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Comparing the influence of native and invasive intraguild predators on a rare native oyster

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ABSTRACT

Invasive species can cause complex, unpredictable changes in community dynamics because they do not share an evolutionary history with native species, meaning interactions could be much stronger or weaker than expected. A field experiment tested hypotheses generated from previous laboratory experiments about interactions in an invaded tri-trophic intertidal food chain that is also characterized by asymmetric intra-guild predation. Cages controlled access of a top predator (native cancrid crabs) and an intermediate (or intraguild) prey (invasive oyster drills, *Ocenebra inornata*) to a resource (native oysters, *Ostrea lurida*) in order to explore the separate and combined effects of these predators on a native ecosystem engineer of conservation concern. Though crabs were predicted to have a strong negative effect on oysters via direct predation, the presence of oyster drills had the strongest impact on oyster survival. Drills consumed up to 80% of oysters in experimental cages per month and accounted for an average of 70% of total mortality when they were present. Contrary to the hypothesis, crabs almost never attacked oysters directly, and consumed drills primarily during only one out of four months. Crabs also did not appear to reduce individual drill feeding rates (i.e. an intimidation effect) or initiate a strong indirect positive effect on oyster survival. This experiment demonstrates that the role of the invasive predator in IGP as well as the strength of the interaction between the native and invasive species combine to influence the dynamics of the system. In addition, these observations underscore the importance of considering non-native predators as obstacles to the recovery of threatened species, as well the value of experimentally identifying, in situ, which of the possible interactions in an invaded food web are ecologically important.

1. Introduction

Introductions of nonnative species can cause significant ecological disruption to resident populations, communities, and ecosystems (Mack et al., 2000). The extent to which an introduced species impacts a community depends in part on the type and strength of interactions with resident species. Yet these interactions can be difficult to predict due to the relatively short shared evolutionary history among the species involved (Payne et al., 2004; Sih et al., 2010). For instance, if a native organism fails to recognize a nonnative predator as a threat, or to respond effectively, the predator could have a strong negative effect on the prey population, potentially leading to further cascading indirect effects in the community (Fritts and Rodda, 1998; Kimbro et al., 2009). Because organisms in ecological communities never interact with only one other species, indirect interactions can have major consequences for community structure (Wootton, 1994a), with many well-described examples from invaded communities (White et al., 2006). In tri-trophic food chains, for example, the top predator interacts directly with intermediate prey via consumption, and indirectly with the resource (prey of the prey) by changing the abundance of the intermediate prey (a consumptive indirect effect) (Menge, 1995; Strauss, 1991; Wootton, 1994a).

In a food chain characterized by intraguild predation (IGP), the top predator both preys on and competes with the intermediate prey by directly consuming the resource (Polis et al., 1989). IGP could theoretically slow the population growth of an invader by reducing the availability of shared prey. In the case of asymmetric IGP, in which only one competitor is a predator of the other, the strength of biotic resistance to the invader will depend on the invader's position in the interaction web. Models of IGP in invaded systems predict accelerated invasion rates when the invader is the intraguild predator (Hall, 2011). This is because the invader can consume either native species, while the native intraguild prey is wholly reliant on their shared resource, a scenario favoring population growth of the invader. On the other hand, if the invader is the intraguild prey, predation and competition from the native intraguild predator could both function to inhibit invader success. The latter of these two scenarios (native intraguild predator, invasive intraguild prey) is less well studied. Understanding the IGP dynamics of an invaded system is critical to management,

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because in some cases removal of a top invasive predator, by releasing population control on an invasive intraguild prey, has been counterproductive to conservation goals (Bergstrom et al., 2009; Courchamp et al., 1999).

The present field study manipulated interactions among a native intraguild predator, an invasive intraguild prey, and a shared native resource species to investigate how these interactions combine to impact the ecologically and economically valuable resource. In the Pacific Northwest USA, invasive Japanese oyster drills (*Ocenebra inornata* Récluz) cause damage that is both ecological, because they consume rare native oysters (*Ostrea lurida* Carpenter), and economic, because they are a pest for the shellfish industry (White et al., 2009). This species of drill was unintentionally introduced in the early 20th century when juvenile Pacific oysters (*Crassostrea gigas* Thunberg), along with shell used as larval settlement substrate, were imported from Asia to supplement the failing native oyster industry (Chapman and Banner, 1949). Subsequent dispersal of drills has been primarily human-mediated because these intertidal whelks develop in benthic egg capsules and emerge as crawl-away juveniles, limiting their natural dispersal rates (Chapman and Banner, 1949). Management of drills by shellfish growers consists of manual removal of egg capsules and adult snails, but these efforts are time-consuming and costly (Buhle et al., 2005), and achieve only limited success at reducing drill populations. Oyster growers suffer losses from drill predation and occasionally abandon beds due to drill infestation. Reclaimed oyster beds are often sites for *O. lurida* restoration, where predation on juvenile oysters by remnant populations of drills could be inhibiting restoration efforts (Buhle and Ruesink, 2009; Wasson et al., 2015). Native cancrid crabs (e.g., *Cancer* (*Metacarcinus*) *magister*, *Cancer productus*, *Cancer gracilis*) co-occur with drills in oyster beds (Holsman et al., 2006) and these crab species can be strong interactors in intertidal communities through predation on molluscs (Yamada and Boulding, 1996).

This crab–drill–oyster system therefore generates the potential for complex trophic dynamics (Fig. 1). Crabs could influence oyster populations via predation on oysters (direct consumptive effects, pathway 3), predation on drills (indirect consumptive effects/trophic cascade, pathways 1 and 2), and by reduction of the per capita effect of drills on oysters (non-consumptive indirect effects, pathway 4) (Abrams, 2007; Lima, 1998; Werner and Peacor, 2003). Previous research in similar systems suggests that the combined and separate effects of crabs and non-native drills are likely context dependent (Kimbro et al., 2009; Wasson et al., 2015). Some of the potential interactions with these species have been studied independently in laboratory experiments, allowing us to hypothesize dynamics that might be observed in natural communities. Laboratory mesocosm studies demonstrated that *O. inornata* eats 50% fewer oysters and hides more often when exposed to chemical cues from *C. productus* attacking, consuming, and digesting conspecific drills (Grason and Miner, 2012a). When given a choice, however, crabs preferentially consume juvenile oysters over drills (Grason and Miner, 2012b). Based on both sets of experiments, we predicted that any positive indirect effect of crabs (both consumptive and non-consumptive) on oysters would be swamped by the negative direct effect of crab predation.

To examine the trophic dynamics of this system in the field, crab and drill access to oysters was manipulated in a four-month caging experiment in Liberty Bay, Washington, an inlet of Puget Sound. Based on forensic observations of shell damage, oyster mortality was attributable to respective predator types. This allowed quantification of the direct effects of each predator type as well as the indirect effects when both predators were present. Lastly, drill feeding rates were measured to distinguish whether any indirect effects were due to changes in drill density, per capita effect, or both.

2. Materials and methods

To determine the separate and combined effects of predators on oyster mortality, the presence and absence of crabs and oyster drills were manipulated over four months (April–August 2011) using enclosure and exclosure cages. The cages were deployed on the mudflats at Scandia on the west side of Liberty Bay, WA (47.72204°N, 122.65412°W) between −0.3 and −0.6 m MLLW. Ongoing native oyster restoration efforts at this site are conducted by a local nongovernmental organization (the Puget Sound Restoration Fund), and oyster recruitment substrate consisting of *C. gigas* shell material was most recently deposited in 2005. The benthic community now includes *O. lurida* that have recruited onto the shell as well as *O. inornata* and large, mature *C. gigas*.

To estimate the effects of both crabs and drills on *O. lurida*, oyster mortality was recorded monthly in a factorial caging experiment consisting of four treatments: no predators, drills only, crabs only, and both drills and crabs (n = 5 cages per treatment). Predator manipulation cages (56 cm L × 56 cm W × 25 cm H) that controlled the access of each predator type to oysters were constructed from plastic mesh (10 mm hole size on top and bottom, 4 mm on sides). In treatments that exposed oysters to crab predation, cages allowed crabs to enter via holes (23 cm L × 10 cm H) on two of the four side panels. The edges of the holes were lined with copper flashing to prevent snails from exiting or entering the cages. This method has previously been

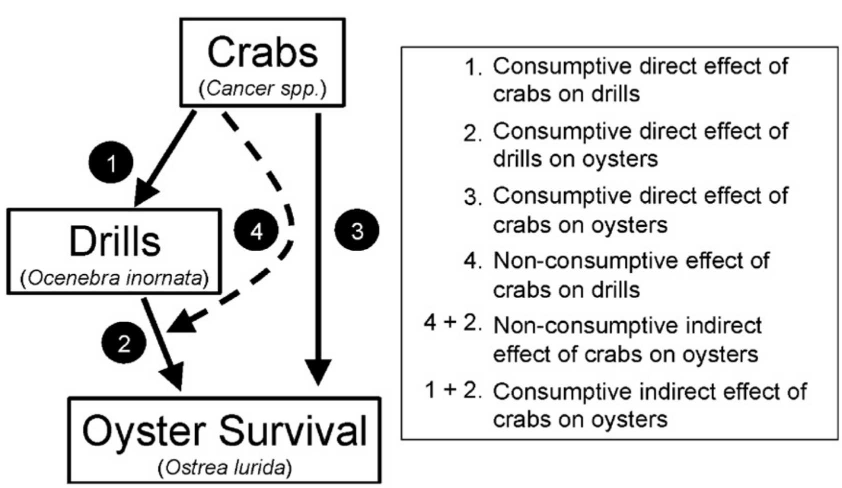

Fig. 1. Diagram of potential interaction pathways in the three-species trophic web investigated here. Arrows point from the initiator species to either the receiving species (solid lines), in the case of consumptive effects, or to the interaction arrow between two species (dashed line), in the case of non-consumptive effects whereby crabs modify the rate at which oyster drills feed on oysters.