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Relative impacts of the invasive Pacific oyster, *Crassostrea gigas*, over the native blue mussel, *Mytilus edulis*, are mediated by flow velocity and food concentration

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Abstract

The ecological impacts of invasive species can be severe, but are generally viewed as highly unpredictable. Recent methods combining *per capita* feeding rates, population abundances and environmental contexts have shown great utility in predicting invader impacts. Here, clearance rates of the invasive Pacific oyster, *Crassostrea gigas*, and native mussel, *Mytilus edulis*, were investigated in a laboratory experiment where oscillatory water flow and algal food concentrations were manipulated. Invasive oysters had lower clearance rates than native mussels in all experimental groups and did not differ among flow velocities or food concentrations. Native mussel clearance rates were higher at 5 cm s^{-1} compared to 0 and 15 cm s^{-1} flow velocities and increased with increasing food concentration. The Relative Impact Potential (RIP) metric was used to assess (i) the influence of flow velocity and food concentration on potential impacts of *C. gigas* on plankton resources and, (ii) the impacts of coexisting reefs, containing both species, on resources compared to monospecific native mussel beds. Greatest Relative Impact Potential of invasive oysters was seen at the lowest flow velocity, but became reduced with increasing flow velocity and food concentration. Relative Impact Potentials of coexisting reefs were generally greater than monospecific native mussel beds, with greatest impacts predicted at lowest flow velocity. We suggest that the greatest ecological impacts and competition potential of *C. gigas* will occur in areas with low flow velocity, but that increased flow will mediate co-existence between the two species.

Keywords
Bivalves; Clearance rate; Ecological impacts; Filter feeding; Hydrodynamics; Invasive species; *Per capita* resource use; Relative Impact Potential

Introduction

The ecological impacts of invasive species can be severe (Simberloff et al. 2013, Dick et al. 2017b) and the rate of invasive species introductions shows no sign of decline (Seebens et al. 2017, 2018). It is therefore necessary to improve our abilities to predict the ecological impacts of current, emerging and future invasive species (Dick et al. 2013, 2017b, Alexander et al. 2014). Recently, the quantification and comparison of *per capita* effects of invasive species, through for example comparative functional responses (inter- and intraspecific comparisons of consumption in relation to resource densities), have been revealed as a strong predictor of invasive species impacts (Dick et al. 2014, 2017b). Invasive species are often associated with higher consumption rates than comparative native species, with these higher *per capita* metrics predicting ecological impact (Dick et al. 2013). Further, the recent incorporation of contexts such as temperature (South and Dick 2017; South et al. 2017) or habitat complexity (Alexander et al. 2012; Wasserman et al. 2016) allow such experiments to increase our understanding and prediction of impacts under various environmental contexts (Dick et al. 2014, Paterson et al. 2015).

Recently, the Relative Impact Potential (RIP), a metric proposed by Dick et al. (2017b), has combined *per capita* resource use with population abundances to better predict the ecological impacts of invasive species. Although Dick et al. (2017b) primarily use functional responses combined with abundance data to produce RIP scores, they suggest that suitable, relevant proxies for such measures can be used in their place. For example, in the case of filter feeders, algal uptake or clearance rates as a measure of *per capita* resource use are more common than functional responses (e.g. Alexander et al. 2015). Similarly, biomass may be an equally relevant metric as a proxy for population abundance depending upon the species in question (Dick et al. 2017b). The RIP combines facets of the 'Total Response' and the 'Parker-Lonsdale' equations (see Dick et al. 2017b and Parker et al. 1999, respectively) into one metric that produces absolute values of species impact on a resource. These absolute values can then be used to compare impact, for example, the baseline impacts of native consumers in relation to invasive species. This approach was highly successful in identifying high impact invaders and indeed RIP scores are correlated tightly with independent measures of the degree of ecological impact of such invaders (Dick et al. 2017b). Here, "impact" is defined as a documented effect on a native population, whereas invasion "success" is best defined as the rate of establishment or spread of a species. The semantic distinction between the two terms should be clarified as no link between the two has been found (Ricciardi and Cohen 2007).

Per capita resource use has traditionally been used in animal ecology to investigate impacts on resources (Holling 1959, 1966, Dick et al. 2017b), whereas plant ecologists use the same method to explicitly study interspecific resource competition (Tilman 1977, Dick et al. 2017a). In ecosystems containing sessile animals that cannot move and search for different resources, such comparative resource use may reveal patterns of interspecific competition as well as impacts on resources. Investigations of interactions between sessile organisms often consider space as the only limiting resource worth studying (Connell 1961). However, local seston depletion can occur above bivalves beds (Wildish and Kristmanson 1984, Dolmer 2000a, b) leading to resource limitation (e.g. Vismann et al. 2016), and hence potential competition between filter feeding species due to their limited ability to actively search for new resources.

While comparative *per capita* resource use has been applied to a range of taxonomic groups, the method has only recently been applied to filter feeders (Alexander et al. 2015, Kemp and Aldridge 2018). However, the incorporation of environmental parameters such as water motion, a fundamental process for filter feeders, have not been included. Sessile suspension feeders rely greatly upon water motion as it is the bulk water column flow that supplies them with fresh food (Genin et al. 1986). Although water motion is necessary for replenishing plankton resources, hydrodynamic forces exerted by the movement of water can also exert destructive forces on organisms, therefore trade-offs between food provision and dislodgement pressures occur (Denny 2006).

The clear majority of work and our understanding of bivalve feeding with regards to water motion has been conducted in uni-directional currents characteristic of estuaries, inland bays and harbours. It is unknown if these studies provide a reasonable basis for the prediction of responses of bivalves to oscillatory water motion characteristic of wind and swell-driven open coasts (Denny and Gaylord 2002). Continuous reversals in flow direction increase turbulence within the water column (Denny et al. 1998), thus it is less likely that seston depletion above bivalve beds would occur. Several studies into the effects of flow velocity on clearance rates of bivalves have been conducted using mussels (*Mytilus* spp.) but with conflicting results. Some studies have found clearance rates to be unaffected by increasing flow velocity while others show significant reductions in clearance rates with increases in flow (Denis 1999; Newell et al. 2001; Widdows et al. 2002; Ackerman and Nishizaki 2004; Nielsen and Vismann 2014). To date, there have been no studies on the influence of water motion on clearance rates of the invasive Pacific oyster, *Crassostrea gigas*.

The Pacific oyster, *C. gigas*, is one of the most 'globalised' marine invertebrates, dominating shellfish production in many regions (Ruesink 2007, Herbert et al. 2016), and is considered invasive in several countries. For example, the Wadden Sea has seen *C. gigas* settle onto beds of the native blue mussel, *Mytilus edulis*, on such a scale that there has been a shift in dominance from native mussels to non-native oysters (Kochmann et al. 2008), suggesting that *C. gigas* can compete with native *M. edulis* for resources and potentially impact those resources to the detriment of the wider community.

The present study thus examined the Relative Impact Potentials of the invasive Pacific oyster, *C. gigas*, and the native blue mussel, *M. edulis*, in relation to effects of oscillatory flow velocity and algal food concentration on their clearance rates. The experimental treatments simulated environmental conditions experienced on inshore coasts. The main objectives were to: (i) assess the influence of oscillatory flow velocity and food concentration on the clearance rates of the two species; (ii) combine *per capita* resource use with field biomass, using the RIP metric to identify conditions that may lead to impacts on plankton resources; and (iii) use the RIP metric to compare the impacts on plankton resources of co-existing bivalve beds with those of monospecific native mussel beds on plankton resources.

Methods

Bivalve collection

In August 2016, adult Pacific oysters, *Crassostrea gigas*, with a shell length 65–105 mm, were obtained from a local commercial oyster farm, Killough Oysters Ltd. Adult native mussels, *Mytilus edulis*, with a shell length of 45–50 mm, were collected from an intertidal rocky shore in Strangford Lough, County Down, Northern Ireland (54°28'11.2"N, 5°32'25.4"W). Animals of these sizes were used as they are representative of adult organisms, thus results from the experiments would provide data for mature populations. Animals were housed at Queen's University Marine Laboratory, Portaferry in large holding tanks (~500L) with through-flowing, sand filtered seawater pumped directly from the adjacent Strangford Lough. Prior to experimental testing, shells were cleaned of any mud and epibionts and returned to the holding tanks for at least 48 hours prior to testing.

Experimental tank system

Clearance rates of the bivalves were determined in an aerated experimental tank system designed to simulate oscillatory water motion (full details of the design can be found in Kregting et al. 2015). The tank system consisted of four tanks where the bivalves were moved back and forth through a stationary body of aerated water to simulate water motion representative of the horizontal oscillatory water motion benthic animals experience at the seabed on shallow inshore coasts. The horizontal oscillatory water motion was simulated in the four laboratory experimental tanks by two horizontal rods mounted above the tanks on a steel frame allowing free oscillatory movement of the rods. The rods were attached to a rotating arm driven by a 12 V car windscreen wiper motor. Two detachable, vertical polypropylene arms with perpendicular base plates were fixed to each rod (arms = 4). Each arm was suspended over a 65 L polypropylene container (60 × 40 × 32 cm). The driving motor was powered using a regulated power supply (Skytronic 0–30 V) which could be altered to control the horizontal velocity of the arms. Three flow scenarios were selected; static (0 cm s^{-1}) and two which oscillated over a distance of 21 cm with amplitudes of 5 and 15 cm s^{-1}.

Either 4 oysters or 10 mussels were attached to the experimental base plates. Different numbers of each species were used in the experiment to keep the area covered by the animals the same, with clearance rates then corrected by biomass (see below). Oysters were attached to the baseplates using cyanoacrylate glue. Mussels were placed onto baseplates and covered with plastic mesh netting to hold them in place allowing natural byssus attachment. Plates with animals attached were placed into 1 µm filtered, UV sterilised seawater for 22 hours to standardise starvation. After the starvation period which allowed sufficient byssus attachment from mussels, the mesh netting was removed from the mussels prior to testing.

Microalgal culture

The microalga *Tetraselmis suecica* was chosen for the experiment, as plankton of this size (~6–10 µm) (Chrétiennot-Dinet et al. 1986, Hansen et al. 1996) are retained with high efficiency by both species (Bougrier et al. 1997; Ward and Shumway 2004). Algae were cultured in 1 µm filtered, UV sterilised seawater using f/2 media and were on-grown until sufficient stock could be maintained in a 150L bag culture.

Clearance rate experiment

Experimental tanks were filled with 30 L of 1 µm filtered, UV sterilised seawater and aerated at one end to ensure the water was well mixed, but not interfering with the oscillatory movement, allowing use of the clearance equation (see below). The selected animals were subjected to a randomly selected flow velocity for 30 minutes before the addition and mixing of a randomly selected, pre-defined volume of algal monoculture (Table 1). To measure algal depletion in the tanks, two 3 ml water samples were taken immediately after the algal monoculture was sufficiently mixed within the experimental tanks and again after 1 hour. Cell concentration of the water samples were analysed using an electronic particle counter (Coulter Z1). Experimental tanks were emptied, cleaned with freshwater, and rinsed with 1 µm filtered, UV sterilised seawater after each trial. This process was carried out for both species at the three flow velocities (0, 5, 15 cm s^{-1}) and five algal culture volumes (4, 8, 16, 32, 64 ml; corresponding cell

Table 1. Volumes of *Tetraselmis suecica* added to experimental tanks with corresponding initial cell concentrations within experimental tanks for clearance trials (mean ± S.E.).

ml of *T. suecica*	Cell concentration (cells ml^{-1}) ± S.E.
4	5954 ± 188
8	8198 ± 265
16	13567 ± 342
32	22221 ± 381
64	42003 ± 664

concentrations in Table 1) with four replicates per experimental group. Due to the experimental setup, accurate measurement of animal valve gape was not achievable however, all animals were visually inspected during feeding trials. After experimentation, the soft tissue of each animal was removed from the shell and dried at 70 °C for 24 hours to determine the shell-free dry weight (SFDW) of each replicate. Control trials without animals in the experimental tanks (n = 2) were conducted to identify any natural reductions in algal concentration over the feeding period due to sinking.

Clearance rate calculations

Due to adequate water mixing within experimental tanks, the 'clearance method' (Riisgård et al. 2013) was used to measure the rates of algal consumption of the bivalves. Clearance rates (CR), measured as the volume of water cleared of particles per hour (*h*) per gram of SFDW (*g*), were calculated as:

$$CR\ (L\ h^{-1}\ g\ SFDW^{-1}) = \frac{V\ (\ln C_0 - \ln C_t)}{t * SFDW}$$

where V is the volume of water in the experimental tank, C_0 and C_t are algal concentrations at time 0 and time t, *SFDW* is the shell-free dry weight of animal flesh in each replicate. SFDW was used to standardise clearance rates between species as, although the area occupied by both species was kept constant, differences in biomass occurred between the two species.

Data analyses

All analyses were performed in R 3.3.1 (R Core Team 2012). One replicate from two separate experimental groups were removed from the analysis due to mussel detachment during the feeding period. A three-factor analysis of variance (ANOVA) compared clearance rates between species (2 levels; *C. gigas* and *M. edulis*), among flow velocities (3 levels; 0, 5, 15 cm s^{-1}), and among food concentrations (5 levels; 4, 8, 16, 32, 64 ml of *Tetraselmis suecica*). Levene's test for homogeneity of variance ($F_{29,88} = 0.9$, $p > 0.05$) and Shapiro-Wilk's test for normality ($p > 0.05$) ensured ANOVA assumptions were met. Significant differences between treatments were compared with Tukey's honest significant difference post hoc test.

Species biomass and the Relative Impact Potential (RIP) metric

A systematic search of the on-line scientific databases *Scopus*, *Web of Science* and *Google Scholar* was used to collect field biomass data for both *Crassostrea gigas* and *Mytilus edulis*. All searches were performed in October 2017 using the search terms (*Crassostrea gigas*

OR *Magallana gigas* OR *Mytilus edulis*) AND (biomass OR abundance OR density) AND (invasive OR non-native OR native). References from retrieved articles were screened for other relevant publications. Literature was selected (Table 2) if biomass estimates were given as total wet weight (WW), shell-free dry weight (SFDW) or ash-free dry weight (AFDW). Data given as WW or AFDW were converted to SFDW using published weight conversion factors for bivalves (Ricciardi and Bourget 1998), as SFDW was used in the clearance rate calculations. Clearance rates averaged across food concentrations, as well as those at the lowest and highest food concentrations for each species from this study, were combined with biomasses for each species to create RIP biplots (Laverty et al. 2017). Biplots represent the Relative Impact Potential of *C. gigas* compared to *M. edulis* to under the contexts of 'flow velocity' and 'food concentration'. Biomass data from the Wadden Sea were also available for reefs where the two species are coexisting, dubbed 'oyssel reefs' (Reise et al. 2017). In these cases, clearance rates averaged across food concentrations, as well as at the lowest and highest food concentrations of each species, were multiplied by their proportional contribution to the overall reef biomass. The proportionally adjusted clearance rates were then combined to give an overall clearance rate for the mixed species reef. Clearance rates combined with biomass data were used to create RIP biplots to represent Relative Impact Potentials of coexisting 'oyssel reefs' compared to monospecific *M. edulis* beds. RIP biplots combine biomass and clearance rate data to give a visualisation of ecological impact with greater impacts being shifted towards the top and right of the plot, and lesser impacts being shifted towards the bottom and left of the plot (Laverty et al. 2017).

Results

Clearance rate experiment

Visual inspection found that all animals were open and appeared to be feeding during experimental trials. Control groups saw changes in algal concentrations < 2% of the changes that occurred in treatments with animals, thus any changes in algal concentration over the feeding period with animals present were attributed to intake by the animals and not sinking.

Overall, clearance rates of *Crassostrea gigas* were significantly lower than those of *Mytilus edulis* (Table 3; Figure 1). There was a significant main effect of flow velocity on clearance rate (Table 3), with clearance rates at 5 cm s^{-1} significantly higher than both other velocities tested (Tukey's HSD, $p < 0.05$). However, the significant 'species' × 'flow' interaction (Table 3) reflects the lack of change in the *C. gigas* clearance rate but increase in *M. edulis* clearance rate at 5 cm s^{-1}.

Overall, clearance rate increased with food concentration (Table 3). The significant 'species' × 'food concentration' interaction (Table 3) reflects that increasing clearance rates over increasing algal food concentrations occurred only for the native *M. edulis* (Tukey's HSD, $p < 0.05$; Fig. 1).

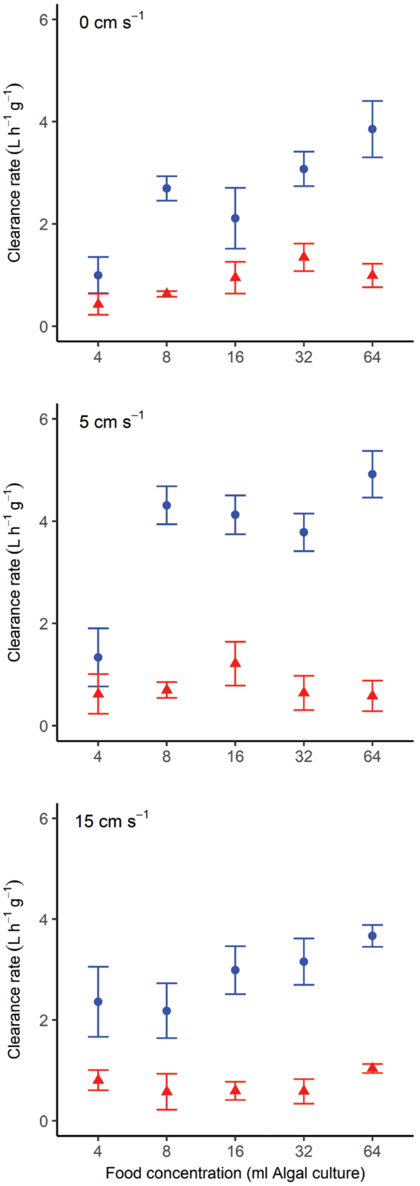

Figure 1. Clearance rates of the native mussel, *Mytilus edulis* (blue circles), and invasive Pacific oyster, *Crassostrea gigas* (red triangles), as a function of algal food concentration at flow velocities of 0, 5 and 15 cm s^{-1}.

Relative impact potentials

Biomass data from the Wadden Sea show that *C. gigas* generally has a higher biomass than *M. edulis*. Combined with average clearance rates from this study, *C. gigas* is shown to have similar Relative Impact Potential to *M. edulis* at 0 and 15 cm s^{-1} flow

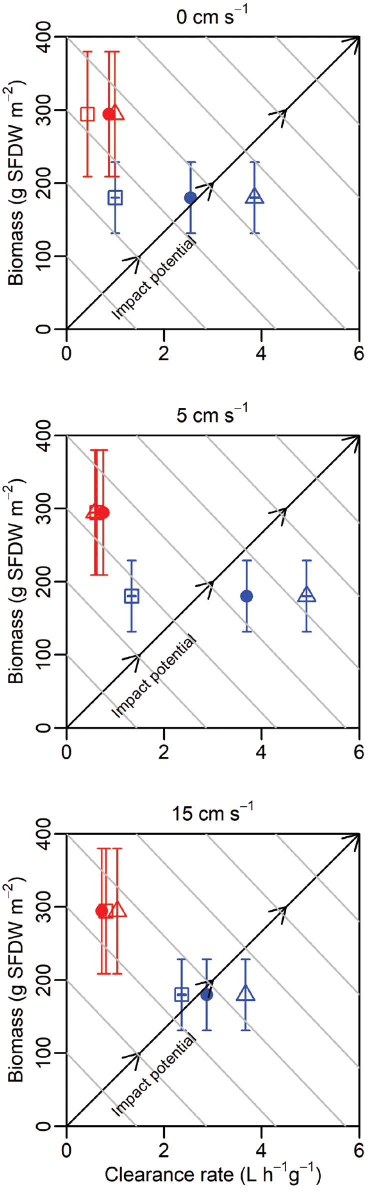

Figure 2. RIP biplots of the native mussel, *Mytilus edulis* (blue), and invasive Pacific oyster, *Crassostrea gigas* (red), using biomass data from the Wadden Sea (mean ± S.E.). Squares indicate clearance rate (CR; L h^{-1} g^{-1}) at minimum food level, circles indicate average CR over all food levels, triangles indicate CR at maximum food level (mean ± S.E.). Impact increases from bottom left to top right.

velocities (Fig. 2). The increased average clearance rate of *M. edulis* at 5 cm s^{-1} reveals that impacts of *M. edulis* at this flow velocity are higher than *C. gigas* (i.e. shifted further to the right, Fig. 2). At low food concentrations, the RIP of *C. gigas* is higher than that of *M. edulis* at both 0 and 5 cm s^{-1} due to reduced *M. edulis* clearance rates

Table 2. Biomass data for *Crassostrea gigas*, *Mytilus edulis*, and coexisting 'oyssel' reefs from the Wadden Sea with corresponding references. Symbols denote separate species biomass contributions to coexisting 'oyssel' reefs.

Species	Biomass (g SFDW m^{-2})	Reference
C. gigas	508†	(Markert et al. 2010)
	348‡	(Markert et al. 2013)
	201*	(Markert et al. 2013)
	118	(Fey et al. 2010)
M. edulis	328	(Markert et al. 2010)
	247†	(Markert et al. 2010)
	85‡	(Markert et al. 2013)
	71*	(Markert et al. 2013)
	166	(Munch-Petersen and Kristensen 2001)
Coexisting reef	755†	(Markert et al. 2010)
	433‡	(Markert et al. 2013)
	273*	(Markert et al. 2013)

Table 3. Three-way ANOVA of the effects of species (2 levels; *Crassostrea gigas* and *Mytilus edulis*), flow velocity (3 levels; 0, 5, 15 cm s^{-1}), and food concentration (5 levels; 4, 8, 16, 32, 64 ml of algal monoculture) on clearance rates.

	Df	Mean Sq	F value	Pr(>F)
Species	1	151.24	275.725	< 0.001
Flow	2	3.28	5.985	<0.01
Food	4	5.83	10.636	< 0.001
Species × flow	2	4.3	7.836	< 0.001
Species × food	4	3.83	6.989	< 0.001
Flow × food	8	1.09	1.985	0.0575
Species × flow × food	8	0.71	1.303	0.2523
Residuals	88	0.55		

(i.e. *M. edulis* toward bottom and shifted left, Fig. 2). At 15 cm s^{-1}, impacts of the two species under low food conditions are similar. High food concentrations indicate greater impacts of *M. edulis* under all flow scenarios due to increased clearance rates.

The total biomass of coexisting reefs was higher than monospecific *M. edulis* beds (Table 2). The elevated average clearance rate of *M. edulis* at 5 cm s^{-1} leads to the impacts of coexisting reefs and monospecific *M. edulis* beds to be similar. At 0 and 15 cm s^{-1}, however, the impacts of coexisting reefs are higher than those of monospecific *M. edulis* beds (Fig. 3). At low food concentrations, impacts of coexisting reefs are shown to be higher than monospecific *M. edulis* beds at all flow velocities (Fig. 3). High food concentrations lead to similar impacts of coexisting reefs and monospecific *M. edulis* beds at 0 and 15 cm s^{-1} but greater impacts of monospecific *M. edulis* beds at 5 cm s^{-1} (Fig. 3).

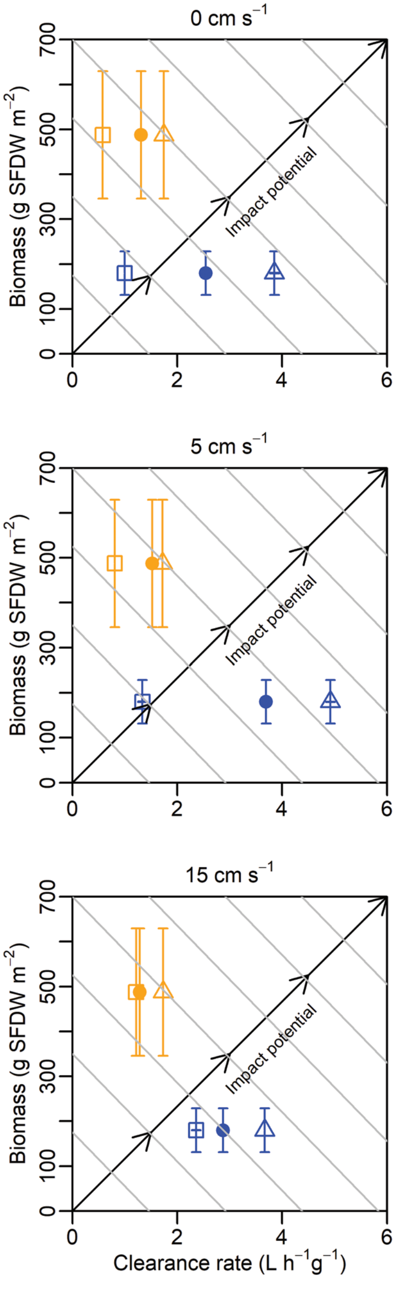

Figure 3. RIP biplots of the native mussel, *Mytilus edulis* (blue), and coexisting 'oyssel' reefs (orange) using biomass data from the Wadden Sea (mean ± S.E.). Squares indicate clearance rate (CR; L h^{-1} g^{-1}) at minimum food level, circles indicate average CR over all food levels, triangles indicate CR at maximum food level (mean ± S.E.). Impact increases from bottom left to top right.

Discussion

Comparative resource use and Relative Impact Potential studies involving native and invasive bivalves to investigate species interactions have not been explored in depth (Alexander et al. 2015, Kemp and Aldridge 2018). This study has thus coupled a comparative resource use concept, with population abundance and the environmental context of oscillatory flow, to examine whether invasion impact on resources and competitive effects by the invasive Pacific oyster, *Crassostrea gigas*, could be predicted based on algal uptake in the different hydrodynamic conditions tested. We found that *per capita* resource use of the invasive Pacific oyster, *C. gigas* was lower than that of native *Mytilus edulis*. However, when accounting for field densities, sites that have seen large invasions of *C. gigas* may experience ecological impacts on resource communities, especially in areas with little water motion.

The flow velocities chosen in this study are within the range that mussels and oysters are likely to experience regularly in open coastal areas, for example, the Wadden Sea (Janssen-Stelder 2000). Changes in flow velocity and food concentration had no effect on invasive *C. gigas* but significantly altered native *M. edulis* clearance rates. Flow velocity and food concentration mediated the Relative Impact Potential of the invasive *C. gigas* over the native *M. edulis*. Low flow velocities and food concentrations led to the RIP of *C. gigas* being higher than that of *M. edulis*, suggesting a greater impact on resources (i.e. plankton) by *C. gigas* under such conditions. Increases in flow and food however, increased the RIP of *M. edulis* due to the increases in clearance rate, thus suggesting a lower comparative impact of *C. gigas* when flow velocity and food concentrations increase. The RIP biplots also show that in reefs where coexistence between the two species occurs, impacts on plankton resources are likely to be greater than monospecific *M. edulis* beds in the majority of flow velocity and food concentration contexts tested.

This is the first study investigating the effects of oscillatory water flow on bivalve clearance rates thus we cannot compare the results found to other studies. Previous investigation into *M. edulis* clearance rates in uni-directional currents have provided mixed results (Ackerman 1999, Denis 1999, Widdows et al. 2002, Ackerman and Nishizaki 2004). Here, we found a uni-modal response of *M. edulis* clearance rates with increasing water velocity. Although unclear, it may be predicted that clearance rates may decrease at lower oscillatory flow velocities compared to uni-directional current velocities due to increased turbulence created by oscillating motion. Such turbulence may inhibit feeding as well as the fact that in oscillatory flows, inhalant siphons would face into the flow 50% of the time, which has been linked with decreased clearance rates (Newell et al. 2001). The lack of influence of flow velocity on the clearance rate of *C. gigas* differed from responses shown by *M. edulis*. No previous studies have investigated the influence of flow velocity on *C. gigas* clearance rates although this species can be found in environments with a wide range of hydrodynamic conditions from high energy to sheltered environments (Wrange et al. 2010, Strand et al. 2012, Dolmer et al. 2014).

Food concentration only significantly increased *M. edulis* clearance rate. This is consistent with patterns observed whereby, at a lower threshold, bivalves can cease filtering (Denis 1999, Riisgård et al. 2013, Sarnelle et al. 2015). This is not shown by *C. gigas* which, although it has a lower clearance rate, appears to maximise its feeding capability even at low food levels.

Here, our measured clearance rates for *C. gigas* were <1 L h^{-1} g^{-1}, which is lower than other studies ranging from 2–11.8 L h^{-1} g^{-1} (Walne et al. 1972, Gerdes et al. 1983, Bougrier et al. 1995, Dupuy et al. 2000). These studies, however, used a range of oyster sizes generally smaller than those used here, which may lead to higher body weight specific clearance rates. Previous studies also measured clearance rates in static systems which provide unrealistic, idealised conditions for filtration. Although our measured clearance rates are lower than other laboratory studies, they are similar to field observations of < 1 L h^{-1} g^{-1} (Wheat and Ruesink 2013). Our measured clearance rates for *M. edulis* are comparable to those of other laboratory studies (examples in Troost et al. 2010).

Although *C. gigas* is a successful invader, it produces varied ecological impacts, both positive and negative depending on context (Padilla 2010, Herbert et al. 2012, 2016). Invasion "success" and "impact" should be distinguished as the two are not necessarily correlated (Ricciardi and Cohen 2007). Common misinterpretation leads to the incorrect use of the terms whereby success should be defined as the rate of establishment and spread whereas impact is a documented effect on native populations. Here, we show that the relatively low *per capita* clearance rates of *C. gigas* found are in line with theory that high relative *per capita* rates are associated with high impact, with the corollary being that low impact should be associated with low *per capita* rates (Dick et al. 2013, 2014, 2017b). By combing *per capita* clearance rates with field biomass data into the RIP metric, we show again that, even with the higher biomass of *C. gigas*, because this is mitigated by lower *per capita* feeding rates, the invader is predicted to have relatively low impact on native resources.

Further, although the RIP would usually be used to assess or predict species impacts on a resource, we contend that it may also be useful in understanding interspecific competition (Dick et al. 2017a), due to the inability of bivalves to move and search for new food resources. Although plankton resources are not thought of to be limiting, it has been shown that seston depletion can occur above bivalve beds (Wildish and Kristmanson 1984, Dolmer 2000a), and that bivalve beds can become food limited (Vismann et al. 2016), which may result in interspecific competition for limited resources. The RIPs shown here suggest that only under low flow and low food conditions may the invader, *C. gigas*, exhibit ecological impacts over, and compete effectively with the native, *M. edulis*. Such areas are therefore most likely to see resource based ecological impacts from *C. gigas*. However, due to daily fluctuations in wind/storm driven changes in flow velocity as well as seasonal variations in plankton abundance, *M. edulis* will not always be outcompeted for resources which is reflected by the regular coexistence found between the two species (Holm et al. 2016; Reise et al. 2017). Although these species may compete for other resources (i.e. space), our data, using measured clearance rates, are fully in line with field patterns of invasive impacts and coexistence, and indeed, the *per capita*, RIP and context-dependency approach could be used more predictively for emerging and potential invasive species impacts (Dick et al. 2017b).

The RIP metric also revealed that the impacts of mixed species 'oyssel reefs' (Reise et al. 2017) on resources are predicted to be greater than baseline impacts of monospecific *M. edulis* beds. The magnitude of these impacts is shown to be greatest in areas with low flow velocities and food concentrations. A lack of investigation into differences in plankton resources over native monospecific *M. edulis* beds compared to those that have been invaded by *C. gigas* cannot allow statements of whether such field impacts have occurred. However, with the RIP clearly a successful predictive tool for invasive species impacts on resources, studies into plankton abundances above native and non-native bivalve beds clearly need further investigation.

Conclusion

Due to the differential effects of flow velocity on *C. gigas* and *M. edulis*, additional investigations into the effects of flow type (i.e. currents vs. waves) may be required to further understand differences in feeding and growth *in situ*, especially as these species are sensitive to interspecific competition. As growth is directly related to feeding, investigation into growth rates in different hydrodynamic conditions, which vary both naturally and due to anthropogenic influences, should be conducted to validate the results of this study. Based on our results, we suggest that areas with little water motion and those where local food limitation may occur are likely to be most at risk of impacts from *C. gigas*. Areas with increased water motion are unlikely to be resource limited due to increased food replenishment however, destructive forces exerted by the water itself may affect species growth and success. The field patterns of low invasion impact and coexistence with the native analogue, *M. edulis*, further highlight the excellent explanatory and predictive power of coupling *per capita* resource use with field abundances for invasion ecology, however, investigation into growth rates under these environmental contexts would achieve an even better understanding of competition between the two species.

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