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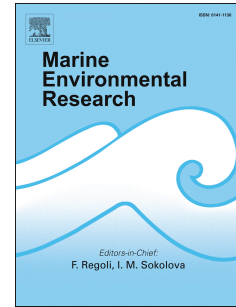
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Patrick W.S. Joyce, James W.E. Dickey, Ross N. Cuthbert, Jaimie, T.A. Dick, Louise Kregting



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1 Using functional responses and prey switching to quantify invasion success of the Pacific
2 oyster, *Crassostrea gigas*

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4 Patrick W.S. Joyce^{1,2*}, James W.E. Dickey², Ross N. Cuthbert², Jaimie, T.A. Dick², Louise
5 Kregting^{1,2}

6

7 ¹School of Natural and Built Environment, Queen's University Belfast, Queen's Marine
8 Laboratory, 12-13 The Strand, Portaferry, BT22 1PF, UK

9 ²Institute for Global Food Security, School of Biological Sciences, Queen's University
10 Belfast, Medical Biology Centre, 97 Lisburn Road, Belfast BT9 7BL, UK

11

12 *Corresponding author email: pjoyce04@qub.ac.uk

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Abstract

Invasive alien species continue to proliferate and cause severe ecological impacts. Functional responses (FRs) have shown excellent utility in predicting invasive predator success, however, their use in predicting invasive prey success is limited. Here, we assessed invader success by quantifying FRs and prey switching patterns of two native predators, the common sea star, *Asterias rubens*, and the green crab, *Carcinus maenas*, towards native blue mussels, *Mytilus edulis*, and invasive Pacific oysters, *Crassostrea gigas*. *Asterias* displayed destabilising type II FRs, whereas *Carcinus* displayed stabilising type III FRs towards both prey species. Both predators exhibited greater search efficiencies and maximum feeding rates towards native compared to invasive prey. Both predators disproportionately consumed native mussels over invasive oysters when presented simultaneously, even when native mussels were rare in the environment, therefore indicating negligible prey switching. We demonstrate that invasion success may be mediated through differential levels of biotic resistance exerted by native predators.

Keywords

Biotic resistance; Crabs; Frequency dependent predation; Invasive species; *Per capita* consumption; Predation; Sea stars

51 Introduction

52 The rate of invasive alien species (IAS) introductions is increasing (Seebens et al.
53 2017, 2018). Many IAS can drive changes in biodiversity (Molnar et al. 2008), habitat
54 (Burlakova et al., 2012) and community structure (Sanders et al. 2003, Guy et al. 2018), often
55 leading to novel species interactions between natives and invaders (Skein et al., 2018).
56 Previously, there has been a sustained focus on the effects of invasive predators on native
57 prey (Dick et al. 2017), with invasive predators perceived to have greater impacts on
58 communities than invasive prey (Salo et al. 2007). The latter can, however, establish in large
59 numbers with the potential to displace native species (Burlakova et al., 2000) and alter
60 predator-prey and competitive interactions (Waser et al., 2015). Predicting the outcomes of
61 such species introductions has been elusive and plagued with contradictory meta-analyses of
62 species traits and lack of application of appropriate methods (Dick et al. 2014).

63 Functional responses (i.e. resource use as a function of resource density), and prey
64 switching (“frequency dependent predation”), are well known, fundamental ecological
65 concepts, however, invasion ecologists have been slow to capitalise on their use in assessing
66 and predicting ecological impacts of invasive species. Comparative functional response (FR)
67 analysis has shown excellent utility in assessing and predicting invader impacts (Dick et al.
68 2014, 2017, Lavery et al. 2017), but with little application to biotic resistance (Twardochleb
69 et al. 2012). Comparative FRs achieve this because they quantify the relative magnitude of
70 invader *versus* native equivalent *per capita* effects, that then translate into population
71 consequences for native resources such as prey species (Dick et al. 2017). Prey switching
72 may complement FR methods (Cuthbert et al. 2018b), as both approaches can inform
73 population level outcomes of species interactions. Prey switching by predators can impact
74 prey population stability by controlling abundant prey species while simultaneously
75 providing refuge for scarce prey (Murdoch 1969). Thus, if invading prey are consumed by

76 native predators that can readily switch between resources, then some level of biotic
77 resistance toward the invader may occur (Sousa et al., 2009; Carlsson et al., 2011).
78 Conversely, predators that do not exhibit such switching behaviour may reduce the
79 abundance of one prey type while allowing the increase of another. Thus, in situations where
80 invasive prey are consumed at a lesser rate than native prey, or are ignored completely, the
81 reduced predation pressure on invasive prey along with continuous removal of native
82 competitors is likely to exacerbate the invasion (Cuthbert et al. 2018a,b). Although this
83 concept appears elementary, there is a distinct lack of investigation into prey switching,
84 especially with regards to invasive species.

85 The Pacific oyster, *Crassostrea gigas*, is one of the most successful invertebrate
86 invaders worldwide (Ruesink 2007, Herbert et al. 2016) and has been documented to colonise
87 and flourish on beds of the native blue mussel, *Mytilus edulis* (e.g. Kochmann et al. 2008).
88 Beds of *M. edulis* that are invaded by *C. gigas* can experience a shift in the dominant
89 ecosystem engineer (Kochmann et al. 2008, Reise et al. 2017a) which may lead to
90 implications for the native community. Not only has oyster reef formation been suggested to
91 alter *M. edulis* population size structure by reducing predation on small mussels (van der Zee
92 et al. 2012), they can also negatively affect foraging in higher trophic levels (Markert et al.
93 2013). However, invasions by Pacific oysters have not led to catastrophic declines in native
94 species and complete dominance of benthos (Reise et al. 2017b) as has been the case with, for
95 example, zebra mussels in many freshwater ecosystems (Ricciardi et al. 1996, 1998). Thus,
96 we expect to find evidence that Pacific oysters suffer some degree of biotic resistance from
97 native species, particularly by predators such as crabs owing to their generalist feeding nature
98 (Walne & Davies 1977).

99 Blue mussels provide an important and abundant food resource for a range of
100 intertidal and subtidal predators including birds, sea stars, and crabs (Ebling et al. 1964;

101 Paine, 1974; Nehls et al., 1997). Throughout Europe, two of the main invertebrate predators
102 of *M. edulis* are the common sea star, *Asterias rubens*, and the European green crab, *Carcinus*
103 *maenas* (Dolmer, 1998; Murray et al., 2007). Seasonal swarming of *A. rubens* onto beds of
104 *M. edulis* has the potential to destroy local populations (Dare 1982) and *C. maenas* has been
105 found to have serious impacts on commercially valuable mussel beds (Murray et al., 2007).
106 Although the diets of *A. rubens* and *C. maenas* often contain mussels, they are considered
107 generalist predators (Miron et al., 2005). This generalist feeding nature suggests an ability to
108 switch between prey species, or show strong preferential feeding on some species, depending
109 on relative abundances available. Mascaró & Seed (2001) observed consumption of *C. gigas*
110 by *C. maenas* thus, these native predators may potentially exert some level of biotic
111 resistance toward *C. gigas*, which may reduce invasion success, but also reduce competitor
112 abundance, hence aiding invader success.

113 Here, we thus employ functional response and prey switching experiments to identify
114 density-dependent predation rates and prey switching/preference of predators towards both
115 invasive and native prey, in isolation and when presented simultaneously. Using two
116 dominant native predators, the common sea star, *Asterias rubens*, and the green crab,
117 *Carcinus maenas*, we aimed to investigate predation of the native blue mussel, *M. edulis*, and
118 the Pacific oyster, *C. gigas*, and the balance of predator driven biotic resistance or facilitation
119 of *C. gigas*.

120 **Methods**

121 *Animal collection and maintenance*

122 Common sea stars, *A. rubens*, were collected by hand from shallow waters in
123 Strangford Lough by snorkelling whilst green crabs, *C. maenas*, were collected using baited
124 crab pots from a rocky shore within 50 m of the sea star collection site (54° 23' 30" N, 05°
125 34' 29" W). Animals were maintained at Queen's Marine Laboratory, Portaferry in through-

126 flowing, sand filtered seawater ($13\text{ }^{\circ}\text{C} \pm 1\text{ }^{\circ}\text{C}$) pumped from the adjacent Strangford Lough.
127 Sea stars were fed whole mussels ($> 40\text{ mm}$ shell length) *ad libitum* and held in uncovered,
128 ~500 L tanks allowing natural light conditions for two weeks prior to feeding trials. All sea
129 stars were size matched for experimental use with maximum arm lengths measuring 70 – 90
130 mm. Green crabs were fed raw herring every two to three days and were held under similar
131 conditions to the sea stars for a minimum of one week prior to experiments. Male crabs were
132 selected to avoid confounding effects of sex and size matched with respect to carapace width
133 (60-70 mm) to minimise variations due to sex and size. Only individuals free of parasites and
134 with both claws intact were used in the experiments. Prior to feeding trials, both sea stars and
135 green crabs were starved for 48 hours to standardise hunger levels. Survivability of all
136 predators were monitored in the laboratory for at least one week after the experiments to
137 ensure all individuals were healthy at the time of feeding. Sea star and green crab
138 experiments were conducted in June 2018 and August 2018, respectively.

139 The prey, juvenile native blue mussels, *Mytilus edulis*, were collected by hand from a
140 local rocky shore ($54^{\circ} 28' 13''\text{ N}$, $05^{\circ} 32' 26''\text{ W}$), and juvenile invasive Pacific oysters,
141 *Crassostrea gigas*, were obtained commercially (Guernsey Sea Farms Ltd, Guernsey). Prey
142 were maintained under the same conditions as predators. Prey animals used in feeding trials
143 had shell lengths of 15 – 20.99 mm, a size which is most often consumed by crabs with
144 carapace widths used here (Mascaró & Seed, 2001) and to avoid any confounding effects of
145 prey size. Although *A. rubens* may prefer larger prey than offered here (Saier 2001) this is
146 likely driven by refuge provision. Dolmer (1998) however, observed no size selection of prey
147 by *A. rubens* when offered in isolation.

148 *Feeding trials*

149 Functional responses (FRs)

150 For sea stars, feeding trials were conducted in $36 \times 26 \times 18$ cm arenas filled with 15
151 litres of continuously aerated, sand filtered seawater pumped from the adjacent Strangford
152 Lough, to which the sea stars were previously acclimated. For the FRs, predators were
153 presented with either native mussel or invasive oyster prey at six densities (1, 2, 4, 8, 15 or
154 30; $n = 4$ per experimental group) which were added to each of the arenas five minutes before
155 the addition of a predator. Trials started at 09:00 and lasted 48 hours, after which predators
156 were removed and remaining live prey counted. Due to the number of sea stars ($n = 40$)
157 necessary for the experiment ($n = 48$ trials), individuals were reused until sufficient
158 replication was complete. Individuals were not exposed to the same treatment twice to avoid
159 pseudoreplication.

160 For green crabs, feeding trials were conducted in $56 \times 36 \times 23$ cm arenas covered
161 with plastic mesh (1 cm mesh size) to allow natural light to penetrate but prevent crabs from
162 escaping. Running sea water, pumped from the adjacent Strangford Lough, was delivered to
163 the arenas via hoses supplying water at a rate of $\sim 1.5 \text{ L min}^{-1}$. For the FRs, predators were
164 presented with either native mussel or invasive oyster prey at six densities (2, 4, 8, 16, 32 or
165 64; $n \geq 3$ per experimental group). Native mussels naturally attached to the base of the arena
166 with byssus threads and invasive oysters were adhered to the base of the arena with a small
167 amount of epoxy putty to simulate natural attachment. Attachment of prey to the bottom of
168 experimental arenas was necessary for feeding trials with green crabs to ensure prey were not
169 washed away or moved by the running water. Prey animals were added to each of the arenas
170 13 hours prior to the feeding period. For consistency, trials started at 09:00 and lasted 8
171 hours, after which predators were removed and the remaining live prey counted. For both
172 predators, controls to capture background mortality of prey included one replicate of each
173 experimental group in the absence of a predator.

174 Prey switching

175 Predators from FR experiments were reused for prey switching experiments after a
176 48-hour starvation period. Switching experiments were performed under the same conditions
177 as the FRs for each of the two predators. For both prey switching experiments, native mussels
178 and invasive oysters were added simultaneously in five different ratios (0:20, 5:15, 10:10,
179 15:5, 20:0; sea stars, $n \geq 7$ replicates per experimental group; green crabs, $n \geq 5$ replicates per
180 experimental group). Sea stars were allowed to feed for 24 hours with consumed prey being
181 replaced after 12 hours to maintain nominal prey ratios. Green crabs were allowed to feed for
182 two hours with consumed prey being replaced every 15 minutes to maintain nominal prey
183 ratios. For both predators, controls to capture background mortality of prey included one
184 replicate of each experimental group without a predator.

185 *Statistical analyses*

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

188 Functional responses

189 Overall prey consumption in FR experiments with respect to the factors 'prey species'
190 and 'prey density' for each predator type was compared using generalised linear models
191 assuming Poisson distributions and log links as counts were not overdispersed in relation to
192 degrees of freedom.

193 Functional response analysis was undertaken using the 'frair' package (Pritchard et al.
194 2017). Logistic regression considering the proportion of prey consumed as a function of
195 initial prey density was used to determine FR types. A type II FR is determined categorically
196 by a significantly negative first order term and a type III by a significantly positive first order
197 term followed by a significantly negative second order term. Akaike Information Criterion
198 (AIC) was applied to select FR models which minimised information loss. We fit flexible FR
199 models for non-replacement of prey (Real 1977, Barrios-O'Neill et al. 2016):

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

200 where N_e is the number of prey eaten, N_0 is the initial prey density, b is the search coefficient,
 201 q is the scaling component, h is the handling time, and T is the experimental time.
 202 Categorically, type II FRs are indicated when $q = 0$, and when $q > 0$ the FR becomes
 203 increasingly sigmoidal. Here, when type II FRs were indicated, q was fixed at 0 and when
 204 type III FRs were indicated, q was fixed at 1. The *Lambert W* function was implemented to fit
 205 the models to the data (Bolker 2008). Non-parametric bootstrapping ($n = 2000$) was used to
 206 produce 95 % confidence intervals (CIs) around the FR curves (Pritchard et al. 2017),
 207 enabling results to be considered at the population-level and thus differences to be inferred on
 208 the basis of CI overlaps.

209 Prey switching

210 In prey switching trials, prey ratios of 5:15, 10:10 and 15:5 were formally included in
 211 analyses to omit singularities in prey choice from analyses (0:20 and 20:0). Overall
 212 consumption was examined using generalised linear mixed effects models using the package
 213 ‘lme4’ (Bates et al. 2015), with ‘proportion available’ integrated as a between factor and
 214 ‘prey species’ as a within factor.

215 Chesson’s selectivity index was used to assess prey preference of sea stars and green
 216 crabs separately towards invasive oysters (Chesson 1978, 1983):

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

217 where r_i is the proportion of prey type i in the diet, p_i is the proportion of prey type i
 218 available, m is the number of prey types, r_j is the proportion of prey type j in the diet, p_j is the
 219 proportion of prey type j available. The value of α_i ranges from 0 to 1 with $\alpha_i > 0.5$ ($1/m$)
 220 inferring positive preference, $\alpha_i < 0.5$ inferring negative preference, and $\alpha_i = 0.5$ inferring no

221 preference for either prey type. Chesson's selectivity indices were transformed to reduce
 222 extremes (0s and 1s):

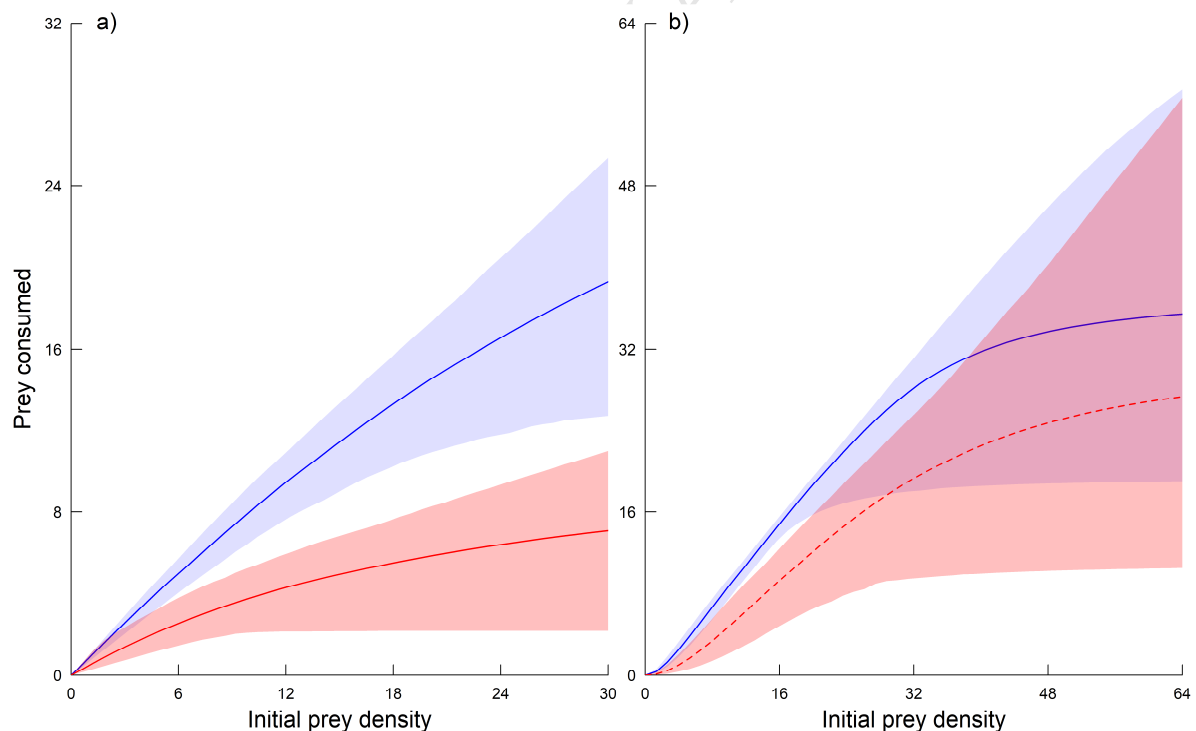
$$\alpha_t = \frac{\alpha_i(n-1) + 0.5}{n}$$

223 where α_t is the transformed output and n is the sample size. Beta regression was then used to
 224 compare observed α_t values towards invasive oysters with predicted values under no
 225 preference (i.e. 0.5) across proportions available separately for each predator type using the
 226 'betareg' package in R (Cribari-Neto & Zeileis 2010).

227 Results

228 Functional Responses

229 Prey survival in controls of both FR experiments was > 99 % thus indicating that prey
 230 were healthy and mortality in all experimental groups could be attributed to predation.



231 Figure 1. Functional responses of a) the common sea star, *Asterias rubens* and b) the green
 232 crab, *Carcinus maenas*, toward invasive oysters, *Crassostrea gigas* (red), and native mussels,
 233 *Mytilus edulis* (blue), with bootstrapped ($n = 2000$) 95 % CIs. Note difference in axes scales.
 234

235 For sea stars, overall, significantly more native mussels were consumed than invasive
236 oysters ($\chi^2 = 40.82$, $df = 1$, $p < 0.001$) and significantly more prey were consumed when
237 greater densities were supplied ($\chi^2 = 173.12$, $df = 5$, $p < 0.001$). A significant ‘prey species \times
238 prey density’ interaction ($\chi^2 = 27.13$, $df = 5$, $p < 0.001$) reflected greater consumptive
239 differences in favour of native mussels at higher prey densities (Fig. 1a).

240 Logistic regression revealed that sea stars exhibited type II FRs towards native
241 mussels and invasive oysters (Table 1). Sea stars exhibited a significantly higher FR towards
242 native mussels than towards invasive oysters, with CIs divergent across most prey densities
243 (Fig. 1a). The search coefficient, b , was higher toward native mussels than invasive oysters
244 (Table 1) and handling time, h , tended to be lower toward native mussels (Table 1).
245 Maximum feeding rates, $1/h$ (i.e. FR curve asymptote), were thus higher when consuming
246 native mussels as compared to invasive oysters (Table 1, Fig 1a).

247 Overall, green crabs consumed significantly more native mussels than invasive
248 oysters ($\chi^2 = 17.37$, $df = 1$, $p < 0.001$) and consumption increased under greater prey densities
249 ($\chi^2 = 463.34$, $df = 5$, $p < 0.01$). A significant ‘prey species \times prey density’ interaction ($\chi^2 =$
250 27.13 , $df = 5$, $p < 0.01$), reflected increased consumption of native mussels compared to
251 invasive oysters under low-intermediate prey densities which is mirrored in the FR (Fig. 1b).

252 For green crabs, results of logistic regression were equivocal between types II and III
253 (Table 1), however, AIC indicated the type III model was the best fit. Green crabs exhibited a
254 type III FR toward invasive oysters. Functional response CIs were divergent at low prey
255 densities but converged above densities of 20 (Fig. 1b). As with sea stars, the search
256 coefficient, b , was higher towards native mussels than invasive oysters (Table 1) and the
257 handling time, h , of native mussels was lower compared to invasive oysters (Table 1).
258 Maximum feeding rates, $1/h$, therefore tended to be higher towards native mussels (Table 1;
259 Fig. 1b).

260 Table 1. Results of logistic regression for both type II and type III models of the common sea
 261 star, *Asterias rubens*, and the green crab, *Carcinus maenas*, towards invasive oysters,
 262 *Crassostrea gigas*, and native mussels, *Mytilus edulis*, considering prey eaten as a function of
 263 prey density. Terms marked * indicate significant terms. Parameter estimates resulting from
 264 flexible FR models are shown.

	<i>Asterias rubens</i>		<i>Carcinus maenas</i>	
	<i>C. gigas</i>	<i>M. edulis</i>	<i>C. gigas</i>	<i>M. edulis</i>
Prey species				
Logistic regression				
Type II FR				
First term	-0.029	-0.041	-0.004	-0.036
<i>P</i> value	0.026*	0.006*	0.323	< 0.001*
Type III FR				
First term	-0.181	-0.104	0.070	0.122
<i>P</i> value	0.016*	0.265	0.002*	< 0.001*
Second term	0.004	0.002	-0.001	-0.002
<i>P</i> value	0.040*	0.489	< 0.001*	< 0.001*
Parameter estimates				
<i>b</i>	0.703	2.046	0.077	0.273
<i>h</i>	0.087	0.026	0.036	0.027
<i>q</i>	0	0	1	1
1/ <i>h</i>	11.494	38.760	30.769	37.175

265

266 Prey switching

267 In sea star switching trials, overall, consumption of native mussels was greater than
 268 invasive oysters ($\chi^2 = 10.55$, $df = 1$, $p < 0.01$), and prey proportions available did not
 269 significantly influence consumption ($\chi^2 = 5.53$, $df = 2$, $p > 0.05$). However, a significant ‘prey
 270 species \times proportion available’ interaction ($\chi^2 = 9.53$, $df = 2$, $p < 0.01$) reflected greater
 271 consumptive differences in favour of native mussels when under equal prey proportions with
 272 invasive oysters.

273 Chesson’s selectivity indices toward invasive oysters were found to be significantly
 274 lower than the null preference value of 0.5 ($\chi^2 = 22.29$, $df = 1$, $p < 0.001$), thus indicating
 275 positive preference for native mussels overall (Table 2, Fig 2). This effect was consistent

276 across all proportions as there was no significant ‘prey species × proportion available’
 277 interaction ($\chi^2 = 2.19$, $df = 2$, $p = 0.33$), reflecting a lack of prey switching and consistent
 278 disproportionate consumptive preference for native mussels over invasive oysters by sea stars
 279 (Fig 2).

280 Overall, green crabs consumed significantly more native mussels than invasive
 281 oysters ($\chi^2 = 10.48$, $df = 1$, $p < 0.001$). Consumption tended to be greater when prey were
 282 available in greater proportions, but this effect was not significant ($\chi^2 = 2.85$, $df = 2$, $p >$
 283 0.05). Consumption rates of each prey species were consistent across prey ratios as the ‘prey
 284 species × proportion available’ interaction was not significant ($\chi^2 = 5.69$, $df = 2$, $p > 0.05$).

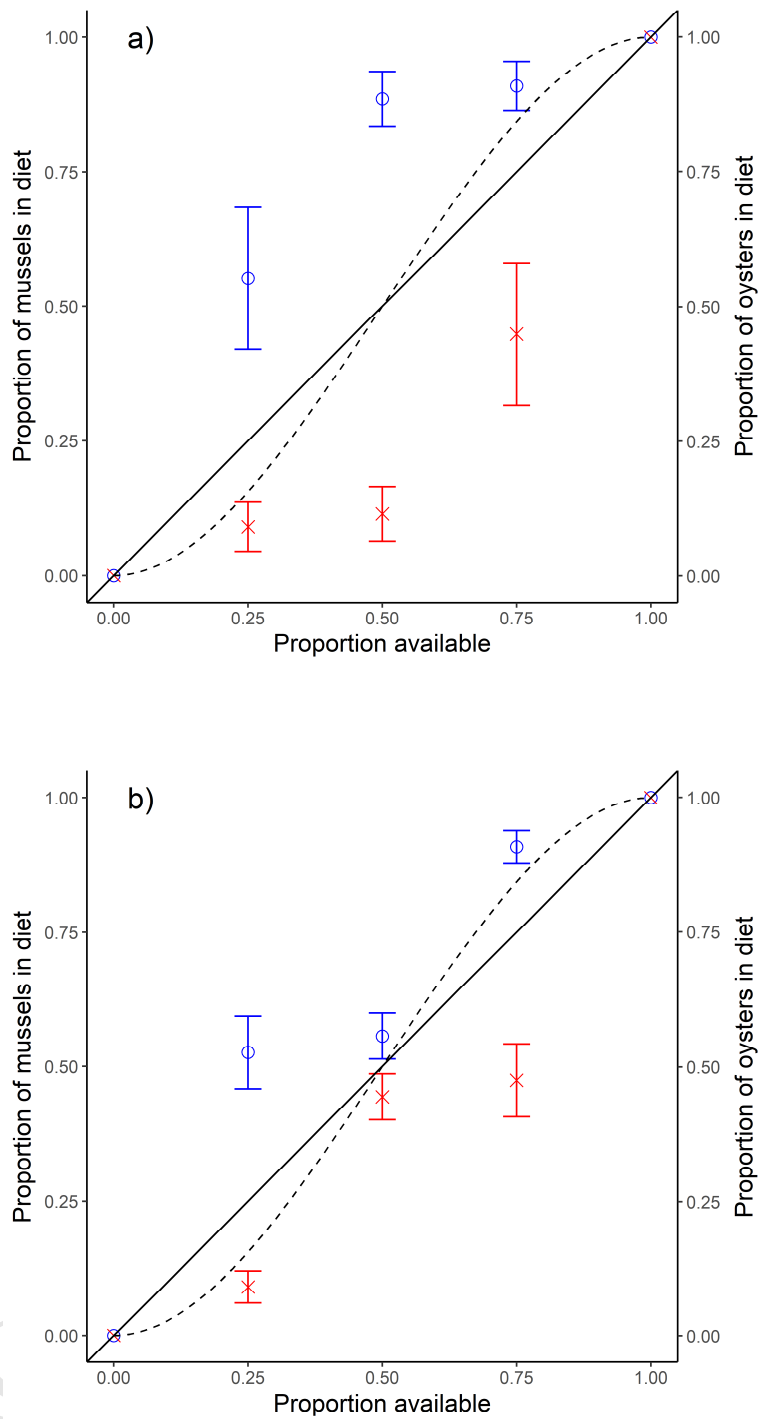
285

286 Table 2. Chesson’s selectivity indices ($\alpha_i \pm$ S.E.) for the common sea star, *Asterias rubens*,
 287 and the green crab, *Carcinus maenas*, toward invasive oysters, *Crassostrea gigas*, and native
 288 mussels, *Mytilus edulis*, at varying prey proportion availabilities. Selectivity indices above
 289 0.5 indicate positive preference whilst indices below 0.5 indicate negative preference of a
 290 prey type.

Predator:prey combination	Proportion available	Chesson $\alpha_i \pm$ S.E.
<i>Asterias rubens</i>		
<i>C. gigas</i>	0.25	0.19 ± 0.08
	0.50	0.11 ± 0.05
	0.75	0.32 ± 0.13
<i>M. edulis</i>	0.25	0.68 ± 0.13
	0.50	0.89 ± 0.05
	0.75	0.81 ± 0.08
<i>Carcinus maenas</i>		
<i>C. gigas</i>	0.25	0.22 ± 0.07
	0.50	0.44 ± 0.04
	0.75	0.24 ± 0.05
<i>M. edulis</i>	0.25	0.76 ± 0.05
	0.50	0.56 ± 0.04
	0.75	0.78 ± 0.07

291

292 Chesson's selectivity indices towards invasive oysters were, again, significantly lower
293 than the null preference values of 0.5 overall ($\chi^2 = 31.49$, $df = 1$, $p < 0.001$), thus indicating
294 positive preference of native mussels over invasive oysters by green crabs (Table 2; Fig. 2b).
295 A significant 'prey species \times proportion available' interaction ($\chi^2 = 12.26$, $df = 2$, $p < 0.01$)
296 reflected reduced preference of native mussels when available at proportions of 0.5, but a
297 lack of prey switching was evidenced overall given a disproportionate preference for native
298 mussels across all choices (Fig. 2).



299 Figure 2. Proportion of either *Crassostrea gigas* (red) or *Mytilus edulis* (blue) consumed
 300 (mean \pm S.E.) as a function of their respective proportional availability for a) the common sea
 301 star, *Asterias rubens*, and b) the green crab, *Carcinus maenas*. The solid line indicates
 302 expected values if no prey preference was to occur. The dashed line indicates a hypothetical
 303 prey switching pattern.

304 **Discussion**

305 With the rate of spread of invasive alien species (IAS) showing little sign of abating
306 (Seebens et al. 2018), invasion ecology needs effective methodologies for assessing and
307 predicting the success and impacts of established, emerging, and future IAS (Dick et al. 2017,
308 Cuthbert et al 2018b, Dickey et al. 2018). Functional responses (FRs) have shown excellent
309 utility in predicting the success and impacts of invasive predators (Dick et al. 2014, Bovy et
310 al. 2015, Xu et al. 2016, Laverly et al. 2017), yet few studies examine FRs toward invasive
311 prey (but see Twardochleb et al. 2012). While FRs have been shown to offer good predictive
312 ability of IAS impacts (Dick et al. 2017), the inclusion of prey switching experiments, with
313 more than one prey species provided simultaneously, could further enhance our knowledge
314 (Cuthbert et al. 2018b). This is because FRs in terms of type (i.e. shape of curve) and
315 magnitude (i.e. maximum feeding rates), plus switching (i.e. “frequency dependent
316 predation”), help quantify the population outcomes of consumer behaviour towards resources
317 (e.g. predator: prey, see Dick et al. 2014).

318 Pacific oysters have invaded ecosystems worldwide but have not had drastic impacts
319 or caused competitive exclusion of other bivalve species (Reise et al. 2017b). To quantify this
320 pattern of invasion we combined FR and prey switching experiments using two native
321 predators, the common sea star, *Asterias rubens*, and the green crab, *Carcinus maenas*,
322 toward the native blue mussel, *Mytilus edulis*, and invasive Pacific oyster, *Crassostrea gigas*.
323 *Asterias rubens* exhibited a higher-magnitude type II FR toward *M. edulis* compared to *C.*
324 *gigas*, while *C. maenas* showed type III FRs towards both prey species, with similar
325 maximum feeding rates between prey types but increased predation upon native *M. edulis*,
326 particularly at low densities. We also found that when prey were offered simultaneously, both
327 predators disproportionately consumed native *M. edulis* over invasive *C. gigas* prey, even

328 when *M. edulis* was rare in the environment, thus suggesting a lack of predator-driven biotic
329 resistance towards *C. gigas* invasion.

330 Although *A. rubens* exhibited destabilising type II FRs towards both prey species,
331 increased search efficiency and decreased handling times were shown toward native *M.*
332 *edulis* compared to invasive *C. gigas*. Consequently, our results indicate that *A. rubens* exerts
333 strong destabilising impacts toward native *M. edulis* due to high predation rates at low prey
334 densities and lower handling times which drive high maximum feeding rates (Dick et al.
335 2013), and reduced predation pressure upon invasive *C. gigas*. In particular, lower handling
336 times of *A. rubens* and *C. maenas* towards *M. edulis* compared to *C. gigas* prey suggests that
337 predators are quicker to open, consume, and digest the native prey, which may be a function
338 of shell morphology or thickness, even though shell length between prey species was
339 matched in experiments (Griffiths & Seiderer 1980).

340 Whilst green crabs displayed greater similarities in maximum feeding rates between
341 prey species, feeding rates were considerably higher towards the native prey. In contrast to
342 sea stars, green crabs displayed equivocal type II and type III FRs toward native *M. edulis*
343 and a more stabilising type III FR toward invasive *C. gigas*. Although unexpected due to the
344 experimental setup, where type II FRs tend to emerge when predators cannot “switch”, type
345 III FRs are likely to be encountered under natural conditions and have previously been found
346 toward mussel prey (Griffen & Delaney 2007). Type III FRs suggest the presence of a low
347 density refuge for prey, reducing the risk of predation when prey fall below a certain
348 threshold (Murdoch & Oaten 1975). The higher search efficiency which *C. maenas* displayed
349 toward native *M. edulis* suggests a greater predatory impact due to a higher rate of prey
350 consumption at low prey densities, which may be more destabilising for native mussel
351 populations at low densities.

352 For generalist predators such as *A. rubens* and *C. maenas*, invasive prey species may
353 provide a novel resource should they be recognised as prey. Ruesink (2007) found significant
354 predation upon *C. gigas* on rocky shores suggesting these ecosystems exert biotic resistance
355 toward the invasion. Here, although *A. rubens* were offered loose prey and *C. maenas* were
356 offered prey under more ‘realistic’ conditions whereby prey animals were attached to the
357 substratum, when native *M. edulis* and invasive *C. gigas* were provided simultaneously, we
358 found that neither predator showed evidence of prey switching behaviour. Native *M. edulis*
359 was disproportionately consumed by *A. rubens* across all prey species proportion
360 combinations, thus sea stars actively sought native *M. edulis* prey, even when availability was
361 low. Mascaró & Seed (2001) investigated prey choice of *C. maenas* towards several bivalve
362 species, however, the proportional availabilities of the prey species were not altered. Such
363 frequency dependent predation is often overlooked, yet is considered a major driver of
364 genetic, phenotypic, and species diversity (Clarke 1962, Greenwood & Elton 1979, Allen
365 1988, Whiteley et al. 1997). Species or polymorphs that are rare in the environment may be
366 disproportionately ignored by predators allowing their abundance to increase and *vice versa*,
367 thus substantially contributing to diversity changes. The lack of switching by both predators
368 indicates that even when occupying low proportions of prey availability, native *M. edulis* are
369 consumed at disproportionately high rates. Invasive *C. gigas* are consumed in low numbers
370 irrespective of availability, and are largely relieved from predation pressure, contrary to the
371 alternative prey hypothesis (Angelstam et al. 1984). This low level of predation suggests a
372 small amount of predator driven biotic resistance towards *C. gigas* which corroborates with
373 its limited ecological impacts (Reise et al. 2017b).

374 Naïveté due to lack of co-evolutionary history is a common concept in invasion
375 ecology however the concept is most often applied to native prey in response to invasive
376 predators (Cuthbert et al. 2018a). Also, it has also been shown that conditioning predators to

377 prey species can occur (Hall et al. 1982). The predators in this study, however, were collected
378 from a site where *M. edulis* is common whereas *C. gigas* is scarce. The feeding of *M. edulis*
379 to *A. rubens* prior to experimental trials is thus unlikely to have provided any extra
380 conditioning to their natural state. The predators here were thus faced with a novel prey
381 choice and the results provide insights into predation patterns at initial states of *C. gigas*
382 invasion. Although the preference for *M. edulis* over *C. gigas* appeared greater for *A. rubens*
383 compared to *C. maenas*, the lack of significant switching shown by both predators further
384 suggests native predator naïveté towards *C. gigas*, and that laboratory conditioning was
385 unlikely a driver of these results. The preference pattern observed may be because neither
386 predator recognises the novel chemical cue of *C. gigas* as potential prey. Certainly, prolonged
387 exposure of predators to *C. gigas* as an available prey source may alter these predation
388 patterns, however we show that biotic resistance to initial invasions is unlikely. Chemical
389 cues are understood to play several roles in predator-prey dynamics (Weissburg & Zimmer-
390 Faust 1994, Leonard et al. 1999, Griffiths & Richardson 2006) and are commonplace in the
391 aquatic environment. Invasive alien species have been shown to produce chemical cues
392 which may facilitate their invasion by inducing behavioural displacement of native species
393 (Raw et al., 2013). Further investigation into chemical detection of invasive prey by native
394 predators should be investigated as evolutionary experience and learning may increase
395 predation on invasive prey species in the future.

396 Although the mechanism as to why *C. gigas* consumption by predators is reduced in
397 this study needs further investigation, comparisons of predation towards trophically similar
398 native and invasive prey gives further insights into predator-driven biotic resistance towards
399 invasions. The disproportionate consumption of *M. edulis* over *C. gigas* may facilitate
400 invasions by reducing predation pressure on invasive *C. gigas* and removing potential
401 competitors for resources (i.e. space) from the system. If such patterns were to occur in the

402 field, then predation pressure may further increase towards *M. edulis* populations.
403 Conversely, it may be predicted that habitat complexity provided by adult *C. gigas* may
404 create structural refugia which could additionally alter consumption by predators (Grabowski
405 & Powers, 2004; Alexander et al., 2012; Bertolini et al., 2018) and lead to *M. edulis*
406 persistence after invasion (Reise et al. 2017b).

407 Of course, other life history traits also contribute to invasion success, such as the high
408 growth rates, or the high fecundity of invaders (Troost 2010). However, the results presented
409 here corroborate with field patterns of *C. gigas* invasion (e.g. Reise et al. 2017b), and further
410 inform patterns of invasion success potentially owing to the lack of biotic resistance shown
411 by native predators. In our FR experiments, green crabs consumed similar numbers of *M.*
412 *edulis* and *C. gigas* at high densities, suggesting they may exert some control over both
413 invasive and native populations. The preference for *M. edulis* over *C. gigas* in the prey
414 switching experiments further informs their interaction, whereby *M. edulis* is
415 disproportionately consumed whilst *C. gigas* is alleviated from predation pressure, inferring a
416 lack of predator-driven biotic resistance towards *C. gigas* invasion. Thus, we advocate the
417 combined use of functional responses and prey switching experiments to understand and
418 predict invader success, impacts on native populations, and strength of biotic resistance from
419 native communities.

420

421 **Author contributions**

422 P.W.S.J., J.W.E.D., L.T.K., & J.T.A.D. conceived the study. P.W.S.J. and J.W.E.D.
423 performed the experiments. P.W.S.J. and R.N.C. conducted statistical analysis. P.W.S.J.
424 wrote the first draft and all authors contributed to writing the final manuscript and gave
425 approval for publication.

426

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431

432 Conflict of interest

433 The authors declare that they have no conflict of interest

434

435 Data accessibility

436 Data will be made accessible from the Dryad Digital Repository on acceptance.

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Using functional responses and prey switching to quantify invasion success of the Pacific oyster, *Crassostrea gigas*

Patrick W.S. Joyce, James W.E. Dickey, Ross N. Cuthbert, Jaimie, T.A. Dick, Louise Kregting

- Functional responses and prey switching may predict invader success
- Predation by two predators towards native and invasive bivalve prey was quantified
- Both predators consumed native prey at a higher rate than invasive prey
- Predators disproportionately consumed native prey when prey occurred simultaneously
- Invasion success is mediated through differential levels of biotic resistance