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On the structuring role of *Saduria entomon* (L.) on shallow water zoobenthos

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In shallow, northern Baltic archipelago waters, predatory epibenthic invertebrates are rare in relation to fully marine environments. One such predator is the relict isopod *Saduria entomon* L., which is faced with a choice of prey organisms of varying ecological origin, including marine or estuarine species on the one hand, and "limnic" species on the other. In clearly sublittoral areas *S. entomon* has no principal invertebrate competitors for food, but in shallow water regions odonata larvae may play a similar regulatory role on the benthic community. Against this background, the structuring role of *S. entomon* for the benthic infauna in shallow brackish waters was tested in relation to (a) one major invertebrate food competitor (*Libellula quadrimaculata*; Odonata), and (b) prey species of varying ecological origin (marine or estuarine, exemplified by *Macoma balthica* and *Corophium volutator*, and "limnic", e.g. *Asellus aquaticus* and larval chironomids). Field and aquarium experiments illustrated that *S. entomon* is technically capable by predation to exhibit a regulatory pressure on all prey items offered, but that the effects at community level are difficult to distinguish from the natural variation within the ecosystem. On shallow bottoms *S. entomon* exhibits similar predatory effects to the larvae of the dragonfly *L. quadrimaculata*. It is concluded that *S. entomon* in shallow Baltic archipelagoes is something of a "universal competitor", capable of affecting populations regardless of their functional origin.

1. Introduction

The isopod *Saduria entomon* is a large, widely dispersed omnivorous predator (Green 1957), occurring in fully marine, brackish and limnic waters (Apstein 1909, Ekman 1920, 1953). In the Baltic Sea *S. entomon* is a glacial relict species found throughout the depth gradient (in the Åland area, for example, it is found from 1–290 m), thus potentially being an important community regulator in a large variety of benthic assemblages (Segerstråle 1966, 1969, 1982, Bagge & Ilus 1973), ranging from the species-poor deep bottoms to the species-rich and productive littoral communities. In shallow water *S. entomon* occurs throughout the year, but feeding and growth is regulated by temperature (Leonardsson 1986). In shallow archipelago areas *S. entomon* is faced with a choice of potential prey organisms of varying ecological origin, namely marine, estuarine and limnic. As

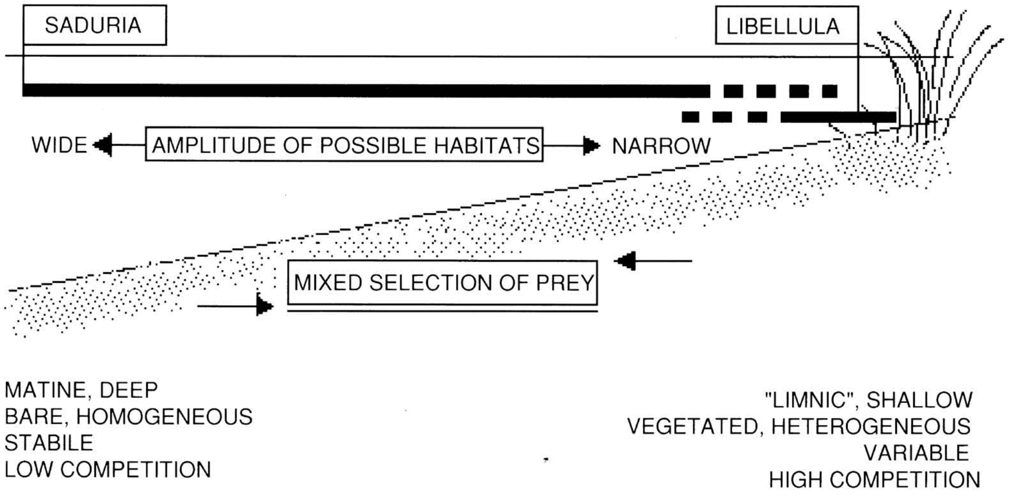

Fig. 1. The principal ecological locations of *Saduria* and *Libellula* in relation to origin, type of habitat, and overall level of competition (as a function of community diversity). The black horizontal bars denote the spatial distribution of the two species, and the zone of overlap is denoted with broken bars.

regards the prey species occurring in deep water, *S. entomon* has no principal epibenthic invertebrate competitors in the northern Baltic Sea, but in shallow areas shrimp, polychaetes and large insect larvae (changing with exposure and substrate), as well as fish (eg. gobies; *Pomatoschistus* spp., flounder; *Plathictys flesus* and ruffe; *Acerina cernua*), are potential competitors for food (Mattila & Bonsdorff 1988, Rönn et al. 1988). Thus the ecological role of *S. entomon* will vary widely even over short geographical distances, depending on the local habitat (e.g. off-shore deep areas in contrast to near-shore shallow locations; Fig. 1). *S. entomon*, on the other hand, is a highly preferred food item for many fish species, such as cod (*Gadus morrhua*) and fourhorn sculpin (*Myoxocephalus quadricornis*), which are both benthic feeding fish (Westin 1970, Haahtela 1975, Leonardsson et al. 1988).

The aim of this study is to illustrate the role of *S. entomon* as a potential structuring factor on benthic infauna of different ecological origins, and its primary competitive strength in shallow water. The other predator (i.e. potential competitor) used is the dragonfly *Libellula quadrimaculata*, the larvae of which spend one or two years in the sediment (Corbet 1980, Pierce & Crowley 1985, Miller 1987). To test whether either of these predators shows any clear selection or preference for marine, estuarine or limnic prey, several available prey-species were used in the experiments (mainly the marine bivalve *Macoma balthica*, the estuarine amphipod *Corophium volutator*, the limnic isopod *Asellus aquaticus* and larval chironomids). This investigation thus relates the role of one specific relict species to theories of ecosystem development, succession and maintenance (Connell & Slatyer 1977, Glasser 1979, Connell 1983, Schoener 1983, Lawton 1987, Menge & Sutherland 1987), and represents a continuation to previous studies of the same habitats (Bonsdorff et al. 1986, Rönn et al. 1988).

2. Material and methods

Field experiments were conducted in the vicinity of Husö Biological Station on Åland (N. Baltic Sea; 60°17′N, 19°49′E) at localities covering the "ecological gradient" ranging from the exposed, outer archipelago to the inner, sheltered bays (cf. Fig. 1). Two different test situations were used, namely studying the effects of artificially increased densities of either of the predators on natural communities, and their effect on the establishment and succession of benthos on initially azoic sediment. To enclose natural sediment, including the existing community at a depth of

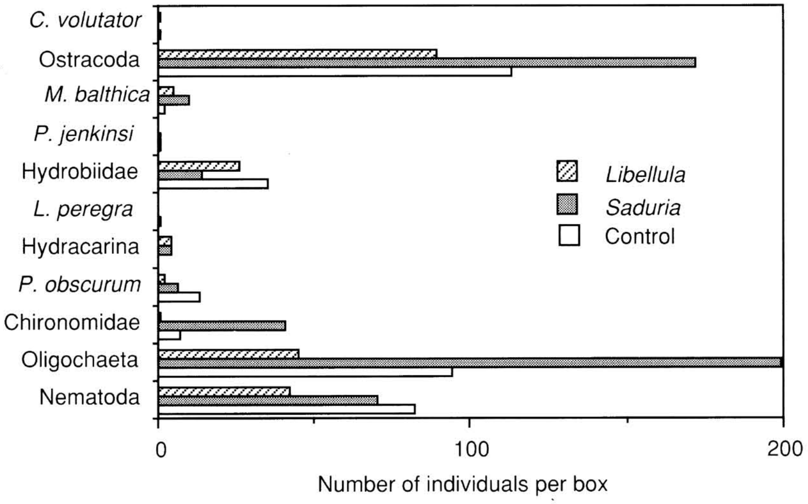

Fig. 2. Number of immigrating individuals per species to colonization boxes with 7 *Saduria* or 7 *Libellula* compared to the control box with no predator. Experimental duration = 4 weeks at a depth of 1.5 m in a semiexposed habitat in the outer archipelago.

1–1.5 m, cylinders of sheet metal (1 m high, ∅=16 cm, covered with a 0.5 mm mesh-net) were used. Three different set-ups were run simultaneously (5 replicates of each) for two weeks, namely with no predators, or with two individuals of either *S. entomon* or *L. quadrimaculata* added. The effects of constant predation and competition on benthic colonization were studied using boxes (30×40×11 cm) filled with defaunated sediment (Bonsdorff & Österman 1985, Bonsdorff et al. 1986, Rönn et al. 1988, Bonsdorff 1989). A set-up similar to the cylinder-tests was used, 7 individuals of each predator being added to separate net-covered boxes. The boxes were left at a depth of about 1.5 m for 4 weeks, after which 15 core samples (∅=2.5 cm) were taken from each box. In all the field experiments reference samples were taken at the beginning and end. All field samples and the sediment in the cylinders were washed on a 0.5 mm screen (the cores from the colonization boxes were washed on a 0.25 mm screen), and treated separately.

The technical ability (predation intensity) to regulate any given prey population was tested in small (10×10 cm; 0.75 l) flow-through aquaria, as described in Bonsdorff & Rönn (1985) and Rönn et al. (1988). In the laboratory, the hydrographical conditions mirrored those at the site of the field experiments (9–17°C, 4–5 ppt salinity, pH 7.9–8.3). All aquarium experiments were run for 7 days, and the predators were starved for 48 hours before each run. The prey species were allowed to acclimatize in the aquaria for about 3 hours before the predators were added. In each test three set-ups (no predators, or one individual of either *S. entomon* or *L. quadrimaculata*) were adopted, and 5 replicates of each set-up were made.

Standard statistical and graphical methods were applied to the data (StatView™ SE + Graphics for the Macintosh; Abacus Concepts, Inc.).

3. Results

3.1. Field colonization experiment

In a field experiment for testing the effect on the benthic community succession of the predators *Saduria entomon* and *Libellula quadrimaculata*, a significant difference ($P<0.05$, one-way ANOVA) was found between both set-ups and the control when comparing the mean number of individuals per sample (Fig. 2). Although the effect of predation on the establishment of the

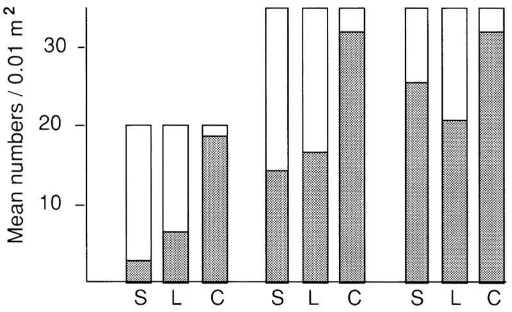

Fig. 3. The predatory effect of *Saduria* (S) and *Libellula* (*L*) on the prey species *Asellus aquaticus, Ostracoda* spp. and *Macoma balthica* compared to control aquaria (C). Shadowed bars = living, and open bars = dead, prey organisms after the experiment (7 days in small flow-through aquaria).

immigrating species was significant, the effects at community level in terms of diversity and evenness were low, and no significant differences between the set-ups were found (*H′*-values were 2.305 for the control community, compared to 2.231 with *Saduria*, and 2.419 with *Libellula*, and *J*-values were 0.666, 0.645 and 0.728, respectively). For the odonata there was a tendency to increased diversity as a result of selective predation, as previously demonstrated for similar communities with the polychaete *Nereis diversicolor* (Rönn et al. 1988). When comparing the effects on dominant species such as *Oligochaeta* spp., *Ostracoda* spp. and larval chironomids, significant differences (P<0.05, one-way ANOVA) were found between all set-ups with respect to the oligochaetes. No significant effect of *L. quadrimaculata* on ostracods and larval chironomids was observed, yet there was a significant difference (P<0.05) between the control box and the box with *S. entomon*, illustrating the relative importance of the relict crustacean in shallow sub-littoral waters.

The results from analyzed cylinder samples show a similar effect of *S. entomon* and *L. quadrimaculata* on the natural zoobenthos community as from the colonization experiment. The effect is emphasized by a higher diversity and evenness in the cylinders with added predators.

3.2. Aquarium experiments

When testing for possible differences in prey selection by *S. entomon* and *L. quadrimaculata* using aquarium experiments, the marine/estuarine species *Macoma balthica, Ostracoda* spp., together with the limnic species *Asellus aquaticus*, were used as prey species. Comparing control aquaria (prey without predators) with set-ups having one predator (*Saduria* or *Libellula*) each, a significant difference (P<0.05, *t*-test) was found. No significant differences between predator set-ups were found, however. The survival rates of the prey organisms used varied between 90.0 and 91.4% in the controls, and 15.0 and 74.2% in the predation experiments. The direct predatory effects of both *Saduria* and *Libellula* are summarized in Fig. 3. Additional experiments have further supported the hypothesis that *S. entomon* has the capacity to regulate prey populations of different origin.

4. Discussion

The results from both the field and the laboratory demonstrate the potential of *S. entomon* and *L. quadrimaculata* to affect the biotic environment in terms of predation. Previous studies on *S. entomon* have largely disregarded predation, but the present findings support the initial assumption that the glacial relict *S. entomon* is able to compete successfully with specialized predators such as *L. quadrimaculata* in very shallow waters as well. Being an omnivorous predator (Green 1957) capable of living throughout the depth gradient in the Baltic Sea, *S. entomon* must be considered as an important overall community regulator (Segerstråle 1982). Comparing the predatory effect of *L. quadrimaculata* on shallow water areas (Benke 1976) with the effect of *S. entomon*, one may expect competition for food between these two predators as they exhibit no significant difference in prey selection. Furthermore, fish and polychaetes are also potential competitors for food in shallow areas (Mattila & Bonsdorff 1988, Rönn et al. 1988).

Applying empirical feeding models (Linton & Davies 1988) to the laboratory data, the regulatory capacity of *Saduria* and *Libellula* on the prey items studied should also be significant in the field. The results of the manipulative field experiments (Fig. 2) in fact support the results concerning principal population effects at community level. The present data is also in agreement with the general finding that trophic infaunal complexity is partly regulated through internal predation, as summarized for marine environments by Commito & Ambrose (1985). *S. entomon* also forms an important link in the food web connecting the benthic environment with the fish community, as it is a major food item of some benthic feeding fish (Westin 1970, Haahtela 1975, Leonardsson et al. 1988).

In conclusion, it seems evident that the glacial relict isopod *S. entomon*, occurring across a very wide amplitude of habitats (McCrimmon & Bray 1962, Narver 1968) has adapted to a broad variety of habitats, and is capable of competing for food successfully even in marginal habitats with predators such as *L. quadrimaculata*, which are highly specialized in their own environment. Thus *S. entomon* is yet another example of the relative importance of the zoobenthos as a structuring agent within the benthic community (Arntz 1980, Commito & Ambrose 1985, Rönn et al. 1988).

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