

Effects of predator richness and habitat heterogeneity on prey suppression in an estuarine food chain

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ABSTRACT: Predator influence on the structure of prey communities can be mediated by habitat heterogeneity, the effects of which may cascade to the base of the food webs, altering producer biomass and species composition. We carried out a mesocosm experiment manipulating the identity and richness of predators and habitat heterogeneity to test their influence on resource use effectiveness, competition among predators, and trophic cascades in a model estuarine system with 3 trophic levels (microalgae, mysids, and the predators blue crab *Callinectes sapidus*, sand shrimp *Crangon septemspinosa*, and grass shrimp *Palaemonetes pugio*). We hypothesized that increasing predator species richness would increase mysid suppression because of complementarity among predators, that complementarity would be better expressed in more heterogeneous habitats, and that higher mysid suppression would increase algae biomass through cascading effects. Assemblages with multiple predators were more effective at suppressing prey than the average single predator, but not in comparison to the most effective predator (i.e. no transgressive overyielding). Predator diversity effects increased with habitat heterogeneity, possibly because it allowed interspecific complementarity among predators to be expressed. Moreover, habitat heterogeneity dampened intraspecific predation and/or negative behavioral interactions between predators. A trophic cascade was not observed because of the low mysid grazing impact on microalgae, probably related to the omnivorous feeding of mysids. Our findings indicate that the loss of both biodiversity and habitat heterogeneity should alter the energy flux in marine food webs; therefore, both must be considered for the proper management of natural ecosystems.

KEY WORDS: Biodiversity · Ecosystem functioning · Habitat structure · Predator richness · Trophic cascade · Food webs · Complementarity · Omnivory

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INTRODUCTION

The loss of biodiversity, i.e. variety of species, genes, or functional traits, has negative consequences for several ecosystem functions, e.g. the capacity of communities to use resources, produce biomass, decompose, and recycle nutrients (Stachowicz et al. 2007, Gamfeldt et al. 2015). Consequently, declines in biodiversity can also impair ecosystem services, such

as the production of renewable resources and resistance to climate events (Cardinale et al. 2012, Isbell et al. 2015, Duffy et al. 2016). Most studies concerning biodiversity effects on ecosystem functioning have focused on terrestrial producers (Cardinale et al. 2006, 2011), because they constitute the base of the food webs and are easier to manipulate than consumers in higher trophic levels. Predators, in contrast, usually have complex behaviors and present complex

trophic interactions, such as intraguild predation (Polis & Holt 1992, Finke & Denno 2004). Nevertheless, there is recent evidence that the relationship between species richness effects and consumption is stronger for predators than for producers and detritivores (Griffin et al. 2013, Gamfeldt et al. 2015). Thus, an alteration in predator species identity and diversity may alter top-down controls and cascade through consumers to the base of the food webs (Duffy et al. 2005, 2007, Bruno & Cardinale 2008).

Experimental evidence shows that ecosystem effects of changing diversity are generally consistent across taxa and ecosystems (Cardinale et al. 2006, Stachowicz et al. 2007); however, the responses may vary considerably according to habitat heterogeneity (Griffin et al. 2009, Godbold et al. 2011). An increase of habitat heterogeneity often strengthens diversity effects, apparently because it allows resource partitioning to be better expressed, i.e. complementarity effects among species to be manifested (Duffy 2009, Griffin et al. 2009). Habitat heterogeneity may be promoted by foundation species, such as oysters, corals, and kelps, which create complex habitats for other species, and are thus often essential for the structure, resilience, and functioning of ecosystems (Gutiérrez et al. 2003, Altieri & van de Koppel 2014). The biogenic structure of foundation species provides refuge, which attenuates physical and biological stresses (e.g. wave action and predation pressure, respectively), often enabling the coexistence of abundant and diverse communities (Stachowicz 2001). Habitat heterogeneity can also mediate trophic interactions by influencing competition among predators (Grabowski & Powers 2004, Hughes & Grabowski 2006), strength of trophic cascades, and occurrence of intraguild predation (Finke & Denno 2002, 2006, Grabowski et al. 2008).

Despite the importance of habitat heterogeneity in mediating the relationship between trophic interactions, biodiversity and ecosystem functioning, to our knowledge no study has manipulated predator richness (3 or more species) and habitat heterogeneity concomitantly. Here, we carried out a mesocosm experiment manipulating the identity and richness of estuarine predator species (blue crab *Callinectes sapidus*, sand shrimp *Crangon septemspinosa*, and grass shrimp *Palaemonetes pugio*) and habitat heterogeneity to test their influence on resource use

effectiveness, competition among predators, and the trophic cascade to basal prey. We hypothesized that increasing predator species richness and habitat heterogeneity would each increase suppression of intermediate prey (mysid crustaceans) because of complementarity among predators that is better expressed in more complex habitats, and that these impacts should reduce grazing by mysids on basal prey (microalgae) through a cascading effect of predator richness on microalgae.

MATERIALS AND METHODS

Experimental design

We carried out a mesocosm experiment in outdoor tanks supplied with water from the York River estuary, Virginia, USA, where the organisms were collected. Flowing estuarine water was filtered through 150 µm mesh bags to avoid invasion of large organisms, but allowing colonization by microalgae. Water was distributed to the mesocosms through a dump-bucket system. We manipulated predator species richness and habitat heterogeneity in the presence/absence of prey through 14 distinct treatments (Table 1), implemented in 70 mesocosms of 18 l, from 22 October to 5 November 2013 (14 d). We used a replacement design, i.e. we manipulated predator richness and identity maintaining the number of individual predators constant at 3 individuals per mesocosm. We chose a replacement instead of an additive design because the former more rigorously detects

Table 1. Experimental design. Initial number of mysids (intermediate consumers) and of each predator species, and habitat complexity level (homogeneous or heterogeneous) in each treatment

| Treatment | Mysid | Predator | | | Habitat |
|-----------|-------|-------------|--------------|-----------|---------------|
| | | Sand shrimp | Grass shrimp | Blue crab | |
| 1 | 15 | 0 | 0 | 0 | Homogeneous |
| 2 | 15 | 3 | 0 | 0 | Homogeneous |
| 3 | 15 | 0 | 3 | 0 | Homogeneous |
| 4 | 15 | 0 | 0 | 3 | Homogeneous |
| 5 | 15 | 1 | 1 | 1 | Homogeneous |
| 6 | 0 | 1 | 1 | 1 | Homogeneous |
| 7 | 0 | 0 | 0 | 0 | Homogeneous |
| 8 | 15 | 0 | 0 | 0 | Heterogeneous |
| 9 | 15 | 3 | 0 | 0 | Heterogeneous |
| 10 | 15 | 0 | 3 | 0 | Heterogeneous |
| 11 | 15 | 0 | 0 | 3 | Heterogeneous |
| 12 | 15 | 1 | 1 | 1 | Heterogeneous |
| 13 | 0 | 1 | 1 | 1 | Heterogeneous |
| 14 | 0 | 0 | 0 | 0 | Heterogeneous |

interspecific and intraspecific predation, as well as complementarity effects among multiple predators (Byrnes & Stachowicz 2009). The 14 treatments (5 replicates each) included: (1) mysids alone (predator control), to evaluate mysid survival without predators; (2–4) monocultures of each of the 3 predators with prey; predator polycultures (5) with and (6) without prey; (7) algae alone (consumer control treatment), containing neither predators nor prey, as a baseline to evaluate grazing impact on algae (Table 1: homogeneous habitat treatments); and (8–14) all of these same treatments within a physically structured habitat (Table 1: heterogeneous habitat treatments). Thus, the food chain in the mesocosms had 3 levels: benthic microalgae (basal prey), mysids (intermediate prey) and predators (top consumers). Mesocosms were open at the top, but covered with screens to prevent predator escape.

Community assembly

One week prior to the introduction of predators, 15 adult mysids (intermediate prey) were introduced into the mesocosms and allowed to acclimate. We chose mysids as prey because they are one of the main intermediate consumers in coastal waters (Miyashita & Calliari 2016), including the Chesapeake Bay (Markle & Grant 1970, Latour et al. 2008). Mysids are hyperbenthic organisms, having a major role in benthic–pelagic coupling, as they usually stay close to the bottom during the day and migrate to the water column during nighttime (Jumars 2007). We selected the numerically dominant mysid species in the field at the time of the experiment: *Americamysis bahia*. Adults of *A. bahia* reach a total length of approximately 6 mm. Mysids are omnivorous: they eat detritus, algae, and small invertebrates (Mauchline 1980).

We introduced 3 predator individuals into each mesocosm (number potentially representative of natural predator abundances in estuarine systems), either 3 of a single species, or one of each of the 3 species in the combined treatment (polyculture). The predators chosen, and their individual mean \pm SE wet mass and length, were the sand shrimp *Crangon septemspinosa* (0.27 ± 0.08 g; 31.1 ± 0.9 mm), the grass shrimp *Palaemonetes pugio* (0.20 ± 0.04 g; 28.7 ± 0.7 mm), and juveniles of the blue crab *Callinectes sapidus* (0.76 ± 0.33 g; 15.9 ± 0.9 mm). We selected predators of each species of similar size to avoid biomass differences among mesocosm replicates. These highly abundant predators in the Chesapeake Bay

(Douglass et al. 2010) are omnivorous (Morgan 1980, Taylor & Peck 2004, Douglass et al. 2011, Seitz et al. 2011) and are expected to consume mysids (Price 1962, Morgan 1980, Fantle et al. 1999). The 3 predator species play an essential role in the carbon flux of marine coastal waters, as they serve as a major link between the base of the food webs (producers and primary consumers) and upper-level consumers, such as birds (Kent 1986) and fish species (Scharf & Schlicht 2000, Clark et al. 2003, Kelly & Hanson 2013).

The mesocosms representing the homogeneous habitat were left without any structure, whereas the heterogeneous habitat was created by introducing the macroalga *Gracilaria* sp. and dry shells from the eastern oyster *Crassostrea virginica* into the mesocosms 48 h prior to the introduction of mysids. We selected dry oyster shells of similar size in enough quantity to cover only the bottom of the mesocosms. *Gracilaria* sp. was defaunated before its introduction into the mesocosms by soaking in freshwater for 2–3 h, followed by careful visual inspection after rinsing in freshwater. We added approximately 10 g of *Gracilaria* sp. wet mass in each mesocosm. *Gracilaria* sp. was weighed after removing excess water using a salad spinner (70 revolutions).

At the end of experiments, all invertebrates (mysids and predators) from the mesocosms were fixed in 70% ethanol for counting at the laboratory. To quantify microalgal biomass (chlorophyll *a*), microalgae were randomly sampled at a fixed depth from the wall of the mesocosms (2 samples of 10 cm²) and analyzed with a spectrophotometer (Jeffrey & Humphrey 1975). *Gracilaria* sp. wet mass was measured as described above.

Statistical analyses

We calculated the reduction of mysid abundance as the response variable to test the predators' efficiency, whereas change in microalgal biomass was used to test for cascading effects. Mysid reduction was calculated as the difference between the mean abundance of mysids in the absence of predators and their mean abundance in each predator treatment. The initial and final abundance of mysids in the predator-free treatments in both homogeneous and heterogeneous habitats were compared with a *t*-test to verify mysid survival without predators during the experiment. The influence of habitat heterogeneity on mysid survival without predators (Table 1: Treatments 1 and 8) and on final biomass of microalgae without con-

sumers (Table 1: Treatments 7 and 14) was also examined through a *t*-test by comparing the homogeneous treatment with its analogous heterogeneous treatment. One-way ANOVA was applied to homogeneous and heterogeneous treatments separately to verify differences in mysid suppression and microalgal biomass. *Gracilaria* sp. mass was also analyzed with 1-way ANOVA among those treatments in which it was stocked. Finally, differences in mysid abundance, microalgal biomass, and predator survival (number of predators that survived until the end of the experiment; all treatments containing predators were included in the analysis) between treatments were analyzed with 2-way ANOVA (factors: predator species composition and habitat heterogeneity). Significant treatment effects were clarified through post hoc Tukey's HSD tests. Homogeneity of variances and normality of the data were tested, and when necessary a log ($x + 1$) transformation was used to normalize the data (only the predator survival data had to be transformed) to meet the statistical assumptions of ANOVA.

We used a planned linear contrast to compare the mean prey suppression of the monocultures with the polyculture to test for non-transgressive overyielding effects. The occurrence of transgressive overyielding was also verified by comparing the best-performing monoculture with the polyculture.

RESULTS

Suppression of mysid prey differed strongly among predator treatments, but all predators were more effective in the heterogeneous habitat (Fig. 1). Habitat heterogeneity alone did not influence mysid abundance (*t*-test, $p = 0.540$) or microalgal biomass ($p = 0.321$), as the control treatments of both variables did not differ significantly between homogeneous and heterogeneous habitats. Moreover, mysid mortality and/or recruitment was negligible without predators, as indicated by no significant differences between their initial and final abundances in the control treatments during the experiment (*t*-test, $p > 0.06$). Predator treatment and habitat heterogeneity affected mysid suppression (2-way ANOVA, $p < 0.001$), but there was no interaction among treatments ($p = 0.44$; Table 2). The grass

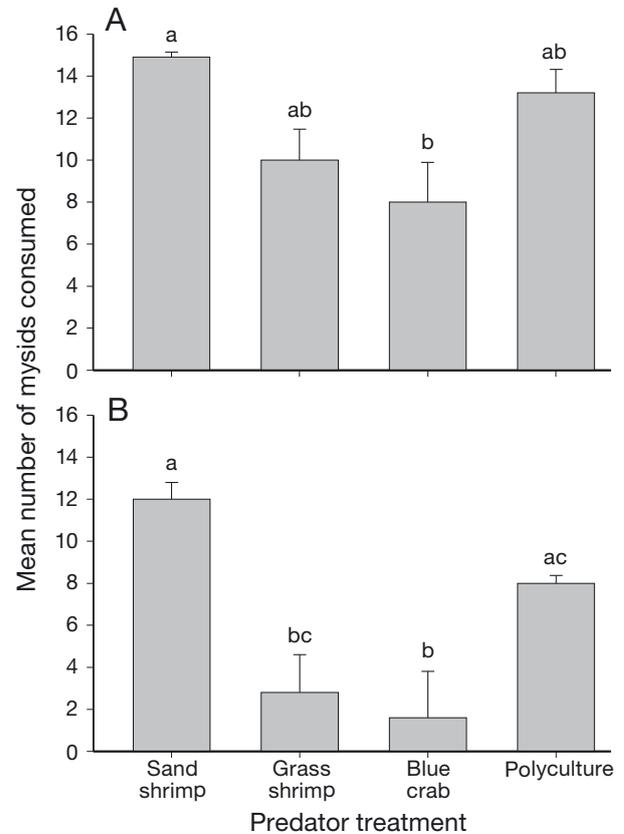


Fig. 1. Mean number of mysids consumed in each predator treatment in the (A) heterogeneous and (B) homogeneous habitats. Error bars represent the standard error. Bars with different letters are significantly different according to Tukey's HSD ($\alpha = 0.05$)

Table 2. Results of 2-way ANOVAs related to suppression of mysid abundance, microalgae biomass and (log) predator survival. Significant *p*-values ($p < 0.05$) are in **bold**

| Response variable and factor | df | SS | MS | <i>F</i> | <i>p</i> |
|------------------------------|----|--------|---------|----------|------------------|
| Prey suppression | | | | | |
| Predator | 3 | 461.6 | 153.9 | 15.464 | <0.001 |
| Habitat | 1 | 176.4 | 176.4 | 17.729 | <0.001 |
| Predator × Habitat | 3 | 27.6 | 9.2 | 0.925 | 0.44 |
| Error | 32 | 318.4 | 9.9 | | |
| Total | 39 | 984 | | | |
| Microalgae biomass | | | | | |
| Predator | 3 | 0.073 | 0.0243 | 1165 | 0.338 |
| Habitat | 1 | 0.0546 | 0.0546 | 2613 | 0.116 |
| Predator × Habitat | 3 | 0.0281 | 0.00938 | 0.449 | 0.72 |
| Error | 32 | 0.668 | 0.0209 | | |
| Total | 39 | 0.824 | 0.0211 | | |
| Predator survival | | | | | |
| Predator | 4 | 0.0974 | 0.0244 | 3.351 | 0.019 |
| Habitat | 1 | 0.0907 | 0.0907 | 12.482 | 0.001 |
| Predator × Habitat | 4 | 0.163 | 0.0406 | 5.59 | 0.001 |
| Error | 40 | 0.291 | 0.00727 | | |
| Total | 49 | 0.641 | 0.0131 | | |

shrimp (ANOVA, $p < 0.0001$) and the blue crab ($p = 0.004$) preyed significantly on mysids only in the heterogeneous habitat (Fig. 1), whereas the sand shrimp and the predator polyculture suppressed mysids significantly in both habitats ($p < 0.005$).

We did not observe transgressive overyielding, i.e. the total in the predator polycultures did not exceed that of the sand shrimp, which was the best-performing single predator species in both homogeneous and heterogeneous habitat treatments. Although the predator polyculture consumed more mysids (mean \pm SE; homogeneous habitat: 8.0 ± 0.8 mysids; heterogeneous habitat: 12.6 ± 1.1 mysids) compared with the mean of the 3 predator monocultures (homogeneous habitat: 5.5 ± 1.5 mysids; heterogeneous habitat: 10.3 ± 1.1 mysids), they did not differ significantly (planned linear contrast, homogeneous habitat: $p = 0.161$; heterogeneous habitat: $p = 0.158$), indicating absence of non-transgressive overyielding effects.

Microalgal biomass had lower values in the blue crab and grass shrimp monocultures in the homogeneous habitat, which may suggest some microalgae grazing by these predators (Fig. 2). However, microalgal biomass did not vary significantly between treatments in homogeneous and heterogeneous habitats (ANOVA, $p > 0.42$; Fig. 2) and was not affected by predator species composition (2-way ANOVA, $p = 0.338$), habitat heterogeneity ($p = 0.116$), or their interaction ($p = 0.72$; Table 2). Thus, no trophic cascades were observed, as predator reduction of mysid abundance did not influence microalgal biomass.

Change in *Gracilaria* sp. wet mass was lower in the monocultures and the predator-free control treatment, and higher in the predator polyculture without prey and the microalgae-alone treatment (Fig. 3). This result may indicate some *Gracilaria* sp. consumption by mysids and predators, although the treatments did not differ significantly (ANOVA, $p = 0.165$).

Predator survival was affected by predator treatment (2-way ANOVA, $p = 0.019$), habitat heterogeneity ($p = 0.001$), and their interaction ($p = 0.001$; Table 2). This was evident mainly for the blue crab (Fig. 4), which had significantly higher survival rates in the heterogeneous habitat (Tukey's HSD, $p < 0.001$).

DISCUSSION

Our experiment showed that predator species differed strongly in ability to suppress prey, multi-species predator assemblages were more effective than the average single predator, and predator effectiveness and survival were enhanced by habitat hetero-

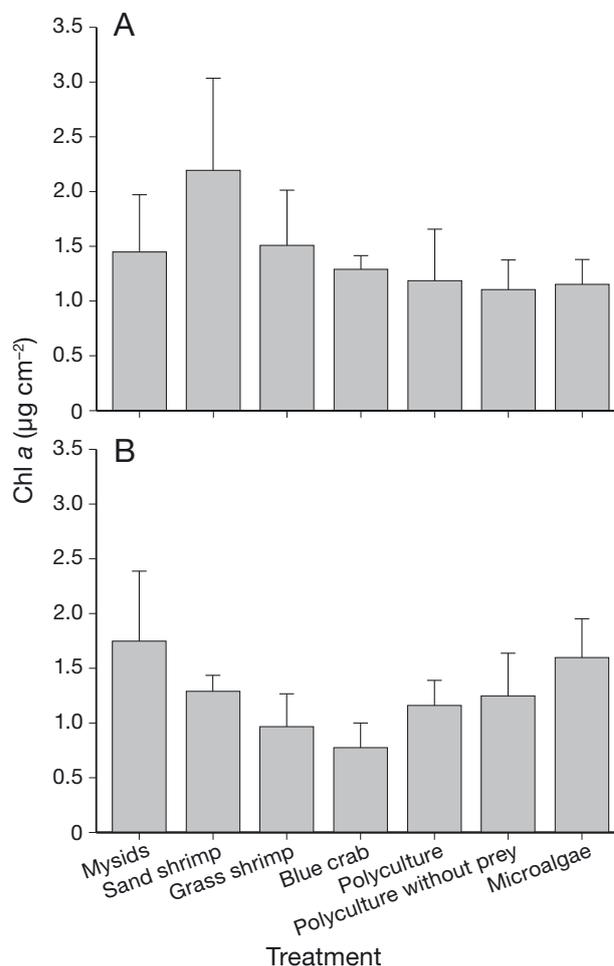


Fig. 2. Mean microalgal biomass in each treatment in the (A) heterogeneous and (B) homogeneous habitats. Error bars represent the standard error

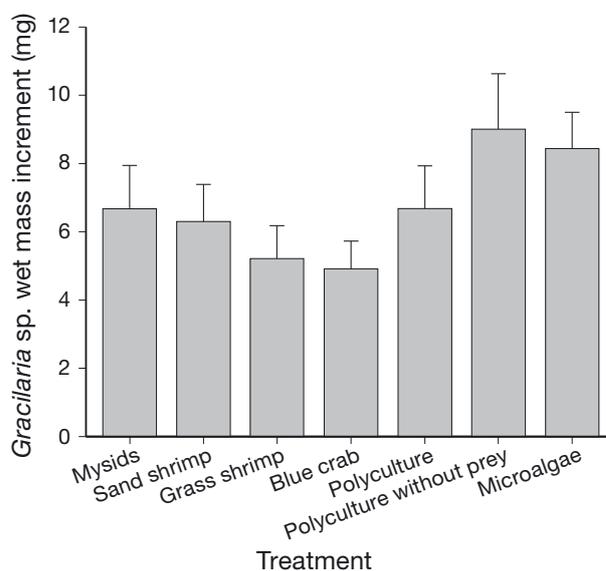


Fig. 3. Mean *Gracilaria* sp. wet mass increment during the experiment. Error bars represent the standard error

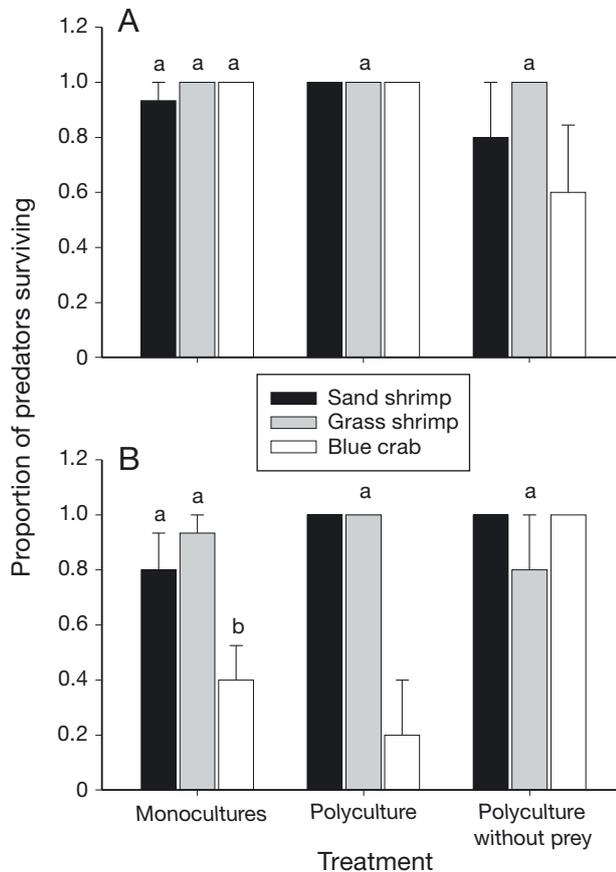


Fig. 4. Mean proportion of predators surviving at the end of the experiment in each predator treatment in the (A) heterogeneous and (B) homogeneous habitats. Error bars represent the standard error. Bars with different letters are significantly different according to Tukey's HSD ($\alpha = 0.05$)

generality. All predator treatments were more efficient at suppressing prey in the more heterogeneous habitat; however, the importance of habitat heterogeneity was singular for each species, probably related to the specific behavior and feeding mode of each predator. The sand shrimp was the most effective predator species in both homogeneous and heterogeneous habitats, and apparently was the species least dependent on habitat heterogeneity to suppress prey. The 3 predator species used in the experiment are bottom dwellers, but the sand shrimp, in contrast to the grass shrimp and the blue crab, is a nocturnal opportunistic predator (Taylor & Peck 2004) that migrates to the water column during nighttime (Brown et al. 2014). This migratory behavior may have increased predator-prey encounter rates, which may explain the higher mysid suppression by the sand shrimp independently of habitat heterogeneity. Conversely, the grass shrimp and the blue crab only preyed effectively on mysids in the more heterogeneous habitat.

These 2 predators generally occur in association with foundation species such as submerged aquatic vegetation and oyster reefs (Douglass et al. 2010, Shervette et al. 2011), where they usually have higher predation success (Ryer 1987, Gregg & Fleeger 1998) and survival (Hovel & Lipcius 2002, Mattila et al. 2008) than in more homogeneous environments, as observed in our experiment. The grass shrimp especially took advantage of the physical structure provided by *Gracilaria* sp., to which it was frequently seen clinging, as already shown for this shrimp species (Khan et al. 1997). The vertical structure provided by the macroalgae seemed to: (1) segregate the grass shrimp from the other 2 predator species; (2) allow this generalist shrimp predator to access prey higher in the water column; and (3) provide a refuge from which to ambush the mysids. For the blue crab, habitat heterogeneity visibly influenced survival rates, likely because of its high intraspecific aggressiveness (Mansour & Lipcius 1991, Clark et al. 1999) and cannibalistic behavior (Hines et al. 1990, Moksnes et al. 1997). Therefore, the higher prey suppression of the blue crab in the more heterogeneous habitat was probably a consequence of less agonistic behavior and/or reduced intraspecific predation. Thus, the distinct interaction of each predator species with habitat heterogeneity allowed interspecific niche partitioning among the 3 predators to be better expressed, resulting in higher prey suppression because of complementarity effects (Cardinale et al. 2004, Griffin et al. 2009).

The pattern of highest predation by the sand shrimp, followed by the predator polyculture, indicates that both predator identity and diversity influenced the efficiency of the assemblage to remove prey (Bruno & O'Connor 2005, Douglass et al. 2008). Our data are consistent with results of a meta-analysis that showed that predator richness generally enhances prey suppression relative to the mean performance of predator monocultures, but not in comparison to the most effective predator (Griffin et al. 2013). This trend implies that maximum prey suppression, i.e. energy fluxes from prey to predator assemblages, would diminish with loss of predator diversity only if the most effective predator disappears (and assuming that predator density remains constant). However, in natural ecosystems, different species usually maximize distinct ecosystem processes (Duffy 2009, Lefcheck et al. 2015); hence, reduced predator diversity is likely to alter any of several processes mediated through top-down forcing and cascade through consumers to producers (Finke & Denno 2004, Duffy et al. 2007, Bruno & Cardinale

2008), consequently affecting ecosystem functions such as production and decomposition.

Despite the ubiquity of trophic cascades in the marine benthos (Shurin et al. 2002), we did not observe any sign of the influence of predator identity and diversity on the occurrence of a trophic cascade. We expected a trophic cascade whereby predator richness indirectly increases algal biomass via predation on grazing mysids. Yet, mysids did not graze on benthic microalgae to a significant extent, probably because they are omnivorous generalist consumers (Mauchline 1980, Jumars 2007). Thus, in addition to benthic microalgae, they might have fed on other food sources, such as detritus, phytoplankton, and tiny invertebrates (e.g. harpacticoid copepods), present in the mesocosms. Conversely, mysids seemed to consume *Gracilaria* sp.; however, no trophic cascade was observed in this case either, because predators also seemed to feed on this macroalgae. In this case, the omnivorous character of predators dampened a trophic cascade (Bruno & O'Connor 2005, Johnson et al. 2014).

In summary, we observed that complementarity effects between predator species were fostered in a more heterogeneous habitat, apparently because of niche partitioning, which leads to higher prey suppression and survival of predators. These findings indicate that the loss of both biodiversity and habitat heterogeneity can alter processes that affect energy flux in marine food webs, although the exact consequences are hard to predict because of their complex interaction. Therefore, conservation of both biodiversity and habitat heterogeneity are considerations for the appropriate management of natural ecosystems.

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