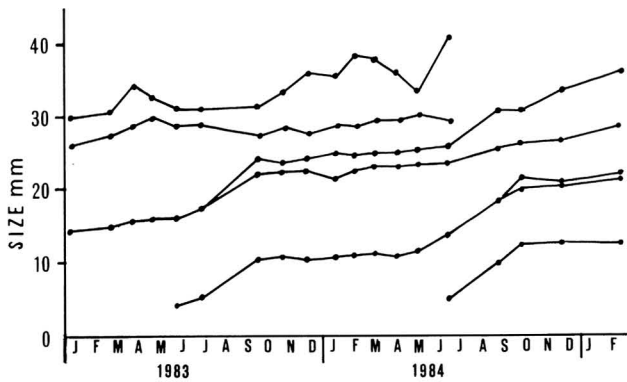
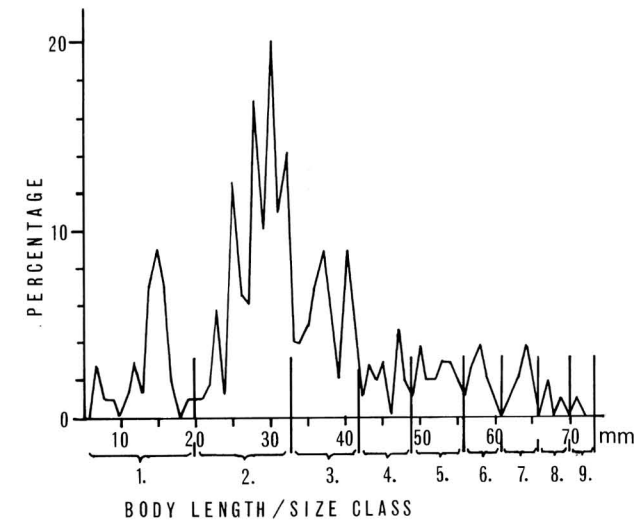


Fig. 2. In a *Saduria entomon* sample from Kleipėd in April 1957, nine size classes were distinguished by Nikitina & Spasskii (1963). (Above). Usually three, but sometimes two or four age classes could be distinguished in a *Saduria* population of the northern Bothnian Sea (Leonardsson 1986). (Below). Simplified.

Leonardsson (1986) studied a *Saduria* population in the Bothnian Bay for over two years. The mancas were found in June in both years, and formed a well defined size-group (age class) one year later (Fig. 2). After one more year the development of ova commenced in females. Some females matured during the autumn, but the largest fraction did so in January–May. The young were released in June. Spent females occurred in June and July. Mature males were found whenever sampled, but their proportion in the oldest age class reached a peak during the winter. Most of both females and males apparently died after reproduction. The length of the life cycle would thus be three years.

This is in keeping with Ankar & Elmgren (1976), who have estimated the life-span of *S. entomon* in the Askö area as 3.3 years. Kopacz & Wiktor (1986) have observed the co-existence of at least two generations of *S. entomon* in the Gulf of Gdańsk, and suggest that the life-span does not exceed three years. Nikitina & Spasskii (1963) have calculated the life-span of *S. entomon* by Klaipėd in the western Baltic proper as 8–9 years (Fig. 2), i.e. three times higher than stated in the studies mentioned above. In agreement with the others is the age of maturity: two years for some and three for the majority of females.

If the experiment by Haahtela (p. 273), had been continued and *S. entomon* would have grown

at about the same rate as they did during the first two years, females would have reached the maximum size recorded in the study area during their third year of life, but males not until a year later. Hence, the age could be as high as 4–5 years. It is, however, not easy to accept the idea that *Saduria* males of the Bothnian Sea, despite the optimal conditions for the species, could have attained a body length of 88 mm (males) or 68 mm (females) in this period of time, as this would mean an average annual growth of 21 and 17 mm respectively. Until further studies are carried out, the definite age of *S. entomon* remains obscure.

Whether *S. entomon* reproduce throughout the year is a question that has long troubled biologists. In earlier papers (Apstein 1909, 1922, Ekman 1920, Bogucki 1948) a general opinion seemed to be that as in the lakes and the ocean (cf. Ekman 1920), this relict species reproduces in the Baltic throughout the year, although mainly in May–September. This is not the whole truth because the statement was apparently based on the occurrence of the egg-bearing females. If we focus our attention on females with fully developed embryos, as did Nikitina & Spasskii (1963), Leonardsson (1986), Kopacz & Wiktor (1986), or particularly on spent females and newly released juveniles (Leonardsson 1986), it becomes evident that, as stated above, in coastal areas reproduction takes place in the period March–September, and most intensively in June (Fig. 3). In deep open water areas the situation may be different (Leonardsson 1986).

7. Reproductive biology

Precopulation of *S. entomon* has often been observed in aquaria and also within the samples (Haahtela 1977, Leonardsson 1985). In the aquaria it continued for 10 to 18 hours, or rarely for several days (Haahtela 1977). Larger males tend to chase away smaller precopulating males, then proceeding to take over the female (Leonardsson 1985). The actual insemination has not been recorded.

The average time for brooding the eggs until the release of the young in the laboratory (10°C) was 65 days, the maximum being 136 days (Leonardsson 1985). Data on the body length of

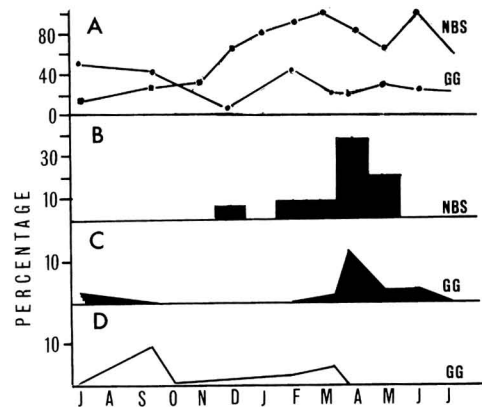


Fig. 3. Reproduction of *Saduria entomon* takes place in the spring and early summer. This is verified by the increase in the percentage of mature males to all males during the first half of the year and the decrease in the summer (A), the occurrence of females with developed embryos from February to July (B and C) and specimens <10 mm long mainly in the autumn (D). GG = Gulf of Gdansk, NBS = Northern Bothnian Sea. From Kopacz & Wiktor (1986) and Leonardsson (1986). Simplified.

brooding females and on fecundity has been published by Apstein (1909), Nikitina & Spasskii (1963), Romanova as cited in Ivanova & Vasilenko (1987), Kopacz & Wiktor (1986) and Leonardsson (1986). According to these studies the body length of the smallest reproducing female varies between 25 and 32 mm, depending on the mean body size of the population. The fecundity varied from 75 to 605, increasing in direct proportion to the size of the female. The relationship between fecundity (F) and female body length (X) has been described by Leonardsson (1986) to be $F = -200 + 12X$, $r = 0.800$. He did not find any correlation between female size and individual egg size. Kopacz & Wiktor (1986) noticed that the minimum body length of egg-bearing females in the winter was considerably greater than it was in the summer, and that the number of eggs for females of the same size was less in the winter than in the summer.

Males mature at a much larger size than females (Nikitina & Spasskii 1963, Haahtela 1977,

Leonardsson 1986). Most adults seem to die after reproduction, but some females moulted into an intergenerative phase, shedding their marsupium. Also, some males may reproduce more than once (Leonardsson 1986). Haahtela (1978b) has observed the same and thinks that males, when once matured, never lose their copulatory stylets and probably never moult again. This is in disagreement with Kovalevskii (1864) and Skorikova (1906).

8. Feeding, diet and predators

Green (1957) has studied the feeding mechanism of *S. entomon*. The species is an omnivorous scavenger, living on dead fish and such objects as it may find on the sea bottom. *Saduria* is also an effective predator. In the laboratory experiments it could capture and eat specimens of *Daphnia magna*, *Asellus aquaticus*, large specimens of *Artemia salina*, and various chironomid larvae (Green 1957). Segerstråle (1933) also mentions chironomid larvae, and, together with Apstein (1909), amphipods. Among the latter *Pontoporeia affinis* in particular is preyed upon (Hessle 1924). Potential food is effectively detected at a long distance by the aid of the antennular chemoreceptors, the aesthotasks (Pynnönen 1985).

Leonardsson (1989) has found that cannibalism is an important mortality factor and a population regulating mechanism in *S. entomon*. In shallow Baltic areas the consumption of invertebrates by *Saduria* seems to have a marked influence on the structure of the bottom communities (Sandberg & Bonsdorff 1989).

More than 10 of the fish species living in the Baltic are known to feed on *S. entomon* (Haahtela 1962a, b, Hansson 1984). The main predators of the species are cod (*Gadus morrhua*) and dab (*Limanda limanda*) (Hessle 1924, Uzars 1969), father lasher (*Myoxocephalus scorpius*) (Apstein 1909) and fourhorn sculpin *Myoxocephalus quadricornis* (Hansson 1984, Leonardsson et al. 1987).

Nikitina & Spasskii (1963) have pointed out that predation by cod regulates the population of *S. entomon*, the size of the devoured isopods being different at different seasons. Seasonal variation was also observed in the size of *Saduria* preyed on by fourhorn sculpin in the coastal areas of the Bothnian Bay. There the selection of large speci-

mens (the oldest year-class) might favour a lowering of the reproductive age (Leonardsson et al. 1987). At greater depths mature *Saduria* are much larger and apparently also older (Haahtela 1975). Leonardsson et al. (1987) think that this might be the result of diminished or non-existent predation pressure.

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