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Impacts of mussel invasions on the prey preference of two native predators

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Running headline: Impact of invasion on prey preference

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1 **Lay summary**

2 Alien prey alter food choices available to native predators and when these prey are not selected
3 for consumption, their invasion may be facilitated. We show that even predators with a broad
4 diet may actively avoid alien prey and selectively feed on native species, despite alien prey
5 being more abundant and easier to consume. This lack of predation pressure combined with the
6 removal of competing native prey offers two sources of facilitation of prey invasions.

7

8 **Impacts of mussel invasions on the prey preference of two native predators**

9 Running headline: Impact of invasion on prey preference

10

11 **Abstract**

12 Biotic invasions can result in the displacement of native species. This can alter the availability
13 of native prey and the choices made by native predators. We investigated prey selection by two
14 native South African predators, the west coast rock lobster *Jasus lalandii* and the starfish
15 *Marthasterias africana* in response to the invasive mussels, *Mytilus galloprovincialis* and
16 *Semimytilus algosus*, and native mussels *Aulacomya atra* and *Choromytilus meridionalis*. As the
17 diets of lobsters and starfish are broad and have been suggested to reflect prey availability, we
18 hypothesized that they would consume the most abundant prey, regardless of its native or alien
19 status. Laboratory studies presented predators with varying proportions of native and invasive
20 mussels that represented pre- and post-invasion scenarios. Mussel parameters (shell strength,
21 adductor muscle size and energy content) that may be of importance in selection by predators
22 were compared among species. Both predators exhibited preference towards the native mussel
23 *C. meridionalis*, even when it was the least abundant prey. The selection of native species
24 occurred despite mussel parameters suggesting invasive species would be easier to consume.

25 These findings highlight the potential for facilitation of prey invasions, especially when
26 predators avoid alien prey and select for native comparators that may offer resistance to the
27 invasion through inter-specific competition. It is presently unclear how often such lack of
28 predator-driven biotic resistance acts in combination with indirect facilitation, but interrogating
29 the behaviors that drive such outcomes will advance our understanding of successful invasions.

30

31 **Keywords:** alien species impact, biotic resistance, *Mytilus galloprovincialis*, *Semimytilus*
32 *algosus*, species interactions

33 **INTRODUCTION**

34 Invasions by alien species are occurring globally at an ever increasing rate (Bumbeer and Moreira
35 2016), a trend that is expected to continue owing to the link between invasions and the expansion of
36 human trade and travel (Harding 2003; Occhipinti-Ambrogi 2007). With the ability to drive
37 biodiversity loss by bringing about changes in habitat (Crooks 1998) and community structure
38 (Grosholz 2002; Sadchatheeswaran et al. 2015), the introduction of alien species can also lead to
39 novel interactions between native and invasive organisms (Freeman and Byers 2006; Alexander et al.
40 2015a).

41

42 Novel interactions occurring between predators and prey (e.g. consumptive or trait-mediated
43 interactions (Werner and Peacor 2003; Jermacz and Kobak 2017)), are of particular importance in
44 biological invasions (Sih et al. 2010). However, there is often a focus on the role of invasive predators
45 and their effects on native prey (Carlsson et al. 2009), likely as a result of the impacts of invasive
46 predators being perceived as greater than those resulting from invasive prey (Salo et al. 2007). There
47 is, however, a growing awareness of the role that invasive prey species may have on native systems
48 (Carlsson et al. 2009). Invasive prey often establish in large numbers (Sousa et al. 2009), with the
49 potential to competitively displace native species (Sadchatheeswaran et al. 2015). They may
50 subsequently present a novel food source that, if in high enough abundance, can induce a predatory
51 switch in resource selection in native predators (Sousa et al. 2009). The invasion of round gobies
52 *Neogobius melanostomus* in Lake Erie (USA), for example, was suggested to influence a shift in the
53 prey preference of the native and endangered Lake Erie Water Snake *Nerodia sipedon insularum*, a
54 phenomenon that was attributed to the high abundance of this alien prey (King et al. 2006).

55

56 There are instances where such a switch by native predators towards the consumption of invasive prey
57 can invoke biotic resistance (García and Protogino 2005; Sousa et al. 2009; Carlsson et al. 2011;
58 Freestone et al. 2013). While this can act to limit the abundance and distribution of invasive prey
59 (MacNeil et al. 2013), such switches from feeding on a native resource to a novel, invasive species
60 might not occur readily or may not be possible. Indeed, native predators may fail entirely to recognize
61 novel invasive prey organisms as a new or additional food source (Robinson et al. 2015). Even in
62 cases where native predators recognize invasive prey as food, but do not consume it to the same
63 degree as native prey, it could have considerable implications. These can include freeing invasive
64 prey from the predatory pressure normally experienced in its native range and ultimately increasing
65 the probability of successful invasion, as per the enemy release hypothesis (Colautti et al. 2004). The
66 inability of native predators to switch their preferences towards a novel, abundant food source may
67 also result in decreased fitness (e.g. reduced body condition and growth) compared to co-occurring
68 predators that are able to feed extensively on novel prey (Carlsson et al. 2009). Moreover, predators
69 that avoid invasive prey and continue to consume native resources can, to some extent, facilitate
70 invasions of the alien species through the removal of native competitors (i.e. the preferred native prey
71 species) (Needles et al. 2015). Switching from familiar to novel prey items has been suggested to
72 occur in generalist predators (Jaworski et al. 2013). Although clear definitions of generalists vs
73 specialists are illusive (Futuyma and Moreno 1988; Vamosi et al. 2014), in the context of predators
74 generalists are most often categorized based on their consumption of various species of prey that often
75 display morphological differences (for example see Hughes and O'brien 2001; Finlay-Doney and
76 Walter 2012; Gianguzza et al. 2016). It is this characterization that we apply in this study.

77

78 Marine ecosystems, including estuaries and coastal regions, are considered among the most heavily
79 invaded on earth (Ruiz et al. 1999; Castorani and Hovel 2016), and marine invasive species constitute

80 a serious threat to these native systems. In South Africa there have been a number of prominent
81 marine invasions, and of particular importance has been the establishment of two alien mussels,
82 *Mytilus galloprovincialis* and *Semimytilus algosus* (Grant and Cherry 1985; de Greef et al. 2013).
83 *Mytilus galloprovincialis* has been present along the South African coastline for more than 30 years
84 (Grant and Cherry 1985) with a widespread west and south coast distribution (Robinson et al. 2005).
85 The more recently introduced *S. algosus* was first documented on the west coast in 2009 (de Greef et
86 al. 2013), and spread onto the south coast in ca. 2015. These invasions have occurred at the expense
87 of the native mussels *Aulacomya atra* and *Choromytilus meridionalis*, that have been displaced along
88 many stretches of coastline (Robinson et al. 2007; Sadchatheeswaran et al. 2015). Mussels represent
89 an important food source for various intertidal and subtidal native predators, including whelks, marine
90 birds, starfish and rock lobsters (Griffiths and Hockey 1987; Caro et al. 2008; Alexander et al. 2015a).
91 It has, therefore, been suggested that the large abundances of *M. galloprovincialis* and *S. algosus*
92 could represent a new food source for marine predators in the region (de Greef et al. 2013). Indeed,
93 the native predatory whelk *Trochia cingulata* has been shown to shift feeding towards invasive
94 mussel species *M. galloprovincialis* and morphologically similar *S. algosus* (Alexander et al. 2015b).
95 However, knowledge of the impacts of these mussel invasions on subtidal predators is lacking and,
96 given a recent range expansion of *S. algosus* onto the south coast, it has become important to
97 determine how subtidal predators in this extended range are responding to this novel prey.

98

99 Two subtidal predators that occur along the west and south coast are the west coast rock lobster *Jasus*
100 *lalandii* and the spiny starfish *Marthasterias africana* (formerly misidentified as the European species
101 *Marthasterias glacialis*) (Wright et al. 2016). Rock lobsters are considered to have an important role
102 in the structuring of subtidal communities through predation (Tegner and Levin 1983; Barkai and
103 Branch 1988a; Robles et al. 1990; Andrew and Macdiarmid 1991; Babcock et al. 1999; Mayfield et al.

104 2000a; Blamey and Branch 2012). While there is evidence of rock lobsters consuming the invasive
105 mussel *M. galloprovincialis*, at least under laboratory conditions (Nicastro et al. 2007), no studies
106 have considered if *S. algosus* has been incorporated into its diet and/or whether it's presence has an
107 effect on the selection of prey. Starfish are similarly considered important benthic predators that have
108 impact at a variety of scales, shaping populations and assemblages within their respective
109 communities (Verling et al. 2003; Himmelman et al. 2005). In South Africa, the native starfish *M.*
110 *africana* has been shown to exhibit a preference toward mussels (Penney and Griffiths 1984).
111 Although it is recognized that species in this genus are capable of exerting strong predation pressure
112 on prey populations (Verling et al. 2003), the majority of studies to date have focused on the
113 importance of predation on intertidal communities (Gaymer et al. 2004). Nonetheless, the impact of
114 starfish in subtidal communities is likely to be even greater in subtidal systems as the environmental
115 stressors characteristic of intertidal habitats (e.g. frequent aerial exposure) no longer play a role
116 (Gaymer et al. 2004). In previous studies, rock lobsters and starfish have been described as generalists
117 (Penney and Griffiths 1984; Mayfield et al. 2000a; Verling et al. 2003), based on their tendency to
118 feed on a large variety of prey (e.g. mussels, winkles, sea urchins, fish, limpets, whelks, barnacles,
119 algae, and sponges) (Penney and Griffiths 1984; Mayfield et al. 2000a; Mayfield and Branch 2000)),
120 with their diets often reflecting prey availability (Menge 1972; Penney and Griffiths 1984; Mayfield
121 et al. 2000b).

122

123 Against this background the aim of this study was (1) to determine the prey preference of *J. lalandii*
124 and *M. africana* when exposed simultaneously to native (*A. atra* and *C. meridionalis*) and invasive
125 (*M. galloprovincialis* and *S. algosus*) mussel prey in a laboratory setting, and (2) to examine how
126 these preferences might vary in a scenario where invasive prey species are most abundant. Based on
127 research conducted prior to the invasions of *M. galloprovincialis* and *S. algosus* (Branch 1978;

128 Griffiths and Seiderer 1980), it was hypothesized that *J. lalandii* and *M. africana* would select for the
129 native mussel *C. meridionalis*, but when offered higher proportions of invasive *M. galloprovincialis*
130 and *S. algosus*, both predators would select for the more abundant alien prey species. The results from
131 this study will offer insight into whether there is potential for biotic resistance against the ongoing
132 invasion of *S. algosus*, or whether these important subtidal predators avoid the invasive prey, a
133 situation that could subsequently facilitate further spread of *S. algosus*.

134

135 **METHODS**

136 **Specimen collection and maintenance**

137 The four mussel species used in this study were sampled from monospecific mussel beds along the
138 west coast of South Africa (between 33°49'S, 18°28'E and 34°02'S, 21°38'E). Starfish and rock
139 lobsters were collected from subtidal sites on the south coast and then used in trials in 2015 and 2016,
140 respectively. As *S. algosus* has only recently (ca. 2015) spread to the south coast, these sites were
141 selected as native predators along the south coast are not considered to have been exposed to this prey
142 for a substantial period of time. For all experiments, mussel size ranged between 20 – 30 mm. In rock
143 lobster trials, individuals with carapace lengths of 65 – 75 mm were used and in starfish trials,
144 individuals with arm lengths that ranged between 50 – 80 mm were used. These size ranges were
145 selected as previous work has established preferred prey size matching for both lobsters (Griffiths and
146 Seiderer 1980) and starfish (Penney and Griffiths 1984).

147

148 Upon collection, all specimens were returned to the laboratory at Stellenbosch University and
149 maintained in holding tanks with aerated artificial seawater at a salinity of 30 – 35 ppt. and at a
150 constant temperature of 15 °C. Water changes were carried out daily for predators, and twice daily for
151 mussels. Mussels were supplied with algal culture every two days prior to experiments. In order to

152 standardize hunger levels across all replicates, rock lobsters and starfish were starved for a period of
153 seven days prior to experiments. However, during trials starfish took longer to commence feeding (ca.
154 20 days), which could be an indication that starfish require a longer period of time to become
155 acclimatized to laboratory conditions, or that a longer starvation period might be needed as a result of
156 their comparatively slower feeding rates (Penney and Griffiths 1984).

157

158 **Feeding trials**

159 Feeding trials were conducted separately for individual lobsters and starfish. Lobster trials were
160 undertaken in tanks with bases measuring 40 x 27 cm and filled with 11L seawater whereas starfish
161 trials took place in circular tanks of 23 cm diameter filled with 5L seawater. Individual rock lobsters
162 and starfish were presented with one of three diet treatments consisting of the four mussel species
163 scattered haphazardly on the floor of the tank in varying proportions that represented different mussel
164 invasion scenarios (Table 1). ‘Pre-invasion’ and ‘Post-invasion’ diets provided reference to the
165 invasion of *S. algosus*, with the ‘Baseline’ diet simply consisting of equal proportions of all prey
166 species (Table 1). To account for potential differences driven by the sex of lobsters (Mayfield et al.
167 2000a), every diet treatment was replicated nine times each for males and females, with the exception
168 of the ‘Baseline’ diet where logistical constraints resulted in only eight replicates for males. Lobsters
169 respond rapidly to visual cues (Hirtle and Mann 1978) and, as such experiments were monitored only
170 once daily to avoid possible disturbances that could interfere with normal feeding behavior. Lobsters
171 that molted during the acclimatization period or during trials were not used in experiments.

172 Experiments with lobsters were run for a total of 10 days. In starfish trials, nine replicates of each of
173 the three diets were employed (Table 1). However, due to their comparatively slower feeding rate
174 (Penney and Griffiths 1984), starfish trials ran for a total of 40 days.

175

176 Monitoring of experiments for both predators consisted of the identification, removal and replacement
177 of consumed mussels in order to maintain constant proportions of the respective diets throughout
178 experiments. Controls for both the predator experiments were three replicates of each diet containing
179 mussels in the absence of any predator to confirm that mussel mortality during trials was attributable
180 to predation and not due to other confounding factors.

181

182 **Chesson selectivity index**

183 The Chesson selectivity index was used in order to assess the prey preference of lobsters and starfish
184 towards the mussel species across the three diets (Chesson 1978). Selection toward particular species
185 of prey was determined through the equation:

186

$$187 \alpha_i = \frac{(r_i/p_i)}{\sum_i(r_i/p_i)}; i = 1, \dots, n$$

188

189 where r_i is the percentage of a particular species in the diet (consumed), p_i the percentage of that same
190 particular species in the overall habitat (on offer) and n the total number of mussel species in the
191 overall habitat (on offer). When $\alpha = 1/n$ the absence of selective predation is indicated, whereas $\alpha <$
192 $1/n$ infers negative selection (avoidance) and $\alpha > 1/n$ infers positive selection (preference). The use of
193 this particular selectivity index is justified as it takes into account the presence of other prey items,
194 thus incorporating the presence of multiple species (and in varying proportions) that are present in the
195 overall habitat of the predator.

196

197 Assessments of prey preference indices for both rock lobsters and starfish were undertaken with
198 repeated measures ANOVAs. For lobsters, 'diet' and 'sex' were employed as between factors, and
199 index for each mussel species as a within factor. For starfish, 'diet' was designated a between factor

200 and index for each mussel species as a within factor. Data were arcsine transformed prior to statistical
201 analyses. All analyses were carried out in SPSS (Version 24.0).

202

203 **Mussel morphology and energetic content**

204 To investigate some of the underlying factors that could explain prey preference, several
205 characteristics of the prey species were assessed. These included among species differences in (1)
206 shell strength that can mechanically limit the ability of lobsters to crush mussels (Juanes 1992), (2)
207 adductor muscle size that may influence opening of mussels by starfish (Reimer and Harms-Ringdahl
208 2001), and (3) energetic content that may make particular species more sought after by predators
209 (Creswell and McLay 1990). Ten individuals of each mussel species from the size class utilized
210 during the feeding experiments were used to compare morphometric characteristics and total energy
211 and were collected from the same sites as those used in the feeding trials.

212

213 Shell strength was measured using a Zwick 1484 universal tensile tester and pressure was applied at a
214 rate of $2 \text{ mm}\cdot\text{s}^{-1}$. Shells were separated and the point of fracture was established for both valves, the
215 average of which was used as a representation of individual mussel shell strength (Mackenzie et al.
216 2014). All shells were orientated in the same way during testing i.e. the shell length along the
217 horizontal axis of the instrument with the outer shell facing upwards. The size of adductor muscles
218 was determined by weight (Reimer and Tedengren 1997). After collection, posterior adductor muscles
219 were separated from the rest of the flesh and dried to a constant weight at $60 \text{ }^\circ\text{C}$, after which they
220 were weighed to the nearest 0.01 mg. Energetic content (kJ/individual) was determined by the
221 equation: mean kJ/g x dry flesh weight (g). This was determined by removing the flesh from mussels
222 and drying samples to a constant mass at $60 \text{ }^\circ\text{C}$ to gain the dry flesh weight for each individual.
223 Samples were then ground into powder form and the energy content (kJ/g) was determined by bomb

224 calorimetry. This measure was then used to determine the energetic content per individual. Both
225 morphometric characteristics and energetic content were compared among mussel species using a
226 one-way ANOVA followed by Tukey's HSD test.

227

228 **RESULTS**

229 Control experiments without predators had 100% mussel survival. Therefore, mussel mortality in
230 feeding trials with lobsters and starfish was considered to be as a result of predation.

231

232 **Rock lobsters**

233 No significant differences in mussel consumption were detected between male and female lobsters in
234 the 'Baseline' diet ($F_{3,45} = 3.45$, $P = 0.061$), 'Pre-invasion' diet ($F_{2,32} = 1.424$, $P = 0.256$), or the
235 'Post-invasion' diet ($F_{3,48} = 0.288$, $P = 0.834$). Repeated measures ANOVAs considering the Chesson
236 selectivity indices for all respective mussel species revealed that there was a significant main effect of
237 mussel species ($F_{3,150} = 16.574$, $P < 0.001$, Fig. 1a). This was driven by stronger selection for the
238 native mussel *C. meridionalis*, as revealed through post hoc pairwise comparisons, where Chesson
239 selectivity indices for *C. meridionalis* compared to other species were significantly different ($P <$
240 0.001) in all cases. There was no significant effect of 'diet' ($F_{2,50} = 1.969$, $P = 0.15$), and the 'diet' x
241 'prey' interaction was also non-significant ($F_{6,150} = 1.005$, $P = 0.42$). It was notable that rock lobsters
242 consumed all the flesh of mussels that they opened, suggesting that acceptance or rejection of prey
243 was decided before consumption began.

244

245 **Starfish**

246 Repeated measures ANOVAs assessing the Chesson indices revealed a significant main effect of prey
247 species ($F_{3,15} = 11.323$, $P < 0.001$, Fig. 1b). Post-hoc pairwise comparisons revealed that this was

248 driven by a significantly greater selection of the native mussel *C. meridionalis* compared to the other
249 mussel species ($P < 0.001$ in all cases). Similarly to lobsters, starfish consumed all mussels that they
250 opened.

251

252 **Mussel morphology and energetic content**

253 Shell strength was found to vary among mussel species ($F_3 = 179.580$, $P < 0.001$) with the native
254 mussel *A. atra* demonstrating the highest mean shell breaking force ($252.7N \pm 36.04$ SD) (Fig. 2a).
255 No difference in shell strength was found between *M. galloprovincialis* ($174.7N \pm 16.19$) and *C.*
256 *meridionalis* ($161.1N \pm 5.45$), while the emerging alien *S. algosus* had the weakest shells ($41.2N \pm$
257 10.46). The size of adductor muscles also varied among species ($F_3 = 121.465$, $P < 0.001$) and was
258 driven by *A. atra* having significantly larger muscles than all other species (Fig. 2b). There was a
259 significant difference in energy offered by the four mussel species ($F_3 = 13.92$, $P < 0.001$). Notably,
260 the mean energy content of *S. algosus* individuals ($10, 5$ kJ ± 0.3 SE) was significantly greater than
261 both native species *A. atra* (8.8 kJ ± 0.5) and *C. meridionalis* ($6, 6$ kJ ± 0.38) (Fig. 2c), while the
262 preferred native species *C. meridionalis* had the lowest energy, differing significantly from all species
263 except *M. galloprovincialis* (Fig. 2c).

264

265 **DISCUSSION**

266 Invasions by alien species can result in the displacement of native species (Crooks 2002; Shinen et al.
267 2009), leading to dramatic changes in the availability of native prey as a resource for predators
268 (Carlsson et al. 2009). Native predators that are able to switch from feeding on native prey to novel
269 invasive prey may unlock an abundant new food source (Barber et al. 2008). However, there is also
270 the possibility that predators may avoid novel invasive prey due to unfamiliarity, and may continue to
271 select and consume native species, despite a potentially greater availability of the novel resource

272 (Carlsson et al. 2009; Robinson et al. 2015). This study investigated this phenomenon with regards to
273 two native South African subtidal predators, the west coast rock lobster and the spiny starfish, and
274 their selection preferences towards native and invasive mussel prey. Both of these predators
275 demonstrated preference for the same native mussel *Choromytilus meridionalis*, even in diet
276 treatments where proportions of the invasive mussels, *Mytilus galloprovincialis* and *Semimytilus*
277 *algosus*, were dominant. These results suggest avoidance of novel prey in both these important
278 consumers, despite them being generalist predators that can be expected to easily incorporate novel
279 prey into their diets (Rodriquez et al. 2006; Carlsson et al. 2009).

280

281 The avoidance of both the invasive mussel species by native lobsters and starfish was unexpected.
282 While the avoidance of *S. algosus* by native predators could most easily be explained by
283 unfamiliarity, the avoidance of *M. galloprovincialis* was surprising given the long time period this
284 invasive mussel has been present on the South African coastline (Grant and Cherry 1985). However,
285 fieldwork conducted in the same area after the completion of the present study revealed that, despite
286 the intertidal dominance of *M. galloprovincialis* (Robinson et al. 2005), this species was virtually
287 absent from subtidal sites from which predators were collected (Skein, unpublished data). In fact, *M.*
288 *galloprovincialis* was recorded from only one site during extensive subtidal surveys representing less
289 than 4% of mussels present. This suggests that despite the well-established presence of this invader in
290 intertidal habitats, subtidal predators may in fact not have encountered it and may consequently be
291 unfamiliar with feeding on this prey.

292

293 Nonetheless, to confirm that avoidance of the invasive mussels by lobsters and starfish was in fact the
294 result of unfamiliarity, it is important to consider other factors that may affect prey choice by
295 predators. In this study, comparisons of shell strength revealed that the invasive mussels *M.*

296 *galloprovincialis* and *S. algosus* do not have stronger shells than the native mussel species. In fact, *S.*
297 *algosus* had the weakest shells of all four species but was still not selected for by lobsters, despite
298 them crushing mussel shells to access their prey. Starfish utilize a different approach to handling prey
299 and pry open mussel prey. However, the avoidance of the invasive mussels by these predators could
300 not be explained by adductor muscle strength, as the invasive mussels did not have larger adductor
301 muscles than the native mussels. It is interesting to note that the avoidance of the native *Aulacomya*
302 *atra* by lobsters is likely reflective of its strong ribbed shell. Previous comparative studies of the
303 native mussels *A. atra* and *C. meridionalis* have illustrated that a larger force is required by rock
304 lobsters to crush and detach *A. atra* than *C. meridionalis* of equal lengths (Griffiths and Seiderer
305 1980), and this, coupled with a high level of unfamiliarity towards the invasive mussels, is a potential
306 mechanism behind the preference toward *C. meridionalis* observed in this study. Similarly, the
307 selection for *C. meridionalis* by starfish likely relates to the larger adductor muscles of *A. atra* which
308 together with avoidance of *M. galloprovincialis* and *S. algosus* drives the choice for *C. meridionalis*.

309

310 A primary driver of prey choice is the ability of predators to handle prey and effectively access the
311 energetic reward they offer (Hughes and Dunkin 1984). In this case, *C. meridionalis* in fact offers the
312 lowest reward in terms of energetic content, a finding that aligns with a previous intertidal study that
313 compared *C. meridionalis*, *A. atra* and *M. galloprovincialis* (van Erkom Schurink and Griffiths 1991).
314 This indicates that energetic gain did not govern the predator's selection of prey. It was notable that
315 acceptance or rejection of prey by both predators took place before mussels were opened. This,
316 together with findings on shell strength, adductor muscle size and energetic content suggests that prey
317 choices by these predators may reflect one of two scenarios; (1) unfamiliarity with the alien mussels
318 or (2) prey choice may not be governed by the traditional optimal foraging theory framework that
319 assumes prey is selected in a way that maximizes energetic gain. Recent research suggests that some

320 predators might not forage to optimize net energetic gain, but rather manage the intake and balance of
321 macronutrients (Machovsky-Capuska et al. 2016a). It has been suggested that various fitness-related
322 aspects (e.g. egg production (Jensen et al. 2012), longevity (Lee et al. 2008), immunity (Le Couteur et
323 al. 2014)) are linked to the ability of predators to actively select for particular nutrients while
324 foraging. In order to determine whether the predators studied here are foraging in this way, would
325 require additional studies that consider the nutritional composition of different prey species. However,
326 it is unlikely that taxonomically different organisms such as rock lobsters and starfish have the same
327 nutritional requirements, given the large differences in their physiology and life histories. As such, the
328 selection and avoidance of the similar prey species by both predators is likely explained by
329 unfamiliarity of avoided prey rather than by prey nutritional composition. As *S. algosus* is thought to
330 only recently have invaded the south coast, we suggest that the most likely explanation for our results
331 is unfamiliarity. However, if this species did invade earlier, it is possible that subtidal predators might
332 have had previous exposure to this prey and drivers of prey selection that were not considered in this
333 study may be at play.

334

335 Positive selection towards *C. meridionalis* occurred across all diet treatments, even when proportions
336 of other species were greater. This was an unexpected finding given the broad diets of the predators in
337 the study (Barkai and Branch 1988a, b; Edgar 1990; Mayfield and Branch 2000; Mayfield et al.
338 2000a) and discounted our *a priori* hypotheses. It has been suggested that generalist predators, such as
339 rock lobsters and starfish, switch to alternative prey as the density of their main prey declines (Reif et
340 al. 2001; Kjellander and Nordström 2003). According to the alternative prey hypothesis (Angelstam et
341 al. 1984), the predation pressure on such an alternative should increase as the density of the most
342 selected prey decreases (Pöysä et al. 2016). The results of this study demonstrate, however, that both
343 predators continue to select *C. meridionalis* even in instances when it is the least abundant prey

344 species. If this was to occur in the field, then predatory forces may contribute to increased pressure on
345 populations of this species. The positive selection towards *C. meridionalis* demonstrated by both rock
346 lobsters and starfish may in fact facilitate the continued invasion of the non-native mussel species. By
347 increasing the availability of primary rock space through predation of native competitors, these
348 predators might be removing potential barriers for further invasive spread (Needles et al. 2015) . The
349 fact that *S. algosus* has spread more than 350 km along the open coast in just eight years (Robinson,
350 unpublished data) may well be reflective of such facilitation.

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354 This does not present the first observation of native predators failing to select for invasive prey (e.g.
355 López et al. 2010; Veiga et al. 2011). However, in other cases, the avoided invasive prey were
356 suggested to possess physical characteristics that might hinder predation from native predators. In
357 contrast this study found that alien prey were unlikely to offer predators such constraints.

358 Additionally, we demonstrate that two important native predators, select for native over invasive
359 mussel prey species despite the fact that they were offered in reduced proportions. In the broader
360 context, these findings highlight that predator-driven biotic resistance may not manifest, even in the
361 context of generalist predators. Importantly, when such prey avoidance coincides with selection of
362 native prey that may have offered invasion resistance through inter-specific competition, native
363 predators may indirectly facilitate invasions. While it is presently unclear how often such facilitation
364 acts, interrogating the behaviors that drive such outcomes will advance our understanding of
365 successful invasions.

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544 **FIGURE LEGENDS**

545 **Figure 1:** Chesson selectivity indices (\pm SE) for four mussel species as offered in the three 'diet'
546 treatments to (a) rock lobsters *Jasus lalandii* (males and females grouped) and (b) starfish
547 *Marthasterias africana*. For 'Baseline' and 'Post-invasion' diets, values above solid line = positive
548 selection. For 'Pre-invasion' diet, values above dashed line = positive selection. Values below lines
549 are indicative of avoidance and values on lines of neutral selection. Empty bars = native species; filled
550 bars = invasive species.

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552 **Figure 2:** Mean (\pm SD) (a) shell strength, (b) adductor muscle weight and (c) energetic content (\pm SE)
553 of the native mussels *Aulacomya atra* and *Choromytilus meridionalis* (empty bars) and the invasive
554 mussels *Mytilus galloprovincialis* and *Semimytilus algosus* (filled bars). Bars not sharing common
555 letters are significantly different (Tukey's HSD test, $P < 0.05$).

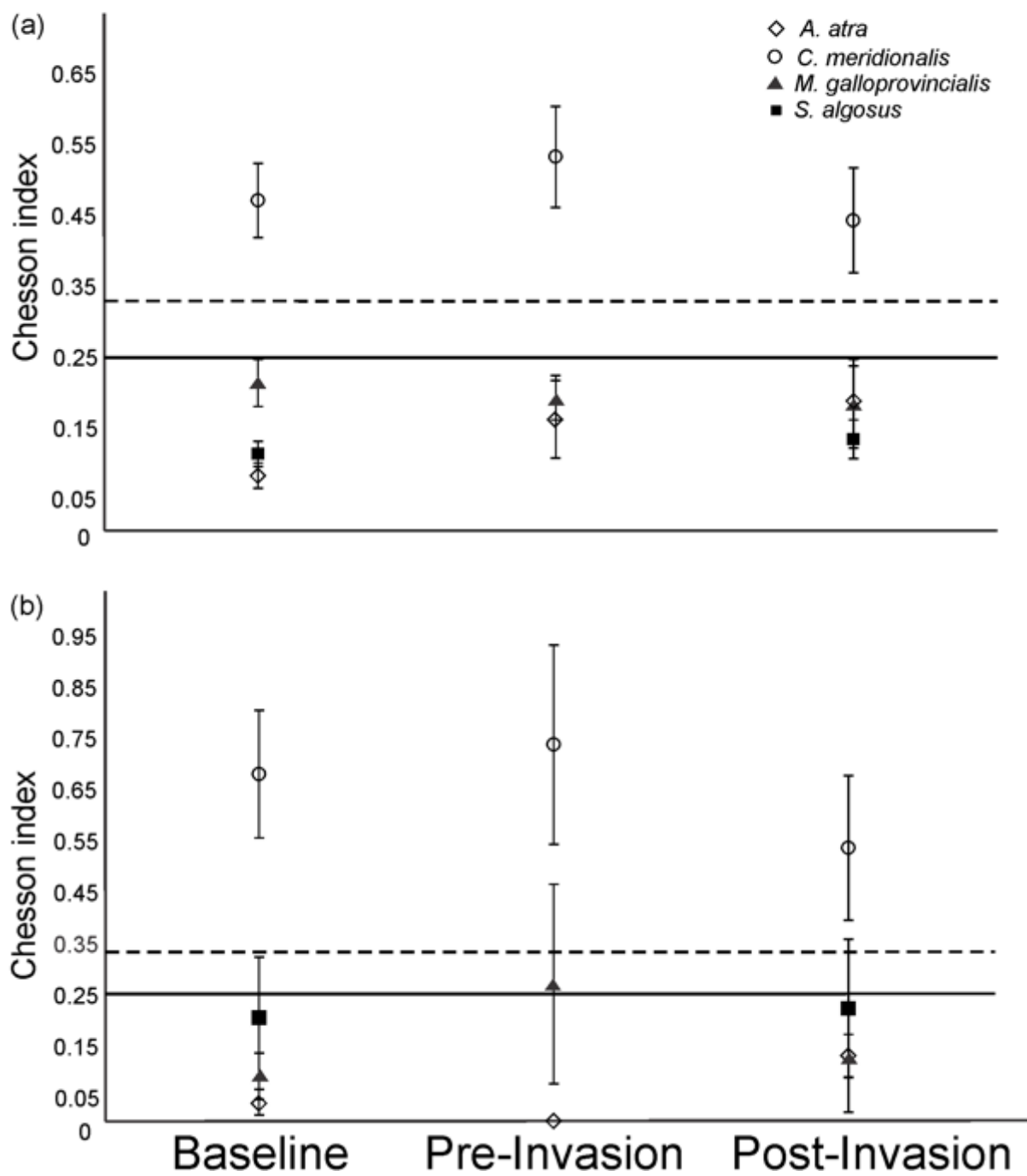
556 **TABLES AND TABLE LEGEDNS**

557 **Table 1:** Diet treatments offered to rock lobsters and starfish, with 'Pre-invasion' and 'Post-invasion'
 558 diets reflecting the more recent invasion of the mussel *S. algosus*. The numbers in the table reflect the
 559 number of mussels offered per species per diet.

Mussel Composition

Diet	<i>A. atra</i> (native)	<i>C. meridionalis</i> (native)	<i>M. galloprovincialis</i> (invasive)	<i>S. algosus</i> (invasive)
Baseline	6	6	6	6
Pre-invasion	6	6	12	0
Post-invasion	3	3	9	9

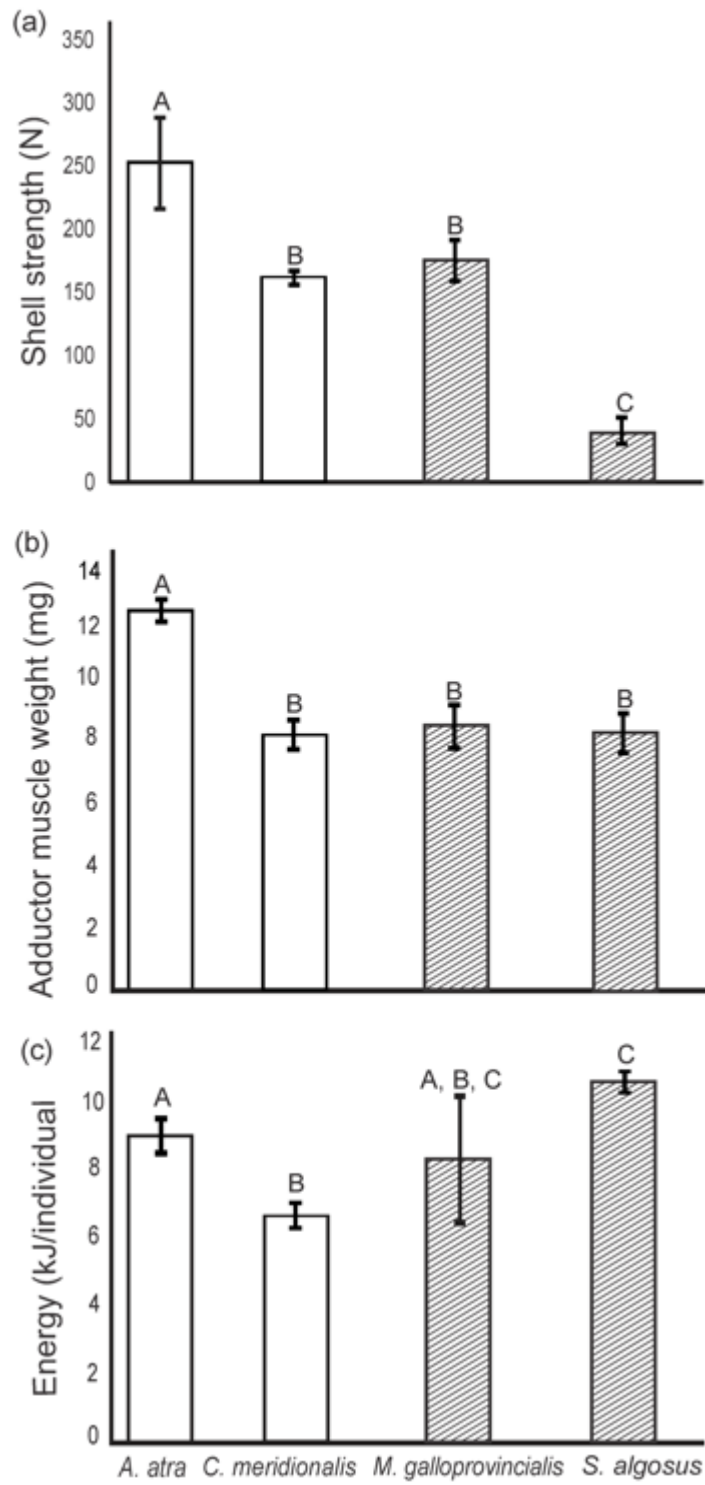
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579 **Figure 1.**



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581 **Figure 2.**

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