Competition between the introduced polychaete *Marenzelleria* sp. and the native amphipod *Monoporeia affinis* in Baltic soft bottoms

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ABSTRACT: The North American spionid polychaete *Marenzelleria* cf. *viridis* was reported from the Baltic Sea for the first time in 1985. The species has spread rapidly and now dominates many soft-bottom communities, where it dwells in burrows down to 30 cm deep in the sediment. In the Baltic Sea, below 10 m water depth, the macrobenthic community is composed of only a handful of species, among which the amphipod *Monoporeia affinis* is a key member. This species is highly mobile; it swims actively at night but remains burrowed in the sediment during the day. Due to similarities in feeding mode and sympatric occurrence, the polychaete may compete with the amphipod for both food and space. One plausible outcome of interactions between the 2 species is that the amphipod, the more mobile species, would avoid areas where the more sessile polychaete is present in high numbers. In the laboratory, we tested the hypothesis that, if given the choice, the amphipod avoids burrowing in sediment with high polychaete abundances. The amphipod burrowed in significantly lower numbers in patches with high polychaete abundance compared to those with lower abundance. Also, plastic tubes mimicking polychaete body structure were not avoided by the amphipods, indicating that the physical tube structure of the polychaetes does not explain the amphipod's choice of burrowing site. Furthermore, the amphipod did not increase or prolong swimming activities as a function of higher worm density, indicating that increased swimming activity over dense polychaete patches and subsequent migration away from them is not a likely explaination of why this amphipod burrow less frequently in patches of high polychaete abundance.

KEY WORDS: Alien species · Native species · Behaviour · Interference · Competition · Benthos · Baltic Sea · Laboratory experiment

INTRODUCTION

The field of invasion-ecology was introduced by Elton (1958) and has since then gained increasing attention, especially for commercially important terrestrial habitats.

During the last 2 centuries, the rate of species introductions into marine and brackish-water ecosystems has increased exponentially (Gollasch 1996, Cohen & Carlton 1998, Leppaekoski & Olenin 2000a, Ruiz et al. 2000). In San Francisco Bay, for example, over 230 introduced species have been reported, and these now constitute between 40 and 100 % of the most abundant species (Cohen & Carlton 1998). Over 100 species have been transferred to the Baltic Sea area during the same period, and between 3 and 29 % of all Baltic Sea species are considered to be of recent (< 200 yr) foreign origin (Leppaekoski & Olenin 2000a). Some of the introduced species have inhabited the native community in relatively low numbers with no apparent effects, while others have quickly reached high population densities and sometimes dominate the community, seemingly at the expense of native species (Cohen & Carlton 1998, Leppaekoski & Olenin 2000b).

A large amount of the aquatic invasion literature deals with patterns, processes and theories regarding when, where and which species will invade a particular native community. Most of the studies have been descriptive, and many of the experimental studies have focused on effects of introduced predators (Ler-

oux et al. 1990, Dick et al. 1999, 2002, Hill & Lodge 1999, Dick & Platvoet 2000, Grosholz et al. 2000, Brousseau et al. 2001, Nystrom et al. 2001, Dick et al. 2002, Holloway & Keough 2002, Jensen et al. 2002, Lohrer & Whitlatch 2002, Walton et al. 2002, Ross et al. 2003, Stenroth & Nystrom 2003).

Apart from 2 studies indicating that, despite competitors, some invaders succeed through superior conversion efficiency (Hill et al. 1993, Byers 2000), little experimental data is available on competition between introduced and native animals. A few studies have demonstrated various forms of interference competition (Race 1982, Marchetti 1999, McDonald et al. 2001, 2001, Janssen & Jude 2001, Usio et al. 2001) and some have shown increased mortality or reduced growth in native species in the presence of an invader (Kotta et al. 2001, Kotta & Ólafsson 2003).

One recent, successful invader in the Baltic Sea is the North American polychaete *Marenzelleria* cf. *viridis* (Verrill, 1873) (Polychaeta: Spionidae), which was observed in the southern Baltic Sea for the first time in 1985, and was probably introduced as pelagic larvae with ballast water (Bick & Burckhardt 1989). Subsequently, it has spread more than 1000 km, as far as the oligohaline Gulf of Bothnia (Stigzelius et al. 1997, Leonardsson 2000) and Bothnian Bay (Leonardsson & Karlsson 2002).

Marenzelleria cf. *viridis* lives in tubes extending about 10 to 35 cm into the sediment (Zettler et al. 1994). It spends most of its time in its tube, but partially emerges when feeding from the sediment surface or suspension-feeding from the water column (Dauer et al. 1981, Bock & Miller 1999). Occasionally it has also been observed swimming during early spring (a behavior that has been related to reproduction: Dauer et al. 1980, Russell 1995), and it has been found in the stomachs of several fish species (Winkler & Debus 1997). *Marenzelleria* cf. *viridis* prefers sandy sediment, but seems to settle in all sediments with low clay content (Dauer et al. 1981, Gruszka 1999) at water depths ranging from <1 to 90 m (Lagzdins & Pallo 1994, Kube et al. 1996).

One of the most ecologically important and dominant native species in the Baltic Sea benthic community between 10 and about 80 m is the deposit-feeding amphipod *Monoporeia affinis* (Lindström) (Ankar & Elmgren 1976, Ankar 1977, Laine et al. 1997). It is a benthic species inhabiting the top 5 cm of the sediment (Byren et al. 2002) that displays nocturnal swimming activity in the water column (Donner & Lindström 1980). The reasons for its nocturnal migration pattern are not known, but have been suggested to be related to predator avoidance during moulting (Cederwall 1990), reproduction and when searching for suitable substrates (Donner et al. 1987).

Marenzelleria cf. *viridis* was shown to reduce growth in *Monoporeia affinis* in a laboratory experiment by Kotta & Ólafsson (2003). It is likely that the 2 species compete for food, as *M.* cf. *viridis* feeds mainly on surface deposits of material from primary production (Dauer et al. 1981), and *M. affinis* seems to rely mainly on the same food source and, to a lesser extent on bacteria involved in the degradation of primary producers (Aljetlawi et al. 2000). *M. affinis* has been shown to be food-limited for most of the year (Elmgren et al. 2001) and has been observed to avoid patches of low and also of extremely high food levels (J. Wenngren pers. obs.). Another possibility is that the 2 species minimise competition by avoiding patches of high competitor abundance. As *M. affinis* is the more mobile of the 2 species, it is probable that it avoids burrowing in patches with high densities of *M.* cf. *viridis*. We tested this hypothesis with an experiment in which *M. affinis* could choose between sediment patches containing different densities of *M.* cf. *viridis*. Our results showed that *M. affinis* clearly avoids sediment with high densities of this polychaete and we therefore ran a further experiment, using plastic worm mimics to determine if mere physical presence would explain the results. In a third experiment, we tested the null-hypothesis that the worms have no effect on the diurnal swimming pattern of the amphipods.

MATERIALS AND METHODS

Expt 1: Choice experiment with live polychaetes. This and the following experiments were performed in a thermo-constant room at ambient sea-temperature ±2°C. We used a large plastic container (length/width/height = 80/60/30 cm; Fig. 1) holding 48 smaller jars (380 ml, 53 cm² surface area) filled with sieved natural sediment and worms at 6 different densities (0, 2, 4, 6, 10 or 20 individuals per sediment jar, corresponding to 0, 380, 750, 1130, 1890 and 3780 individuals m⁻²) replicated 8 times in a randomized block design (Fig. 1). *Marenzelleria* cf. *viridis* was collected on 3 to 4 May 2001 at 0.5 to 0.8 m depth from a sandy beach about 40 km southwest of Stockholm (59° 2′ 29″ N, 17° 41′ 45″ E). The sand was sieved through a 1 mm screen, and the worms were removed and stored in aerated brackish water without food until the experiment 4 d later. Amphipods were collected from a 30 m deep station about 2 km west of Askö laboratory (59° 49′ 29″ N, 17° 46′ 12″ E) at the beginning of April by sampling sediment with a benthic sled (Blomqvist & Lundgren 1996). The sediment was sieved through a 1 mm screen and 1+ year-class individuals were isolated. Additionally, fine sediment for the experimental units was taken from the same area with a van Veen
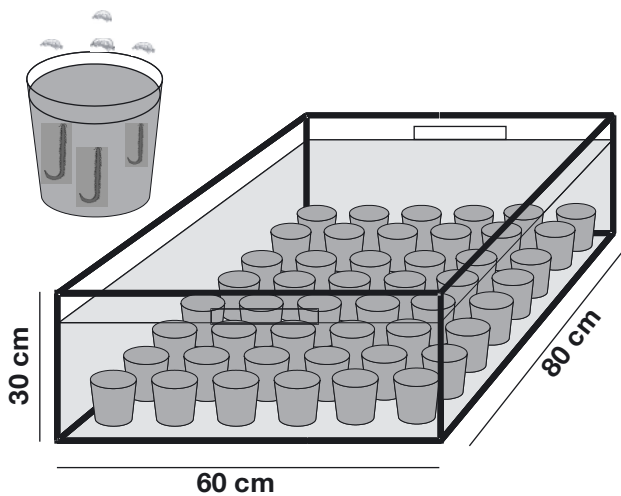
Fig. 1. Design of the choice experiments

grab and, before addition to the jars, sieved through a 0.5 mm aperture sieve to remove all macrofauna and homogenised by stirring.

The worms were added to the sediment surface of the jars, and the container was then filled with water and left overnight. Worms that had not dug into the sediment by the following morning were replaced (a total of 5 individuals). The worms were allowed to acclimatise with a continuous filtered brackish water supply of about 30 l h^{-1}. After about 1 wk, the water flow was shut off and 480 individuals of *Monoporeia affinis* were added to the container, corresponding to about 2000 individuals m^{-2} sediment surface, a normal field density in the 10 to 40 m depth range in this area (Ankar & Elmgren 1976).

The amphipods were left for 4 d in dim light to establish diurnal burrowing and swimming activities. At noon on the 4th day, when practically all amphipods had burrowed into the sediment, the water level was lowered to isolate the jars from each other. The contents of the jars were sieved through a 1 mm sieve and all amphipods counted. A 1-way ANOVA was performed on transformed data (ln[$x+2$]), Bartlett's chi-square = 9.3, p = 0.10) to ensure homogeneous variance. The data were also analysed for potential block-effects using 1-way ANOVA, as the data set as a whole did not meet the criteria for a 2-way ANOVA design.

Expt 2: Choice experiment with physical hindrance. This experiment was performed at the same time of the year and in the same way as Expt 1, but in the following year and using vertical PTFE (polytetra-fluoroethylene) tubes as worm mimics. The tubes were placed vertically and randomly in the jars, flush with the sediment surface, and were of similar dimensions (length 50 mm, diameter 1.3 mm) to the worm tubes.

We used the same densities as for the worms. Amphipods (1+ year class) and sediment were collected from a station about 5 km east of Askö (58° 49′ 28′′ N, 17° 47′ 13′′ E) because of unusually low amphipod densities at the previously sampled station. The analysis was performed on transformed amphipod densities (ln[$x+2$]), Bartlett's chi-square 3.33, p = 0.65). The data were also analysed for potential block-effects using 1-way ANOVA, as the data set as a whole did not meet the criteria for a 2-way ANOVA design.

Expt 3: Swimming experiment. This experiment determined whether the presence of the worms resulted in the amphipods spending more time swimming in the water column by counting the number of swimming amphipods in jars with different worm densities. Counting was performed once every hour for 24 h. The experiment was repeated twice, first with amphipods acclimatised to worms for 1 wk before counting, and then with amphipods with no previous acclimatisation to worms in the laboratory. The jars (diameter 9.5 cm, height 22 cm) contained 0, 4 or 11 worms and 12 0+ amphipods (corresponding to 0, 700 and 1900 worms and 2100 amphipods m^{-2}) and each treatment was replicated 5 times. Each jar was connected to a brackish water supply and a 5 mm outflow pipe covered with a 1 mm meshed nylon net to prevent the amphipods from escaping. The experiment was carried out in November 2002 in a 8:16 h light:dark regime of weak green light. Since the eye of *Monoporeia affinis* is sensitive mainly to green light (550 nm) (Donner 1971), red light was used during counting to disturb the amphipods as little as possible.

Amphipods and sediment were collected at the same location as in the second choice experiment (Expt 2) 2 d before the swimming experiment was set up, and were stored in aerated brackish water in a thermo-constant room. The sediment was treated as in the 2 previous experiments. The worms were collected from the same location as in the first choice experiment (Expt 1) and stored in aerated brackish water for 5 d before the experiment was set up.

The jars were supplied with a continuous brackish water flow during acclimatisation. The water was shut off just before counting began. After the first 24 h counts, the microcosms were again supplied with flowing brackish water, and the outflow nets were removed for 1 wk to allow the amphipods to escape before new amphipods were added for a second counting. Thus, the same worms were used in both experiments. A net placed at the end of the whole set-up trapped the escaping amphipods, allowing us to determine when the majority had escaped (all but 5 individuals). At the end of the second experimental run, the sediment from each jar was sieved and the worms were counted.

RESULTS

Expt 1: Choice experiment with live polychaetes

The number of amphipods in the jars differed significantly among treatments (ANOVA, p < 0.001; Table 1). *Monoporeia affinis* was present in higher numbers in sediment jars with 0, 2, 4 or 6 individuals of *Marenzelleria* cf. *viridis* than in sediment jars with 10 and 20 individuals (Tukey's HSD, p < 0,01, Fig. 2). There was no significant difference among blocks (ANOVA, p = 0.67) (Table 1).

Loss caused by handling and mortality among worms and amphipods was about 15 and 6% respectively. Some worms moved between jars during the experiment: 3 worms were found in different 0 treatment jars after the experiment, and in 3 other low-density jars the number of worms had also increased by 1 per jar. The average number of worms decreased during the experiment in all but the 0 treatment. The final average number of worms in the 6 treatments was 0.4, 1.6, 3.4, 5, 9 and 16.4 respectively.

Expt 2: Choice experiment with physical hindrance

There was no significant difference in amphipod densities among the treatments (ANOVA, p = 0.92, Fig. 3) but there was a significant block-effect (ANOVA, p < 0.001; Table 1). Mortality or loss of amphipods was about the same as in Expt 1 (4%).

Expt 3: Swimming experiment

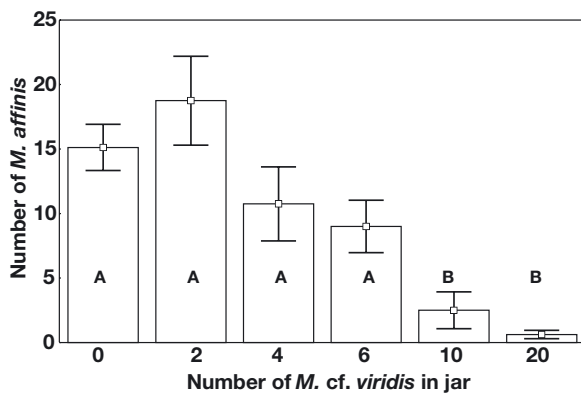There was no visible difference in swimming activity between treatments regardless of whether or not the

Table 1. ANOVA of choice experiments

Expt	Source of variation	df	*F*	p
Avoidance of worms (1)	Block	7	0.706	0.67
	Treatment	5	20.84	<0.001
Avoidance of tubes (2)	Block	7	6.525	<0.001
	Treatment	5	0.282	0.92

amphipods had been acclimatised to the polychaetes (Fig. 4). The loss of worms was between 0 and 73% (mean 32.5%, SD = 25.4) but there was no significant difference between treatments. Only 1 worm was found in the net trap at the end of the set-up after exchange of the amphipods, indicating that mortality was the main reason for the low number of worms recovered at the termination of the experiment

DISCUSSION

It is clear from our results that *Monoporeia affinis* avoids burrowing in patches of high *Marenzelleria* cf. *viridis* abundance, at least under laboratory conditions. The amphipods did not respond to plastic tubes in the same way as to worms, and thus mere physical hindrance is an unlikely explanation. This result was not surprising, since field sediment usually contains a large number of particles similar in size to the worms. The amphipods are thus accustomed to contact with large objects in the sediment. This does, however, not rule out interference as the most likely explanation for the results in the first experiment, since the amphipods may still sense and react to both chemical and/or tactile signals from the worms.

Chemical substances involved in communication between interacting species are believed to be an
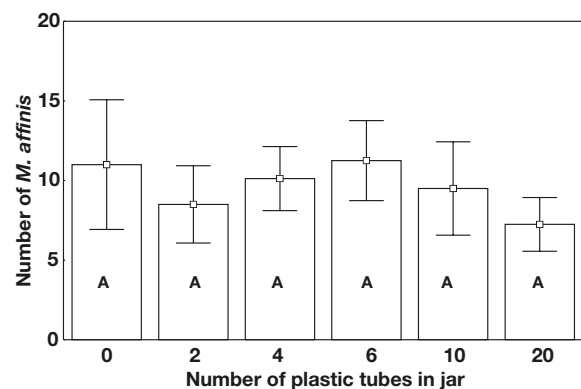

Fig. 2. Average number of *Monoporeia affinis* recovered in jars with different numbers of *Marenzelleria* cf. *viridis* (n = 8, *y*-bars indicating ±SE). Common letters indicate homogenous groups

Fig. 3. Average number of *Monoporeia affinis* recovered in jars with different numbers of plastic tubes (n = 8, *y*-bars indicating ±SE). Common letters indicate homogenous groups
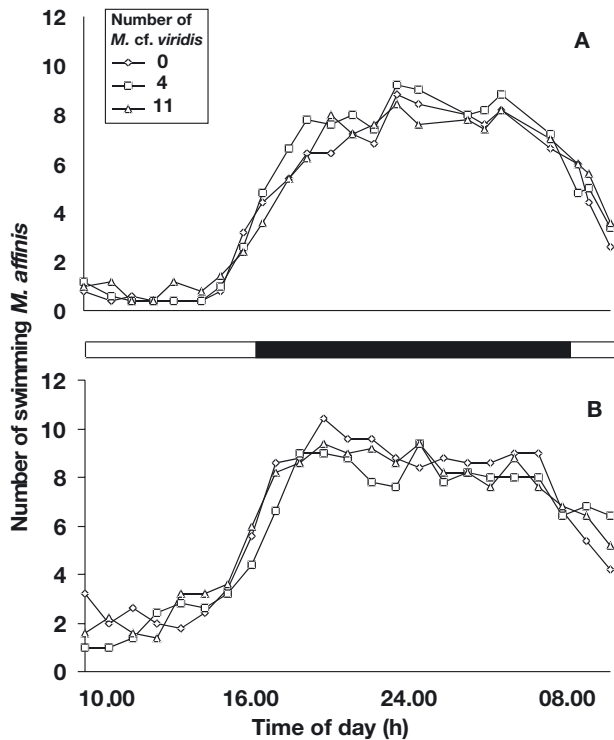
Fig. 4. *Monoporeia affinis* and *Marenzelleria* cf. *viridis.* Average number of swimming *M. affinis* in jars containing 3 densities of *M.* cf. *viridis* during 24 h (n = 5). *M. affinis* (A) acclimatised and (B) not acclimatised to *M.* cf. *viridis*

important feature in interference competition and predation among benthic invertebrates (Woodin 1991, McClintock & Baker 1997). *Marenzelleria* cf. *viridis* is known to produce at least 1 chlorinated compound that could have such effect (Fielman et al. 1999). The amphipods have well-developed chemical receptors (Hallberg et al. 1997), which could conceivably allow them to sense the worms and thereby avoid worm encounter. Taking into account that both species are newly sympatric in distribution, such a mechanism is probably rather general in function. A generality of response is also supported by our observations that *Monoporeia affinis* avoids burrowing in sediments containing high densities of the Baltic clam *Macoma balthica* (L) (authors′ pers. obs).

Jensen & André (1993) found that the shallow-water amphipods *Corophium volutator* (Pallas) and *C. araneum* (Crawford) avoided the polychaete *Nereis diversicolor* (Müller) in experimental conditions. They suggested competition by interference as an explanation for the amphipods′ migration away from the polychaete. *C. volutator* has also been shown to migrate away from mechanically disturbed sediment (Ronn et al. 1988).

Other explanations concerning exploitation of resources are also possible. If, for example, *Marenzel-*

leria cf. *viridis* depletes the available food from the sediment surface, *Monoporeia affinis* could migrate away to other areas with presumably better conditions. *M. affinis* have earlier been shown to choose actively among different food levels (Wenngren et al. 2003). We did not investigate the chlorophyll concentration or organic content in the sediment, but as the deposition layer on the surface was evenly mixed throughout the whole sediment volume during preparation, we assume that the food levels were comparatively low. Therefore, it is unlikely that *M.* cf. *viridis* significantly affected food availability for the amphipods at such low levels during the short experimental period. Similar results were obtained by DeWitt & Levinton (1985) investigating the distribution of the amphipod *Microdeutopus gryllotalpa* (Costa) in response to the mud snail *Ilyanassa obsoleta* (Say) over approximately the same time span. They concluded that food exploitation did not explain amphipod distribution, as they found no difference in chlorophyll concentration between the different treatments.

Monoporeia affinis is very sensitive to hypoxia and anoxia (Modig & Ólafsson 1998), and has been shown to avoid patches of high sulphide concentration and low oxygen concentration when given the choice of more favourable areas (Ólafsson & Limén 2002). *Marenzelleria* cf. *viridis* appears to be less sensitive to hypoxia owing to its ability for anaerobic energy production (Schiedek 1997). It has also been reported that *M. affinis* increases swimming frequency (but decreases swimming duration) at low oxygen levels (Johansson 1997). Had the oxygen levels at surface of sediments containing high densities of polychaetes been critically low during Expt 1, the amphipods would have swum away from those jars and moved to nearby jars with presumably better conditions. However, Expt 3 did not reveal increased or prolonged swimming of amphipods over jars with high worm densities, making this explanation unlikely.

Although no worms were observed to swim in the water above the jars in Expt 1, some individuals must have swum up from the sediment and actively moved to a nearby jar. This observation, together with our observations (J. Wenngren pers. obs.) of pelagic feeding fishes with stomachs filled with *Marenzelleria* cf. *viridis* during winter, supports the idea that adult *M.* cf. *viridis* swims up into the water column to reach new habitats (Kube et al. 1996).

This study has demonstrated that an invader can affect the distribution patterns of a keystone native species. This specific interaction has not been documented in the field, where *Marenzelleria* cf. *viridis* densities in our areas do not exceed about 700 individuals m^{-2}, and it is not clear how important it is in relation to other factors regulating *Monoporeia affinis*

population dynamics. *M. affinis* are known to vary considerably in abundance between years, but in the Gulf of Riga, a massive population decrease coincided with the invasion of *M.* cf. *viridis* (Cederwall et al. 1999), possibly facilitating the invasion process. If the behaviour shown by *M. affinis* in our experiment reflects that in the field, it could decrease the overlap in the distributions of these 2 species.

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