

Delicious critters make prime real estate: the effects of an invasive ecosystem engineer on functional diversity in Willapa Bay, WA

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14 March 2020

Abstract

By creating habitat complexity, ecosystem engineers can have an outsized effect on their environments and communities, particularly when introduced to a new area. While a number of studies have focused on changes in species richness and abundance related to biogenic habitat complexity, few have used a trait-based approach to evaluate how those changes could affect ecological processes. The goal of this study was to compare communities on, under, and near reefs of an invasive and farmed oyster, *Crassostrea gigas*, in Willapa Bay, Washington, by categorizing organisms in terms of their feeding strategy and their mobility. We collected sediment cores from mud under and adjacent to the reef, along with oyster clumps from the reef itself, and calculated the abundance and richness of each functional group. Taxa richness and abundance were higher on oyster shells than either sediment group, and communities from the sediment groups were more similar to each other than to those on oysters. Our results support the claim that greater habitat complexity is linked to higher functional biodiversity and to major shifts in community composition.

1.0 Introduction

In the marine intertidal, habitat complexity often has a dramatic effect on biodiversity and community composition. More complex habitat structures can offer refugia, create a new food source or trap nutrients, buffer communities from harsh environmental conditions, and provide settlement sites for organisms who might otherwise be absent from an ecosystem. As a result, they support a different, often more diverse array of organisms than could be found on smooth bare rock or uniform sediment. In otherwise homogenous environments, biogenic complexity can be created by ecosystem engineers, organisms that alter their environment through their behavior or growth (Jones et al 1994). In their native ranges, ecosystem engineers usually give a region's overall biodiversity a boost and can support critters that would otherwise be endangered or locally extinct. As invaders, they have an outsized effect on local ecosystems: in addition to more typical interspecific interactions like competition or predation, they can dramatically change the structure or chemistry of their surroundings, depriving some locals of their habitat and possibly attracting more non-local species (Kjørboe et al 2018, Kochmann et al 2008). The

Pacific oyster, *Crassostrea gigas*, is both an ecosystem engineer and the most widespread invasive oyster worldwide, due to a combination of aquaculture and its own volunteer settlement (Barille et al 2017, Dumbauld et al 2001). They are likely to increase still in range as global ocean temperatures rise (Barille et al 2017). Given their global ubiquity and heavy presence along the Washington coast, an understanding of their impact on local ecosystems is critical to aquaculture regulation and environmental management going forward (Cadotte et al 2011). By counting organisms found on oyster reefs and in mud, we aimed to discover whether high complexity and low complexity communities differed as a result of oyster aquaculture in southwestern Washington.

While traditional ecology has used taxonomy as the basis of biodiversity measures, recent years have seen a shift towards studying ecosystems by tracking their distribution of functional traits, defined as any characteristic of an organism that influences its interactions with other species or with its environment (Cianciaruso et al 2009, Kjørboe et al 2018). Unlike taxonomic divisions, trait-based ecology emphasizes an organism's role in an ecosystem and has the potential to reveal deeper changes in a community (Cianciaruso et al 2009). A shift from a mobile-dominated community to a sessile-dominated one probably speaks to greater change, for example, than a shift in dominance from one mobile species to another. As global climate change and species invasions alter marine environments, some traits may become more adaptive while others are selected against, allowing trait distributions to act as a “canary in the coalmine” for broader changes in communities (Kjørboe et al 2018). In our case, a simple and obvious trait to focus on was the mobility of organisms present on reefs, and in or on mud. By forming reefs on intertidal mudflats that previously lacked much hard substrate, *C. gigas* may promote the settlement of other sessile organisms, increasing their presence in a region (Crooks 2002). They may also offer protection for mobile organisms, particularly those that would be unable to burrow in soft sediment to escape predation or desiccation (Barbosa et al 2019).

Our other chosen fundamental trait was feeding type, which has been used frequently by other trait-based ecology studies, given its relevance to a community's trophic structure (Barbosa et al 2019, Cianciaruso et al 2009, Kjørboe et al 2018). While often linked to mobility, it could differ in important ways. As an example, while most predators are mobile, anemones are sessile. It can also reflect differences not only in substrate type, but in other environmental factors such as turbidity, wave energy, depth, and resource availability. Although it may not necessarily mean a higher overall biodiversity, a wide range of feeding types in an ecosystem is indicative of a high number of trophic levels in the local food chain. It should supply us with a more complete image of ecosystem health, as well as offering more practical knowledge to be used in management of *C. gigas* (Cadotte et al 2011).

To determine differences in overall community structures between the reefs and their surroundings, we asked how richness and abundance of taxa with different mobilities and feeding

strategies differed between the oyster reefs, the sediment below oysters, and the nearby mudflat. We predict that both diversity and assemblage of functional groups will differ between oyster reefs and adjacent mud, since they are radically different habitats. Oyster reefs will likely have a higher richness and abundance of sessile organisms because they serve as a hard attachment point for sessile organisms. Because mobility and feeding type are closely linked, they will also likely have a higher abundance and richness of autotrophs and suspension feeders, who are often sessile. The probable decrease in turbidity over the reef will also better support photosynthesis and filter feeding than the fine sediment of the mudflat itself. It seems reasonable that similar substrates would be home to similar species, so we predicted that sediment taken from below the oyster reef would more closely resemble adjacent mud than the reef above it. Both are soft sediment and would contain taxa with traits conducive to living in that environment. Overall, oyster reefs would have a higher abundance and richness than sediment samples, because of their higher habitat complexity.

2.0 Methods

2.1 Field collection: Samples were collected on January 25, 2020 at a -0.28 m low tide from on, below, and near an oyster reef composed predominantly of *Crassostrea gigas*, offshore of Nahcotta Public Access, Willapa Bay, WA (46° 29.729' N, 124° 01.594' W). The area was an intertidal estuarine mudflat surrounded by oyster aquaculture and eelgrass beds, with a well-established reef and little human disturbance due to its distance from shore. To sample the reef itself, we selected a roughly 10 cm² oyster clump at each location and placed it into a labelled plastic bag ("On Oyster"). Next, using a cylindrical core 10 cm in diameter and height, we collected separate sediment samples from directly beneath the oyster clump ("Under Oyster"), and from 1 m away from the oyster clump on the open mudflat ("Mud"). Each was then sieved using a 1 mm mesh and placed in its own labelled bag. In total, four separate oyster clumps were collected. Each was counted as one replicate, with each habitat representing a different sample.

2.2 Laboratory processing: In the lab, we placed each sediment sample in a labelled petri dish and covered it with seawater brought back from the site. Each dish was then inspected, both by eye and under a dissecting scope, and any living or recently dead organisms were identified as an anemone, ascidian, barnacle, bryozoan, clam, crab, oyster, polychaete worm, shrimp, slipper shell, snail, sponge, tanaid, ulvoid, or red algae. Algae were counted according to their individual holdfasts, and bryozoan colonies counted as a single individual. No other taxa were found. We then washed the oyster clumps into a 10 mm sieve and placed the sieve contents into a petri dish to be examined like the others. Oyster

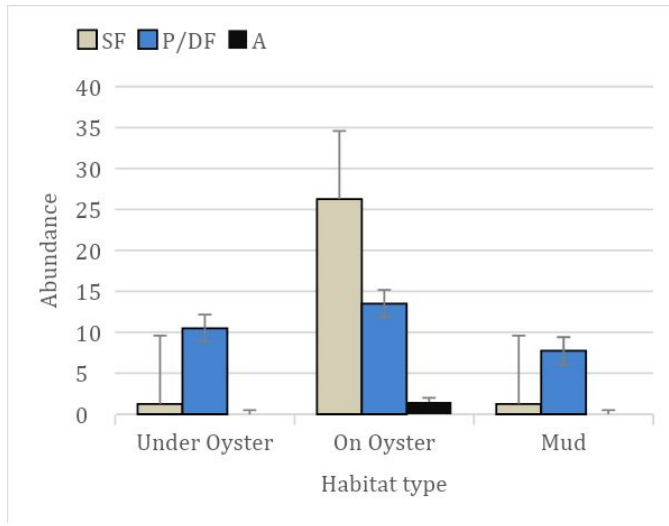
clumps themselves were checked for any epiphytes or epifauna, including juvenile oysters that appeared less than one year in age. The result was a record of which taxa were present and in what quantity.

2.3 Statistical analysis: We sorted collected taxa into functional groups based on feeding types and on mobility. Each taxon was categorized as either mobile (tanaid, shrimp, crab, and polychaete) or sessile (remaining), and as a suspension feeder (ascidian, barnacle, bryozoan, clam, oyster, slipper shell, and sponge), autotroph (ulvoid and red algae), or predator/deposit feeder (tanaid, shrimp, crab, snail, anemone, and polychaete), according to whichever strategy dominated that group. Predators and deposit feeders were grouped together because we did not identify organisms to a specific enough taxonomic level to differentiate between the two. Our predictor variables were substrate type (mud, under oyster, on oyster) and functional group, with richness and abundance as our response variables. Our data were not normal, so all counts were increased by 1 and log transformed before running tests. They did not, however, fail an equal variance Levene's test, and overall met the parameters for a typical two-factor ANOVA. In total, we ran four two-factor ANOVA tests, each with habitat type as one factor, and functional group as the other. In two tests, mobility was the second factor, and in the other two, feeding type. Of the two, one test was run on abundance, and the other on richness. To compensate for running four tests, our alpha level was lowered to 0.0125 (Bonferroni correction).

3.0 Results

Overall, taxa richness and abundance were higher on oyster shells than either below oyster reefs or in the mud adjacent to oyster reefs. Below oyster and mud samples resembled each other more than either did to the oyster samples.

3.1 Feeding types

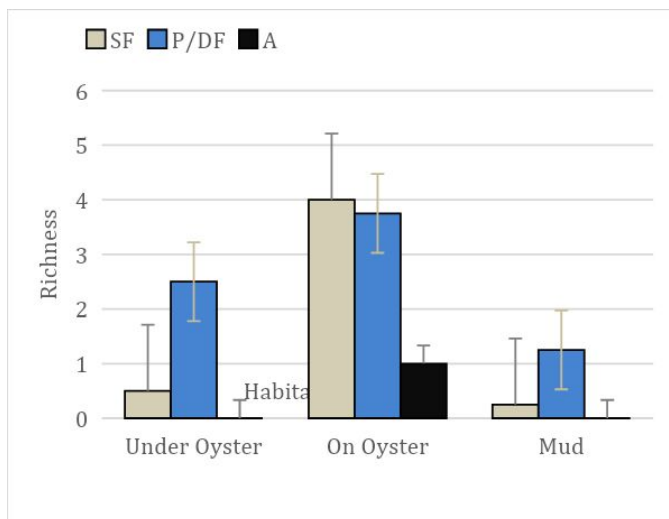


3.1.1 Abundance: Feeding types differed significantly in abundance (Table 1). Autotrophs were the least abundant overall, and only present on oyster shells (Figure 1). Predators and deposit feeders were of roughly equal abundance across habitats, but suspension feeders roughly five times as abundant on oysters (Figure 1). On oyster samples had higher abundance than either sediment types (Table 1). Because predators and deposit feeders dominated sediment

samples, while suspension feeders dominated the oyster reef samples, there was a significant interaction effect.

	<i>Df</i>	<i>Sum Square</i>	<i>Mean Square</i>	<i>F value</i>	<i>P value</i>
<i>Feeding type</i>	2	26.068	13.034	37.872	1.46e-08 ***
<i>Habitat</i>	2	12.547	6.274	18.229	9.77e-06 ***
<i>Interaction</i>	4	6.530	1.632	4.743	0.00498 *
<i>Residuals</i>	27	9.292	0.344		

Table 1: results of a two factor ANOVA with abundance of taxa as a function of habitat type and feeding type.



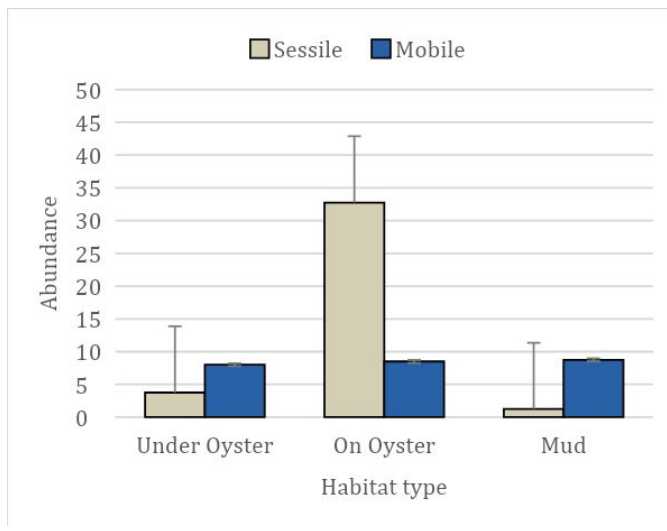
3.1.2 Richness: Feeding types differed significantly in richness as well (Table 2). Richness for autotrophs and suspension feeders was again highest on oysters than in sediment, although suspension feeders did not actually differ significantly from predators/deposit feeders (Figure 2). Overall, autotrophs were significantly less rich than the

other feeding types (Table 2). In-group variation was higher, which may have contributed to a non-significant interaction effect (Figure 2).

	<i>Df</i>	<i>Sum Square</i>	<i>Mean Square</i>	<i>F value</i>	<i>P value</i>
<i>Feeding type</i>	2	5.879	2.9395	36.847	1.92e-08 ***
<i>Habitat</i>	2	5.602	2.8010	35.111	3.08e-08 ***
<i>Interaction</i>	4	1.129	0.2823	3.539	0.0191
<i>Residuals</i>	27	2.154	0.0798		

Table 2: results of a two factor ANOVA with richness of taxa as a function of habitat type and feeding type.

3.2 Mobility

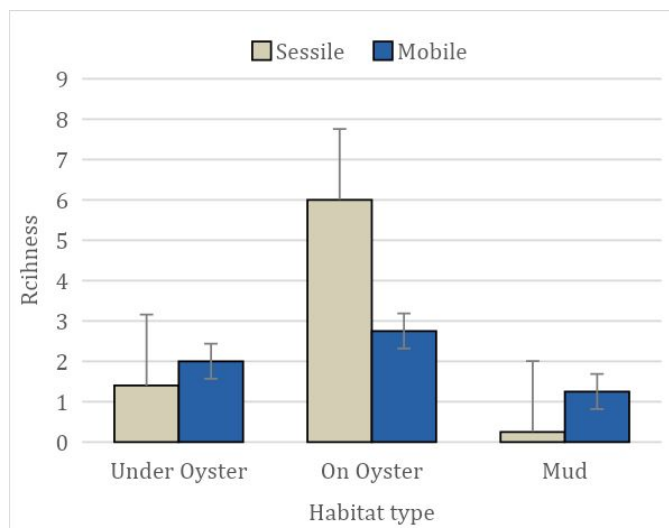


3.2.1 Abundance: Abundance did not differ significantly between mobile and sessile organisms irrespective of habitat (Table 3, *Mobility*). Both were present in roughly equal quantities, although their distributions differed. There was a significant difference in overall abundance between habitat types, with abundance far higher on oysters than either sedimentary substrate (Table 3). There was also an interaction effect, with mobile organisms divided equally between the three

habitats, but sessile organisms dramatically more abundant on oysters (Table 3).

	<i>Df</i>	<i>Sum Square</i>	<i>Mean Square</i>	<i>F value</i>	<i>P value</i>
<i>Mobility</i>	1	1.125	1.125	2.589	0.12500
<i>Habitat</i>	2	8.502	4.251	9.781	0.00133 *
<i>Interaction</i>	2	7.690	3.845	8.847	0.00211 *
<i>Residuals</i>	18	7.823	0.435		

Table 3: results of a two factor ANOVA with abundance of taxa as a function of habitat type and mobility



3.2.2 *Richness*: Once again, there was no significant difference in richness overall between the two attachment types (Table 4). Like abundance, richness was higher overall on oysters than on either of the soft sediment samples. Mobile taxa did not differ between habitats, but sessile taxa had a significantly higher richness on oysters (Table 4).

	<i>Df</i>	<i>Sum Square</i>	<i>Mean Square</i>	<i>F value</i>	<i>P value</i>
<i>Mobility</i>	1	1.04	1.042	0.926	0.348673
<i>Habitat</i>	2	58.58	29.292	26.037	4.87e-06 ***
<i>Interaction</i>	2	24.08	12.042	10.704	0.000865 ***
<i>Residuals</i>	18	20.25	1.125		

Table 4: results of a two factor ANOVA with abundance of taxa as a function of habitat type and mobility

4.0 Discussion

Our results support the claim that greater habitat complexity is linked to higher functional biodiversity. Oyster reefs had equal or higher abundance and richness of all traits examined compared to both sediment types, as was expected based on prior studies. Given that sediment cores taken from under oysters resembled mud cores more than they did oyster shell samples, it is reasonable to conclude that these differences can be linked to habitat structure. We can therefore conclude that introduced oysters are acting as ecosystem engineers, altering community composition in a dramatic way, and providing new habitat for species that would not otherwise be local to an area.

Past studies on bivalve reef biodiversity have found varied results, depending in part on the location and type of reef examined. On a superficial level, our results closely match those of two European teams working at similar latitudes, who found that species richness, abundance, and biomass were higher on *C. gigas* reefs than in sediment on estuarine mudflats (Herbert et al 2017, Lejart & Hily 2011). This suggests that the Pacific oyster has a similar effect on overall biodiversity throughout its temperate range, with consequent effects on its adopted ecosystems. Our conclusion that its structural complexity is a major factor in increasing biodiversity concurs with that of two north German studies that compared *C. gigas* reefs to those of a native *Mytilus* (Kochmann et al 2008, Markert et al 2010). Certain taxa were found to be more abundant on the invasive oyster reefs, indicating a major shift in species assemblage (Kochmann et al 2008). *C. gigas* reefs were also associated with overall higher biodiversity than either mudflats or native reefs (Markert et al 2010). While still an ecosystem engineer, the smooth shells of mussels create a less complex habitat than the tangled crenellations of *C. gigas*. Their results were in line with what we would predict if increased habitat complexity indeed correlated with increased biodiversity. Intriguingly, one study that also examined trophic groups on and off *C. gigas* reefs found opposite results to ours (Lejart & Hily 2011). They found that carnivores dominated invasive oyster reefs in northern France, while suspension feeders (excluding the oysters themselves) were more abundant in mudflats (Lejart & Hily 2011). Part of this may be due to the presence of other traits in our populations that went unmeasured. While most of our suspension feeders were not able to thrive in sediment, theirs may have other adaptations that allow them to. Another possibility is simply that they had more clams and other burrowing suspension feeders, either because they dug deeper when collecting samples or because French burrowers live closer to the surface. Finally, unlike ours, their estuary had no century-long history of Pacific oyster aquaculture, which may have resulted in a different trait distribution. More precise transoceanic comparisons are needed.

It is unlikely that differences in our methods caused our opposing results. Aside from the issue of a small sample size, we had the advantage of using a relatively simple sampling method similar to that used by Herbert et al (2017). The same method can be applied to other intertidal mudflats and bivalve reefs for sampling macroscopic epibionts and infauna.

The discord between our results and those found by Lejart and Hily (2011) clearly show that more study is needed to understand how oyster reefs and habitat complexity affect the distribution of traits in a muddy estuarine ecosystem. Because *C. gigas* is a widespread introduced species, the possibility that it has opposite effects on community structure in different regions of the world behooves us to investigate further. It could be that management of the species in one part of the globe must take a different tack than management in another. It would also be meet to expand the horizons of the study and attempt to draw a link to the density of surrounding aquaculture. Willapa Bay has a long history of intensive oyster farming, with decades of regular chemical usage to control pests (Dumbauld et al 2001). Its effects on functional traits present in the bay is unknown. Finally, our study exclusively looked at spatial variation across a small area. For a full view of community differences, we would need to do a long-term study that looked at changes across several seasons or years. Given the relatively rapid change our oceans are undergoing, it is possible that our present results will bear little resemblance to future ones.

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Acknowledgements

Many thanks to my collaborators, Chris Jendrey, Chiko Meng, Anna Lank, and Elena Subbotin. They did all the actual collecting because I was busy standing in a harbor at night putting eelgrass in plastic bags. Thank you to Robin Fales, as well, for giving me the opportunity to put eelgrass in plastic bags. Thanks as well to Drs. Jennifer Ruesink and Melissa Frey, for an excellent quarter.