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Joyce, P., Dick, J. T. A., & Kregting, L. (2020). Lack of biotic resistance to an invasive bivalve irrespective of season or hydrodynamic disturbance. *Journal of Experimental Marine Biology and Ecology*, 528. <https://doi.org/10.1016/j.jembe.2020.151382>

Published in:

Journal of Experimental Marine Biology and Ecology

Document Version:

Peer reviewed version

Queen's University Belfast - Research Portal:

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Lack of biotic resistance to an invasive bivalve irrespective of season or hydrodynamic disturbance

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Abstract

Coastal ecosystems are subject to a wide variety of abiotic variation including seasonal fluctuations and hydrodynamic disturbance, which can influence species distributions. Additionally, introductions of invasive species are creating biotic pressures within coastal ecosystems, which can influence biological interactions. With the recent development of combining comparative functional responses, prey switching and biotic resistance theory in invasion ecology, invasion success and ecological impacts of invaders can be better quantified. Further, the incorporation of environmental contexts with these approaches allows predictions of invader success under a range of ecological scenarios. We examined the functional responses and prey switching propensities of the native European green crab, *Carcinus maenas* (Linnaeus, 1758), towards native blue mussels, *Mytilus edulis* (Linnaeus, 1758), and invasive Pacific oysters, *Crassostrea (Magallana) gigas* (Thunberg, 1793), under the abiotic contexts of season (winter vs summer) and hydrodynamic disturbance level (high vs low). In general, when each prey species was offered separately, *C. maenas* maximum feeding rates were higher towards native *M. edulis* compared to invasive *C. gigas*. In addition, handling times were lower, and thus maximum feeding rates were higher, in summer compared to winter. Hydrodynamic disturbance level had no significant influence on handling times or maximum feeding rates towards either prey species. When prey species were offered simultaneously, *C. maenas* disproportionately consumed native *M. edulis* over invasive *C. gigas* irrespective of proportional availability. In addition, increased hydrodynamic disturbance further increased the disproportionate consumption of *M. edulis* over *C. gigas*. We thus demonstrate that *C. maenas* offers little biotic resistance to invasions of *C. gigas* under a range of abiotic contexts, and indeed some of these contexts may exacerbate the invasion. We suggest that combined functional response and prey switching

studies provide a wealth of information regarding invasion success and biotic resistance towards invasive species under environmental variation.

Keywords

Functional Response; Invasive species; *Per capita* consumption; Predation; Prey switching

Introduction

Coastal ecosystems are subject to a wide range of abiotic conditions including varied temperature, nutrient availability, water turbidity and hydrodynamic condition. Biotic interactions within ecosystems are likely to differ among seasons owing to changes in physical parameters including day length, rainfall, wind speed and temperature, among others. Variation in temperature occurs naturally over daily and seasonal cycles and is one of the main abiotic factors affecting physiological processes such as growth, feeding and locomotion due to its influence on metabolic rate (Brown et al., 2004). Several investigations show that increases in temperature can decrease the time taken to consume food items and therefore increasing predator maximum consumption rates, especially in ectotherms (Zamani et al., 2006; Vasseur et al., 2014; Zhang et al., 2016; Laverty et al., 2017). Since predation is a critical factor in structuring coastal communities (Paine, 1974; Grosholz et al., 2000), changes in predation rates throughout seasons may have implications for prey populations as well as stocks of commercially important species such as bivalves (Murray et al., 2007; Sanchez-Salazar et al., 1987).

While hydrodynamic variability, such as differences in wave height and period or current speeds, are considered a major driver of species distributions (Denny, 2006), effects of hydrodynamics on species interactions are still understudied. Different hydrodynamic conditions can lead to changes in biotic processes such as altering growth rates (Millar et al.,

2019), fertilisation success (Kregting et al., 2013), and nutrient uptake (Morris et al., 2008). In active foragers, hydrodynamic stress can alter foraging success through mechanisms including limiting chemosensory detection (Weissburg et al., 2002) and locomotion (Kawamata, 1998). Over the last 100 years, significant wave heights in the North Atlantic have increased by 0.01 metres yr⁻¹ (Bertin et al., 2013; Castelle et al., 2018) and, more recently, coastal infrastructure such as renewable energy developments and aquaculture have been linked to altered hydrodynamic conditions (Lin et al., 2016). Such changes in localised hydrodynamic environments may thus impact biotic processes and species interactions, further altering these ecosystems.

Alongside abiotic change, coastal ecosystems are facing increased pressures from biotic change *via* the ever increasing number of invasive species introductions (Seebens et al., 2017, 2018). Invasive species can have severe impacts on recipient communities, including altering the physical habitat (Burlakova et al., 2012), community structure (Guy et al., 2018), and biodiversity (Molnar et al., 2008). Invasive predators are perceived to have greater ecological impacts than invasive prey species and thus have received greater attention (Salo et al., 2007). However, invasive prey species can also induce ecological impacts through the displacement of native species (Burlakova et al., 2000) and alteration of predator-prey dynamics (Waser et al., 2015).

Comparative functional responses (FRs; resource use as a function of resource availability) have shown excellent utility in quantifying ecological impacts caused by invasive species (Dick et al., 2017). Functional responses typically exist in three forms; linear (Type I), hyperbolic (Type II), and sigmoidal (Type III) (Holling, 1959). Type I FRs are typically constrained to filter feeders due to their minimal handling times and need to constantly forage (Jeschke et al., 2004). Type II FRs are considered potentially prey population destabilising owing to high proportional predation at low prey densities, whereas

Type III FRs may impart stability in prey populations by providing prey refuge at low prey densities (Murdoch & Oaten 1975). Functional responses can offer insights into consumer attack rates (instantaneous resource capture rate by the consumer) and handling times (time spent ingesting and digesting prey). Comparing the magnitude of FRs is a particularly effective method of quantifying impacts of invasive predators on prey resources owing to their higher consumption rates compared to trophically analogous natives (Dick et al., 2017).

In addition to FRs, the approach of determining prey switching patterns (Murdoch, 1969) may further inform invasion success, ecological impacts and predation driven biotic resistance towards invasive species, particularly invasive prey (Cuthbert et al., 2018; Skein et al., 2018). Predator driven biotic resistance towards invasive prey species, that is, the ability of an ecosystem to resist its invasion or control its population, has the potential to occur if native predators are able to switch between resources and recognise the invasive prey species as a novel food source (Sousa et al., 2009; Carlsson et al., 2011). However, invasive prey may also go unrecognised by native predators. For example, in South Africa, both rock lobsters and starfish were found to prefer native over invasive bivalve prey despite bivalve morphology suggesting the invaders would be easier to consume (Skein et al., 2018). Also, native predators may lack the ability to consume invasive prey or switch between resources. Such predation patterns may lead to continuous consumption of native prey while simultaneously relieving the invasive prey from predation. Although the incorporation of ecological contexts such as temperature (South et al., 2018) and habitat complexity (Alexander et al., 2012) into FR investigations has been shown to improve their utility, recent investigations into prey switching have not yet utilised the incorporation of abiotic contexts (Cuthbert et al., 2018; Skein et al., 2018).

The Pacific oyster, *Crassostrea gigas* (*Magallana gigas*; Salvi & Mariottini, 2016; Bayne et al., 2017), is one of the most globalised invasive marine invertebrates on coastal rocky

shores (Herbert et al., 2016), and can have impacts on ecosystems including changing benthic species assemblages (Markert et al., 2009; Guy et al., 2018) and sediment chemistry (Green et al., 2013). In many areas, *C. gigas* invades and replaces native blue mussels, *Mytilus edulis*, as the dominant ecosystem engineer (Troost, 2010; Kochmann & Crowe, 2014; Reise et al., 2017). The native *M. edulis* forms extensive beds and provides a vital food source for a wide range of organisms (Ebling et al., 1964; Paine, 1974) and is thus a vital part of coastal ecosystems. Shifts from native *M. edulis* to invasive *C. gigas* dominance may affect food webs and foraging of predators (Markert et al., 2013). Although *C. gigas* may provide a novel food source for some predators (Wright et al., 2018), consumption relies on predator recognition and ability to open *C. gigas* shells.

Throughout Europe, the green crab, *Carcinus maenas*, is one of the most common predators of *M. edulis* in coastal communities (Paine, 1974), which often makes up large quantities of *C. maenas* diets (Murray et al., 2007). Although considered a generalist predator (i.e. they can switch between resources), *C. maenas* is likely to exert very limited biotic resistance on *C. gigas* (Joyce et al., 2019). However, it is not understood whether such patterns of predation are consistent under varied abiotic conditions, with such environmental context dependencies recognised as critical in shaping invader success versus failure (Dick et al., 2017).

Owing to the overlapping distributions of *C. maenas*, invasive *C. gigas*, and native *M. edulis* along European coastlines, where thermal and hydrodynamic regimes are highly variable, we examined predation patterns of *C. maenas* towards the two bivalve prey species. More specifically, we examined the FR of native *C. maenas* towards the two prey types separately, at two different times of year, to investigate seasonal effects, and also examined two levels of hydrodynamic disturbance (high and low) to simulate changes in hydrodynamic conditions. We also examined prey switching patterns of *C. maenas*, whereby the two prey

species were presented simultaneously across a range of proportional availabilities, using two levels of hydrodynamic disturbance. Overall, these combined approaches assess whether such abiotic conditions may alter the level of biotic resistance towards *C. gigas* by *C. maenas*.

Methods

Animal collection and maintenance

Green crabs, *Carcinus maenas*, were collected using baited crab pots from a rocky shore where *C. gigas* occurrence is low (54° 23' 30" N, 05° 34' 29" W) and housed at Queen's University Marine Laboratory, Portaferry, in through-flowing, sand filtered seawater pumped from the adjacent Strangford Lough. The collected predators were held in ~500 L tanks and fed raw herring *ad libitum* for at least one week prior to trials to acclimate them to laboratory conditions. In experiments, we used only male *C. maenas* with a carapace width of 60-70 mm and that had both claws intact and were free from visible, external parasites. As females go through cycles of egg development seasonally, this may potentially affect their foraging requirements because of changes in energy allocation. Therefore, we used only males to reduce any associated variability in feeding rates. Prior to feeding trials, individuals were starved for 48 hours to standardise hunger levels. After use in the experiments, predators were maintained in the laboratory for one week to ensure animals were healthy and feeding had not been affected by imminent moulting.

Juvenile invasive Pacific oysters, *Crassostrea (Magallana) gigas*, were obtained from a commercial spat producer (Guernsey Sea Farms Ltd, Guernsey), while juvenile native blue mussels, *Mytilus edulis*, were collected by hand from a local intertidal rocky shore (54° 28' 13" N, 05° 32' 26" W). These prey were maintained under the same conditions as the predators and were size matched with respect to shell length (15 – 20.99 mm), thus avoiding confounding prey size effects. Collection of animals occurred in December 2017 and August 2018 for winter and summer experiments, respectively.

Feeding trials

Functional responses

Functional response feeding trials were conducted in $56 \times 36 \times 23$ cm outdoor mesocosms covered with 1 cm plastic mesh, thus preventing crabs from escaping but allowing natural light to penetrate. Experiments were conducted in December 2017 (winter) and August 2018 (summer) to measure the seasonal influence on predation rates. A temperature logger (Aqualogger 520PT, Aquatec Group, Hampshire, UK) located on the Portaferry Quay measured water temperature every 15 minutes at the time of experiments, which were 6.2 ± 0.1 °C and 14.0 ± 0.2 °C during winter and summer, respectively (Kregting *unpublished data*). To manipulate disturbance levels, running sea water, pumped from the adjacent Strangford Lough, was supplied to the areas by either (1) hoses supplying water at a rate of ~ 1.5 L min⁻¹ from a height of 5 cm above the experimental mesocosm, simulating a low disturbance regime, or (2) by weighted overhead dump buckets that emptied every ~ 1 minute from a height of ~ 0.7 m, delivering ~ 4 L of water to 2 mesocosms, simulating a high disturbance regime characteristic of increased wave exposure (Mrowicki & O'Connor, 2015). Mesocosms were provided with either invasive *C. gigas* or native *M. edulis* prey at 6 densities (2, 4, 8, 16, 32 or 64; $n \geq 3$ per experimental group). Prey were adhered to the base of each mesocosm: *C. gigas* were attached by using a small amount of epoxy putty to simulate natural attachment, whereas *M. edulis* were allowed to attach to the base of mesocosms naturally with byssus threads. Prey were left in mesocosms for 13 hours prior to the feeding period to allow sufficient attachment strength of *M. edulis*. Predators were added to the mesocosms at 09:00 and removed after 8 hours and the remaining live prey quantified. Controls consisted of one replicate of each experimental group in the absence of a predator to quantify any background mortality of prey.

Prey switching

A prey switching experiment was performed under the same general conditions as the FRs. The experiment was only performed in summer 2018 as *C. maenas* are likely to be more active under warmer temperatures, which would allow for better discrimination of prey switching behaviour. Invasive *C. gigas* and native *M. edulis* were added simultaneously in three ratios of the two species (5:15, 10:10, 15:5; $n = 5$ per experimental group) and adhered to the mesocosm base as per the FR experiment. Predators were added to the mesocosms and allowed to feed for 2 hours, with consumed prey being replaced every 15 minutes to maintain nominal prey species ratios. Replaced prey were adhered to the base of the mesocosms using epoxy putty. Pilot results indicated that *C. maenas* showed no preference for *M. edulis* prey that were naturally attached to the mesocosm floor or those attached with epoxy putty. Controls consisted of one replicate of each experimental group in the absence of a predator to quantify any background mortality of prey.

Conclusions from the summer low disturbance treatment FR and low disturbance prey switching experiment have previously been presented in Joyce et al. (2019) and represent 25% and 50% of the FR and prey switching data, respectively, in this study. Here, we show that incorporating abiotic contexts into experiments can substantially increase the knowledge surrounding consumer-resource relationships and thus the utility of the FR and prey switching data.

Statistical analyses

Functional responses

Overall prey consumption in FR trials was compared using a generalised linear model assuming Poisson distribution and log link as counts were not overdispersed in relation to degrees of freedom. Consumption was compared with respect to the factors: prey species, prey density, season and disturbance level. Non-significant interactions between terms were systematically removed to reduce the model with χ^2 via analysis of deviance used for model

simplification as well as reporting the effect sizes using the *car* package in R (Fox & Weisburg, 2011). Significant effects and interactions were compared using Tukey's post hoc comparisons via the *lsmeans* package in R (Lenth, 2016).

Functional response analysis was undertaken using the 'frair' package (Pritchard et al., 2017). Logistic regression was used to infer FR types with respect to the proportion of prey consumed as a function of initial prey density. Categorically, Type II FRs are indicated by a significantly negative first order term, whereas Type III FRs are indicated by a significantly positive first order term followed by a significantly negative second order term. Information loss was minimised by using Akaike Information Criterion (AIC) for FR model selection. Flexible FR models for non-replacement of prey were fitted (Barrios-O'Neill et al., 2016; Real, 1977):

$$N_e = N_0(1 - \exp(bN_0^q(hN_e - T)))$$

where N_e is the number of prey consumed, N_0 is the initial prey density, b is the search coefficient, q is the scaling component, h is the handling time, and T is the experimental time. When $q = 0$ Type II FRs are indicated, and when $q > 0$ the FR becomes increasingly sigmoidal, allowing a continuum of FR types ranging from Type II to Type III. Here, q was fixed at 0 when Type II FRs were indicated, and q was fixed at 1 when Type III FRs were indicated. The Lambert W function was used to enable model fitting (Bolker, 2008). Data were non-parametrically bootstrapped ($n = 2000$) to produce 95 % confidence intervals (CIs) allowing the FRs to be compared by CI overlap (Pritchard et al., 2017).

Prey switching

The number of prey of each species consumed was examined using a generalised linear mixed effects model using the package *lme4* (Bates et al., 2015) to account for repeated measures. The number of prey individuals consumed was analysed with regards to the factors: prey species, proportion of each prey type available and disturbance level. Each

replicate (i.e. each individual mesocosm) was included as a random factor with prey species treated as a within subject variable to account for multiple measurements within individual mesocosms. Interactions between terms were systematically removed to reduce the model with χ^2 via analysis of deviance used for model simplification as well as reporting the effect sizes.

Chesson's selectivity index (Chesson, 1978, 1983) was used to assess prey preference of *C. maenas* towards invasive *C. gigas* when available in various proportions and under different disturbance levels. Chesson's index was calculated as:

$$\alpha_i = \frac{(r_i/p_i)}{\sum_{j=1}^m (r_j/p_j)}$$

Where r_i is the percentage of prey type i in the diet (consumed), p_i is the percentage of prey type i available (on offer within the experimental mesocosm), m is the number of prey types, r_j is the percentage of prey type j in the diet (consumed), p_j is the percentage of prey type j available (on offer within the experimental mesocosm). Chesson's index, α_i , ranges from 0 to 1 with $\alpha_i > 1/m$ (here, $1/m = 0.5$) inferring positive preference, $\alpha_i < 0.5$ inferring negative preference, and $\alpha_i = 0.5$ inferring no preference for either prey type. Chesson's indices were transformed to reduce extreme values (0s and 1s) via the transformation:

$$\alpha_t = \frac{\alpha_i(n - 1) + 0.5}{n}$$

where α_t is the transformed output and n is the sample size. Beta regression compared α_t values towards invasive *C. gigas* with predicted values of no preference (i.e. 0.5) across proportional availabilities and disturbance levels using the betareg package (Cribari-Neto & Zeileis, 2010).

All statistical analyses were undertaken in 'R' version 3.4.2 (R Development Core Team, 2017).

Results

Functional responses

Prey survival was 100% in controls (no predators) and thus prey were determined to be healthy at the time of the experiments and all experimental prey mortality was attributed to predation.

Overall, significantly more native *M. edulis* were consumed than invasive *C. gigas* ($\chi^2 = 45.91$, $df = 1$, $p < 0.001$) and significantly more prey were consumed when more were available ($\chi^2 = 199.65$, $df = 5$, $p < 0.001$). Season affected predation with significantly more prey being consumed in summer compared to winter ($\chi^2 = 57.50$, $df = 1$, $p < 0.001$), however, disturbance level did not significantly affect predation ($\chi^2 = 0.0351$, $df = 1$, $p < 0.55$). A significant prey species $\times$ season interaction reflects the reduced consumptive difference between seasons for native *M. edulis* compared to invasive *C. gigas* ($\chi^2 = 5.53$, $df = 1$, $p < 0.05$). Tukey post hoc comparisons revealed that greater consumption of native *M. edulis* compared to invasive *C. gigas* occurred in both seasons (both $p < 0.05$), consumption in summer was greater than in winter for both species (both $p < 0.05$), however, consumption of native *M. edulis* in winter was similar to consumption of invasive *C. gigas* in summer ($p > 0.05$).

Functional responses were generally Type II with one categorical Type III response in summer towards invasive *C. gigas* within the low disturbance treatment. Two further responses returned equivocal Type II and Type III responses, however, in these cases lower AIC values for Type III models suggested reduced information loss. One case (*M. edulis* prey, high disturbance, summer) returned no significant responses due to extreme consumption. Due to the invertebrate predator type and experimental setup, that is, a confined space with a lack of habitat structural complexity (Alexander et al., 2012; Barrios-O'Neill et al., 2015), a Type II response was selected (Table 1).

In winter, FRs towards native *M. edulis* were greater than towards invasive *C. gigas* (Fig. 1A & C), however, 95% CIs overlapped at prey densities above ~38 for both disturbance levels. Greater search coefficients and lower handling times were observed towards native *M. edulis* compared to invasive *C. gigas* (Table 1).

In summer, the FR towards native *M. edulis* was higher than invasive *C. gigas* in the high disturbance treatment (Fig. 1B). Within the low disturbance treatment, Type III FRs were shown with 95% CI overlap at prey densities above 20, however, predation towards native *M. edulis* at densities below 20 was greater than towards invasive *C. gigas* (Fig. 1C). Although 95% CIs overlapped at high prey densities, lower handling times, and thus greater maximum feeding rates, tended to be shown towards native *M. edulis* compared to invasive *C. gigas* (Table 1).

For each prey species $\times$ disturbance combination within winter and summer, respectively, functional response CIs overlapped across all prey densities, thus disturbance level had no significant effect on predation (Fig. 1).

Under the high disturbance treatment, *C. maenas* consumption of both prey species was greater in summer than in winter, with 95% CIs showing no overlap at any prey density (Fig. 1A & B). The search coefficients towards both prey species, b , were greater and handling times, h , were lower in summer compared to winter (Table 1).

Under the low disturbance treatment, consumption of *M. edulis* prey was similar between seasons with 95% CIs overlapping across all prey densities (Fig. 1C & D). Similarly to the high disturbance treatment, the search coefficient, b , was greater and handling time, h , was lower in summer compared to winter. For invasive *C. gigas* prey under the low disturbance treatment, different FR types occurred between summer and winter with the FR in summer being Type III and winter being Type II (Fig. 1C & D). Functional Response 95% CIs overlapped at prey densities below 15 and above 50, thus consumption was significantly

increased in summer compared to winter at intermediate prey densities only. The search coefficient, b , was lower in summer compared to winter due to the Type III response shown in summer. Handling time, h , was lower, and thus maximum feeding rate was greater, in summer compared to winter (Table 1).

Prey switching

Significantly more native *M. edulis* were consumed compared to invasive *C. gigas* ($\chi^2 = 39.04$, $df = 1$, $p = <0.001$) and a main effect of proportion available shows that more prey were consumed when available in greater proportions ($\chi^2 = 37.34$, $df = 2$, $p = < 0.001$). Disturbance level did not significantly alter consumption ($\chi^2 = 0.09$, $df = 1$, $p = 0.77$).

Chesson's selectivity indices towards invasive *C. gigas* were significantly lower than the null preference value of 0.5 ($\chi^2 = 15.13$, $df = 1$, $p < 0.001$; Table 2). A significant prey species $\times$ proportion available $\times$ disturbance interaction ($\chi^2 = 6.1148$, $df = 2$, $p = 0.047$) reflects the greater preference for native *M. edulis* in the high disturbance treatment when available at a proportion of 0.5 (Fig. 2). Thus, *C. maenas* exhibited a lack of switching behaviour and disproportionately consumed native *M. edulis* across treatments, however, preference for native prey appears greater under increased disturbance (Fig. 2).

Discussion

In a changing world, understanding how organisms respond to environmental variability is necessary for quantifying and predicting how future environmental scenarios will affect these responses. In the marine environment, drivers of ecosystem change include abiotic influences such as seasonal change and hydrodynamic variation (Brown et al., 2004; Reguero et al., 2019), as well as biotic influences such as invasive species (Seebens et al., 2018). Functional responses and, more recently, combining these with prey switching approaches (i.e. frequency dependent predation), have been used to quantify invasion success of invasive prey species as well as ecological impacts of invaders (Cuthbert et al., 2018;

Skein et al., 2018; Joyce et al., 2019). However, these combined approaches have thus far lacked the inclusion of abiotic contexts. From our experiments investigating such predation patterns, *Carcinus maenas* FRs tended to be greater toward native *M. edulis* compared to invasive *C. gigas* under all season and disturbance scenarios. FRs also increased in magnitude from winter to summer, but were unaffected by disturbance levels. When both prey species were offered simultaneously, across a range of proportional availabilities, *C. maenas* disproportionately consumed native *M. edulis* over invasive *C. gigas*, and the disproportionate consumption of native *M. edulis* increased under high disturbance levels. Thus, *C. maenas* displays limited biotic resistance towards *C. gigas* invasions which is likely to become further reduced in areas with greater hydrodynamic disturbance.

As intertidal species, *Carcinus maenas*, *M. edulis* and *C. gigas* are subjected to a wide range of environmental fluctuations including temperature variation. Such abiotic variables can affect species distributions and density due to crab migrations during different seasons (Aagaard et al 1995), and through spawning during summer (Seed & Suchanek, 1992). The higher magnitude FRs of *C. maenas* exhibited in summer compared to winter, towards both native *M. edulis* and invasive *C. gigas*, was expected owing to metabolic theory (Brown et al., 2004). Increased temperatures during summer drive an increase in metabolic rate compared to winter, thus increasing predation (Brown et al., 2004; Elner, 1980; Sanchez-Salazar et al., 1987). Increased metabolic rate has been shown to decrease handling times, the FR parameter h , and thus increase maximum feeding rates, $1/h$, of predators, especially ectotherms (Vasseur et al., 2014; Zhang et al. 2016; but see South et al., 2018), potentially destabilising populations and communities (Daugaard et al., 2019). Although these results appear likely to be driven by changes in temperature, it should be considered that changes in season also brings changes in factors such as day length and wind. Such factors also have the potential to partially explain the observed results as photoperiod can influence crab

373 physiology and thus foraging activity (Hyde et al. 2012). Wind speed can also change
374 hydrodynamics, however, further investigation is required to fully understand the relative
375 influences of these other parameters. The results presented here suggest that it is within
376 summer that *C. maenas* will exert greatest predation pressure on prey species and commercial
377 bivalve stocks will receive the greatest impacts from predation (Murray et al., 2007).
378 However, further investigations across multiples of each season and throughout the year
379 would give a clearer insight into seasonal variation of *C. maenas* predation.

380 Hydrodynamic variability also alters biotic processes including settlement ability
381 (Fuchs & DiBacco, 2011) and searching and consumption capabilities (Kawamata, 1998;
382 Gagnon et al., 2003; St-Pierre & Gagnon, 2015). Here, however, the influence of
383 hydrodynamic disturbance on consumption was small, causing subtle, but not significant
384 changes to FRs. Although the influence of hydrodynamic disturbance is small, some
385 explanations of drivers behind the changes can be suggested when combined with the
386 changes in season. During winter, FRs of *C. maenas* towards *M. edulis* changed from Type II
387 to Type III when hydrodynamic disturbance increased. This change may be due to cold
388 temperatures reducing crab muscle functioning (Blundon, 1989), which can potentially limit
389 their foraging (Matheson & Gagnon, 2012) and ability to open hard shelled prey. Reduced
390 temperature and muscle functioning, in this case, leads to a slight increased influence of
391 hydrodynamic disturbance on crab reducing foraging efficiency (Robinson et al. 2011),
392 especially at low prey densities. In summer, the influence of hydrodynamic disturbance was
393 unclear due to the equivocal Type II and Type III responses towards *M. edulis* prey under the
394 low disturbance treatment, and the lack of significant FR under the high disturbance
395 treatment. We hypothesise that the increase in muscle function under the warmer
396 temperatures during summer (Blundon, 1989) allows *C. maenas* to better withstand the

influence of physical disturbance and permits continuous feeding and possibly reducing the low density refuge for prey under high disturbance levels.

Under all treatment combinations, *C. maenas* exhibited lower handling times, and thus higher maximum feeding rates, towards native *M. edulis* compared to invasive *C. gigas*. The lower handling times infer that *C. maenas* are quicker to consume the native prey compared to the invasive prey. Crabs show preference for prey of different sizes depending on both crab size, prey size and prey species (Mascaró & Seed, 2001). The results found here are consistent with previous investigations where *C. maenas* show a preference for mussel over oyster prey (Mascaró & Seed, 2001; Miron et al., 2005; Pickering & Quijon, 2011; Joyce et al., 2019). There are two potential mechanisms to explain the preference for *M. edulis* over *C. gigas*. Firstly, although prey in these experiments were matched for size in terms of shell length, morphological differences and differences in shell strength between the two species is likely to induce the differences in handling times found (Pickering & Quijon, 2011; Campbell et al. 2019). Given that shell thickness is a good predictor of shell strength and that crabs use their chelae either to crush the shells of their prey or to chip away at the valve edges to force shells open (Elner 1978), it can be assumed that shell thickness directly relates prey vulnerability to predators. Although shell strength and thickness in this investigation were not measured, it can be suggested that *C. gigas* of a similar length to *M. edulis* have thicker shells. Secondly, another potential mechanism driving differences in predation of the two species is predator naïveté. As the predators used in this study were obtained from an area where *C. gigas* remains rare, they may not recognise *C. gigas* as a potential prey species, either due to chemical stimuli (e.g. Carthy et al. 2017) or shell morphology (Mascaró & Seed, 2001) which may reduce consumption. Although the mechanism behind the preference of prey type requires further investigation, the greater maximum feeding rates towards native *M. edulis* compared to invasive *C. gigas* indicates that

C. maenas will generally exert greater impact over *M. edulis* populations compared to *C. gigas* populations.

Although considered a generalist predator that readily switches between resources, the disproportionate consumption of *M. edulis* over *C. gigas* by *C. maenas* when a choice is offered applies limited biotic resistance towards *C. gigas* invasions. We found that the disproportionate consumption of native *M. edulis* over invasive *C. gigas* by *C. maenas* (Joyce et al., 2019) was strengthened under the high disturbance treatment. Again, this preference for native *M. edulis* over invasive *C. gigas* prey could be attributed to shell morphology and strength (Mascaró & Seed, 2001; Pickering & Quijon, 2011). Foraging efficiency and consuming prey is energy demanding and can become reduced in high energy environments (Robinson et al. 2011). The increased energy demand for resisting the high disturbance treatment in this case is likely to have driven *C. maenas* to selecting native *M. edulis* prey even more often than under the low disturbance treatment to optimise its foraging. This demonstrates that physical disturbance further increases the predator selectivity towards native prey compared to invasive prey and thus, under increased hydrodynamic disturbances, *C. gigas* invasions may be exacerbated. Prey switching and prey preference is a major driver of species diversity (Allen, 1988), whereby those that are rare in the environment are disproportionately ignored by predators allowing their abundance to increase. Here, however, the continuous disproportionate consumption of *M. edulis* over *C. gigas* independent of both proportional availability and hydrodynamic disturbance level shows that little biotic resistance towards *C. gigas* invasions will occur under a range of conditions.

The disproportionate consumption of *M. edulis* over *C. gigas* coupled with the low handling times and generally higher maximum feeding rates observed towards *M. edulis* shows potential for significant impacts on *M. edulis* populations by predators. Prey switching studies show excellent utility in understanding predation patterns towards native and invasive

prey at different stages of invasion (Alexander et al., 2015; Skein et al., 2018). In these experiments, *C. gigas* was a novel prey for *C. maenas* as crabs were collected from an area where *C. gigas* occurrence is low. As *C. maenas* possesses a good learning ability (Roudez et al., 2008) and can transfer handling skills towards novel prey (Hughes & O'brien, 2001), future research into their prey switching propensities should be conducted after prolonged exposure to *C. gigas* which is common (e.g. Markert et al. 2009).

Although the prey switching experiment was only conducted in summer, it can be assumed that preference shown for *M. edulis* over *C. gigas* prey would extend into winter when then physical demands of foraging are higher. We concede that the hydrodynamic disturbance used here may not truly represent the physical forces experienced at the seabed when waves are present. Although the same method has previously been used to investigate the influence of waves on ecosystem processes within rocky shore communities (Mrowicki & O'Connor, 2015; White et al., 2018), the effects may be more simulative of waves crashing in tidal pools on rocky shores. As crabs are known to migrate with tides (Hunter & Naylor, 1993; Silva et al., 2010) and feeding taking place when submerged, these predators are more likely to be affected by oscillating horizontal water motion. Although some information can be taken from these experiments regarding physical disturbance levels, further investigation into predation by *C. maenas* should be conducted using horizontal oscillations in water direction, along with varying speeds, to better simulate realistic field conditions.

Due to large anthropogenic influences on coastal hydrodynamics and invasive species introductions, identifying how these factors influence species interactions is important for understanding future ecological interactions. We have shown that predation by *Carcinus maenas*, at least in its native range, is more affected by changes in season than hydrodynamic disturbance. The greater predation pressure towards *M. edulis* is likely to lead to greater population impacts on *M. edulis* compared to invasive *C. gigas* populations. Further,

increased hydrodynamic disturbance led to greater disproportionate consumption of native *M. edulis* prey over *C. gigas* prey compared to low disturbance levels suggesting that ecosystems with greater disturbance may be more susceptible to invasion success. Certainly, further investigation into predation patterns of *C. maenas* in its invasive range would provide more information as to whether patterns similar to those observed here occur. We show not only that the use of FRs can quantify potential population impacts by native predators towards native and invasive prey, but that combining this with prey switching studies further inform predator-prey interactions and give a greater understanding of invasion success and predator driven biotic resistance under various environmental contexts.

Competing Interests

The authors declare that the research was carried out without any competing interests.

Data availability

Data will be made available on manuscript acceptance

Acknowledgements

This work was funded by the Department for the Economy, Northern Ireland and part of SuperGen Marine Energy Research Consortium II, which was funded by the UK Engineering and Physical Science Research Council. The authors extend their thanks to the anonymous reviewers whose comments improved the manuscript significantly.

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769 Figure 1. Functional responses of green crabs, *Carcinus maenas*, towards invasive oyster,
770 *Crassostrea gigas*, and native blue mussel, *Mytilus edulis*, prey in winter (A & C) and
771 summer (B & D) and under high (A & B) and low (C & D) disturbances. Shaded areas
772 indicate bootstrapped (n = 2000) 95% CIs. The summer-low disturbance treatment data have
773 previously been published in Joyce et al. (2019).
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776 Figure 2. Proportion of either *Crassostrea gigas* (red) or *Mytilus edulis* (blue) in the diet of
 777 *Carcinus maenas* (mean $\pm$ S.E.) as a function of their respectively proportional availability at
 778 high and low disturbance levels. The solid line indicates expected values if no prey
 779 preference was to occur. The dashed line indicates a hypothetical prey switching pattern. The
 780 low disturbance data have previously been published in Joyce et al. (2019).

Tables

Table 1. Results of logistic regression for both Type II and Type III FR models towards invasive *C. gigas* and native *M. edulis* during winter and summer and under high and low disturbance levels models, considering prey eaten as a function of prey density. Terms marked * indicate significant terms. Parameter estimates resulting from models are shown. The scaling component, q , was fixed at 0 or 1 depending on the FR Type selected.

	Winter			
	High disturbance <i>C. gigas</i>	<i>M. edulis</i>	Low disturbance <i>C. gigas</i>	<i>M. edulis</i>
Logistic regression				
Type II FR				
First order	-0.026	0.037	-0.0269	-0.0237
<i>P</i>	<0.001*	<0.001*	<0.001*	<0.001*
AIC	152.23	353.27	271.65	373.59
Type III FR				
first order	0.0163	0.1201	0.0398	0.0410
<i>P</i>	0.589	<0.001*	0.1254	0.066
second order	-0.0005	-0.0021	-0.0009	-0.0008
<i>P</i>	0.146	<0.001*	0.007*	0.003*
AIC	152.11	305.24	266.50	366.91
Parameter estimates				
<i>b</i>	0.2445	0.1192	0.3420	1.1263
<i>q</i>	0	1	0	0
<i>h</i>	0.2265	0.0634	0.1470	0.0309
$1/h$	4.41466	15.750	6.7986	32.309
	Summer			
	High disturbance <i>C. gigas</i>	<i>M. edulis</i>	Low disturbance <i>C. gigas</i>	<i>M. edulis</i>
Type II FR				
First order	-0.0124	-0.0099	-0.0039	-0.0358
<i>P</i>	0.002*	0.204	0.323	<0.001*
AIC	225.71	71.56	480.78	207.30
Type III FR				
first order	-0.0832	-0.0523	0.0702	0.1217
<i>P</i>	<0.001*	0.2877	0.002*	<0.001*
second order	0.0009	0.0005	-0.0009	-0.002
<i>P</i>	0.002*	0.3763	<0.001*	<0.001*
AIC	218.01	72.752	471.52	190.11
Parameter estimates				
<i>b</i>	0.7437	2.6705	0.0773	0.2727
<i>q</i>	0	0	1	1
<i>h</i>	0.0292	0.0039	0.0325	0.0269
$1/h$	34.195	252.75	30.769	37.155

787 Table 2. Chesson's selectivity indices ($\alpha_i \pm \text{S.E.}$) for *Carcinus maenas* towards invasive
788 oysters, *Crassostrea gigas*, and native mussels, *Mytilus edulis*, at high and low disturbance
789 levels. Selectivity indices above 0.5 indicate preference whilst indices below 0.5 indicate
790 avoidance of prey.

	Proportion available	Chesson alpha $\pm$ S.E.
High disturbance		
<i>C. gigas</i>	0.25	0.22 $\pm$ 0.07
	0.5	0.19 $\pm$ 0.01
	0.75	0.12 $\pm$ 0.05
<i>M. edulis</i>	0.25	0.88 $\pm$ 0.05
	0.5	0.81 $\pm$ 0.12
	0.75	0.78 $\pm$ 0.07
Low disturbance		
<i>C. gigas</i>	0.25	0.22 $\pm$ 0.07
	0.5	0.44 $\pm$ 0.09
	0.75	0.24 $\pm$ 0.05
<i>M. edulis</i>	0.25	0.76 $\pm$ 0.05
	0.5	0.56 $\pm$ 0.04
	0.75	0.78 $\pm$ 0.07

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