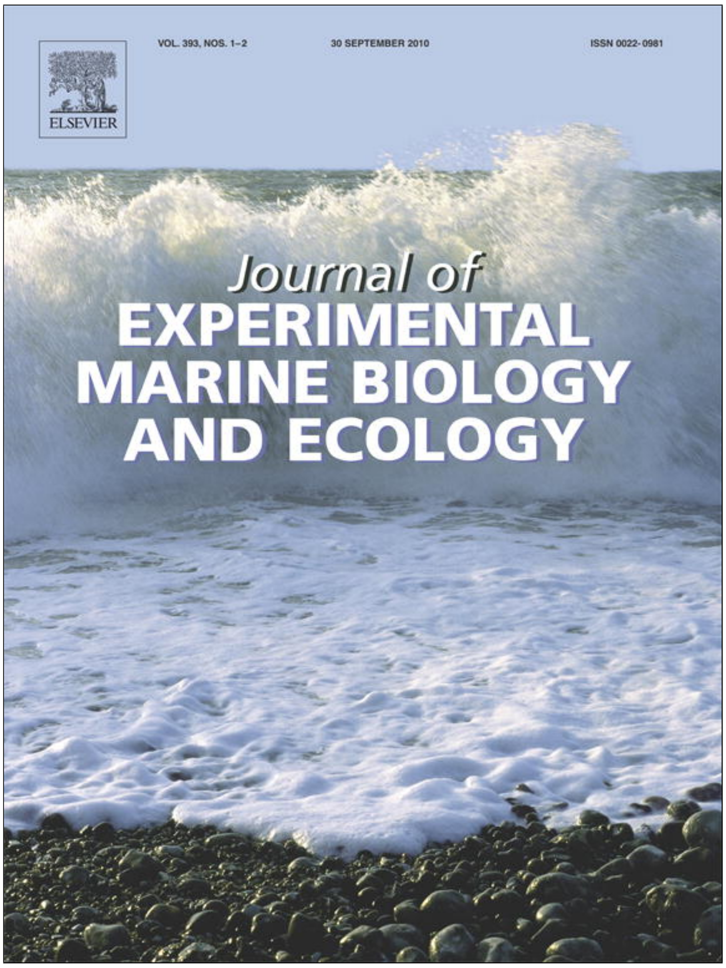
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Sediment preference and burrowing behaviour in the sympatric brittlestars *Ophiura albida* Forbes, 1839 and *Ophiura ophiura* (Linnaeus, 1758) (Ophiuroidea, Echinodermata)

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ABSTRACT

Ophiura albida and *Ophiura ophiura* are widespread and highly abundant brittlestar species occurring sympatrically on soft bottoms along the western European coasts. Laboratory choice experiments revealed that *O. albida* preferred staying on fine rather than on coarse sediments, whereas *O. ophiura* did not distinguish between these types of sediment. Sediment-specific burrowing behaviour of the two species was investigated under different stress and food conditions in order to evaluate relations of predator avoidance and feeding strategies with the observed sediment preference. In the presence of a predator, *O. albida* burrowed preferentially in fine sediment while coarse sediment did not seem to support quick burrowing for efficient escape. Conversely, *O. ophiura* tended to escape the predator by fleeing across the sediment surface rather than by burrowing, reflecting its unselectivity towards different sediment types. For *O. albida*, stationary burrowing behaviour suggests deposit feeding, predating and/or scavenging on infaunal organisms to be the predominant feeding behaviour rather than hunting for epibenthic prey organisms; more so, as this foraging strategy reduces the species' exposure to predators. In contrast, *O. ophiura* seems to be a true hunter and predator for epibenthic prey which was reflected in the experiments by low burrowing activities in presence of food enriched sediments. We suggest that in *O. albida* and *O. ophiura* the evolution of different mechanisms of predator avoidance has been associated with the evolution of contrasting foraging strategies, supporting the species' coexistence in broadly overlapping habitats and explaining their distribution on different types of sediment in the German Bight (North Sea).

1. Introduction

Particle size and organic content have been the most commonly considered features for characterising sediment types and linking them to distributional patterns of a number of different taxa (Hagmeier, 1925; Stripp, 1969; Salzwedel et al., 1985; Quinn and Hickey, 1990; Bourassa and Morin, 1995; Rees et al., 1999; Freeman and Rogers, 2003). In ophiuroid echinoderms, studies on particle size selection and sediment preference have mainly focused on infaunal and cryptic species (Woodley, 1975; Clements and Stancyk, 1984; Sides and Woodley, 1985; Hendler and Littman, 1986), considering lifestyle, feeding mechanisms and protective strategies (Ursin, 1960; Buchanan, 1964; Warner, 1971; Tyler and Banner, 1977; Summers and Nybakken, 2000). Laboratory studies on the burrowing amphiurid brittlestar *Microphiopholis gracillima*, for example, showed that this species distinctly integrated both grain size and organic content into its habitat choice as it is reflected in the species' distributional pattern observed in the field (Zimmerman et al., 1988).

While the burrowing lifestyle of infaunal brittlestars is considered an evolutionary adaptation to predator avoidance (Sköld, 1998), epibenthic brittlestars, for example from the genus *Ophiura*, have evolved other strategies to avoid predators, to temporarily hide from them or even to endure encounters. These include autotomy, rapid escape, deimatic behaviour and unwieldy shape, cryptic colouring and seeking shelter in crevices or under rocks (Fell, 1966; Hendler, 1984; Emson and Wilkie, 1980; Sköld and Rosenberg, 1996; Sköld, 1998). Although leading an epibenthic lifestyle, burrowing – referring to a position just slightly below the sediment surface mostly with the arm tips still exposed above sediment level – has been reported to be a common response to potential stressors (e.g. predators or illumination) in *Ophiura albida* and *Ophiura ophiura* (Moore and Cobb, 1985; Sköld and Rosenberg, 1996; Sköld, 1998). MacGintie (1949) suggested that deposit feeding in *O. sarsi* may be related to burrowing behaviour which is likely to apply to other *Ophiura* species as well. Hereby the animals were observed dabbing their tube-feet over an organically enriched sediment surface and

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raking through the sediment with their arms followed by the subsequent burrowing of the entire body disc.

Experimental studies on sediment preference and burrowing behaviour in epibenthic brittlestars of the genus *Ophiura* are scarce. While Caspers (1979) reported that *O. albida* and *O. ophiura* selected distinctly different sediment types during early larval settlement, possible sediment preferences of adults so far could only be derived from observational monitoring studies and field sampling and have not revealed any clear patterns (Süßbach and Breckner, 1911; Gerdes, 1977; Salzwedel et al., 1985; Dahm, 1993; Kühne and Rachor, 1996; Niermann, 1997; Volbehr and Rachor, 1997; Boos and Franke, 2004).

O. albida and *O. ophiura* are common representatives of the boreo-lusitanian fauna distributed from Norway and Iceland to the Mediterranean and even as far as the Azores (Hyman, 1955; Ursin, 1960). Both species are considered omnivorous and have been reported to exhibit a wide range of feeding mechanisms including predation, scavenging as well as surface and sub-surface deposit feeding (Feder, 1981; Warner, 1982; Sköld and Rosenberg, 1996). In turn, they are predated upon by a number of demersal fishes such as haddock, plaice, dab and other flatfish and by various echinoderms and crustaceans making them important links in local food-webs and faunal communities (Fenchel, 1965; Warner, 1971; Pihl, 1994; Sköld, 1998; Summers and Nybakken, 2000). *O. albida* and *O. ophiura* are found sympatrically and in abundances of up to 700 ind. m^{-2} (Goldschmid, 1996) on a variety of different soft-bottom sediments in the southern North Sea including all grades of mud, gravel, sand and broken shell (Süßbach and Breckner, 1911; Salzwedel et al., 1985; Dahm, 1993; Kühne and Rachor, 1996; Niermann, 1997; Boos and Franke, 2004, 2006).

Common traits in *O. albida* and *O. ophiura* suggest that the two species have similar ecological requirements and are therefore likely to compete for shared resources. According to the classic ‘competitive exclusion principle’, however, two species cannot realize the same ecological niche (Hutchinson, 1957 in Soberón and Peterson, 2005; Hardin, 1960). The co-occurrence of *O. albida* and *O. ophiura* on soft-bottom sediments, therefore, indicates ecological differences between the two species that allow for their coexistence. While niche segregation among ecological equivalents is common in most communities (Ross, 1986), the mechanisms and factors allowing for the coexistence of species occupying the same habitat and utilizing the same resources, are often unknown.

In order to give a mechanistic explanation for the coexistence of *O. albida* and *O. ophiura* in the field, we studied possible sediment preferences of the species in the laboratory. Building on these results, we identified factors relating to sediment preferences. In detail we ask the following questions: Do *O. albida* and *O. ophiura* have different sediment preferences? If so, are the preferences related to burrowing behaviour performed as predator avoidance and/or feeding strategy? Can differences in these strategies explain for niche segregation and, thus, the coexistence of *O. albida* and *O. ophiura*?

To answer these questions, we applied single- and mixed-species sediment choice experiments with *O. albida* and *O. ophiura* at different densities in the laboratory. Subsequently, we investigated the burrowing behaviour of the two species on different sediment types under different stress and food conditions.

2. Materials and methods

2.1. Sampling of animals and sediment treatment

From June to July 2003, *O. albida* and *O. ophiura* were collected by dredging in the close vicinity of the island of Helgoland, German Bight (North Sea). Cultures of the two species of approximately 70 individuals each were maintained separately in 60 × 45 × 40 cm flow-through aquarium tanks at 16 °C and a light–dark cycle of 16:8 h in the seawater laboratory of the Helgoland Marine Station. Sediment was collected with a van Veen grab (0.1 m^2) and offered as natural, untreated substratum. The ophiuroids were fed daily *ad libitum* with a mixed diet of commercial fish-food (TetraMin®), tissue bits of blue mussels *Mytilus edulis* and small pieces of the isopod *Idotea baltica*. Leftover food particles were removed daily.

In all experiments only undamaged, i.e. non-regenerating adult individuals were used. All experiments were run at a constant temperature of 16 °C. Sediment for experimental usage originated from van Veen grab samples taken along with the sediment sampled for maintenance purposes. Approximately 50 l of sediment was dried and fractionated to different grain sizes by sieving through a cascade of sieves with decreasing mesh sizes (3360, 1800, 1000, 500, 250 and 125 µm). Subsequently, sediment fractions of two specific grain sizes were used throughout all experiments: 1000–1800 µm and 125–250 µm. They will hereafter be referred to as coarse and fine sediment, respectively. Because this procedure is labour intensive and yields only relatively small quantities, the experimental sediments were used repeatedly. Prior to any experimental procedure, the sediments and basins were thoroughly washed with hot tap water in order to remove organic remains and chemical cues from animals of preceding experiments and to prevent microbial growth.

2.2. Experimental setup

2.2.1. Sediment preference

Either half of a round basin (Ø = 45 cm, height = 15 cm) was laid out with a 2-cm-thick layer of coarse and fine sediment, respectively, and then carefully filled up with seawater. Randomly chosen individuals of the respective species (mean disc diameter for *O. albida*: 7.4 ± 0.7 mm and for *O. ophiura*: 12.7 ± 1.3 mm) were placed on the sediment, where the two sediment types bordered on each other. The numbers of individuals used in the experiments were chosen according to similar experiments by Sköld (1998). The maximum density of ophiuroids used in the present experiments was still low enough to allow for the animals' unimpeded migration in the basin throughout the experimental procedure (personal observation). The following numbers of individuals were used in single- and mixed-species trials; all trials were run with three replicates each:

- 5 individuals of *O. albida* and *O. ophiura*, respectively, in single-species treatments (for species-specific sediment preference)
- 10 individuals of *O. albida* and *O. ophiura*, respectively, in single-species treatments (for intraspecific or ‘density’ effects)
- 5 individuals of either species in mixed-species treatments (for interspecific or ‘species’ effects).

After a 2-h period of acclimatization to the artificial environment, the sediment choice of the ophiuroids was monitored constantly over a period of 8 h. Ophiuroids are known to react negatively to light by seeking shelter under rocks, in crevices or by burrowing in sediments when illuminated (Fell, 1966; Moore and Cobb, 1985; Hendler, 2004). Moore and Cobb (1985) not only confirmed a negative phototaxis in *O. ophiura* but also showed distinct behavioural reactions in individuals that were exposed to different gradients of illumination. In order to prevent effects of directional photic stimuli on the animals' spatial distribution, the experiments were performed in the dark and were videotaped under infra-red light. Later the position of each individual at any given time was traced back on the screen. The moments in time of a sediment boundary crossing, i.e. when at least three legs of an individual had entirely crossed over to the respective other sediment type, were recorded for the entire trial duration. In this way, the total time spent on fine and coarse sediment was calculated for each individual.

2.3. Burrowing behaviour

The burrowing behaviour of *O. albida* and *O. ophiura* on coarse and fine sediment was tested under different conditions of (i) a stressor and (ii) food. An ophiuroid was determined 'burrowed', as soon as its dorsal disc surface came equal with the sediment surface, independent of parts of the disc or the arms still being visible.

2.3.1. Stress

The burrowing behaviour in presence and absence (control) of a stressor, the edible crab *Cancer pagurus*, was studied using a round aerated basin (Ø = 45 cm, height = 15 cm) with a 2-cm-thick layer of coarse and fine sediment, respectively. *C. pagurus* was chosen as a predatory stressor as it is known to cause mechanical disturbance when browsing in dense epibenthic brittlestar populations (e.g. *Ophiothrix fragilis*) (Warner, 1971). We used medium sized *C. pagurus* with a mean carapax width of 8.4 ± 1.2 cm. 10 conspecific ophiuroids (mean disc diameter for *O. albida*: 7.6 ± 0.9 mm and for *O. ophiura*: 12.8 ± 1.5 mm) were transferred into the experimental basin and left for 2 h to acclimatize. After the acclimatization period, one individual of *C. pagurus* was introduced to the experiment. The number of burrowed ophiuroids was recorded every 5 min for a total period of 30 min. Three replicates were run for each sediment type, treatment (control and trial) and ophiuroid species.

2.3.2. Food

The burrowing behaviour was studied in presence and absence (control) of food using 5 l (17 × 15 × 25 cm) flow-through aquaria with a 2-cm-thick layer of the respective sediment. In each set of food trials, the sediments in the aquaria were enriched by mixing them with 2 g of commercial fish food (TetraMin®), bits of tissue of 5 medium sized mussels (*M. edulis*), approximately 15 g of isopod pieces (*I. baltica*) and freshly hatched nauplii of the brine shrimp *Artemia salina*, concentrated from 1 l (3.5 ml cysts/l seawater). After sedimentation of the food enriched sediment, food particles were available in the sediment as well as on the sediment surface meeting the requirements of the main feeding mechanisms in the genus *Ophiura*, i.e. epi- and endobenthic carnivory (scavenging and predation) and surface and subsurface deposit feeding.

In the experimental trials, three individuals of the same species (mean disc diameter for *O. albida*: 6.7 ± 1.5 mm and for *O. ophiura*: 13.7 ± 1.5 mm), which had been starved for 2 days, were each transferred into a tank. After 2 h of acclimatization to the artificial environment, the number of burrowed individuals was recorded every 30 min for a total period of 8 h. Five replicates with three individuals each were run for each sediment type, treatment (control and trial) and ophiuroid species.

2.4. Statistical analysis

All calculations were performed at the 95% confidence level using computer software GraphPad Prism (3.0), STATISTIKA (7.1) or SPSS (15.0.0).

Ophiuroid sediment preference in single-species trials was analysed with a nested ANOVA with species and density as crossed fixed effects factors and experiment (with individuals as replicates) as random effects factor being nested in combinations of species and density. According to Zar (1999), we tested the two fixed effects factors and their interaction against the experiment mean square. In mixed-species comparisons, we used a crossed two-way ANOVA with species as fixed and experiment as random effects factor. Here we tested species against the interaction between the two factors and treatment as well as the interaction itself against the error mean square. In both analyses, we used the proportion of time spent on the coarse sediment as the response variable. Although Levene's test of homogeneity of error variances indicated clear deviations from this assumption (both $P<0.01$), we chose these analyses because inspections of plots of residuals against predicted values indicated no obvious deviations from normality and homogeneity of error variances (neither arcsin nor rank transformations improved fit to assumptions). To increase power and since no other factor than species nor any interaction revealed significance, we finally tested the data of both experiments pooled using a nested ANOVA with treatment as nested random effects factor and species as well as experimental condition (single vs. both species) as fixed effects factors. Both factors and their interaction were tested against the treatment mean square.

The burrowing behaviour of ophiuroids in both the stress and the food trials was analysed with repeated measures ANOVAs. Species (with levels: *O. albida* and *O. ophiura*) and sediment (with levels: coarse and fine) were treated as between subject factors having fixed effects, and experimental treatment (with levels: control and trial run) was included as a within subjects factor having fixed effects. Data + 1 were log-transformed to meet the assumptions of normal distribution and homogeneous error variances (checked by visual inspection of the plot of the residuals against the predicted values and Levene's test: all except one $P>0.31$).

3. Results

3.1. Sediment preference

In the single-species treatments, the sediment choice of *O. albida* and *O. ophiura* tended to differ at low densities (nested ANOVA: $F_{1,8}=4.99$, $P=0.056$) but not at high densities ($F_{1,8}=0.09$, $P=0.77$). However, the interaction between density and species was statistically not significant ($F_{1,8}=0.69$, $P=0.43$; Fig. 1). In fact, *O. albida* tended to spend more time on fine sediment (mean ± SD = 284.9 ± 120.6 min) than on coarse sediment (mean ± SD = 195.0 ± 120.7 min), whereas *O. ophiura* did not do so (222.4 ± 210.8 and 257.7 ± 210.8 min, respectively). In mixed-species experiments, we found no difference in sediment choice of the two species (ANOVA: $F_{1,2}=1.61$, $P=0.33$). Neither the treatment ($F_{1,2}=0.036$, $P=0.96$) nor the interaction between treatment and species had a significant effect on the sediment choice of the two species ($F_{1,2}=0.43$, $P=0.66$). Pooling all data sets of each species revealed that *O. albida* spent more time on the fine sediment than did *O. ophiura* ($F_{1,14}=6.44$, $P=0.024$). The number of conspecifics and heterospecifics had no effect on sediment choice ($F_{1,14}=1.26$, $P=0.28$) and the interaction between density and sediment was, again, not significant ($F_{1,14}=0.06$, $P=0.80$).

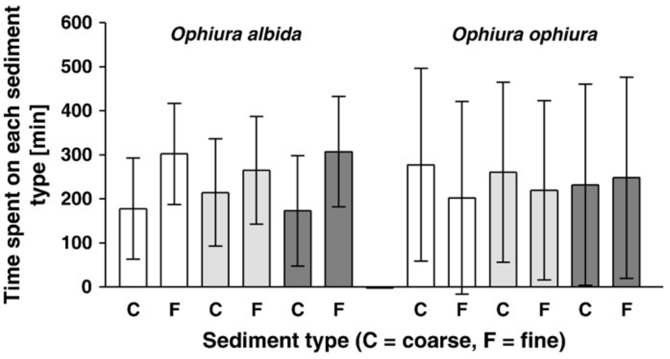

Fig. 1. Total time spent on coarse and fine sediment by *Ophiura albida* and *Ophiura ophiura* in different densities and species compositions; white bars = single-species treatments (5 animals), light grey bars = single-species treatments (10 animals) and dark grey bars = mixed-species treatments (5 + 5 animals); mean ± SD ($N=15$ and 30, respectively).

3.2. Burrowing behaviour

3.2.1. Stress

The presence of the predator *C. pagurus* differentially influenced the burrowing behaviour of *O. albida* and *O. ophiura* on different sediment types (repeated measures ANOVA, species × condition × sediment type interaction: $F_{1,8} = 6.32$, $P = 0.04$; Fig. 2). *O. albida* showed higher burrowing activity in stress treatments than in stress-free conditions, whereas it was the opposite for *O. ophiura*. In both species, more animals were burrowed in fine than in coarse sediment ($F_{1,8} = 6.08$, $P = 0.04$). Accordingly, the interaction between species and sediment was not significant ($F_{1,8} = 0.20$, $P = 0.67$). *O. albida* generally showed higher burrowing activity than did *O. ophiura* ($F_{1,8} = 7.90$, $P = 0.023$). Further interactions were not detected.

3.2.2. Food

Food availability in the sediment differentially influenced the burrowing behaviour of *O. albida* and *O. ophiura* (interaction species × feeding condition: $F_{1,16} = 7.92$, $P = 0.012$; Fig. 3). Burrowing activity of *O. albida* was enhanced in the presence of food whereas food enrichment of the sediment had no effect on the burrowing behaviour of *O. ophiura*. The two species also differed in their response to the sediment type (repeated measures ANOVA interaction, species × sediment: $F_{1,16} = 13.92$, $P = 0.002$). More individuals of *O. albida* were found burrowed in fine than in coarse sediment. The burrowing behaviour of *O. ophiura* was similar on both sediment types. Further interactions were not detected.

4. Discussion

When given a choice between the two sediment types, *O. albida* in all treatments, spent more time on fine sediment than on coarse sediment. The addition of conspecifics or heterospecifics did not alter this tendency making, intra- and interspecific effects on substrate selection negligible within the tested range of densities. *O. ophiura*, in contrast, showed no preference for any of the sediment types under study and was always found randomly distributed. It also did not respond to the addition of conspecifics or heterospecifics.

In both, the stress and the food trials, *O. albida* and *O. ophiura* generally showed higher burrowing activity on fine than on coarse sediment. On fine sediment, *O. albida* burrowed more often when the predator *C. pagurus* was present compared to when it was absent, while the opposite was found for *O. ophiura*. In the food trials, *O. albida* burrowed more often in fine sediment when it was enriched with food as when food was lacking. In contrast, *O. ophiura* generally remained on top of the sediment, independent of food enrichment.

Our results suggest that burrowing plays a greater role in the behavioural strategies (predator avoidance, foraging) of *O. albida* than in those of its congener *O. ophiura*. *O. albida* exhibited burrowing behaviour as a protective mechanism when encountering a potential predator. These findings are in accordance with earlier studies by Sköld (1998), where *O. albida* showed very little effort in fleeing, but remained still or covered itself slightly with sediment when exposed to a predator.

Burrowing in *O. albida* was observed more often on fine than on coarse sediment. Coarse sediments might present mechanical problems to burrowing (Stancyk, 1970 in Zimmerman et al., 1988; Woodley, 1967, 1975), thus not allowing for a quick escape in case of danger. Alternatively, being burrowed in coarse sediments may not provide an efficient protection from predators. Ehrenhauss et al. (2004) showed that due to enhanced water flow through larger pore sizes, transport rates of particles and dissolved chemical cues were higher in medium and coarse sands than in fine sands. Thus, burrowing as a protective mechanism against chemically orientated predators may be less efficient in coarse sediments as opposed to fine sediments. This effect may offer an explanation for the observed preference for fine sediments in *O. albida*.

In contrast to *O. albida*, *O. ophiura* does not seem to make use of burrowing as a protective mechanism against potential predators. In the present experiments *O. ophiura* tended to escape rapidly across the sediment surface on both fine and coarse sediment. This behaviour makes *O. ophiura* rather unselective towards sediment types as it does not seem to depend on a particular grain size to seek shelter from predators. These findings may explain for the lack of a clear preference in the sediment choice experiments.

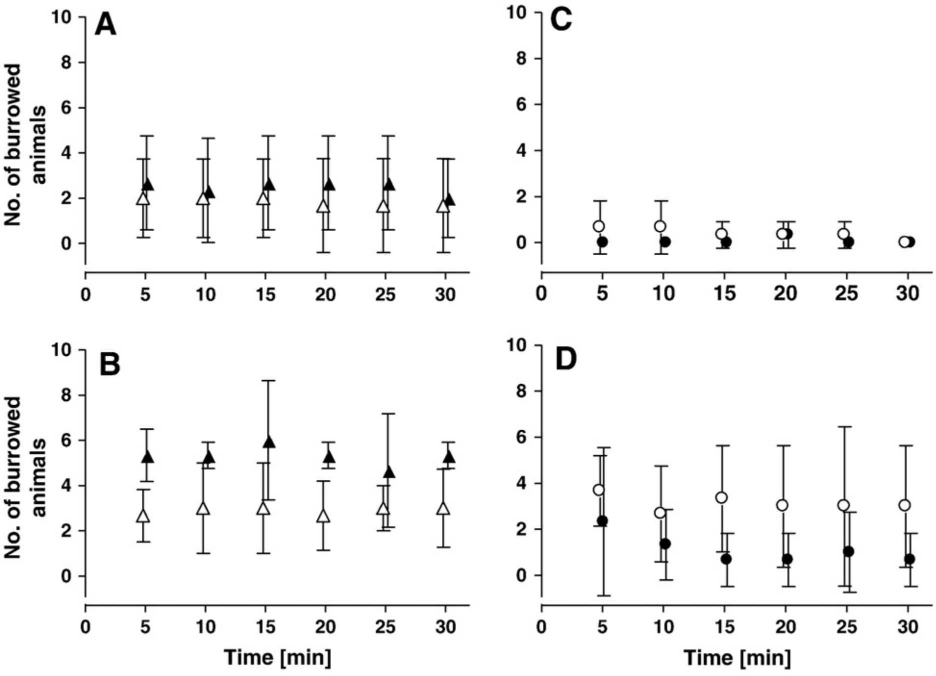

Fig. 2. Number of burrowed individuals of *Ophiura albida* (▲△) in coarse (A) and fine (B) and *Ophiura ophiura* (●○) in coarse (C) and fine (D) sediment in presence (black symbols) and absence (white symbols) of predator stress over time; mean ± SD ($N = 3$).

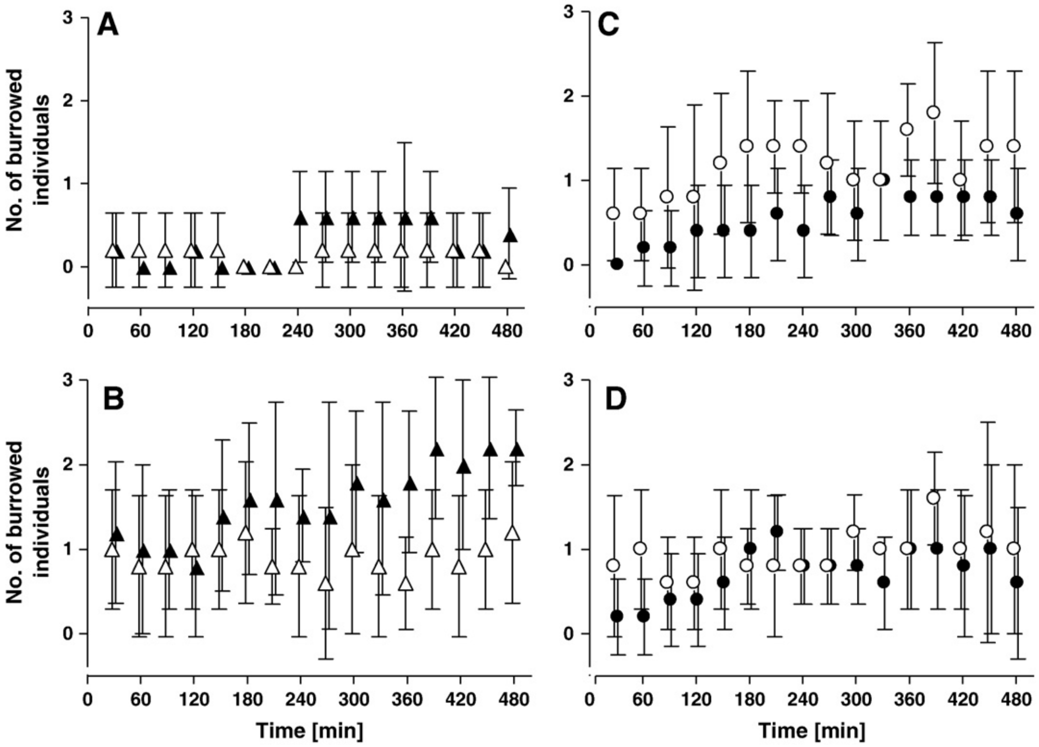

Fig. 3. Number of burrowed individuals of *Ophiura albida* (▲△) in coarse (A) and fine (B) sediment and *Ophiura ophiura* (●○) in coarse (C) and fine (D) sediment in presence (black symbols) and absence (white symbols) of food over time; mean ± SD ($N=5$).

The tendency in *O. ophiura* of rather digging itself out of the sediment and presenting itself when under threat is in accordance with the defence or escape mechanisms of epibenthic ophiuroids described by Sköld (1998). Horizontal locomotion in brittlestars typically takes place by using the entire arms instead of individual tube feet (Lawrence, 1987). By alternately moving two arms in the desired direction, the animals generally lift up their body over the surface dragging behind the other three arms (Lawrence, 1987). With a maximum disc diameter of approximately 30 mm and an arm length of four times the disc diameter (Mortensen, 1927), *O. ophiura* is able to cover a larger distance much faster than *O. albida*, which is only about half the size of *O. ophiura*. This may explain the efficacy of a rapid escape in *O. ophiura* when under threat, whereas burrowing may be the better alternative for the smaller and slower moving *O. albida*. More so, as burrowing in slow moving species, like in most amphiurid ophiuroids, seems to be the predominant mechanism to seek shelter from predators such as demersal fishes (i.e. the dab *Limanda limanda*) or star fish (Fenchel, 1965; Summers and Nybakken, 2000; Saborowski and Buchholz, 1996). In addition, disc autotomy is also considered a very common mechanism of predator avoidance (Emson and Wilkie, 1980). With regard to autotomy, Stancyk (in Emson and Wilkie, 1980) suggested that not only does it enhance the chance of surviving predatory attacks, but, because of a smaller body size after autotomy, it may also allow for less resistance when burrowing in case of threat.

Being less active, slower and smaller than its congener, burrowing may make *O. albida* not only less prone to visually and/or chemically orientated predators. It may also reflect the species' stationary foraging behaviour, which includes subsurface deposit feeding as well as preying or scavenging on smaller infaunal organisms in the top layers of fine grained sediments, rather than hunting and actively searching for prey. Support is given by Eichelbaum (1910) and Jangoux and Lawrence (1982) who found comparably high amounts of sediment in stomach content analyses of *O. albida* in comparison to remains of small benthic organisms. Eichelbaum (1910) related more than 75% of ingested material to sediment ('bottom material') and designated *O. albida* as a deposit feeder. As fine grain sized sediments contain enhanced organic content and thus offer surface and subsurface deposit feeders substantial nutriment (Summers and Nybakken, 2000), they may also provide better feeding grounds for other infaunal organisms and potential prey objects, than do coarse grain sized sediments (Salzwedel et al., 1985). In turn, this may offer another explanation for the preference for fine sediment in *O. albida* observed in the present experiments.

Studying the stomach content and feeding behaviour of *O. ophiura*, Feder (1981) identified 41 prey organisms from different endo- and epibenthic taxa, including specimens of the congener *O. albida*. Because of the species' fairly unselective feeding behaviour (Tyler, 1977) and broad food spectrum, Feder (1981) designated *O. ophiura* as a predominant predator of small benthic organisms from a variety of different habitats, which, again, makes this species rather unspecific towards a certain sediment type.

Based on our results, we suggest that predator avoidance may play a primary role in explaining the differences between *O. albida* and *O. ophiura* with respect to substrate choice (preference for fine over coarse sediment in *O. albida*; no such preference in *O. ophiura*). The two species have evolved different strategies to escape or avoid potential predators and these differences are related to differences in the species' predominant foraging strategies. Differences in feeding habits, thus, may be considered the main factor allowing for the species' broad overlap in habitat use and coexistence observed in the field. In both species, increasing numbers of conspecifics as well as the presence of heterospecifics did not affect the outcome of sediment choice experiments within the small range of densities studied. While both species under study are known to perform a wide variety of predator avoidance strategies and feeding mechanisms, we were able to focus on some predominant behavioural responses to explain for an observed distribution of brittlestar populations in the German Bight (North Sea). Performances of additional feeding habits may play a role when looking into possible effects of competitive interactions on both, the intra- and interspecific level. These, however, have not been investigated in the present study.

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