Journal of Experimental Marine Biology and Ecology 412 (2012) 117–125

Contents lists available at SciVerse ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Inter- and intraspecific interactions among green crabs (*Carcinus maenas*) and whelks (*Nucella lapillus*) foraging on blue mussels (*Mytilus edulis*)

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ARTICLE INFO

Article history:
Received 27 June 2011
Received in revised form 27 October 2011
Accepted 15 November 2011
Available online 3 December 2011

Keywords:
Blue mussels
Dogwhelks
Green crabs
Intraguild predation
Kleptoparasitism
Multiple predator effects

ABSTRACT

Blue mussels (*Mytilus edulis*) play an important role in many coastal marine communities, regulating biodiversity and serving as food for many predators. Interactions between predators mediate their impact on mussel prey, and thus have indirect effects on the mussel bed community. We studied the effects of predator density and species composition on mussel predation by green crabs (*Carcinus maenas*) and dogwhelks (*Nucella lapillus*). We conducted an experiment in which predators at high and low natural intertidal densities were enclosed with mussels, in either single- or multiple-predator species treatments. Biomass consumed by each species in each treatment was determined and effects of multiple predators on consumption rates were estimated. Mean size of mussels eaten by each predator species was also measured and compared between treatments. Feeding by whelks and crabs was inhibited by conspecifics, and whelk foraging was also depressed in the presence of crabs. The presence of whelks had a positive effect on crab foraging, which may have moderated the negative effects of intraspecific competition between crabs. Sizes of mussels consumed did not differ statistically between treatments. In mixed-species treatments, crabs appear to have kleptoparasitized mussels being eaten by whelks, possibly facilitating consumption of larger mussels by crabs. Results indicate that interactions between invertebrate predators of blue mussels cause shifts in the feeding patterns of these predators, and are therefore an important part of mussel bed community dynamics.

1. Introduction

Predation and competition are important determinants of the structure of biological communities (Hairston et al., 1960; Holt, 1977; McQueen et al., 1989; Menge and Sutherland, 1976). These are negative interactions in that they result in negative effects on one or both organisms. Positive interactions, in which the presence of one species in some way benefits another, also play important roles in community dynamics (Bertness and Leonard, 1997; Peterson and Heck, 2001), for example, when foraging activity of one consumer facilitates the feeding of another (Eklöv and VanKooten, 2001). Trophic dynamics in natural communities may be further influenced by intraguild predation (IGP), in which predators that should be potential competitors for the same prey species also engage in predator–prey interactions with each other (Arim and Marquet, 2004; Polis and Holt, 1992). The intermediate consumer in IGP often undergoes some change in its traits or behavior to avoid predation (Dill et al., 2003; Navarrete et al., 2000; Polis and Holt, 1992; Trussell et al., 2003), resulting in trait-mediated indirect interactions (TMIIs) between consumers and prey.

In intertidal communities, filter-feeding invertebrates, including mussels, are an important basal food source in numerous food webs (Menge and Branch, 2001). The abundance of such dominant filter-feeders controls community diversity through competition with other species for space and food (Enderlein and Wahl, 2004; Hamilton, 2000), and through provision of secondary space (Lee and Ambrose, 1989), but is itself influenced by predation (Menge and Sutherland, 1976). In Passamaquoddy Bay, Bay of Fundy, Canada, the blue mussel *Mytilus edulis* forms dense beds in the intertidal zone that sustain such communities. Predators of blue mussels in this region include green crabs (*Carcinus maenas*), dogwhelks (*Nucella lapillus*), sea stars (*Asterias* spp.), and diving ducks, the most abundant of which are common eiders (*Somateria mollissima*) (Hamilton, 2000). Interactions among these predators may affect predation rates and may play an important role in defining the dynamics of mussel bed communities within this region.

The green crab is an invasive European decapod crustacean (Carlton and Cohen, 2003). It has a very broad diet and hunts using olfactory and tactile stimuli (Crothers, 1968). Crabs examine prey items before consuming them and then crush or chip the shells of prey with their chelae (Elner, 1978). They are also highly aggressive competitors, with interference by conspecifics potentially inhibiting crab feeding (Griffen and Williamson, 2008; Huntingford and Taylor, 1997; Rovero et al., 2000). This interference sometimes takes the form of kleptoparasitism, in which one crab steals mussel prey from another (Smallegange et al.,

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doi:10.1016/j.jembe.2011.11.012

2006). Such inhibition may be less severe at higher prey densities because predators spend less time searching for prey (Smallegange et al., 2006), though interference competition does still occur at these densities and thus may cause predation rates to be less than additive.

Dogwhelks are gastropod molluscs that feed on mussels, periwinkles, and barnacles (Crothers, 1985). Whelks search for prey using olfaction (Hughes and Dunkin, 1984), bore through the shells of prey using a combination of radular scraping and chemical dissolution (Carriker and Williams, 1978), then digest the tissue inside. The smell of feeding conspecifics may stimulate whelks to feed (Hughes and Dunkin, 1984), constituting a positive effect of whelk density on feeding rates. However, whelks may also engage in interference competition with conspecifics, either by displacing each other from mussel prey (Hughes and Dunkin, 1984) or engaging in kleptoparasitism at higher densities (Morton, 2010). Therefore, the net effect of whelks on each others' feeding remains uncertain.

Dogwhelks are occasionally eaten by green crabs (Aschaffenburg, 2008; Crothers, 1968; Trussell et al., 2003), which is a form of intraguild predation. Whelks can sense chemical risk cues in seawater that signal the presence of predatory crabs in their environment (Appleton and Palmer, 1988), and respond by reducing their feeding rates (Aschaffenburg, 2008; Trussell et al., 2003; Vadas et al., 1994). Thus, when both predator species are present in the system, their net effect should be less than additive, which represents an emergent effect of multiple predators in the system (d'Entremont, 2005; Sih et al., 1998).

Competitive interactions between predators sometimes lead to prey switching (Huntingford and Taylor, 1997; Rovero et al., 2000). Green crabs and dogwhelks have a preferred range of mussel prey sizes, related to predator size (Elner and Hughes, 1978; Hughes and Dunkin, 1984; Juanes, 1992; Enderlein et al., 2003). However, predators can become less selective when other conditions affect their ability to forage. For example, when crabs are stressed, such as after starvation (Morris, 2008), the size of mussels on which they feed becomes more variable. Similar changes in prey size selection may also occur when whelks and crabs are stressed by competition. Although this was not noted in dichotomous choice trials in the laboratory (Smallegange et al., 2008), in nature crabs may encounter a wider range of mussels more frequently and thus could be more flexible in their feeding preferences.

We used predator enclosures to investigate the effects of intra- and interspecific interactions between green crabs and dogwhelks on consumption by each species of blue mussels. We hypothesized that negative interactions between predators would lead to depression of foraging rates when more predators were present, with crab and possibly whelk feeding depressed at higher densities due to competition, and whelk feeding depressed in the presence of crabs due to responses to crab risk cues. Such patterns have been investigated before (d'Entremont, 2005), but not at natural predator densities in the field. We also hypothesized that such interactions would cause predators to alter prey sizes chosen to minimize competitive interactions, perhaps with predators becoming less selective under competitive stress (sensu Morris, 2008, and Smallegange et al., 2008) and feeding on mussels of sub-optimal sizes.

2. Materials and methods

2.1. Study site

Work was conducted at Pagan Point, St. Andrews, New Brunswick, Canada (45°4′ N, 67°2′ W), in the littoral zone of Passamaquoddy Bay in the Bay of Fundy. Experimental cage structures were set up at approximately 1.3 m above mean lower low water (MLLW), and were rarely exposed for more than two hours during each low tide.

2.2. Densities and sizes of predators and prey

Based on preliminary surveys of a natural mussel bed in the study area in June 2009 we estimated the density of blue mussels to be 2067 (±822) mussels m^{-2} (mean±SD). We also surveyed densities and sizes of dogwhelks and green crabs along five 30-m transects; two in mussel beds and three in adjacent rockweed (*Ascophyllum nodosum*)-covered areas. Dogwhelks averaged 25.5 (±3.4) mm (mean±SD) in shell height and green crabs averaged 34.0 (±11.9) mm in carapace width. Mean density (±SD) of whelks was 50 (±15) whelks m^{-2}. Because the distribution of observed whelk densities (range 12 to 300 whelks m^{-2}) was skewed with many values below the mean and a few extremely high ones we estimated a typical low density as the median density, 44 whelks m^{-2}, and a typical high density as the 90th percentile, 122 whelks m^{-2}. Mean density (±SD) of crabs was 20 (±17) crabs m^{-2}. Distribution of crabs was patchy and non-normal, so we set typical low and high densities as those that we observed frequently in the field. A typical low density was estimated at approximately 10–12 crabs m^{-2} and a typical high density at approximately 30–33 crabs m^{-2}.

2.3. Predator treatments

Predator densities used in the experiment were 4 whelks (low) or 11 whelks (high), and 1 crab (low), or 3 crabs (high) in their respective cages. Densities were calculated based on an estimated foraging area of 0.09 m^2 (30 cm×30 cm tile covered with mussels) rather than the total cage area of 0.82 m^2 because our focus was on predator interactions, which would occur in foraging areas. Although crabs do take food away from foraging patches (Smallegange et al., 2010), when they leave the competitive interaction between them ends. Six predator treatments were used: low density whelk (LW), high density whelk (HW), low density crab (LC), high density crab (HC), low density crab with low density whelk (LCW), and high density crab with high density whelk (HCW). The different densities of single predator species tested effects of intraspecific interactions on predator foraging, while treatments with both predators present together tested effects of interspecific interactions. This design is additive as opposed to substitutive (sensu Griffen, 2006) because the large difference in size and foraging rates between the two predator species makes it impossible to freely substitute them, precluding the latter approach. However, because we use low and high densities in both single and multiple species treatments, it is possible to partially address the issue, as discussed by Griffen (2006), of whether effects of interspecific interactions on feeding rates stem from predator density or predator identity.

2.4. Field experiment

We conducted three 2-wk experimental trials between July and September 2009, with new predators and prey used for each trial. Duration of trials was selected based on observations of predator feeding during a 20-day preliminary experiment.

Cages were constructed of lobster wire and measured 0.91 m× 0.91 m×0.3 m high. All sides were covered in 0.5-cm mesh. A mesh skirt along the bottom was dug into the substrate to prevent external predators from moving underneath the cages. Two rocks of moderate size with attached rockweed were placed within each cage to provide natural refuges for predators at low tide (Fig. 1a). We set up the cages in five replicate sites (blocks) with each site containing six cage treatments (Fig. 1b). Space limitations required sites to be organized into two rows, but differences among sites in exposure/submersion times were less than 10 min during most tides. Locations of sites and treatments within each site were allocated randomly.