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1 Rapid learning in a native predator shifts diet preferences towards invasive prey

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32 **Abstract**

33

34 Biological invasions often exert negative impacts on native communities and can disrupt
35 a range of biotic interactions such as those between predators and prey. For example,
36 when invasive species alter the foraging landscape, native predators can fail to
37 recognise them as profitable prey because of unfamiliarity. This study therefore
38 investigated whether a native predator (rock lobster *Jasus lalandii*) can develop a new
39 preference for an invasive prey (mussel *Semimytilus patagonicus*) following conditioning
40 through a short-term exposure. Conditioned lobsters, exposed to only *S. patagonicus*
41 for a month, demonstrated a significant change in preference for the novel invasive
42 prey, which was found to contrast with non-conditioned lobsters that continued to show
43 predator preferences toward a native mussel (*Choromytilus meridionalis*). There is
44 therefore potential for native predators such as *J. lalandii* to adapt and switch towards
45 feeding on an abundant invasive prey, even if they avoid it at first. This indicates that
46 rapid learning can occur in a species exposed to novel food resources and
47 demonstrates that native species can adapt to biological invasions.

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50 **Keywords**

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52 Rapid learning, biological invasions, invertebrate predator, prey choice

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63 Introduction

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65 Invasions by non-native species can exert negative impacts on a range of biotic
66 interactions [1], including disruption to predator-prey relationships [2]. However, whilst
67 the effects of non-native predators on native prey communities have been well
68 documented (e.g. [3–5]), the impacts of non-native prey on native predators are
69 comparatively understudied. Invasive prey species may displace competitively inferior
70 native prey, subsequently altering the native predator prey-base [6]. This can in turn
71 present native predators with several challenges, including the physical handling of
72 morphologically unusual prey [7] or overcoming toxic defence mechanisms of some
73 non-native species [8].

74

75 The ability of a predator to switch from familiar to novel prey is important in the context
76 of efficient resource utilisation [9,10], and ‘conditioning’ (i.e. continuous exposure)
77 towards new prey is a mechanism through which this can occur. Such adaptive learning
78 is thought to occur more frequently in generalist predators compared to specialists,
79 which often have fine-tuned adaptations to handle fewer, more specific prey types [11].
80 Various factors have been proposed to influence conditioning, including past feeding
81 experience [12,13], frequency of prey encounters [14] and predator handling capabilities
82 [11]. This concept of learning by native predators has often been investigated in relation
83 to novel *toxic* prey [15–17], however as an adaptive response to invasions by *non-toxic*
84 prey, it has received less research attention.

85

86 In South Africa, the west coast rock lobster *Jasus lalandii* is an important subtidal
87 generalist predator with a preference for mussel prey [18,19]. However, the mussel
88 prey-base for this species is beginning to change due to the invasion by *Semimytilus*
89 *patagonicus* (formerly *S. algosus*), which is beginning to form a significant part of the
90 subtidal mussel community that comprised the native species *Choromytilus meridionalis*
91 and *Aulacomya atra* [20]. Previous work conducted in this region has shown that *J.*
92 *lalandii* avoids *S. patagonicus*, preferring to select native *C. meridionalis* [21]. In
93 comparison to native mussels, the invasive species offers the greatest energetic reward

94 and has the weakest shells, making it a profitable prey choice for most mussel
95 predators [21]. Therefore, it is suggested avoidance occurs because of unfamiliarity with
96 the novel species, which many south coast rock lobster populations have yet to
97 encounter.

98
99 The aim of this research was thus to determine whether the avoidance of *S.*
100 *patagonicus* by the rock lobster *J. lalandii* can be overcome through continuous
101 exposure (i.e. conditioning) to this invasive prey. As *J. lalandii* is a predator with a
102 flexible diet and invasive *S. patagonicus* is currently the most profitable mussel prey, it
103 was predicted that rock lobsters would switch from feeding on less profitable native
104 mussels to *S. patagonicus* once they become familiar with this species.

105
106

107 **Methods**

108
109 Mussels (*C. meridionalis*, *A. atra* and *S. patagonicus*) and rock lobsters *J. lalandii* of a
110 standardised length were collected from the wild to be used in predation trials (see
111 electronic supplementary information for details on collection sites and sizes of animals
112 used).

113
114

115 Phase 1: Predator conditioning

116
117 During a conditioning period, individual rock lobsters (n=20) were exposed to *S.*
118 *patagonicus* prey only. This was conducted in individual cages (0.045 m³ in volume)
119 situated in the field (see electronic supplementary information) to ensure that rock
120 lobsters were exposed to *S. patagonicus* in the presence of naturally occurring cues. An
121 initial seven-day starvation period was conducted to allow for acclimatisation and to
122 standardise rock lobster hunger level. This was followed by four weeks of conditioning
123 where *J. lalandii* were fed with *S. patagonicus* in crushed and whole forms. The total
124 number of mussels (n = 40) provided to each lobster per week was kept constant

125 throughout conditioning. The ratio of crushed to whole mussels was however
126 progressively adjusted as rock lobsters became more familiar with this prey species,
127 with only whole mussels offered in the final week (electronic supplementary information,
128 Table S1).

129

130

131 Phase 2: Determining the influence of conditioning on prey preference

132

133 To determine whether conditioning induced a switch in preference from *C. meridionalis*
134 to *S. patagonicus*, mussel selection from conditioned lobsters (Phase 1) was compared
135 to that of non-conditioned individuals from the same population. The prey preference of
136 conditioned and non-conditioned *J. lalandii* (n=20 per treatment) took place in the
137 laboratory (see electronic supplementary information). Feeding trials lasted seven days
138 after a seven-day acclimatisation and starvation period. Rock lobsters were provided
139 with one of two diet treatments which was either a 'current diet' or 'future diet' (n=10 per
140 diet for conditioned and non-conditioned lobsters). Diets comprised different proportions
141 of the three subtidal mussel species of interest reflecting their current and projected
142 occurrence in the field (Table 1; [20]). Mussel consumption was tracked daily, and
143 availability was kept constant throughout the trials.

144

145

146 Statistical analyses

147

148 All statistical analyses were conducted in R version 3.1.1 (R Core Team, 2016). The
149 difference in overall prey consumption between non-conditioned and conditioned
150 lobsters was analysed using a generalised linear model (GLM) with a quasi-Poisson
151 error distribution and log link. Chesson selectivity indices [22] were calculated for each
152 prey species (native *C. meridionalis* and *A. atra* and invasive *S. patagonicus*) through
153 the formula:

154

155

$$\alpha_i = \frac{(r_i/p_i)}{\Sigma(r_j/p_j)} ; j = 1, \dots, n$$

156 where r_i/p_j is the proportion of a particular species in the diet (consumed), p_i/p_j the
157 proportion of that species present in the overall habitat (on offer) and n the total number
158 of prey species in the overall habitat (on offer). When $\alpha = 1/n$ neutral selection/the
159 absence of selective predation in rock lobsters is indicated, whereas $\alpha < 1/n$ infers
160 negative selection (avoidance) and $\alpha > 1/n$ positive selection (preference). This
161 selectivity index is appropriate in this case as it accounts for the presence and
162 proportion(s) of multiple species in the feeding landscape.

163 Chesson selectivity indices for different mussel prey species in each diet treatment for
164 both conditioned and non-conditioned lobsters were first arcsine transformed due to
165 their proportional nature and then assessed using Friedman's ANOVAs. This was
166 followed by Conover post hoc tests to detect differences between Chesson selectivity
167 indices of prey species within each diet treatment. To establish whether conditioning
168 altered selection of a particular prey species, the Chesson selectivity indices of each
169 prey species as selected by conditioned and non-conditioned lobsters in each diet
170 treatment were compared using t-tests with a Bonferroni correction to account for
171 multiple comparisons.

172

173

174 **Results**

175

176 There was no statistical difference in the overall consumption of prey between non-
177 conditioned and conditioned lobsters (GLM: $F_{1,27} = 0.411$, $p = 0.53$). There was however
178 a significant difference in the selection of mussel species by non-conditioned *J. lalandii*
179 in both diet treatments (current diet: $\chi^2_{2} = 7.153$, $p = 0.027$, Fig. 1a; future diet: $\chi^2_{2} =$
180 7.517 , $p = 0.023$, Fig. 1b). Here, lobsters showed a positive selection towards the native
181 mussel *C. meridionalis* regardless of the proportions in which it was present in the
182 overall diet. However, this selection was not found to statistically differ from the novel
183 prey, *S. patagonicus*, in the current diet (Fig. 1a). Prey selection by conditioned *J.*

184 *lalandii* also differed significantly in both diet treatments (current diet: $\chi^2_2 = 6.869$, $p =$
185 0.032 , Fig. 1c; future diet: $\chi^2_2 = 9.867$, $p = 0.007$, Fig. 1d), and conditioning of *J. lalandii*
186 to *S. patagonicus* drove significantly greater selectivity for the invasive species
187 compared to native prey. This selection was evident regardless of the proportions in
188 which prey were offered to *J. lalandii*.

189

190 Chesson selectivity indices for invasive *S. patagonicus* were significantly greater in
191 conditioned lobsters fed on both the current ($t_{11} = 2.402$, $p = 0.035$; Fig. 2a) and future
192 diets ($t_{14} = 4.084$, $p = 0.001$; Fig. 2b). This was accompanied by a decreased preference
193 for the native *C. meridionalis*, as reflected by the lower selection for this species in
194 conditioned lobsters in both the current ($t_{11} = 3.115$, $p = 0.009$; Fig. 2a) and future diets
195 ($t_{14} = 2.656$, $p = 0.019$; Fig. 2b). Finally, the selection index for native *A. atra* remained
196 low regardless of predator conditioning and regardless of diet treatment (current diet: t_{11}
197 $= 0.706$, $p = 0.495$, Fig. 2a; future diet: $t_{14} = 0.221$, $p = 0.828$, Fig. 2b).

198

199

200 **Discussion**

201

202 The ability of predators to adapt to an altered prey base as a result of biological
203 invasions is important for ensuring that they will be able to incorporate such prey should
204 native resources decline or become fully displaced [7,23,24]. Therefore native predator
205 species that are able to do this may be more successful in the face of invasion fronts
206 that move through habitats, displacing native species rapidly [10]. This is likely to be
207 especially true of predators that can learn to adopt to consume new prey across short
208 timescales. As such, we demonstrate in this study that, despite initial avoidance, a
209 native predator, the rock lobster *J. lalandii*, can come to preferentially select an invasive
210 mussel *S. patagonicus* through a period of rapid learning.

211

212 After a short conditioning phase of four weeks, rock lobsters changed their diet
213 preferences, as measured using Chesson selectivity indices [22], from the dominant
214 native mussel *C. meridionalis* to the recent invader *S. patagonicus*. What was

215 noteworthy was that this occurred irrespective of the proportions of each prey species
216 appearing in the diet, with 'current' diets containing a greater number of native mussels
217 whilst 'future' diets contained more invasive mussels. The invasion of *S. patagonicus* on
218 the west coast of South Africa was first detected in 2009 [25], having recently been
219 found to have spread to the south coast [20]. Whilst this species represents a
220 morphologically similar prey to the native prey base, previous work reported that *J.*
221 *lalandii* avoided it for reasons that are not clear [21]. Native predators, however, could
222 be expected to shift towards feeding on a novel prey when there are low associated
223 search- and handling times, and when it offers higher energetic rewards compared to
224 other prey, as predicted by classic foraging theory [26]. It is also noteworthy that no
225 preference was observed in any of the treatment combinations towards the native
226 mussel *A. atra*. Of the mussels on offer in this study, this species has the greatest shell
227 strength and adductor muscle weight with an intermediate energy content [21] and was
228 therefore likely not selected due to a trade-off between these measures.

229

230 The invasive mussel *S. patagonicus* is a more profitable prey, offering the greatest
231 energetic reward with the weakest shells [21], and it is therefore possible that the native
232 predator is unfamiliar with other aspects of its presence such as its chemical signature.
233 It is therefore likely that over the conditioning period, *J. lalandii* identified cues from
234 novel *S. patagonicus* and through continuous exposure learned to associate it with a
235 profitable food choice, leading to preference development. This ultimately drove rock
236 lobsters to seek out *S. patagonicus*, despite the presence and relative abundances of
237 co-occurring native *C. meridionalis* and *A. atra* in the experimental arenas. Here, a
238 preference for *S. patagonicus* developed following exclusive exposure to this species
239 for four weeks, however in a natural setting containing more prey species, the
240 development of this preference may be delayed. It is also unknown whether this
241 preference would persist over longer time periods or whether *J. lalandii* can retain a
242 memory for this new species. However, the strong feeding switch to *S. patagonicus*
243 observed in this study suggests that it might still be possible for rock lobsters to develop
244 a preference for it in a setting where they will often encounter this species, which is

245 likely given the invasion history of *S. patagonicus* to date where it rapidly forms dense
246 beds that exclude competitors [27,28].

247

248 Conditioning through continuous exposure can lead to the development of a chemical
249 'search image' for a specific prey, which can subsequently improve the ability to locate
250 and ingest that prey [29]. Such chemoreceptive plasticity has been shown to be
251 important in animals that are omnivorous, long-lived, and found in various habitat types,
252 all of which can lead to variation in prey availability [30]. Thus, even though rock
253 lobsters are known to be generalist predators, variability in prey preference at an
254 individual level can be extreme. In addition, it has been suggested that rock lobsters
255 may have a genetic predisposition to act on chemical cues from prey that are profitable
256 [31]. The ability to develop a chemical 'search image' for a particular prey (promoted
257 through continuous exposure) can in itself be viewed as a mechanism that enhances
258 the detection and intake of profitable prey and is likely important here with the new
259 preference towards invasive, novel prey.

260

261

262 **References**

263

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357

358

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365

366

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368

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371

372

373 **Figure legends**

374

375 **Figure 1.** Median (interquartile range, minimum and maximum) Chesson selectivity
376 indices for three prey species (*Choromytilus meridionalis*, *Aulacomya atra* and
377 *Semimytilus patagonicus*) as predated upon by non-conditioned rock lobsters in (a)
378 current and (b) future diet treatments, and conditioned rock lobsters in (c) current and
379 (d) future diet treatments. Dots represent outliers. Boxes with different letters differ
380 significantly (Conover post hoc with Bonferroni correction). Values above the dashed
381 line = positive selection (preference), on the line = neutral selection, below the line =
382 negative selection (avoidance).

383

384

385 **Figure 2.** Species-specific comparisons between Chesson selectivity index values
386 (mean \pm 1 standard error) for prey (*Choromytilus meridionalis*, *Aulacomya atra* and
387 *Semimytilus patagonicus*) as predated upon by non-conditioned and conditioned *Jasus*
388 *lalandii* in the (a) current and (b) future diet treatments. Values above the dashed line =
389 positive selection (preference), values on the line = neutral selection and values below
390 the line = negative selection (avoidance).

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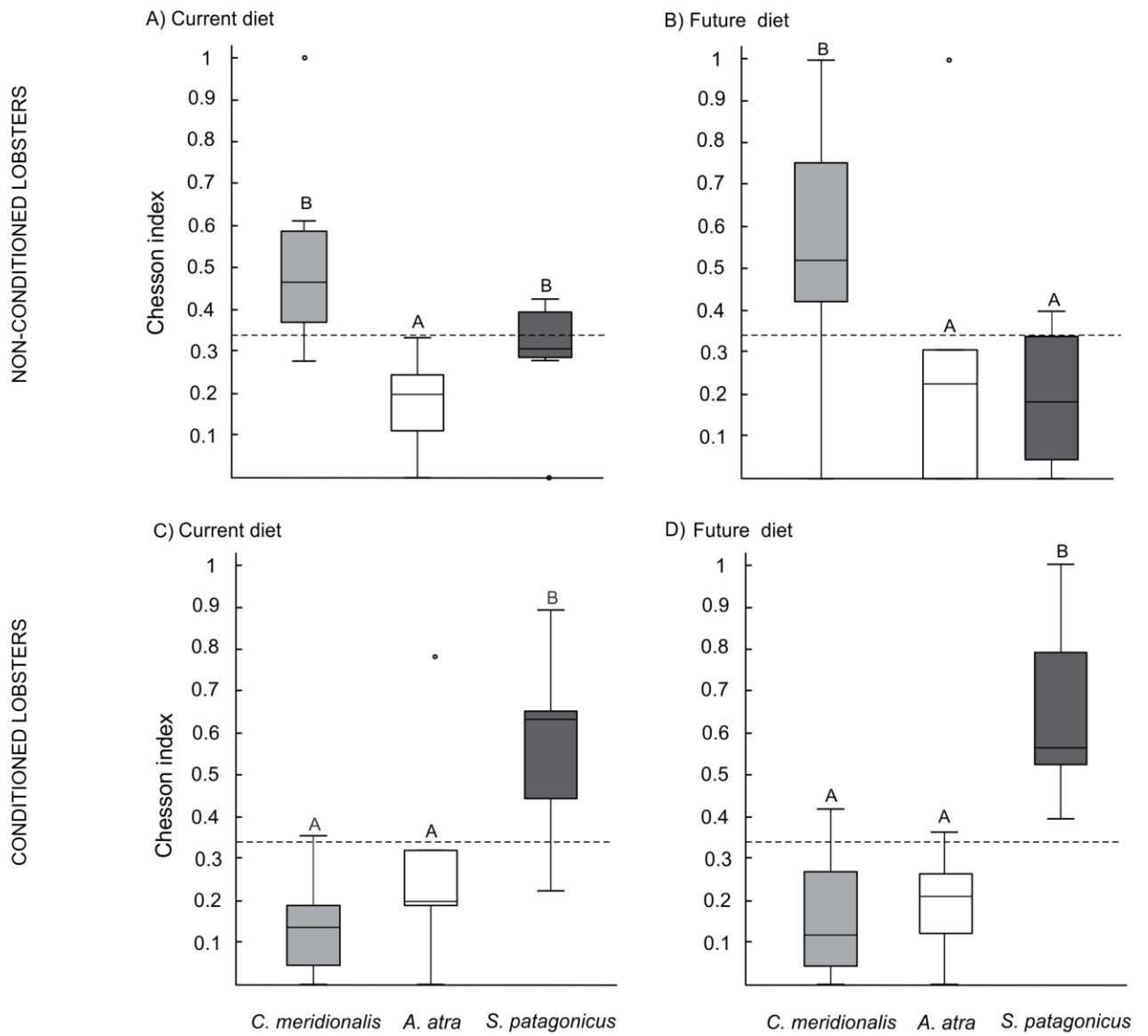
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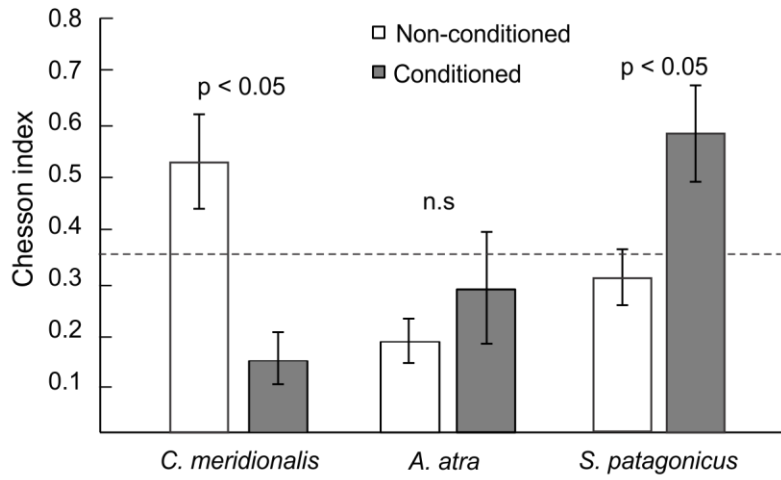


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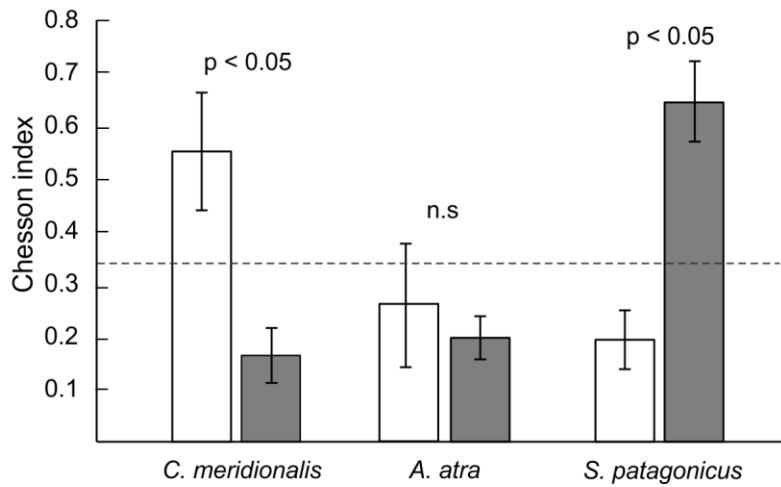
400 Figure 1.

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A) Current diet



B) Future diet



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Figure 2.

414 Table 1. Proportions of native *C. meridionalis* and *A. atra*, and invasive *S. patagonicus*
415 that were presented to rock lobsters in current and future diet scenarios.

Scenario	<i>C. meridionalis</i>	<i>A. atra</i>	<i>S. patagonicus</i>
Current	1	2	1
Future	1	1	2

416

417

418 Rapid learning in a native predator shifts diet preferences towards invasive prey

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420

421 Electronic Supplementary Information

422

423

424 Specimen collection

425

426 This study was conducted in 2018 in the Western Cape, South Africa. Mussels were
427 collected from monospecific beds at Bloubergstrand (33°48'01"S, 18°27'42"E) and
428 Muizenberg (34°5'23"S, 18°29'45"E) with shell lengths of 20 – 30 mm. Rock lobsters (70
429 – 100 mm carapace length) were collected from Kalk Bay on the south coast. This site
430 was chosen as, by the time of our experiments, *Semimytilus patagonicus* had only
431 recently spread to the south coast (2015) and was not known from the collection site.
432 Thus, rock lobsters *Jasus lalandii* in this region would have had little to no exposure to
433 this species. Experimental trials took place during winter when SST in northern False
434 Bay ranges between 14 - 15 °C (Dufois & Rouault, 2012). Salinities are typically
435 between 33 - 36 ppt. Laboratory conditions had similar temperature and salinity ranges.

436

437

438 Phase 1: Predator conditioning

439

440 The first phase of predator conditioning took place at False Bay Yacht Club, Simon's
441 Town (34°11'37"S, 18°26'08"E). Twenty lobsters were kept in separate cages (0.045
442 m³). These cages were covered with plastic mesh (0.5 x 0.5 cm) to exclude other
443 potential prey organisms from entering the cages. After a seven-day acclimatization
444 period, *J. lalandii* was fed with *S. patagonicus* in crushed and whole forms. The total
445 number of mussels given to each lobster per week was kept constant throughout the
446 conditioning phase (n = 40) and were added to each cage on the same day each week,
447 and not supplemented daily. Mussels were added via snorkelling to prevent the cages
448 from being removed from the water to minimise disturbance to lobsters. As minimising
449 disturbance was a priority during this time, we were unable to quantify the exact number
450 of uneaten mussels. However, observations through the mesh cage indicated that
451 lobster feeding was saturated during this time with ~30 mussels consumed each week.
452 It was suspected that avoidance of *S. patagonicus* already documented in non-
453 conditioned lobsters may have been driven by unfamiliarity based on a different shell
454 morphology/chemical cue. Thus, crushed mussels were used to introduce lobsters to
455 the cues of this species and "teach" them to associate these cues with that particular
456 shell shape over time. The ratio of crushed to whole mussels was then progressively
457 adjusted, with only whole mussels offered in the final week (Table S1).

458

459 Table S1. Ratios of *S. patagonicus* in crushed and whole forms as adjusted over the
460 predator conditioning phase.

461

Week	Crushed : Whole
1	30 : 10
2	20 : 20
3	10 : 30
4	0 : 40

462

463

464 Phase 2: Determining the influence of conditioning on prey preference

465

466 The prey preference of conditioned and non-conditioned *J. lalandii* took place in the
467 laboratory where single rock lobsters were kept in 38 L tanks in aerated seawater with
468 daily water changes. It should be noted here that non-conditioned lobsters were caught
469 from the field before being moved immediately into their acclimatization period in the lab
470 before feeding trials. Strict permit requirements along with a high poaching incidence in
471 the area resulted in the decision that it was too much of an experimental risk to have all
472 lobsters (conditioned plus non-conditioned) required in these trials suspended in cages
473 at the yacht club. Non-conditioned lobsters therefore remained in the wild for a month
474 prior to the trials, experiencing the same background water conditions as the nearby
475 yacht club whilst at the same time having access to a full natural diet.

476

477 After the seven-day acclimatization period, rock lobsters were given either one of two
478 treatments: a 'current diet' or a 'future diet', each containing different proportions of the
479 three subtidal mussel species (native *Choromytilus meridionalis* and *A. atra*, and
480 invasive *S. patagonicus*) that occur in the region where rock lobsters were collected.
481 Proportions of mussel species in the 'current diet' was based on the latest assessment
482 of subtidal mussel populations in this region (Skein et al. 2018). Daily checks of
483 experimental tanks included the identification, removal and replacement of consumed
484 mussels so that proportions of different prey species were kept constant throughout the
485 experiments.

486

487 Statistical analyses

488

489 During feeding trials, some rock lobsters moulted or did not feed at all, an indication that
490 they were soon to moult (Mayfield et al. 2000). These individuals were therefore
491 excluded from statistical analyses. Consequently, although trials began with 10
492 replicates for each diet treatment in conditioned and non-conditioned lobsters, analyses

493 of conditioned lobsters included six replicates for the 'current diet' treatment and eight
494 for the 'future diet' treatment, while for non-conditioned lobsters there were seven
495 replicates of the 'current diet' and eight for the 'future diet'.

496

497

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