

Behavioural responses to chemical cues of predation risk in a three-trophic-level Baltic Sea food chain

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ABSTRACT: Behavioural responses of 2 Baltic benthic crustaceans to chemical substances from predators were studied using infrared video-recording in the laboratory. This is the first study of behavioural responses to species-specific chemical substances in a 3-trophic-level food chain. Exposure to chemical substances from a predatory fish, the short-horned sculpin *Myoxocephalus scorpius* (L.), caused the isopod *Saduria entomon* (L.) to remain buried in the sediment most of the time and decreased its foraging success on the amphipod *Monoporeia affinis* (Lindström). *M. affinis* decreased its swimming activity when exposed to water from *S. entomon* feeding on *M. affinis*, whereas water from unfed *S. entomon* had no such effect.

KEY WORDS: Chemical cues · Three-trophic-level food chain · *Monoporeia affinis* · *Saduria entomon* Fish · Benthos · Behaviour · Baltic Sea

INTRODUCTION

In the aquatic environment, the use of chemical cues is probably universal (Dodson et al. 1994). Prey and predators can often discover and localise each other through chemical cues, which may profoundly influence their interactions (Sih 1986, Rittschof 1993, Abrahams 1994, Rochette et al. 1994). The life-history strategy (Crowl & Covich 1990), behaviour (Folt & Goldman 1981, Dodson et al. 1994, Duval et al. 1994), activity pattern (Sih 1986, Holomuzki & Short 1988) and morphology (Appleton & Palmer 1988, Larsson & Dodson 1993) of potential prey may be significantly affected by the presence of predators. Conventional optimal foraging theory predicts that predators should maximise their net rate of energy intake (Hughes 1980). Factors influencing the rate of energetic acquisition, e.g. energy reserves and potential risks from predators, have been taken into consideration (Sih 1982, Vadas et al. 1994) and also included in models (Mangel & Clark 1986, Gilliam & Fraser 1987, Burrows & Hughes 1991,

McNamara & Houston 1992). To maximise fitness, foragers should weigh potential energy gain against mortality risk (Dill & Fraser 1984, Abrahams & Dill 1989).

Predation risk can be perceived through visual, mechanical and chemical cues (Busdosh et al. 1982). Many aquatic invertebrates have small, poorly developed, non-image-forming eyes, sensitive mainly to changes in light intensity (Dodson et al. 1994), but possess well-developed chemoreceptors (Laverack & Ardill 1965, Pynnönen 1985, Larsson & Dodson 1993, Kaufman 1994). Chemical receptors and chemical cues can be used in darkness and by animals that have poor vision or do not see at all. Chemical cues may be molecules large enough to be species-specific, such as proteins (Atema 1988). Concentration and/or composition of the cue makes it possible to recognise a predator and whether it is actively feeding, has recently fed or is starving (Phillips 1978, Appelberg et al. 1993). Alarm substances, originating from predator-mediated release by injured conspecifics, reveal the presence of a predator (Appleton & Palmer 1988, Alexander & Covich 1991a, Hugie et al. 1991, Houtman & Dill 1994, Vadas et al. 1994) and may affect behaviour, growth rate, and morphology (Sih 1986, Appleton & Palmer 1988).

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The question addressed here is whether chemical substances from predators influence the behaviour of 2 Baltic benthic crustaceans. Thus, the aims of my experiments were to determine: (1) whether exposure to chemical substances from a predatory fish, the short-horned sculpin *Myoxocephalus scorpius* (L.), affected the behaviour of the predatory isopod *Saduria entomon* (L.); (2) whether the rate of predation by *S. entomon* on its natural prey, the amphipod *Monoporeia affinis* (Lindström), changed in fish conditioned water; (3) whether exposure to the odour of starved *S. entomon* affected the activity and behaviour of *M. affinis*; and (4) whether *M. affinis* reacted to waterborne substances from *S. entomon* and its prey while the isopod killed, ate and digested individuals of *M. affinis*. The species chosen represent a naturally occurring 3-trophic-level system found in the species-poor Baltic benthic community. To my knowledge, this is the first study of the importance of behavioural responses to species-specific chemicals in a 3-trophic-level food chain.

MATERIAL AND METHODS

Study area, species studied, collection and treatment of sediment and animals. This study was carried out in the northwestern Baltic proper at the Askö Laboratory on the east coast of Sweden (58°49'N, 17°38'E). On the species-poor sub-thermocline benthic bottoms in this area, the amphipod *Monoporeia affinis* is one of the most abundant and productive species, with a natural abundance in 1981 to 1993 of 80 to 2100 1 yr old (1+) *M. affinis* m⁻² at 27 m depth in the Askö area (station 6017 of the National Swedish Environmental Monitoring Program). *M. affinis* is a night-active surface-forager that mainly dwells in the upper 5 cm of the sediment (Hill & Elmgren 1987, Lopez & Elmgren 1989, Lindström et al. 1991). Late in the evening, the amphipods leave the bottom for excursions into the water column (Lindström & Lindström 1980). When they return to the bottom, they dig a new hole, in which they lie on the back. By moving the pleopods, water is efficiently circulated into the burrow (Lindström 1991).

Abundances of the predatory isopod *Saduria entomon* ranged from 0 to 110 ind. m⁻² during the same period (Cederwall 1990, pers. comm.). In the late 1980s and early 1990s, *S. entomon* was easily caught in the study area, but by the summer of 1994, when this study was performed, sufficient numbers could not be obtained. *S. entomon* was therefore collected in the Norrby archipelago, northern Bothnian Sea (63°30'N, 19°50'E), at a salinity of ca 4 psu. In the laboratory, the euryhaline (Lockwood & Croghan 1957) *S. entomon*

acclimatised almost without mortality to a gradual increase in salinity from 4 to 6.5 psu, the salinity in the Askö area. *S. entomon* is a predator and a scavenger that possesses an array of feeding behaviours, and is reported to be mainly nocturnal (Westin & Aneer 1987). The eyes of *S. entomon* are small, with maximal sensitivity to green wavelengths, which dominate at the depths where this isopod lives. However, food is located and recognised via chemoreceptors and chemical cues (Pynnönen 1985). *S. entomon* has 2 types of chemoreceptors, viz. distance chemoreceptors on the first antennae and contact chemoreceptors on the mouth parts. Intact antennae are crucial for bilateral antennular chemoreception (Pynnönen 1985) of odours, such as those coming from dead fish. Small *S. entomon* avoid water from larger cannibalistic conspecifics (Leonardsson 1991).

In the Baltic, *Saduria entomon* is the main diet for the short-horned sculpin *Myoxocephalus scorpius* (Haahtela 1990) and is also eaten by the fourhorn sculpin *M. quadricornis* (L.) (Westin 1970, Aneer 1975). The short-horned sculpins used in the experiments were caught with a gill net and kept in 60 l containers at ca 7°C.

Sediment and *Monoporeia affinis* were collected close to the laboratory, at 30 m depth, using a benthic sled (Blomqvist & Lundgren 1996). The sediment was sieved through a 300 µm metal mesh net and kept cold prior to use. The amphipods were stored in aerated water in a thermostat controlled room (7°C), with a daily 17 h light:7 h dark cycle simulated with a dim green light; the same light cycle as used in the experiment. The day before the start of the experiment, individual *M. affinis* were randomly picked in batches of 5 and inspected under a stereomicroscope to ensure that only intact amphipods were used.

The energy reserves of a predator often affect its foraging intensity (McNamara & Houston 1986). Even though Leonardsson (1991) found no difference in consumption rates for starved or fed *Saduria entomon*, the isopods in my experiments were deprived of food 2 d prior to the start of the experiment. *S. entomon* can survive starvation for months with little mortality (author's unpubl. obs.). Only non-gravid isopods with intact antennae were used.

General experimental set-up. Square plastic aquaria, placed in two 100 l troughs (0.88 m²) (Fig. 1), were used as containers. The aquaria had a sediment area of 310 cm² and 11 cm high walls, each of which had a 75 cm² rectangular hole covered with a 0.2 mm mesh net, allowing water but not animals to pass through. The sediment depth was 3.5 cm, just reaching the holes in the aquarium walls. Below the 100 l troughs, two 140 l troughs (0.93 m²), one containing sea water and one prepared water, were placed. Sea

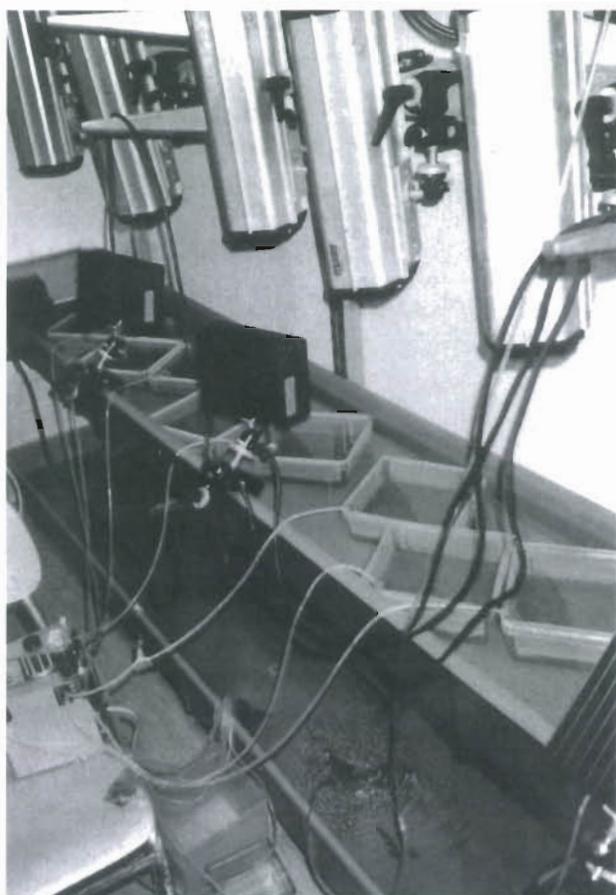


Fig. 1. Experimental set-up. Aquaria were connected to sea or prepared water (lower trough) via a peristaltic pump. Video-cameras were placed above the aquaria. Infrared light emitters (to the left of the aquaria) made video-recording possible in the dark

water was pumped into the aquaria in one of the upper troughs, and prepared water into the aquaria in the other upper trough. Water flow into each aquarium, $0.8 \pm 0.11 \text{ h}^{-1}$, was regulated with a multi-channel peristaltic pump (Alitea, Stockholm, Sweden). The sea water came from 16 m depth; it was filtered through sand (grain size 0.6 to 0.8 mm) and cooled (ca 7°C , salinity 6.5 psu) before reaching the troughs and was aerated once in the troughs. Cue water was prepared for each experiment. The fish, unfed isopod and fed isopod experiments were run consecutively, and the experimental equipment was thoroughly cleaned prior to the start of a new experiment to avoid contamination between experiments. Using milk as a tracer, it was shown that the whole water volume of the experimental aquaria was reached by the incoming fluid in less than 10 min.

Twelve video-recording cameras (Ikegami ICD-42EAC) sensitive in the infrared region of the light spectrum were placed above the aquaria (Fig. 1). Lamps emitting sufficient infrared light ($>880 \text{ nm}$) for the registering cameras were used. The light sensitivity of *Monoporeia affinis* declines sharply towards the red end of the spectrum (Donner 1971), as does that of *Saduria entomon* (Lindström et al. 1991), and neither species can detect infrared light (Donner & Lindström 1980, Lindström et al. 1991). Time-lapse recording started prior to the addition of *S. entomon*. A sequential video-switcher activated the recording cameras in turn from camera 1 to 12 and then repeated the procedure. Recording time was registered on the videotape, and intervals between moving pictures as seen on the TV monitor were 2.2 or 4.1 s, respectively, for 24 h and 48 h long time-lapse recordings. It was not possible to quantify accurately the number of amphipods swimming at a given time, hence swimming activity was registered as present as soon as a single amphipod was seen swimming. As the recording time was registered on the videotape it was possible to determine the duration of the different activities of the animals.

When terminating the experiments, the sediment was sieved, and amphipods retained on a $500 \mu\text{m}$ mesh metal net were preserved in 4% buffered formalin and stained with Rose Bengal. The length of the amphipods was measured on straightened out animals from the tip of the rostrum to the end of the last urosome segment with an image analyzing system (Zeiss, MOP video-plan). Isopod length was measured from the anterior end of the head shield to the tip of the telson.

Fish experiment. In order to test whether chemical substances from predatory fish influence the behaviour of *Saduria entomon*, and ultimately the survival of its amphipod prey (*Monoporeia affinis*), the following 4 treatments were set up: (1) *S. entomon* and *M. affinis* in untreated sea water (8 aquaria), (2) *S. entomon* and *M. affinis* in fish-treated water (8 aquaria), (3) controls with *M. affinis* alone in untreated sea water (3 aquaria), and (4) *M. affinis* in fish-treated water (3 aquaria). This gave a total of 22 aquaria, 12 of which

Table 1 Experimental set-up of the fish experiment. Fish were not fed during the experiment

Treatment	No. of aquaria	No. filmed	No. of <i>S. entomon</i> aquarium ⁻¹	No. of <i>M. affinis</i> aquarium ⁻¹
Sea H ₂ O + <i>S. entomon</i> + <i>M. affinis</i>	8	6	1	30
Fish H ₂ O + <i>S. entomon</i> + <i>M. affinis</i>	8	6	1	30
Sea H ₂ O + <i>M. affinis</i>	3	0	–	30
Fish H ₂ O + <i>M. affinis</i>	3	0	–	30

were video-recorded (6 each of treatments 1 and 2) (Table 1). Video-recordings were made in 48 h time-lapse mode for a total of 72 h.

Thirty adult *Monoporeia affinis* ($\bar{x} \pm SE$, 7.8 ± 0.2 mm long) were gently added to each box at the start of the experiment. One *Saduria entomon* (30 ± 1 mm) per aquarium was added in treatments 1 and 2.

Fish-treated water was prepared in one of the lower 140 l troughs by keeping 3 *Myoxocephalus scorpius* (total weight ca 1 kg) in sea water for 24 h prior to the start and during the entire fish experiment. Sea water and fish-treated water were refilled twice a day into the troughs (Fig. 1). The fish-treated water for refilling was prepared in 3 troughs, each of which held nothing but 1 short-horned sculpin (ca 0.3 kg) in 45 l sea water.

Unfed isopod experiment. The experiment was designed to test whether *Monoporeia affinis* reacted to water which had contained unfed *Saduria entomon*. *M. affinis* were assigned at random to either of 2 treatments: water from unfed isopods, or untreated sea water. Each treatment had 8 aquaria, 6 of which were video-recorded (for 22 h) as above (Table 2). Thirty *M. affinis* (average size 7.8 ± 0.2 mm) were added to each aquarium. The unfed isopod-treated water was prepared by keeping unfed isopods (37 specimens, total weight ca 24 g) in natural sea water in one of the lower 140 l troughs (Fig. 1) for 48 h prior to and during the entire experiment. Water was not refilled.

Fed isopod experiment. To test if substances from *Saduria entomon* killing, eating and digesting *Monoporeia affinis* affected the behaviour of other *M. affinis*, fed-isopod-treated water, i.e. sea water containing 34 isopods (mean body length ca 30 mm, total weight ca 22 g) and 340 amphipods (ca 7.7 ± 0.2 mm) from a 140 l trough, or untreated sea water from another 140 l trough was added to aquaria, each containing 30 *M. affinis*. The aquaria were video-recorded in 24 h time-lapse mode for 22 h (8 aquaria per treatment, 6 of which were video-recorded) (Table 3). In the fed-isopod-treated water trough, isopods were fed *M. affinis* 2 d prior to the experiment and during the entire experiment. During this 3 d period, a total of 290 amphipods were consumed, i.e. ca 8 per isopod. Water was not refilled.

Statistics. One-factor analysis of variance (ANOVA) was used, except when variance was heterogeneous according to Cochran's or Bartlett's test (balanced or unbalanced treatments respectively). Significant results were followed by the Tukey test for unequal N

Table 2. Experimental set-up of the unfed isopod experiment. Isopods were not fed during the experiment

Treatment	No. of aquaria	No. filmed	No. of <i>M. affinis</i> aquarium ⁻¹
Unfed-isopod-treated H ₂ O + <i>M. affinis</i>	8	6	30
Sea H ₂ O + <i>M. affinis</i>	8	6	30

Table 3. Experimental set-up of the fed isopod experiment. Isopods were fed amphipods during the experiment

Treatment	No. of aquaria	No. filmed	No. of <i>M. affinis</i> aquarium ⁻¹
Fed-isopod-treated H ₂ O + <i>M. affinis</i>	8	6	30
Sea H ₂ O + <i>M. affinis</i>	8	6	30

(= TT). When homogeneity of variances could not be obtained through data transformation, the Mann-Whitney *U*-test was used. A paired *t*-test tested for differences in the light/dark activity of *Saduria entomon*. Amphipod activity data was analysed using 2-factor repeated measures ANOVA. Calculations based on a pilot study indicated that 8 replicates would be needed to achieve a power of 0.8 in order to detect a difference of at least 30% in amphipod survival (Zar 1984).

RESULTS

Fish experiment

During the 72 h experimental period, *Saduria entomon* spent only $0.8 \pm 0.3\%$ (36 min) of its time at the sediment surface in fish-treated water, but significantly longer, $7.9 \pm 3.3\%$ (340 min), in the sea water treatment (ANOVA, $F_{1,9} = 13.8$, $p = 0.005$). One *S. entomon* in the sea water treatment moulted and was excluded from the analysis. No differences in activity during the light and dark periods were found within the fish treatment (paired *t*-test, $p > 0.05$) or within the sea water treatment (paired *t*-test, $p > 0.05$) (Fig. 2).

Survival of *Monoporeia affinis* in the controls for the fish (29 ± 1 specimens) and sea water (29 ± 1 specimens) treatments and in the *Saduria entomon* with fish-treated water treatment (26 ± 1 specimens) was significantly better than in the *S. entomon* with sea water treatment (19 ± 2 specimens) (ANOVA, $F_{3,17} = 12.21$, $p = 0.0002$; TT, $p < 0.05$) (Fig. 3).

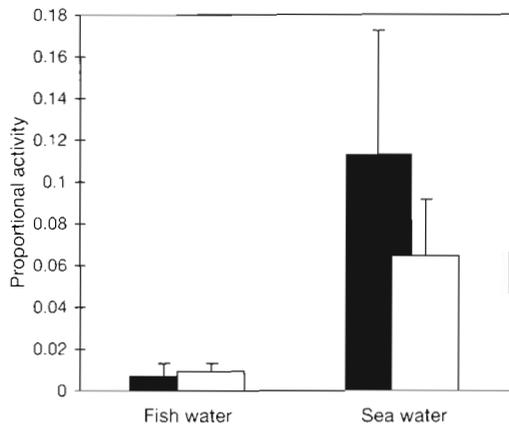


Fig. 2. Proportional activity of *Saduria entomon* in the fish experiment. Mean + standard error of the mean. Black denotes the dark period and white the light period

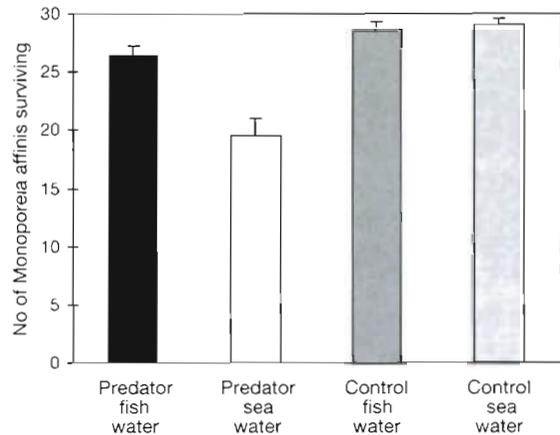


Fig. 3. Number of *Monoporeia affinis* surviving in the presence and absence (control) of *Saduria entomon* in the fish experiment. Mean + standard error of the mean

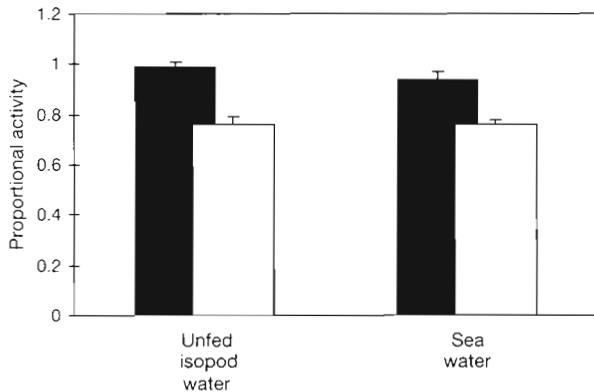


Fig. 4. *Monoporeia affinis* proportional activity in the dark and light periods in the unfed isopod experiment. Mean + standard error of the mean. Black denotes the dark period and white the light period

Unfed isopod experiment

Amphipod survival was high, $97 \pm 1\%$, in both treatments (ANOVA, $F_{1,14} = 0.43$, $p = 0.52$), with a similar swimming activity, $82 \pm 1\%$ (of the total experimental time) in sea water and $83 \pm 2\%$ in unfed-isopod-treated water (Table 4); and for both treatments swimming was significantly more intense in the dark (Fig. 4, Table 4). All *Saduria entomon* survived.

Fed isopod experiment

Amphipod survival was 100% in sea water and $96 \pm 2\%$ in fed-isopod-treated water (Mann-Whitney U -test, $p = 0.003$, $n = 16$). All isopods survived. Amphipod swimming activity was significantly affected by the origin of the added water (Table 5). In fed-isopod-

treated water, swimming was reduced, occurring for only $16 \pm 4\%$ of the total experimental time, while in sea water the corresponding figure was $72 \pm 6\%$. In both treatments, *Monoporeia affinis* was proportionally more active during the dark period (Fig. 5, Table 5).

DISCUSSION

Predation risk often affects prey behaviour (Alexander & Covich 1991b, Legault & Himmelman 1993), and potential prey often shift into safer habitats (Dill 1987, Lima & Dill 1990, Sih 1993, Jachner 1995) or spatially within habitats (Phillips 1977, Alexander & Covich 1991b, Dix & Hamilton 1993) to avoid predation. Risk of predation usually reduces locomotor activity of prey (Lima & Dill 1990, Sih 1993), which improves the chance of avoiding detection by the predator. *Monoporeia affinis* and *Saduria entomon* were both less mobile in the presence of odour from their natural predators, and both spent more time within the sediment.

The fish experiment indicates that *Saduria entomon* reacts to perceived predation risk with decreased

Table 4. Unfed isopod experiment. Two-factor repeated measures ANOVA performed on *Monoporeia affinis* proportional activity during a light or dark period in unfed-isopod-treated water or sea water (cue)

Source of variation	df	F	p
Cue	1	0.79	0.4159
Light/dark	1	54.94	0.0007
Cue \times light/dark	1	0.17	0.6961

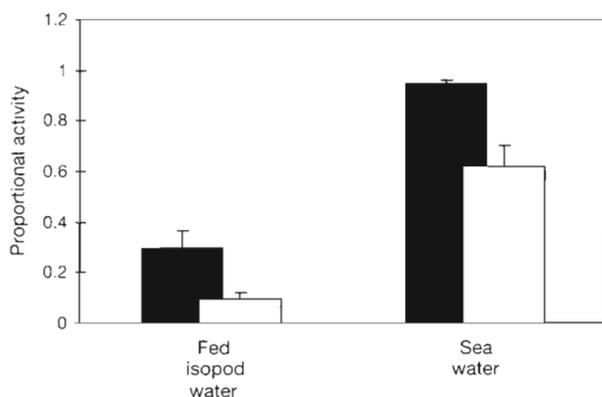


Fig. 5. *Monoporeia affinis* proportional activity in the dark and light periods in the fed isopod experiment. Mean + standard error of the mean. Black denotes the dark period and white the light period

Table 5. Fed isopod experiment. Two-factor repeated measures ANOVA performed on *Monoporeia affinis* proportional activity in a light or dark period in fed-isopod-treated water or sea water (cue)

Source of variation	df	F	p
Cue	1	184.50	0.00004
Light/dark	1	62.04	0.00053
Cue × light/dark	1	1.19	0.32570

activity. When exposed to fish-treated cue water, the activity of *S. entomon* at the sediment surface decreased; Leonardsson (1991) found a similar reaction for small *S. entomon* exposed to chemical cues from predatory larger conspecifics. In spite of the depressed activity of *S. entomon*, amphipods were still eaten, albeit at a slower rate than when fish odour was absent.

When *Saduria entomon* was burrowed in the sediment, the antennae and head were occasionally seen, but the body was mostly hidden. In sea water, antennae were seen more frequently and for longer periods than in the fish-treated water. Once the antennae had been withdrawn into the sediment, they were very difficult to detect, except when exposed again at the same, or nearly the same, spot where they had been seen earlier. However, movement of a totally burrowed *S. entomon* could sometimes be followed through ridgelike structures 'moving' over the sediment surface, with some amphipods escaping from the sediment just ahead of the moving isopod. When neither parts of the body nor ridgelike structures were seen, the isopods remained undetected until appearing again at the sediment surface. No estimates of antennal exposure or of behaviour within the sediment can thus be presented.

Saduria entomon in sea water stayed mainly just below the sediment surface, with flicking antennae showing, thus increasing the exposure of its chemical receptors to odour cues (Schmitt & Ache 1979). Short-horned sculpins are visual foragers with a diel foraging cycle, being diurnal in winter and nocturnal in summer (Westin & Aneer 1987). The sculpins do not search for food within the sediment, but use an ambush technique (L. Westin pers. comm.). Foraging methods used by *S. entomon* include ambushing, or sit and wait, behaviour; sediment surface food search (fast active hunt, i.e. when the isopod swims or moves on, or just below, the sediment surface with its body showing); and burrowing food search (slow active hunt, used when food is searched for at depth in the sediment, with the body hidden in the sediment) (Green 1957, Pynnönen 1985, Ejdung & Bonsdorff 1992). The foraging methods used by *S. entomon* change with exposure to fish-treated cue water, suggesting a perception of increased predation risk. Although quick rushes over the sediment surface might have provided *S. entomon* with food, the isopod seemed to search for food mainly within the sediment when exposed to fish odour, video sequences sometimes showing movements of *S. entomon* within the sediment. The change in behaviour, and use of a habitat spatially separated from that normally foraged in by short-horned sculpins, should lower encounter rates between short-horned sculpins and *S. entomon* and increase isopod survival. However, predator avoidance behaviours often lower food encounter rates (Sih 1993), while energy continues to be used for maintenance and locomotion (Norberg 1977). Evidently, *S. entomon* searched for prey down in the sediment, and the number of prey consumed decreased, as often found when predatory fish are present (Holmuzki & Short 1988).

As sculpins in nature include amphipods in their diet (Westin 1970), they directly affect amphipod survival. This laboratory study of a benthic 3-trophic-level system, with fish odour present during the whole experiment, reflects a near distance predator-prey situation in the field. In the experiment, the presence of fish odour had an indirect positive effect on amphipod survival, since the activity of the predatory isopod decreased. *Saduria entomon* in the experiment could only avoid the perceived predator by burrowing and decreasing its activity, but in nature another avoidance behaviour, emigration, is possible (Sparrevik & Leonardsson 1995), and probably important.

Recently, the first steps in the characterization of kairomones released by planktivorous fishes have been made (Loose et al. 1993, von Elert & Loose 1996). The specific substances released in my experiment are unknown. Additional research is needed to determine

the chemical composition of the substances, their natural concentrations and their rate of degradation.

Recognition of chemical cues emitted by predators or injured conspecifics may increase prey survival, and many aquatic organisms possess this ability (Phillips 1978, Hugie et al. 1991, Covich et al. 1994, Duval et al. 1994). Large crustaceans obtain chemical information by producing currents (Atema 1988), and *Monoporeia affinis* may receive a continuous flow of information on predation risk from chemical cues, which enter its burrow with the currents created by its beating pleopods. The swimming activity of *M. affinis* decreased drastically in water with cues from *Saduria entomon* fed *M. affinis*, indicating that *M. affinis* is able to evaluate the degree of risk connected with the chemical information received. The 'dietary history' of a predator often affects prey responses (Duval et al. 1994). Lack of response to a non-foraging or starving predator has been reported also in the sea urchins *Strongylocentrotus purpuratus*, in the freshwater snails *Physella virgata* and *P. gyrina* and the cladoceran *Daphnia galeata mendotae* (Phillips 1978, Crowl & Covich 1990, Stirling 1995, Turner 1996).

The Baltic benthic ecosystem has been considered as fairly simple, due to its low macro- and meiofaunal diversity (Elmgren 1978). Large areas in the Baltic are covered by fine grained sediments, over which chemoreception works better than on coarse (ca 2 to 3 mm) substrates (Weissburg & Zimmer-Faust 1993). Taking chemical predator-prey interactions into consideration will increase the complexity of interactions in this system. This laboratory study demonstrates that the predator-prey interactions investigated are affected by a variety of chemical cues from predators and prey. Further studies are required to evaluate better the importance of such chemical cues in the field, and of indirect interactions between species caused by chemical cues, in this community.

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