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Prey vulnerability and predation pressure shape predator-induced changes in O₂ consumption and antipredator behaviour

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18

19 Predators regulate prey abundance (direct predation) as well as influencing their metabolism
20 and behaviour (indirect effects) through the perception of risk. Antipredator traits are informed
21 by individual experience of risk, which may vary over environmental gradients and through
22 ontogeny. As prey grow, individual vulnerability generally diminishes, and the reduction in
23 individual vulnerability with ontogenetic growth can potentially lead to size refugia, ultimately
24 nullifying the impacts of direct predation. Despite the ecological importance of the indirect
25 effects of predation and the disproportionate influence larger individuals have on ecological
26 level processes, there has been little focus on the potential indirect effects of predation risk on
27 invulnerable prey. Using a combination of field and laboratory experiments, we measured the
28 changes in routine oxygen consumption of vulnerable and invulnerable size classes of the
29 intertidal snail *Nucella lapillus* (dogwhelk), exposed to effluent from its crab predator *Carcinus*
30 *maenas*. To test the potential influence of prior experience of predation risk, measurements
31 were conducted on populations naturally exposed to different levels of predation pressure. Field
32 results showed that only invulnerable snails modified their routine oxygen consumption in the
33 presence of risk, and this occurred across all populations. Oxygen consumption rates in the
34 laboratory, however, contradicted the pattern, with only vulnerable prey responding to the
35 perception of risk. Metabolic responses of both vulnerable and invulnerable prey under field
36 and laboratory conditions are discussed in the context of asset protection and prey energetic
37 state. Observations of snail behaviour in the laboratory showed that dogwhelks from exposed
38 shores, where predatory risk is higher, were more likely to exhibit antipredator behaviour.
39 Importantly, our findings provide evidence that the indirect effects of predators remain
40 influential even after prey are no longer susceptible to direct predation and add to the growing
41 body of evidence highlighting the ecological importance of indirect predation.

42 Keywords: antipredator behaviour, indirect effects, *Nucella lapillus*, oxygen consumption,
43 physiological response, predation, size refuge, threat-sensitive behaviour, trait-mediated
44 indirect interaction (TMII), vulnerability

45

46 In many species, exposure to a predatory cue elicits a series of coordinated, adaptive
47 physiological responses, which influence antipredator behaviour (Hawlena, Kress, Dufresne,
48 & Schmitz, 2011; Van Dievel, Janssens, & Stoks, 2016) and may come at an energetic cost
49 (Hawlena & Schmitz, 2010; Kamenos, Calosi, & Moore, 2006; Slos & Stoks, 2008). Such
50 physiological and behavioural responses, as well as promoting prey survival, lead to localized
51 reductions in foraging rates or changes in habitat use that can cause trophic cascades with
52 lasting effects on local population densities and community structure (Schmitz, Beckerman, &
53 O'Brien, 1997; Schmitz, Krivan, & Ovadia, 2004; Trussell, Ewanchuk, Bertness, & Silliman,
54 2004; Werner & Peacor, 2003). The energetic costs of predator-induced stress responses have
55 been suggested as potential explanations for reductions in prey fitness, and consequently
56 changes in prey demography (Boonstra, Hik, Singleton, & Tinnikov, 1998; Creel, Christianson,
57 Liley, & Winnie, 2007; Preisser, Orrock, & Schmitz, 2007; Slos & Stoks, 2008), ecosystem
58 nutrient dynamics (Hawlena & Schmitz, 2010), energy flow through trophic levels (C M
59 Matassa & Trussell, 2014) and may possibly account for food chain length in some systems
60 (Trussell, Ewanchuk, & Matassa, 2006b).

61 The threat of predation varies both temporally and spatially at the individual and population
62 level (Lima & Bednekoff, 1999; Lima & Dill, 1990). Natural variation in ambient predation
63 pressure among populations has led to the evolution of adaptive physiological and behavioural
64 responses to predation, which may be adjusted by local conditions (Donelan & Trussell, 2018;
65 Handelsman et al., 2013; Holopainen, Aho, Vornanen, & Huuskonen, 1997). For example, the
66 resting metabolic rate of frog tadpoles, *Rana temporaria*, exposed to short-term risk increases,

67 leading to an enhanced ability to escape predators. However, with longer exposure metabolic
68 rates drop, showing acclimation to predator risk by reducing energetic demands which may
69 underpin risk-averse behaviour while foraging (Steiner & Van Buskirk, 2009). This individual
70 experience of local predation pressure can also inform the subsequent generation, through
71 epigenetic programming (Jablonka & Raz, 2009; Love, McGowan, & Sheriff, 2013). This trait
72 is particularly important for direct developing offspring, whose experience of risk is likely to
73 correlate strongly with that of their parents (Dixon & Agarwala, 1999; Poethke, Weisser, &
74 Hovestadt, 2010). For instance, offspring dispersal (a predator avoidance trait) in the lizard
75 *Zootoca vivipara* increases as a consequence of maternal predator-related stress, decreasing the
76 potential predation pressure experienced by offspring during the most vulnerable stages of
77 development (Bestion, Teyssier, Aubret, Clobert, & Cote, 2014). In this way, parental input
78 and individual experience combine to produce more suitable adaptive ecotypes (Donelan &
79 Trussell, 2015; Giesing, Suski, Warner, & Bell, 2011) with natural selection acting to reinforce
80 local adaptations (Guerra-Varela et al., 2009; Mäkinen et al., 2008).

81 At the level of the individual, several factors including learned behaviours and ontogenetic
82 somatic growth can result in a change in the suite of predators that threaten prey and, in many
83 cases, result in a reduction in overall predation pressure (Paradis, Pepin, & Brown, 1996;
84 Scharf, Juanes, & Rountree, 2000). Larvae of the three-spined stickleback, *Gasterosteus*
85 *aculeatus*, use predator size relative to their own as a measure of predation risk and modify
86 their foraging behaviour accordingly, thus optimizing energy intake while minimizing the risk
87 of being eaten (Bishop & Brown, 1992). This type of threat-sensitive behaviour is further
88 enhanced when prey are able to adjust their behaviour relative to their encounter rates with
89 different predators (Rochette, Maltais, Dill, & Himmelman, 1999). Legault and Himmelman
90 (1993) showed that this kind of threat-sensitive behaviour exists in several marine invertebrate

91 prey, but that correlations between encounter rates and antipredator behaviour vary between
92 species.

93 Ontogenetic somatic growth can be an escape strategy in and of itself, with many prey species
94 able to grow to size refugia and escape direct predation completely (Chase, 1999). Little is
95 known regarding the way in which prey that have reached a size refuge respond to the threat
96 of predation (Lundvall, Svanbäck, Persson, & Byström, 1999; Werner et al., 1983), although
97 links between size-related vulnerability and antipredator behaviour have been shown in certain
98 aquatic gastropods (DeWitt, Sih, & Hucko, 1999; Rochette & Himmelman, 1996). In their
99 study into the potential for the aquatic snail *Physa gyrina* to express behavioural compensation
100 for morphological vulnerability to a crayfish predator (*Orconectes rusticus*), DeWitt et al
101 (1999) showed that larger less vulnerable snails demonstrate reduced levels of antipredator
102 behaviour. Considering the disproportionate impact larger individuals have on demography
103 and resources (Etter, 1989; Paine, 1976), it is perhaps surprising that little interest has been
104 shown in the indirect effects predators have on prey that have reached size refugia.

105 The purpose of this study was to investigate how differences in prey size, and hence
106 vulnerability to direct predation, affect the physiological and antipredator response in prey. In
107 addition, we examined how these effects were modified by prior experience of predation risk,
108 based on habitat (sheltered or exposed shores). We used a widely adopted intertidal predator–
109 prey system and implemented a series of field and laboratory experiments, to examine both
110 physiological and behavioural responses of vulnerable and invulnerable prey to predation risk.

111 <H1>Methods

112 <H2>Predator–prey system

113 The green shore crab, *Carcinus maenas*, is an important predator of the dogwhelk, *Nucella*
114 *lapillus* (hereafter referred to as *Nucella*). Both species are found extensively across the North

115 Atlantic and co-occur along a gradient of wave exposure (Crothers 1985). *Nucella* reaches a
116 size refuge from crab predation at 27 mm shell length (Hughes & Elner, 1979). As with many
117 gastropod species, *Nucella* are able to assess predation risk through the detection of differences
118 in concentration of kairomones, waterborne chemical cues inadvertently released by predators
119 (Edgell, 2010; Catherine M. Matassa & Trussell, 2011; Vadas, Burrows, & Hughes, 1994).
120 *Nucella* use differences in the concentration of these chemicals to assess the proximity of a
121 predator (Freeman & Hamer, 2009; Large, Smee, & Trussell, 2011) and therefore are
122 influenced by local hydrodynamic conditions (Freeman & Hamer, 2009; Large et al., 2011).
123 For example, in high-flow, wave-exposed environments, characterized by an elevated degree
124 of mixing, the homogenization of the olfactory seascape created by predatory kairomones
125 affects the chemoreceptive ability of prey (Large et al., 2011; Weissburg, James, Smee, &
126 Webster, 2003; Zimmer & Butman, 2000). Large et al (2011) showed that antipredator
127 behaviour in *N. lapillus* is strongly influenced by hydrodynamic mixing and that *Nucella*
128 chemoreception ability is reduced in very slow- or fast-flowing turbulent water. They argued
129 that on exposed shores, due to the homogenization of different concentrations of chemical cues,
130 *Nucella* are unable to perceive predation risk. Wave action also directly impacts the densities
131 of crabs, with wave exposure being negatively correlated with crab densities (Hughes & Elner,
132 1979; Large & Smee, 2013; Menge, 1983; Rochette, Smee, & Trussell, 2011). Hence
133 populations of *Nucella* can experience varying levels of predation risk depending on local wave
134 action regimes (Freeman & Hamer, 2009; Large et al., 2011; Menge, 1976; Tyler, Stafford, &
135 Leighton, 2014). The effects of wave action combined with inherent differences in predator
136 densities result in the formation of distinct ecotypes of *Nucella*, with plasticity present in both
137 morphological and behavioural antipredator traits (Crothers, 1983; Guerra-Varela et al., 2009;
138 Large & Smee, 2013; Rolán, Guerra-Varela, Colson, Hughes, & Rolan-Alvarez, 2004).

139 <H2>Site selection and predator numbers

140

141 Our field study was conducted at six sites, three wave-exposed and three wave-sheltered,
142 around the coasts of Anglesey, North Wales, U.K. (Fig. 1). Sites were initially selected as
143 wave-sheltered or wave-exposed based on community structure (Ballantine, 1961) and later
144 exposure was calculated using the map-based method to estimate mean wave fetch for each
145 site (Burrows, Harvey, & Robb, 2008). To estimate differences in crab abundance, baited crab
146 traps (60 x 40 cm and 35 cm high, with 500 g of fish) were used at each of the six sites. For
147 each site, crab numbers per trap were counted on 3 consecutive days. A single baited crab trap
148 was placed in the midzone and left for two complete tidal cycles, sampled and then redeployed
149 a further two times, each time ca. 30 m along the shore from the previous location. This allowed
150 us to average crab numbers across the 3 days for each site to provide a mean crab number per
151 trap per site.

152

153 <H2>Field measurements

154 We compared field oxygen consumption rates of two size classes of *Nucella* from exposed (low
155 predator abundance) and sheltered (high predator abundance) shores with and without a
156 predator cue. Small *Nucella*, considered vulnerable to predation ($N = 7$ at each site, mean shell
157 length $14.6 \pm \text{SD } 1.3$ mm) and large, considered invulnerable ($N = 7$ at each site, mean shell
158 length $29.0 \pm \text{SD } 1.6$ mm) were collected from the same tidal height to control for any unknown
159 shore level size gradients (Elner & Hughes, 1978). Field measurements were conducted
160 between 1100 and 1700 on 4–8 October 2017, apart from one sheltered shore which had to be
161 completed during the next tidal cycle (17 October 2017) due to adverse weather conditions.
162 Animals were collected before being exposed to air, as the tide was receding, and subsequently
163 were kept submerged to avoid any potential impacts on oxygen consumption rates (McMahon,

164 1988; Stickle, Moore, & Bayne, 1985). Care was taken not to select individuals that were
165 actively feeding. Individual *Nucella* were carefully placed into closed system respirometers (70
166 x 70 mm and 50 mm high) containing fully aerated filtered sea water to determine oxygen
167 consumption rates. All water used in field measurements was sourced from the laboratories at
168 the School of Ocean Sciences, Bangor University, Menai Bridge, U.K. Changes in water
169 oxygen partial pressure (PO₂) were measured using an optical fluorescence technique (PreSens,
170 Regensburg, Germany, Fibox 4 trace, Fiber Optic Trace Oxygen Meter). Each respirometer
171 was equipped with a single oxygen sensor spot (PreSens) located on the inside of the lid, which
172 allowed for nonintrusive measurement of sea water PO₂ levels at regular intervals. The
173 seawater was filtered (0.45 µm) to reduce contaminating effects of biological activity from
174 microbes and algae, and two controls consisting of respirometers without snails were included
175 during each trial (N=16). Controls for filtered sea water and crab effluent were used to assess
176 any background (microbial) oxygen consumption rates and this was then subtracted from all
177 other measurements in that trial. Sea surface temperature was measured at each site at the
178 beginning of each experiment and respirometers were placed into temperature-controlled water
179 baths to ensure that in situ temperatures were maintained throughout the period of oxygen
180 consumption measurement (mean 14.18 ± SD 0.06 °C across all sites) to prevent temperature-
181 related changes in metabolic rates (Dahlhoff, Stillman, & Menge, 2008).

182 Preliminary trials showed that rates of oxygen consumption were initially elevated when
183 *Nucella* were first placed in the respirometers due to handling stress, but levels fell over the
184 next 25 min as snails settled in the respirometers. Over the next 45 min PO₂ levels fell within
185 the respirometers in a linear fashion which we considered to be routine rates of oxygen
186 consumption as the snails were free to move around within the respirometers. Several studies
187 have shown that exposure to crab effluent influences *Nucella* behaviour and therefore the use
188 of routine rates of oxygen uptake are more appropriate when determining the natural reaction

189 of *Nucella* to the detection of a predator (including the effects of movement). Based on these
190 initial observations, individual snails were inserted into their respiration chambers, sealed and
191 left for 25 min before the initial PO₂ reading was taken. Repeated PO₂ readings were then taken
192 every 5 min for the next 45 min to determine the linear fall in PO₂ over time. Snails therefore
193 spent 70 min in total in their respective respirometers. In each case, care was taken to avoid
194 hypoxia from developing within the respirometers by ensuring that PO₂ levels remained above
195 17 kPa throughout this period. Rates of oxygen consumption were determined from the drop
196 in PO₂ over 45 min by linear regression, minus the background fall in PO₂ from the respective
197 controls. This value was multiplied by the solubility coefficient for oxygen adjusted for salinity
198 and temperature to give whole-body values in ml O₂/h. Values were corrected to STPD
199 (standard temperature and pressure and dry) and expressed as μmol O₂/h.

200 Once a baseline oxygen consumption rate had been established for each snail, they were then
201 subjected to the predation risk treatment. Each snail that had been monitored for baseline
202 oxygen consumption was exposed to predation risk by exchanging the water in the
203 respirometer for water treated through exposure to crabs. This ‘predation risk’ water was
204 created in the field by adding 8–10 large male crabs (mean carapace length ± SD 56.6 ± 4.8
205 mm) to 20 litres of filtered and aerated water for 1 h. *Nucella* were kept submerged during the
206 water change. They were then allowed a further 25 min to acclimatize to the new treatment.
207 Once measurements were complete, all *Nucella* were marked and returned to the laboratory
208 to assess their oxygen consumption rates and behavioural responses to predation risk under
209 controlled laboratory conditions.

210 <H2>Laboratory measurements

211 Individuals collected from the field were housed in a temperature-controlled aquarium at
212 similar temperatures to those in the field (mean 13.9 ± SD 0.9 °C) in fully aerated, recirculated,

213 natural sea water for 1 month before being used in the second experiment. *Nucella* were not
214 exposed to predation risk during this period. They were fed mussels and barnacles ad libitum
215 and then starved for 48 h before their oxygen consumption was measured, to standardize
216 digestive state (C M Matassa & Trussell, 2014). Laboratory measurements followed the same
217 protocol as the field experiment with routine oxygen consumption rates being established prior
218 to measuring them under predation risk conditions. Water temperature was maintained at the
219 respective in situ temperatures. After 25 min of acclimatization, oxygen consumption rates
220 were measured every 5 min for 45 min. As with the field experiment, the same individuals
221 were then exposed to crab effluent and their oxygen consumption rates were measured.

222 To determine whether the two size classes of *Nucella* show typical antipredator responses
223 (cessation of movement, Freeman, Dernbach, Marcos, & Koob, 2014; Vadas et al., 1994), they
224 were observed for 20 s every 5 min, over 45 min, and their precise location noted on a diagram
225 of the respirometer following the approach of Large et al. (2011). Care was taken not to cast a
226 shadow over the respiration chambers to reduce any potential impacts on *Nucella* behaviour.
227 As the exact movement of individuals between 5 min increments could not be known, we used
228 the shortest possible distance between two consecutive increments for our calculations. By
229 combining the distance travelled between all increments, we were able to estimate the total
230 distance travelled during the experiment.

231 <H2>Statistical analysis

232 As the focus of this study was on comparing the effect of predation risk on oxygen consumption
233 rates of vulnerable and invulnerable prey and not directly on the effects of size, analysis was
234 conducted on whole animal rates of oxygen consumption (Dahlhoff et al., 2008; Hayes, 2001;
235 Packard & Boardman, 1999). To assess the potential impact of predation risk on the oxygen
236 consumption rates of vulnerable and invulnerable prey both in the field and in the laboratory,

237 we used a model selection approach using gamma distributed generalized linear mixed models
238 (GLMMs). In both analyses, we used whole animal oxygen consumption rates as a response
239 variable and wave exposure (exposed and sheltered), *Nucella* vulnerability (vulnerable and
240 invulnerable) and predation risk treatment (no predator cue and predator cue) as fully crossed
241 fixed effects. Log-transformed total length was used as a covariate to account for any potential
242 size-related differences within the size ranges selected. We considered site as being nested
243 within wave exposure and *Nucella* ID as a repeated measure (both treated as random effects).
244 We also performed a GLMM with *Nucella* movement as a response variable using the same
245 fixed, nested and repeated terms effects as in previous analyses. The movement results showed
246 overdispersion and were therefore analysed using a negative binomial GLMM. We used the
247 glmm.TMB package to analyse movement results (Brooks et al., 2017).

248 All GLMMs were constructed and compared in R 3.5.0 (R Core Team, 2013) using the
249 lme4 package (Bates, Mächler, Bolker, & Walker, 2015). Backward model selection was
250 achieved using the drop1 function and models with the lowest Akaike information criterion
251 (AIC) were selected (Bolker et al., 2008). When interaction terms were significant at the $\alpha =$
252 0.05 level, Tukey post hoc tests were carried out using the emmeans package (Lenth,
253 Singmann, Love, Buerkner, & Herve, 2004).

254 <H2>Ethical Note.

255 Our experimental protocol complies with all institutional guidelines at Bangor University. No
256 animals were harmed during the experiment. After the experiment, each whelk was returned to
257 its collection location. No permit was necessary to perform the experiments described above.

258 <H1>Results

259 <H2>Field results

260 Exposure calculations (measured as average wave fetch per site) using the Burrows et al. (2008)
261 map-based method concurred with our assessment of exposure with sheltered and exposed
262 shores having a mean wave fetch of 17.89 km (\pm 7.77 SD) and 49.55 km (\pm 10.09 SD),
263 respectively. These values agree with Burrows et al. (2008) assessment of wave-sheltered and
264 wave-exposed shores which they defined as being 20–40 km and 40–60 km, respectively.
265 There was a significant effect of wave exposure on crab numbers per trap (ANOVA: $F_{1,11} =$
266 7.42, $P = 0.016$; Table 1), with wave-exposed sites having an average of 0.89 ± 0.42 crabs per
267 trap compared with wave-sheltered sites which had an average of 41.22 ± 5.81 crabs per trap
268 (Fig. 2). The combination of wave exposure effects on the perception of kairomones (Freeman
269 & Hamer, 2009; Large et al., 2011) and the stark difference in predator densities indicate that
270 *Nucella* were exposed to different levels of predation risk at the two types of site.

271

272 The addition of *Nucella* shell length to all models tested had no impact on the AIC calculated
273 and it was therefore not included in further analysis. Model selection results for our field and
274 laboratory measurements are summarized in Table 2. Background respiration rates were 0.52
275 $\mu\text{mol O}_2/\text{h}$ across treatments. Oxygen consumption rates of vulnerable *Nucella* (mean 3.60
276 $\mu\text{mol O}_2/\text{h}$, SE = 0.25) were lower than those of invulnerable individuals (mean = 16.65
277 $\mu\text{mol O}_2/\text{h}$, SE = 0.85) across all exposure gradients and treatments (gamma distributed GLMM:
278 $N = 65$, $\chi^2_1 = 66.12$, $P < 0.001$; Fig. 3). GLMM analysis showed that the two size classes of
279 *Nucella* reacted differently when exposed to crab effluent (gamma distributed GLMM: $N =$
280 65, $\chi^2_1 = 8.85$, $P = 0.003$). Further post hoc analysis showed that in the presence of predation
281 risk, invulnerable *Nucella* reduced their respiration rates by 36.2% (Table A1), whereas

282 vulnerable individuals showed a slight nonsignificant increase in oxygen consumption rates of
283 6.01% (Table A1). This pattern was consistent across both exposure levels (gamma distributed
284 GLMM: $N = 65$, $\chi^2_1 = 0.45$, $P = 0.49$; Fig. 3).

285 <H2>Laboratory results

286 Overall laboratory background respiration rates contributed in control respirometers were 0.30
287 $\mu\text{mol}/\text{O}_2/\text{h}$. As with the field results, in the laboratory, invulnerable *Nucella* had higher oxygen
288 consumption rates than vulnerable individuals (gamma distributed GLMM: $N =$
289 65 , $\chi^2_1 = 61.48$, $P < 0.001$). However, under laboratory conditions although there was an
290 interaction between treatment and size (gamma distributed GLMM: $N = 65$, $\chi^2_1 = 12.73$, $P <$
291 0.001), it was vulnerable *Nucella* that showed a reduction in respiration rates by 26.8% under
292 predator risk (Table A1), whereas respiration of invulnerable individuals did not differ between
293 treatments (Table A1, Fig. 4). Once again, differences between size classes were the same
294 irrespective of exposure level (gamma distributed GLMM: $N = 65$, $\chi^2_1 = 1.66$, $P = 0.169$).

295 <H2>Laboratory behavioural responses

296 The detection of a predatory cue affected the behaviour of *Nucella*, and its impact was
297 influenced by both prey vulnerability and wave exposure level (Fig. 5). Overall, vulnerable
298 *Nucella* reduced their movement in the presence of a predatory cue, whereas invulnerable
299 *Nucella* did not (negative binomial GLMM: $N = 65$, $\chi^2_1 = 11.84$, $P < 0.001$). Post hoc testing
300 revealed that both size classes moved similar distances in filtered sea water (Fig. 5) but in crab
301 effluent vulnerable *Nucella* reduced their movement (Table A1), whereas invulnerable
302 individuals did not (Table A1). Under predation risk conditions, there was an overall effect of
303 wave exposure on *Nucella* behaviour (Fig. 6; negative binomial GLMM: $N = 65$, $\chi^2_1 = 4.92$, P
304 $= 0.03$). *Nucella* from sheltered shores, naturally exposed to higher ambient levels of predation

305 risk, reduced their movement when exposed to crab effluent (Table A1), whereas *Nucella* from
306 wave-exposed shores remained active (Table A1).

307 <H1>Discussion

308 Short-term metabolic responses of invertebrate prey to predation risk and the resulting
309 antipredator behaviour are not well understood (Canero & Hermitte, 2014; Mitchell, Bairos-
310 Novak, & Ferrari, 2017), and the influence of individual vulnerability even less so (DeWitt et
311 al., 1999). Exposing *Nucella* to a predatory cue affected their routine metabolic rate as well as
312 their antipredator behaviour, but each response was influenced differently by individual
313 vulnerability and wave exposure. When vulnerable and invulnerable *Nucella* were exposed to
314 a predatory cue in the field, moments after being collected, it was the invulnerable size class
315 that reduced its oxygen consumption rate, as opposed to vulnerable ones. Note that *Nucella*
316 were not tethered while in the respiration chamber as our intention was to capture the total
317 oxygen consumption related to the detection and subsequent short-term response to predation
318 risk. Therefore, our results do not allow us to distinguish between a potential physiological
319 response to predation risk and the metabolic cost of the resulting behavioural response.
320 Changes in oxygen consumption rates are therefore a combination of stress-induced changes
321 in metabolic rate as well as behavioural changes. Notwithstanding, our results clearly indicate
322 that predation risk may still influence prey that are otherwise safe from direct predation by
323 specific predators. In addition, by comparing oxygen consumption in the field, in individuals
324 extracted directly from natural conditions, with that of individuals maintained in the laboratory,
325 we have also shown important differences in response. Our results and particularly the
326 differences between the field and laboratory observations are explained in relation to size-
327 related risk taking as well as through potential changes in *Nucella* physiological and energetic
328 state.

329 <H2>Oxygen consumption in vulnerable *Nucella*

330 When vulnerable *Nucella* were exposed to a predatory cue in the field, there was no change in
331 oxygen consumption when compared to respiration in filtered sea water alone. Previous
332 laboratory-based studies show a cessation of movement in the presence of a predatory cue
333 (Large & Smee, 2010; Vadas et al., 1994). However, our field-based results, when framed from
334 the perspective of foraging–risk trade-off, may be explained by Clark’s asset protection
335 principle (APP, Clark, 1994). The APP asserts that foraging decisions relate to the relative
336 amount an individual stands to lose or gain from foraging at a specific time. The APP argues
337 that for a given amount of energy to be gained from foraging at a specific time, smaller
338 individuals have less to lose (less already invested in growth) and proportionally more to gain
339 than a larger individual. In this context, smaller individuals should forage under risky
340 conditions if the potential energy gain is high enough. In essence, it is more favourable for
341 smaller prey to forage during risky periods than larger individuals. Thus, vulnerable *Nucella*
342 under predation risk conditions are likely to continue to search for food due to the high fitness
343 gains, resulting in similar levels of oxygen consumption between our two treatments.

344 In the laboratory, where *Nucella* were fed *ad libitum* and did not experience risk cues or wave
345 action for one month, oxygen consumption responses to risk differed to those in the field.
346 Vulnerable *Nucella* reduced their routine metabolic rate as well as their movement when
347 exposed to a predatory cue. These seemingly contradictory patterns between field and
348 laboratory results may be explained in the context of the risk allocation hypothesis (RAH). The
349 RAH rests on the inextricable link between current energy reserves and decision making under
350 risky conditions, meaning that behavioural changes are not a result of momentary trade-offs,
351 but rather as forming part of an overarching foraging strategy (Burrows & Hughes, 1991; Lima
352 & Bednekoff, 1999; Lima & Dill, 1990; Mangel & Clark, 1986). In essence, low energy
353 reserves force prey to forage irrespective of risk, whereas when energy reserves are high, prey

354 are able to wait out risky periods in order to forage during more favourable ones (Lima &
355 Bednekoff, 1999; Lima & Dill, 1990). One of the important predictions of the RAH is that if
356 prey experience prolonged periods of safety interspersed with short high-risk periods, then prey
357 should stop foraging during the high-risk periods (Lima, 1998). In the laboratory, *Nucella*
358 experienced ‘safe’ conditions, where they were able to increase energy reserves. Thus, when
359 faced with predatory risk they reduced activity as predicted by the RAH which in turn was
360 reflected in a reduction in oxygen consumption. When Matassa and Trussell (2014) tested the
361 response of starved and satiated *Nucella* in the laboratory they found patterns that corroborate
362 our field–laboratory comparisons. Satiated animals did not forage during risky periods whereas
363 starved individuals were forced to forage even under high-risk conditions.

364 <H2>Oxygen consumption in invulnerable *Nucella*

365 Although vulnerable *Nucella* reacted predictably to predation risk in terms of the RAH, the
366 pattern seen in the invulnerable adults was less clear. Under field conditions, invulnerable
367 *Nucella* reduced their oxygen consumption rate in response to a predatory cue. Large
368 invulnerable *Nucella* are much more likely than small vulnerable individuals to have sufficient
369 energy reserves to be able to reduce activity in the presence of increased risk (Feare, 1970).
370 Thus, a reduction in oxygen consumption in the field may be a consequence of a reduction in
371 movement. Although the exact mechanism underpinning this reduction in oxygen consumption
372 is beyond the scope of this investigation (stress response and movement), these observations
373 are important in showing that *Carcinus* is still able to affect *Nucella* even after they have
374 reached a size refuge. This pattern changed after *Nucella* had been housed under ‘safe’
375 conditions in the laboratory. When tested again in the laboratory, where we expected a similar
376 pattern to that seen in the field (with satiated individuals reducing their respiration as well as
377 their movement), there was no reduction in oxygen consumption or movement under the
378 predation risk condition. Clearly the complexity of behavioural and physiological changes in

379 laboratory-housed *Nucella* at a size refuge warrants further study, as these size classes have a
380 disproportionate influence on population dynamics.

381 <H2>Antipredator behaviour

382 Antipredator behaviour was only assessed in the laboratory, and not in the field. Our
383 observations showed an interesting influence of wave exposure (and hence prior experience of
384 predatory threat) on the propensity for *Nucella* to adopt an antipredator behaviour. Wave-
385 sheltered populations (which naturally experience higher predation risk) showed higher levels
386 of antipredator behaviour (cessation of movement) than their wave-exposed counterparts. At
387 the population level, comparisons of the effects of sympatric and allopatric predators on the
388 behaviour of prey have shown that the influence of local ambient predation pressure informs
389 antipredator behaviours (Aschaffenburg, 2008; Large & Smee, 2013; Rochette, Dill, &
390 Himmelman, 1997; Rochette et al., 1999). In comparisons of antipredator behaviour of the
391 common whelk, *Buccinum undatum*, from populations naturally exposed to different suites of
392 predators, Rochette and Himmelman (1996) found that individuals adopt more appropriate
393 antipredator behaviour to sympatric predators than allopatric ones. In *Nucella* investigations of
394 wave exposure effects on behaviour are conflicting. Large and Smee (2013) found that crabs
395 caused a reduction in *Nucella* movement in both wave-sheltered and wave-exposed
396 populations. By contrast, and in accordance with our own work, Freeman et al. (2014) showed
397 lower levels of antipredator behaviour in more predator-naïve populations from exposed
398 shores.

399 <H2>Potential ecological importance

400 The changes in behavioural and physiological traits of prey can have potentially cascading
401 effects on the rest of the biological community. A predator's influence on community dynamics
402 is not limited to their regulation of prey densities (density-mediated indirect interactions,
403 DMIIIs), but also through their influence on prey physiological and behavioural traits (trait-

404 mediated indirect interactions, TMIs). Investigations into the potential strength of DMIs
405 compared to TMIs between *Carcinus* and *Nucella* have shown that direct predation and
406 predation risk exert similar influence on the community dynamics of this rocky shore food
407 chain (Trussell, Ewanchuk, & Matassa, 2006a). Our results indicate that this may in fact be an
408 underestimation of the importance of TMIs as previous studies have only used small size
409 classes of *Nucella* that have lower foraging rates than individuals at the size refuge used in this
410 study (Dunkin & Hughes, 1984). The persistence of the indirect effects of *Carcinus* on *Nucella*
411 even after a size refuge has been reached will mean that TMIs persist for longer than DMIs,
412 increasing their ecological importance. The greater impact larger individuals have on resources,
413 combined with the protracted temporal scale at which prey are influenced by predation risk,
414 may result in a considerable underestimation of the overall impacts predators have on an
415 ecosystem.

416 <H2>Conclusions

417 Our results provide insight into the effects of predators on prey of differing vulnerability and
418 the potential for antipredator behaviours to be influenced by local environmental factors (wave
419 exposure and hence presumed influence of predation risk). Importantly, we have shown that
420 the influence of a predator may be more far reaching than originally thought, as they are able
421 to affect oxygen consumption of prey even after they are no longer susceptible to direct
422 predation. Our contrasting results from field and laboratory experiments show clearly that
423 understanding of prey state (e.g. physiological/energetic condition which is likely to change
424 dependent on handling and husbandry) is critical in generating a holistic understanding of
425 predator–prey responses (e.g. Matassa & Trussell, 2014). Finally, although not consistent
426 across all responses, we found an effect of wave exposure on antipredator behaviour (cessation
427 of movement) indicating an effect of prior experience of predation risk. Further studies into the
428 potential for predators to indirectly influence prey that are not at risk of direct predation will

429 enable us to better appreciate the overall influence predators have on the ecosystem they
430 inhabit.

431

432 **Author Contributions**

433 S.K. and S.J. conceived the study idea and S.K., I.M. and N.W. designed the experiments.

434 S.K. conducted the experiments. S.K., T.C., L.G. and S.J. contributed to the analysis of the

435 data and S.K., T.C., L.G., I.M., N.W. and S.J. contributed to the writing of the manuscript.

436

437 **Declaration of Interest**

438 The authors declare that the research was conducted in the absence of any commercial or

439 financial relationships that could be construed as a potential conflict of interest.

440

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447 **References**

448 Aschaffenburg, M. D. (2008). Different crab species influence feeding of the snail *Nucella*

449 *lapillus* through trait-mediated indirect interactions. *Marine Ecology*, 29(3), 348–353.

450 <https://doi.org/10.1111/j.1439-0485.2008.00227.x>

- 451 Ballantine, W. J. (1961). A biologically-defined exposure scale for the comparative
452 description of rocky shores. *Field Studies*, 1(3), 1–19.
- 453 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects
454 Models using lme4. *Journal of Statistical Software*, 67, 1–48. Retrieved from
455 <http://arxiv.org/abs/1406.5823>
- 456 Bestion, E., Teyssier, A., Aubret, F., Clobert, J., & Cote, J. (2014). Maternal exposure to
457 predator scents: Offspring phenotypic adjustment and dispersal. *Proceedings of the*
458 *Royal Society B: Biological Sciences*, 281, 20140701.
- 459 Bishop, T. D., & Brown, J. A. (1992). Threat-sensitive foraging by larval threespine
460 sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, 31(2),
461 133–138. <https://doi.org/10.1007/BF00166346>
- 462 Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H.,
463 & White, J. S. S. (2008). Generalized linear mixed models: a practical guide for ecology
464 and evolution. *Trends in Ecology and Evolution*, 24(3), 127–135.
465 <https://doi.org/10.1016/j.tree.2008.10.008>
- 466 Boonstra, R., Hik, D., Singleton, G. R., & Tinnikov, A. (1998). The impact of predator-
467 induced stress on the snowshoe hare cycle. *Ecology Monographs*, 79(5), 371–394.
- 468 Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A.,
469 ... Bolker, B. M. (2017). glmmTMB Balances speed and flexibility among packages for
470 Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, 9(2), 378–400.
- 471 Burrows, M. T., Harvey, R., & Robb, L. (2008). Wave exposure indices from digital
472 coastlines and the prediction of rocky shore community structure. *Marine Ecology*
473 *Progress Series*, 353, 1–12. <https://doi.org/10.3354/meps07284>
- 474 Burrows, M. T., & Hughes, R. N. (1991). Optimal foraging decisions by dogwhelks, *Nucella*

475 *lapillus* (L.) - influences of mortality risk and rate-constrained digestion. *Functional*
476 *Ecology*, 5(4), 461–475. <https://doi.org/10.2307/2389628>

477 Canero, E. M., & Hermitte, G. (2014). New evidence on an old question: Is the “fight or
478 flight” stage present in the cardiac and respiratory regulation of decapod crustaceans?
479 *Journal of Physiology Paris*. <https://doi.org/10.1016/j.jphysparis.2014.07.001>

480 Chase, J. M. (1999). Food web effects of prey size refugia: variable interactions and
481 alternative stable equilibria. *The American Naturalist*, 154(5), 559–570.
482 <https://doi.org/10.1086/303260>

483 Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral*
484 *Ecology*, 5(2), 159–170. <https://doi.org/10.1093/beheco/5.2.159>

485 Creel, S., Christianson, D., Liley, S., & Winnie, J. A. (2007). Predation risk affects
486 reproductive physiology and demography of elk. *Science*, 315(5814), 960.
487 <https://doi.org/10.1126/science.1135918>

488 Crothers, J. H. (1983). Variation in dog-whelk shells in relation to wave action and crab
489 predation. *Biological Journal of the Linnean Society*, 20(1), 85–102.
490 <https://doi.org/10.1111/j.1095-8312.1983.tb01591.x>

491 Crothers, J. H. (1985). Dog-whelks: An introduction to the biology of *Nucella lapillus* (L.).
492 *Field Studies*, 6, 291–360.

493 Dahlhoff, E. P., Stillman, J. H., & Menge, B. A. (2008). Physiological Community Ecology :
494 Variation in metabolic activity of ecologically important rocky intertidal invertebrates
495 along environmental gradients. *Integrative and Comparative Biology*, 42(4), 862–871.

496 DeWitt, T. J., Sih, A., & Hucko, J. A. (1999). Trait competition and cospecialization in a
497 freshwater snail: size, shape and antipredator behaviour. *Animal Behaviour*, 58, 397–
498 407. <https://doi.org/10.1006/anbe.1999.1158>

- 499 Dixon, A. F. G., & Agarwala, B. K. (1999). Ladybird-induced life-history changes in aphids.
500 *Proceedings of the Royal Society B: Biological Sciences*, 266(1428), 1549–1553.
501 <https://doi.org/10.1098/rspb.1999.0814>
- 502 Donelan, S. C., & Trussell, G. C. (2015). Parental effects enhance risk tolerance and
503 performance in offspring. *Ecology*, 96(8), 2049–2055.
504 <https://doi.org/doi.org/10.1890/14-1773.1>
- 505 Donelan, S. C., & Trussell, G. C. (2018). Synergistic effects of parental and embryonic
506 exposure to predation risk on prey offspring size at emergence. *Ecology*, 99(1), 68–78.
507 <https://doi.org/10.1002/ecy.2067>
- 508 Dunkin, S. D. B., & Hughes, R. N. (1984). Behavioural components of prey-selection by
509 dogwhelks, *Nucella lapillus* (L.), feeding on barnacles, *Semibalanus balanoides* (L.), in
510 the laboratory. *Journal of Experimental Marine Biology and Ecology*, 79(1), 91–103.
511 [https://doi.org/10.1016/0022-0981\(84\)90032-7](https://doi.org/10.1016/0022-0981(84)90032-7)
- 512 Edgell, T. C. (2010). Past predation risk induces an intertidal whelk (*Nucella lamellosa*) to
513 respond to more dilute concentrations of its predator's scent. *Marine Biology*, 157(1),
514 215–219. <https://doi.org/10.1007/s00227-009-1303-1>
- 515 Elner, R. W., & Hughes, R. N. (1978). Energy maximization in the diet of the shore crab,
516 *Carcinus maenas*. *Journal of Animal Ecology*, 47(1), 103–116.
517 <https://doi.org/10.2307/3925>
- 518 Etter, R. J. (1989). Life-History variation in the intertidal snail *Nucella Lapillus* across a
519 wave-exposure gradient. *Ecology*, 70(6), 1857–1876.
- 520 Feare, C. J. (1970). Aspects of the ecology of an exposed shore population of dogwhelks
521 *Nucella Lapillus* (L.). *Oecologia*, 5(1), 1–18.
- 522 Freeman, A. S., Dernbach, E., Marcos, C., & Koob, E. (2014). Biogeographic contrast of

523 *Nucella lapillus* responses to *Carcinus maenas*. *Journal of Experimental Marine*
524 *Biology and Ecology*, 452, 1–8. <https://doi.org/10.1016/j.jembe.2013.11.010>

525 Freeman, A. S., & Hamer, C. E. (2009). The persistent effect of wave exposure on TMIs and
526 crab predation in *Nucella lapillus*. *Journal of Experimental Marine Biology and*
527 *Ecology*, 372(1–2), 58–63. <https://doi.org/10.1016/j.jembe.2009.02.002>

528 Giesing, E. R., Suski, C. D., Warner, R. E., & Bell, A. M. (2011). Female sticklebacks
529 transfer information via eggs: Effects of maternal experience with predators on
530 offspring. *Proceedings of the Royal Society B: Biological Sciences*, 278(1712), 1753–
531 1759.

532 Guerra-Varela, J., Colson, I., Backeljau, T., Breugelmans, K., Hughes, R. N., & Rolán-
533 Alvarez, E. (2009). The evolutionary mechanism maintaining shell shape and molecular
534 differentiation between two ecotypes of the dogwhelk *Nucella lapillus*. *Evolutionary*
535 *Ecology*, 23(2), 261–280. <https://doi.org/10.1007/s10682-007-9221-5>

536 Handelsman, C. A., Broder, E. D., Dalton, C. M., Ruell, E. W., Myrick, C. A., Reznick, D.
537 N., & Ghalambor, C. K. (2013). Predator-induced phenotypic plasticity in metabolism
538 and rate of growth: Rapid adaptation to a novel environment. *Integrative and*
539 *Comparative Biology*, 53(6), 975–988. <https://doi.org/10.1093/icb/ict057>

540 Hawlena, D., Kress, H., Dufresne, E. R., & Schmitz, O. J. (2011). Grasshoppers alter jumping
541 biomechanics to enhance escape performance under chronic risk of spider predation.
542 *Functional Ecology*, 25(1), 279–288. <https://doi.org/10.1111/j.1365-2435.2010.01767.x>

543 Hawlena, D., & Schmitz, O. J. (2010). Herbivore physiological response to predation risk and
544 implications for ecosystem nutrient dynamics. *Proceedings of the National Academy of*
545 *Sciences*, 107(35), 15503–15507. <https://doi.org/10.1073/pnas.1009300107>

546 Hayes, J. P. (2001). Mass-specific and whole-animal metabolism are not the same concept.

547 *Physiological and Biochemical Zoology*, 74(1), 147–150.
548 <https://doi.org/10.1086/319310>

549 Holopainen, I. J., Aho, J., Vornanen, M., & Huuskonen, H. (1997). Phenotypic plasticity and
550 predator effects on morphology and physiology of crucian carp in nature and in the
551 laboratory. *Journal of Fish Biology*, 50(4), 781–798.
552 <https://doi.org/10.1006/jfbi.1996.0344>

553 Hughes, R. N., & Elner, R. W. (1979). Tactics of a predator, *Carcinus maenas*, and
554 morphological responses of the prey, *Nucella lapillus*. *Journal of Animal Ecology*,
555 48(1), 65–78. <https://doi.org/10.2307/4100>

556 Jablonka, E., & Raz, G. (2009). Transgenerational Epigenetic Inheritance: Prevalence,
557 mechanisms, and implications for the study of heredity and evolution. *The Quarterly*
558 *Review of Biology*, 84(2), 131–176. <https://doi.org/10.1086/598822>

559 Kamenos, N. A., Calosi, P., & Moore, P. G. (2006). Substratum-mediated heart rate
560 responses of an invertebrate to predation threat. *Animal Behaviour*, 71(4), 809–813.
561 <https://doi.org/10.1016/j.anbehav.2005.05.026>

562 Large, S. I., & Smee, D. L. (2010). Type and nature of cues used by *Nucella lapillus* to
563 evaluate predation risk. *Journal of Experimental Marine Biology and Ecology*, 396(1),
564 10–17. <https://doi.org/10.1016/j.jembe.2010.10.005>

565 Large, S. I., & Smee, D. L. (2013). Biogeographic variation in behavioral and morphological
566 responses to predation risk. *Oecologia*, 171(4), 961–969.
567 <https://doi.org/10.1007/s00442-012-2450-5>

568 Large, S. I., Smee, D. L., & Trussell, G. C. (2011). Environmental conditions influence the
569 frequency of prey responses to predation risk. *Marine Ecology Progress Series*, 422, 41–
570 49. <https://doi.org/10.3354/meps08930>

- 571 Legault, J., & Himmelman, C. (1993). Relation between escape behaviour of benthic marine
572 invertebrates and the risk of predation. *Journal of Experimental Marine Biology and*
573 *Ecology*, 170(1), 55–74. [https://doi.org/10.1016/0022-0981\(93\)90129-c](https://doi.org/10.1016/0022-0981(93)90129-c)
- 574 Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. (2004). ‘emmeans’: Estimated
575 Marginal Means, Aka Least-squares Means. R Package version 1.1. [https://CRAN.R-](https://CRAN.R-project.org/package=emmeans)
576 [project.org/ package=emmeans](https://CRAN.R-project.org/package=emmeans).
- 577 Lima, S. L. (1998). Stress and decision making under the risk of preation: recent
578 developments from behavioral reproductive, and ecological perspectives. *Advances in*
579 *the Study of Behavior*, 27, 258–289. [https://doi.org/10.1016/S0065-3454\(08\)60366-6](https://doi.org/10.1016/S0065-3454(08)60366-6)
- 580 Lima, S. L., & Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator
581 behavior: The Predation Risk Allocation Hypothesis. *The American Naturalist*, 153(6),
582 649–659. <https://doi.org/10.1086/303202>
- 583 Lima, S. L., & Dill, L. M. (1990). Behavioral decision made under the risk of predation: a
584 review and prospectus. *Canadian Journal of Zoology*, 68, 619–640.
585 <https://doi.org/10.1086/303202>
- 586 Love, O. P., McGowan, P. O., & Sheriff, M. J. (2013). Maternal adversity and ecological
587 stressors in natural populations: The role of stress axis programming in individuals, with
588 implications for populations and communities. *Functional Ecology*, 27(1), 81–92.
589 <https://doi.org/10.1111/j.1365-2435.2012.02040.x>
- 590 Lundvall, D., Svanbäck, R., Persson, L., & Byström, P. (1999). Size-dependent predation in
591 piscivores: Interactions between predator foraging and prey avoidance abilities.
592 *Canadian Journal of Fisheries and Aquatic Sciences*, 56(7), 1285–1292.
593 <https://doi.org/10.1139/f99-058>
- 594 Mäkinen, T., Panova, M., Johannesson, K., Tatarenkov, A., Appelqvist, C., & André, C.

595 (2008). Genetic differentiation on multiple spatial scales in an ecotype-forming marine
596 snail with limited dispersal: *Littorina saxatilis*. *Biological Journal of the Linnean*
597 *Society*, 94(June), 31–40. <https://doi.org/10.1111/j.1095-8312.2008.00960.x>

598 Mangel, M., & Clark, C. (1986). Towards a Unified Foraging Theory. *Ecology*, 67(5), 1127–
599 1138.

600 Matassa, C M, & Trussell, G. C. (2014). Prey state shapes the effects of temporal variation in
601 predation risk. *Proceedings of the Royal Society B*, 281.
602 <https://doi.org/dx.doi.org/10.1098/rspb.2014.1952>

603 Matassa, Catherine M., & Trussell, G. C. (2011). Landscape of fear influences the relative
604 importance of consumptive and nonconsumptive predator effects. *Ecology*, 92(12),
605 2258–2266. <https://doi.org/10.1890/11-0424.1>

606 McMahon, R. F. (1988). Respiratory response to periodic emergence in intertidal molluscs.
607 *American Zoologist*, 28(1), 97–114. <https://doi.org/10.1093/icb/28.1.97>

608 Menge, B. A. (1976). Organization of the New England rocky intertidal community: role of
609 predation, competition, and temporal heterogeneity. *Ecological Monographs*, 46(4),
610 355–393. <https://doi.org/10.2307/1942563>

611 Menge, B. A. (1983). Components of predation intensity in the low zone of the New England
612 rock intertidal zone. *Oecologia*, 58(2), 141–155. <https://doi.org/10.1007/BF00399210>

613 Mitchell, M. D., Bairos-Novak, K. R., & Ferrari, M. C. O. (2017). Mechanisms underlying
614 the control of responses to predator odours in aquatic prey. *The Journal of Experimental*
615 *Biology*, 220(11), 1937–1946. <https://doi.org/10.1242/jeb.135137>

616 Packard, G. C., & Boardman, T. J. (1999). The use of percentages and size-specific indices to
617 normalize physiological data for variation in body size: Wasted time, wasted effort?
618 *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*,

619 122(1), 37–44. [https://doi.org/10.1016/S1095-6433\(98\)10170-8](https://doi.org/10.1016/S1095-6433(98)10170-8)

620 Paine, R. T. (1976). Size-limited predation: An observational and experimental approach with
621 the *Mytilus-Pisaster* interaction. *Ecology*, 57(5), 858–873.
622 <https://doi.org/10.2307/1941053>

623 Paradis, A. R., Pepin, P., & Brown, J. A. (1996). Vulnerability of fish eggs and larvae to
624 predation: review of the influence of the relative size of prey and predator. *Canadian*
625 *Journal of Fisheries and Aquatic Sciences*, 53(6), 1226–1235.
626 <https://doi.org/10.1139/cjfas-53-6-1226>

627 Poethke, H. J., Weisser, W. W., & Hovestadt, T. (2010). Predator-induced dispersal and the
628 evolution of conditional dispersal in correlated environments. *The American Naturalist*,
629 175(5), 577–586. <https://doi.org/10.1086/651595>

630 Preisser, E. L., Orrock, J. L., & Schmitz, O. J. (2007). Predator hunting mode and habitat
631 domain alter nonconsumptive effects in predator-prey interactions. *Ecology*, 88(11),
632 2744–2751. <https://doi.org/10.1890/07-0260.1>

633 R Core Team. (2013). R: a language and environment for statistical computing. R Foundation
634 for Statistical Computing. Retrieved from <http://www.r-project.org/>

635 Robinson, E. M., Smee, D. L., & Trussell, G. C. (2011). Green crab (*Carcinus maenas*)
636 foraging efficiency reduced by fast flows. *PLoS ONE*, 6(6), 1–8.
637 <https://doi.org/10.1371/journal.pone.0021025>

638 Rochette, R., Dill, L. M., & Himmelman, J. H. (1997). A field test of threat sensitivity in a
639 marine gastropod. *Animal Behaviour*, 54(5), 1053–1062.
640 <https://doi.org/10.1006/anbe.1997.0488>

641 Rochette, R., & Himmelman, J. H. (1996). Does vulnerability influence trade-offs made by
642 whelks between predation risk and feeding opportunities? *Animal Behaviour*, 52(4),

643 783–794. <https://doi.org/10.1006/anbe.1996.0223>

644 Rochette, R., Maltais, M.-J., Dill, L. M., & Himmelman, J. H. (1999). Interpopulation and
645 context-related differences in responses of a marine gastropod to predation risk. *Animal*
646 *Behaviour*, *57*(4), 977–987. <https://doi.org/10.1006/anbe.1998.1061>

647 Rolán, E., Guerra-Varela, J., Colson, I., Hughes, R., & Rolan-Alvarez, E. (2004).
648 Morphological and Genetic analysis of two sympatric morphs of the dogwhelk *Nucella*
649 *lapillus* (Gastropoda:Muricidae) from Galicia (Northwestern Spain). *Journal of*
650 *Molluscan Studies*, *70*(2), 179–185. <https://doi.org/10.1093/mollus/70.2.179>

651 Scharf, F. S., Juanes, F., & Rountree, R. A. (2000). Predator size - prey size relationships of
652 marine fish predators : interspecific variation and effects of ontogeny and body size on
653 trophic-niche breadth. *Marine Ecology Progress Series*, *208*, 229–248.
654 <https://doi.org/10.3354/meps208229>

655 Schmitz, O. J., Beckerman, A. P., & O'Brien, K. M. (1997). Behaviorally Mediated Trophic
656 Cascades : Effects of predation risk on food web interactions. *Ecology*, *78*(5), 1388–
657 1399. [https://doi.org/doi.org/10.1890/0012-9658\(1997\)078\[1388:BMTCEO\]2.0.CO;2](https://doi.org/doi.org/10.1890/0012-9658(1997)078[1388:BMTCEO]2.0.CO;2)

658 Schmitz, O. J., Krivan, V., & Ovadia, O. (2004). Trophic cascades: The primacy of trait-
659 mediated indirect interactions. *Ecology Letters*, *7*(2), 153–163.
660 <https://doi.org/10.1111/j.1461-0248.2003.00560.x>

661 Slos, S., & Stoks, R. (2008). Predation risk induces stress proteins and reduces antioxidant
662 defense. *Functional Ecology*, *22*(4), 637–642. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2435.2008.01424.x)
663 [2435.2008.01424.x](https://doi.org/10.1111/j.1365-2435.2008.01424.x)

664 Steiner, U. K., & Van Buskirk, J. (2009). Predator-induced changes in metabolism cannot
665 explain the growth/predation risk tradeoff. *PLoS ONE*, *4*(7), 2–5.
666 <https://doi.org/10.1371/journal.pone.0006160>

- 667 Stickle, W. B., Moore, M. N., & Bayne, B. L. (1985). Effects of temperature, salinity and
668 aerial exposure on predation and lysosomal stability of the dogwhelk *Thais (Nucella)*
669 *lapillus* (L.). *Journal of Experimental Marine Biology and Ecology*, *93*(3), 235–258.
670 [https://doi.org/10.1016/0022-0981\(85\)90242-4](https://doi.org/10.1016/0022-0981(85)90242-4)
- 671 Trussell, G. C., Ewanchuk, P. J., Bertness, M. D., & Silliman, B. R. (2004). Trophic cascades
672 in rocky shore tide pools: Distinguishing lethal and nonlethal effects. *Oecologia*, *139*(3),
673 427–432. <https://doi.org/10.1007/s00442-004-1512-8>
- 674 Trussell, G. C., Ewanchuk, P. J., & Matassa, C. M. (2006a). Habitat effects on the relative
675 importance of trait- and density-mediated indirect interactions. *Ecology Letters*, *9*(11),
676 1245–1252. <https://doi.org/10.1111/j.1461-0248.2006.00981.x>
- 677 Trussell, G. C., Ewanchuk, P. J., & Matassa, C. M. (2006b). The fear of being eaten reduces
678 energy transfer in a simple food chain. *Ecology*, *87*(12), 2979–2984.
679 [https://doi.org/10.1890/0012-9658\(2006\)87\[2979:TFOBER\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2979:TFOBER]2.0.CO;2)
- 680 Tyler, C. L., Stafford, E. S. S., & Leighton, L. R. R. (2014). The utility of wax replicas as a
681 measure of crab attack frequency in the rocky intertidal. *Journal of the Marine*
682 *Biological Association of the United Kingdom*, *95*(02), 361–369.
683 <https://doi.org/10.1017/S0025315414001210>
- 684 Vadas, R. L., Burrows, M. T., & Hughes, R. N. (1994). Foraging strategies of dogwhelks,
685 *Nucella lapillus* (L.): interacting effects of age, diet and chemical cues to the threat of
686 predation. *Oecologia*, *100*(4), 439–450. <https://doi.org/10.1007/BF00317866>
- 687 Van Dievel, M., Janssens, L., & Stoks, R. (2016). Short- and long-term behavioural,
688 physiological and stoichiometric responses to predation risk indicate chronic stress and
689 compensatory mechanisms. *Oecologia*, *181*(2), 347–357.
690 <https://doi.org/10.1007/s00442-015-3440-1>

- 691 Weissburg, M. J., James, C. P., Smee, D. L., & Webster, D. R. (2003). Fluid mechanics
692 produces conflicting, constraints during olfactory navigation of blue crabs, *Callinectes*
693 *sapidus*. *Journal of Experimental Biology*, 206(1), 171–180.
694 <https://doi.org/10.1242/jeb.00055>
- 695 Werner, E. E., Gilliam, J. F., Hall, D. J., Mittelbach, G. G., Gilliam, J. F., & Mittelbach, G.
696 G. (1983). An experimental test of the effects of predation risk on habitat use in fish.
697 *Ecology*, 64(646), 1540–1548. <https://doi.org/10.2307/1937508>
- 698 Werner, E. E., & Peacor, S. D. (2003). A review of trait-mediated indirect interactions in
699 ecological communities. *Ecology*, 84(5), 363–397. [https://doi.org/10.1007/978-4-431-](https://doi.org/10.1007/978-4-431-56033-3_14)
700 [56033-3_14](https://doi.org/10.1007/978-4-431-56033-3_14)
- 701 Zimmer, R. K., & Butman, C. A. (2000). Chemical signaling processes in marine
702 environment. *The Biological Bulletin*, 198(2), 168–187. <https://doi.org/10.2307/1542522>

703 Appendix

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707 **Table 1** Wave fetch indices for exposed and sheltered sites using the Burrows et al. (2008)
708 map-based method using 32 angular sectors and mean crab number per trap per site

709

710	Site	Wave exposure	Mean fetch (km)	Mean crab number (SE)
711	Moelfre	Sheltered	11.71	54.66 (10.7)
712	Porth Cwefan	Sheltered	26.62	45.66 (4.48)
713	Bull Bay	Sheltered	15.37	23.33 (3.17)
714	Point Lynas	Exposed	55.10	0.00 (0.00)
715	Cemlyn Bay	Exposed	55.64	1.33 (0.88)
716	Trearddur Bay	Exposed	37.89	1.33 (0.88)

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720 **Table 2** Field and laboratory model selection results for the potential influence of predation
 721 risk on wave-exposed and wave-sheltered populations of dogwhelks

722 723		Terms removed	<i>df</i>	Field	Laboratory	Movement
724	3-way factorial		11	700.52	619.47	1478.19
725	2-way interaction	E*T*S	10	700.52	617.67	1476.61
726		T*S	9	706.07	619.47	1486.37
727		E*S	9	696.98	629.18	1478.99
728		E*T	9	696.98	615.74	1475.10
729	Single 2-way interaction	E*S + T*S	8	704.20	627.26	1485.34
730		E*T + T*S	8	705.28	629.54	1488.90
731		E*T + E*S	8	696.58	616.86	1478.19
732	Fixed terms	E*T + E*S + T*S	7	703.37	627.60	1487.41
733		T	6	717.00	643.29	1500.16
734		S	6	766.94	688.82	1485.59
735		E	6	701.87	627.26	1490.31
736	Single fixed terms	T + S	5	785.58	704.94	1499.03
737		E + S	5	715.65	642.90	1503.99
738		E + T	5	765.00	687.03	1488.46
739	Random factor	Site	10	699.21	617.67	1476.19

740

741 E = wave exposure, T = risk treatment, S = size (vulnerability). Models were selected using
 742 generalized linear square models and corrected Akaike information criterion (AICc) for all
 743 dependent variables. Selected models are highlighted in bold.

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746 **Table A1** Post hoc Tukey’s HSD test results for significant interactions from GLMMs conducted on data from field and laboratory experiments

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Experiment	Model	Factor	Contrast		Combination	Estimate	Z ratio	P	
			Levels						
Field O ₂ consumption	O ₂ con ~ Vulnerability + Risk treatment + Wave exposure + Vulnerability * Risk treatment + (1 Site) + (1 Nucella ID)	Risk treatment	No predator	vs	Predator	Vulnerable	-0.0608	-0.609	0.914
						Invulnerable	-0.4573	-5.290	<0.001
Laboratory O ₂ consumption	O ₂ con ~ Vulnerability + Risk treatment + Wave exposure + Vulnerability * Risk treatment + (1 Site) + (1 Nucella ID)	Risk treatment	No predator	vs	Predator	Vulnerable	-0.3379	-5.883	<0.001
						Invulnerable	-0.0555	-1.094	0.644
Laboratory movement analysis	Movement ~ Vulnerability + Risk treatment + Wave exposure + Vulnerability * Risk treatment + Wave exposure * Risk treatment + (1 Site) + (1 Nucella ID)	Risk treatment	No predator	vs	Predator	Vulnerable	-1.6137	-5.052	<0.001
						Invulnerable	-0.2426	-0.984	0.715
		Risk treatment	No predator	vs	Predator	Sheltered	-1.3559	-4.401	<0.001
						Exposed	-0.5004	-1.982	0.157

748 ‘Vulnerable’/‘invulnerable’ refers to level of vulnerability to predators; ‘sheltered’/‘exposed’ refers to level of wave exposure. Statistically
 749 significant models ($P = 0.001$) are in bold.

750 **Figure 1** Map of study sites across the Isle of Anglesey, Wales, U.K.

751 **Figure 2** Mean number (\pm SE) of *C. maenas* caught per trap for exposed and sheltered shores.

752 * $P < 0.01$ (t test).

753 **Figure 3** Field oxygen consumption rates (mean \pm SE) of vulnerable and invulnerable
754 dogwhelks from sheltered and exposed shores in filtered sea water (no predator cue) and under
755 predation risk (predator cue). Different letters indicate significantly different results from a
756 post hoc Tukey's HSD.

757 **Figure 4** Laboratory oxygen consumption rates (mean \pm SE) of vulnerable and invulnerable
758 dogwhelks from sheltered and exposed shores in filtered sea water (no predator cue) and under
759 predation risk (predator cue). Different letters indicate significantly different results from a
760 post hoc Tukey's HSD.

761 **Figure 5** Movement (mean \pm SE) of invulnerable and vulnerable dogwhelks from sheltered
762 and exposed shores in filtered sea water (grey bars) and under predation risk (white bars).
763 Different letters indicate significantly different results from a post hoc Tukey's HSD.

764 **Figure 6** Combined movement (mean \pm SE) of all size classes of dogwhelks from sheltered
765 and exposed shores in filtered sea water (grey bars) and under predation risk (white bars).

766 Different letters indicate significantly different results from a post hoc Tukey's HSD.

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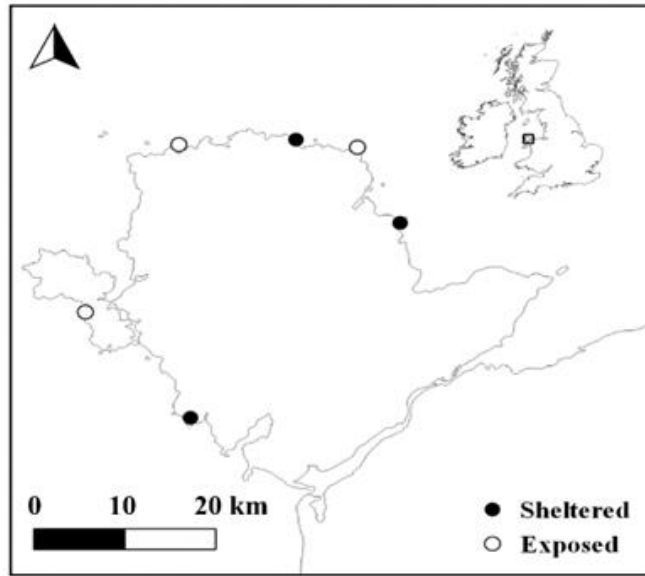
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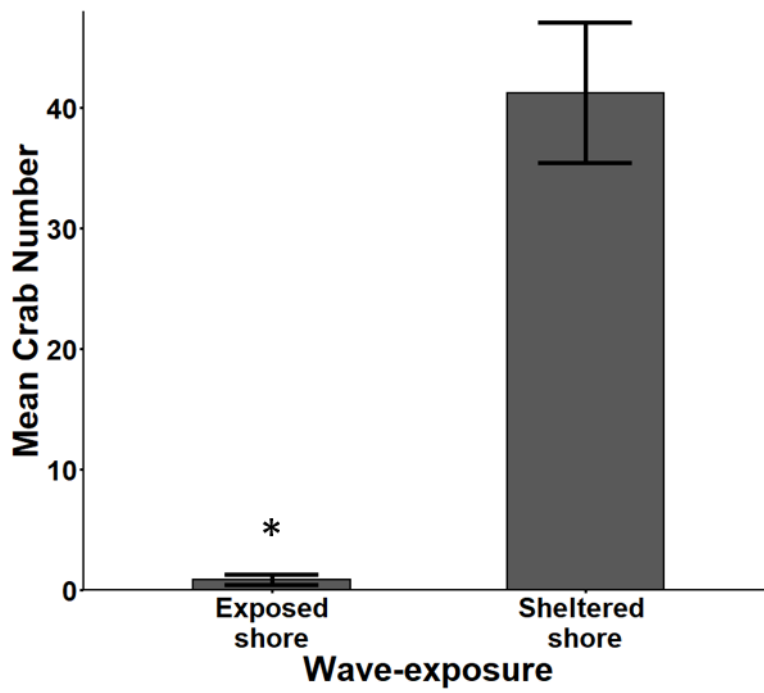
773 **Figure 1**

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775 **Figure 2**

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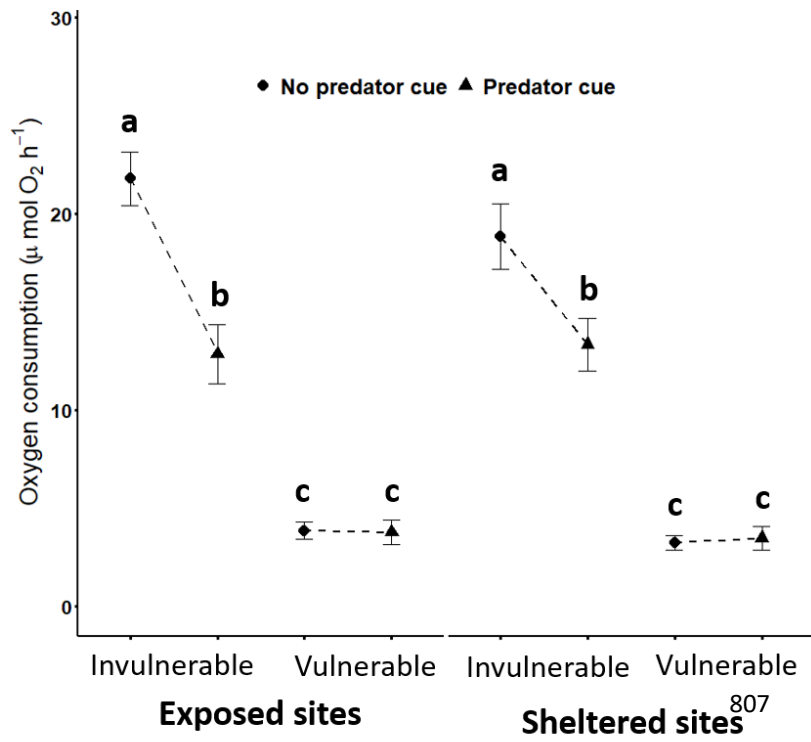
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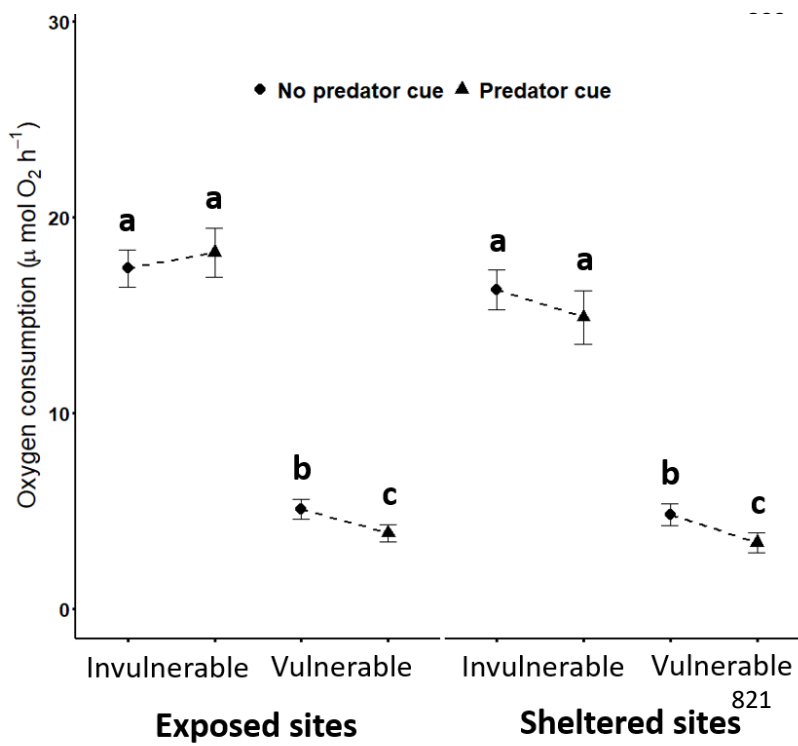
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794 **Figure 3**



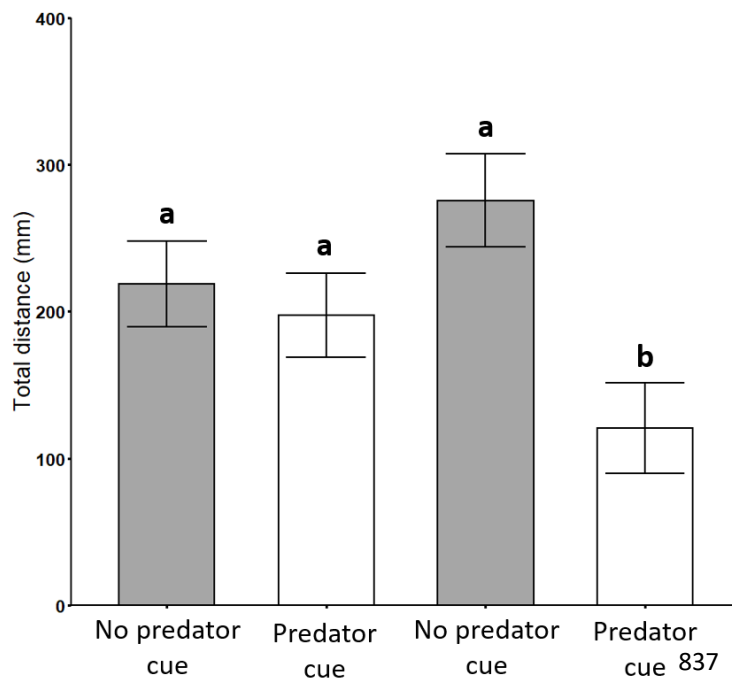
808 **Figure 4**



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824 **Figure 5**



838 **Figure 6** *Invulnerable Nucella* *Vulnerable Nucella* 6

