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Restoration of native oysters in a highly invaded estuary

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ABSTRACT

Restoration of native species may be hampered by competition with non-native species. The outcomes of competition are often context-dependent, with one species dominating under some conditions but not others. Where non-natives differ from natives in their ability to tolerate stressful environmental conditions, restoration practitioners may be able to manipulate conditions or strategically locate restoration projects along naturally occurring stress gradients to favor native species. We tested the responses of native oysters and a suite of non-native sessile invertebrate species (mostly soft-bodied organisms) to varying tidal elevations, shoreline types, and distances from source populations. Cover of non-natives was lower at higher tidal elevation and far from adult populations. Native oyster recruitment was also reduced at the high tidal elevation. At this elevation oyster dominance was increased, but abundance was reduced. To test an adaptive management approach, we moved substrates from the low to high tidal elevations. Cover of non-natives had decreased dramatically one year later, while oyster metrics were unaffected or improved compared to those on substrates remaining at the low elevation. Our study indicates that reduction of non-native species abundance, often an explicit goal of restoration, may be achieved by strategic location of restoration units, although abundance of target species may also be reduced, at least over the short term. However, restoration practitioners may be able to increase abundance of target species and reduce non-natives by applying stress differentially over time, with benign conditions during sensitive early life stages, and increasing stress after target organisms become more tolerant.

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1. Introduction

Restoration frequently occurs in habitats that have been dramatically changed by human activities, which may result in conditions that no longer favor native species (Hobbs and Huenneke, 1992; Miller and Hobbs, 2007). One such change is the introduction of non-native species. Non-native species can pose direct threats to native species as competitors or predators, or by acting as ecosystem engineers, altering their surroundings in ways that negatively impact natives (Carlton, 1999; Crooks, 2002; Mack et al., 2000; Vitousek et al., 1996). The removal of non-native species is often not tractable at the landscape level, but eradication or control can sometimes be successful at smaller scales, allowing restoration of natives to proceed. Another potential option for restoration practitioners is to strategically select environmental conditions that reduce the impacts of non-native species on species targeted for restoration (Daehler, 2003).

The importance of ecological interactions such as competition to species abundance and distribution is often context-dependent, such that some species or communities dominate in a certain set of conditions, but not in others (e.g., Bertness and Calloway, 1994; He et al., 2013: Hutchinson, 1961: Menge and Sutherland, 1987). Restoration practitioners can take advantage of this by identifying and fostering conditions that shift dynamics to favor natives over non-natives (Daehler, 2003). Sometimes this consists of restoring historic conditions under which native species thrive, such as through nitrogen reduction for native grasses and other plants (Blumenthal et al., 2003; Dalrymple et al., 2003, Holzel and Otte, 2003; Perry et al., 2004; Prober et al., 2005), changing topography to increase flooding for meadow and riparian vegetation (Dalrymple et al., 2003; Holzel and Otte, 2003; Nagler et al., 2005), or restoring more natural hydrology regimes for amphibians and a suite of marsh plants (Fuller et al., 2011; Rochlin et al., 2012).

The outcome of biotic interactions can also shift along an environmental stress gradient when native and non-native species differ in their tolerance to stress (Alpert et al., 2000; Daehler, 2003; MacDougall et al., 2006). For example, some native plants outcompete non-natives under grazing or burning regimes or in shady understories;

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thus the creation of these stressful conditions can be a successful restoration approach for invaded grasslands (Buisson et al., 2006; Prober et al., 2005) and mangrove habitats (Chen et al., 2013). When large-scale manipulation of conditions is not an option, restoration practitioners might still be able take advantage of differences in stress tolerances, working within naturally occurring stress gradients and selectively restoring at sites where conditions are more stressful to non-native species than to target native species.

Restoration projects that use the methods described above frequently couple environmental manipulations with seeding or planting in cases where target species are also propagule-limited relative to nonnatives (Frances et al., 2010; Holzel and Otte, 2003). The seed bank or propagule pressure of non-native species at any given site also may need to be taken into account to avoid swamping effects, even when environmental conditions favor natives (Daehler, 2003; Morghan and Seastedt, 1999; Wilson and Gerry, 1995).

To date, much of the restoration work examining the effects of environmental conditions and propagule limitation as they impact native species dominance has occurred in terrestrial plant systems. Here we apply some of these ideas in a marine system, testing several hypotheses about sites and conditions that would favor native oysters over a suite of non-native sessile invertebrates as part of a small-scale oyster restoration project in a Central California estuary.

The Olympia oyster (Ostrea lurida), native to the west coast of North America, is in decline from historic levels throughout its range from British Columbia to Baja California (zu Ermgassen et al., 2012). It is now the focus of restoration efforts in bays and estuaries along the West Coast (Dinnel et al., 2009; Pritchard et al., 2015). Olympia oyster restoration projects typically involve the provision of hard substrate in low intertidal and shallow subtidal zones, which is necessary for oyster settlement, but limited in the soft-sediment estuaries typical of the West Coast. However, many non-native species now found in these estuaries also require hard substrate and may compete with native oysters for settlement space and/or overgrow oysters after settlement (Deck, 2011; Trimble et al., 2009). The issue of competition aside, concerns about the unintentional spread of non-native species through the additions of hard substrate have been raised during the permitting process for native-oyster restoration projects in some locations (Cohen and Zabin, 2009, C.J.Z. pers. obs.). Thus the dual challenge for restoration in these invaded systems is to enhance native species while preventing increased abundance or distribution of non-natives.

The goal of our study at Elkhorn Slough (Central California, USA, Fig. 1) to was examine whether under certain environmental conditions, native oysters could be enhanced relative to a suite of non-native species that are potential space competitors. In particular, we were interested in examining whether oysters were better at facing challenging environmental conditions than the sessile non-native invertebrates with which they co-occur, and if so, whether this could be used in the design of oyster restoration projects. Oysters are shelled bivalves that are adapted to the stressful conditions that are typical of the intertidal zone, such as periods of exposure to air and rapid temperature changes, and of estuarine systems, such as periodic fluctuations in salinity and sedimentation, because of their ability to close their shells (Berger and Kharazova, 1997). In contrast, most of the non-native species on hard substrates at Elkhorn Slough are soft-bodied organisms such as sponges, tunicates and hydroids (Wasson et al., 2001, 2005), which are more vulnerable to desiccation, sedimentation and salinity stress. Non-native oysters are not currently present at Elkhorn Slough (Wasson et al., 2001).

Based on intertidal surveys, we hypothesized that while native oysters and a suite of non-native species broadly overlap in their distribution, there are some conditions under which oysters do better than the non-natives. These conditions, while perhaps not optimal, may be better tolerated by oysters than by the mostly soft-bodied non-natives, and thus could be incorporated into restoration design to promote dominance by oysters on our deployed substrates. For example at Elkhorn Slough, oysters extend higher into the intertidal zone than the non-native tunicate and sponge species (Fig. 2), which in this system are the taxa most likely to overgrow or prevent the settlement of native oysters. Research on eastern oysters (Crassostrea virginica) and Suminoe oysters (Crassostrea ariakensis) on the East Coast of the US found that those oyster species were more tolerant to aerial exposure than many of the other sessile invertebrates with which they co-occur such that that cover of potential competitors was reduced at higher tidal elevations (e.g., Bahr and Lanier, 1981, Bishop and Peterson, 2006; Fodrie et al., 2014). Indeed, it is common practice among commercial oyster growers to periodically expose oyster racks to air to remove soft-bodied fouling species. However, Olympia oyster settlement, growth and/or survival may

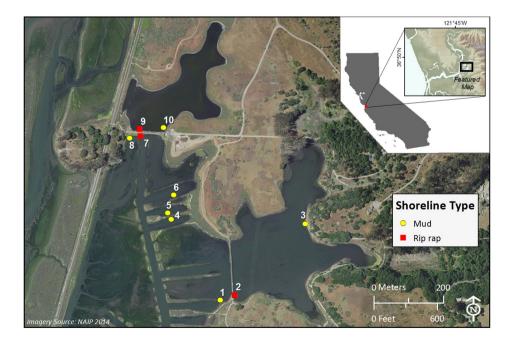


Fig. 1. Location of restoration project (inset); and sites within restoration project.

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