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The Role of Dislodgement in the Territorial Ecology of the Owl Limpet, *Lottia gigantea*

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16   **Highlights:** Territorial owl limpets have the capacity to completely dislodge competing

17   conspecifics, presumably increasing the adaptive value of this behavior.

18

19   Ascertaining the risks and benefits of different behaviors is a central goal of research on

20   territoriality. Although most territorial behavior is ritualized, with concomitant reduced risks for

21   both residents and intruders, this ritualization is generally found to be underpinned by rare,

22   highly consequential, interactions. The agonistic behavior of the intertidal owl limpet, *Lottia*

23   *gigantea*, involves defense of a feeding territory, and includes a relatively explosive thrusting

24   response by territory holders against intruding conspecifics. We here ask whether this thrusting

25   behavior is capable of entirely dislodging intruders from their rocky wave-swept substratum,

26   thereby ridding the resident of future challenges by that intruder. Our field measurements of the

27   strength of territorial thrusts, as well as thrust resistance, indicate that territorial limpets are

28   strong enough to overcome the resistance of small to medium sized (< 40 mm) conspecifics

29   encountered on their territories. Interestingly, at least 44% of the limpets dislodged from the

30   rock substratum during a retreat or territorial response survived in a new location. Growth of

31   these survivors was at least as rapid as that of undisturbed limpets in the old location.

32   We conclude that shell thrusting during the territorial response of *Lottia gigantea* can

33   reduce the cost of territorial defense by dislodging smaller conspecifics, thereby eliminating

34   them from all future interactions. Conversely, the risk incurred by these smaller conspecifics

35   while intruding onto territories of larger individuals is likely mitigated by the surprisingly high

36   survival rate, and subsequent normal growth, of dislodged limpets.

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38   KEY WORDS: risks, benefits, defense, intrusion, waves, retreat, aggression.

39   **Running title:** Territorial dislodgement

40

INTRODUCTION

42   A full understanding of any natural behavior should include knowledge of the costs and

43   benefits of specific behavioral alternatives (Stamps 1994; Hinsch & Komdeur 2010; Rubenstein

44   & Alcock 2018). Such knowledge is particularly important for understanding the evolution of

45   agonistic behavioral systems (Adams 2001). Feeding territoriality is a good example of this: for

46   such territoriality to evolve and persist, costs of defending a territory from multiple intruders

47   must be offset by the benefits of that defense (Ewald & Bransfield 1987; Hinsch et al. 2012;

48   Hinsch & Komdeur 2017b). If there are too many intruders incurring little risk while stealing

49   food from a territorial resident, territorial behavior becomes too costly, and will not persist. On

50   the other hand, if the risk of death or damage to intruders in the face of the resident's territorial

51   defense is too high, intrusion will become rare or absent (Hinsch & Komdeur 2010).   Thus,

52   questions of the risks and benefits of intruding onto a feeding territory, as well as those of

53   defending one, are key to predicting when territorial behavior is likely to evolve/persist. The

54   present study initiates an investigation of these risks and benefits in the limpet, *Lottia gigantea*

55   (Mollusca Gastropoda Patellogastropoda).

56   Patellogastropod limpets comprise a speciose monophyletic clade of gastropods that

57   primarily graze the micro-algae that grows on marine near-shore rocky substrates. World-wide,

58   individuals of some 10 species, scattered among ca 214 species of near-shore patellogastropods

59   (Branch 1975a, 1975b, 1976, 1981, Mmonwa et al. 2017; D. Lindberg pers. comm.; pers.

60   comm.), defend small (< 3000 cm^2) discrete feeding territories from con- and heterospecifics,

61   which intrude in an attempt to feed on the richer algal resources there (Beebe 1942; Galbraith

62   1965; Stimson 1970; Branch 1975a, 1975b, 1976, 1981; Shanks 2002). The only ecological

63   correlate of is that virtually all territorial limpet species live in habitats with relatively high wave

64   activity. However, many non-territorial limpets inhabit such habitats, diminishing the value of

65   this correlate. In any case, these territorial limpet species present a clear opportunity to test

66   hypotheses about territorial ecology in a lineage entirely separate from the vertebrates and

67   insects that comprise the majority of studies on territoriality.   Furthermore, their accessibility

68   and limited territory size make them amenable to experimental manipulation (Stimson 1970,

69   1973; Wright 1982).

70   Among the 26 limpet species found on the west coast of North America (D. Lindberg pers.

71   comm.), only *Lottia gigantea* shows unequivocal territorial behavior (Stimson, 1970; Wright

72   1982, 1989; Wright & Shanks 1993), although limited quasi-aggressive behavior around home

73   scars has been reported for *L. scabra* (Sutherland 1970). *Lottia gigantea* is a long-lived (Wright

74   1989; Fenberg & Roy 2012) patellogastropod, whose territorial individuals defend small (400–

75   2000 cm^2; Stimson 1970) territories from other con- and heterospecific grazers (Stimson 1970,

76   1973; Wright 1982, 1985; Wright & Shanks 1993; Shanks 2002). A resident protects its feeding

77   territory by pursuing and pushing intruders to the perimeter of its territory (Stimson 1970, 1973;

78   Wright 1982). In the present study, we tested whether this territorial behavior is vigorous

79   enough to break the seal of a conspecific intruder with the rocky substratum, making it

80   vulnerable to being washed off the substratum by a passing wave.

81   Previous investigators of territorial behavior in *L. gigantea* have observed such

82   dislodgement, but only of "bait limpets", artificially introduced individuals of *L. gigantea*,

83   previously removed from another area and then placed in the path of a territorial resident

84   (Stimson 1970; Wright 1982). Investigators have generally assumed that naturally intruding

85   conspecifics also risk dislodgement by the bulldozing resident. This assumption is quite

86   significant, because many intertidal ecologists hold that dislodgement necessarily leads to death

4

87   (Denny 1985; Boulding & Van Alstyne 1993; Trussell 1997) as a consequence of predation by

88   mobile (Wells 1980; Pawlik et al. 1986; Silva et al. 2008, 2010) or sessile (Sebens 1981; Ricketts

89   et al. 1992; McQuaid et al. 1999) predators. In any case, the assumption that territorial residents

90   can dislodge intruders has remained untested, because adhesion to the substratum of artificially

91   introduced intruders is severely compromised (Shanks et al. 1986; Smith 1992, 2002; Shanks

92   2002).   Thus, such previously removed "bait limpets" placed in front of moving territorial

93   limpets are likely to be much more weakly adhered to the substratum than unmanipulated

94   moving limpets. Furthermore, because natural territorial encounters are relatively rare and

95   limpet behavior is difficult to observe when the tide is in (Stimson 1970; Wright 1982, 1985,

96   1989), direct observations of natural territorial intrusions in the field are few (Wright 1982, 1985,

97   1989), and observation of dislodgement of natural intruders by residents is lacking.

98   Dislodgement of intruders by territorial limpets is thus the focus of the present study,

99   which asks three questions: (1) Which, if any, conspecific intruders onto territories can be

100   dislodged from the substratum by the thrusts of the resident? (2) If these thrusts do dislodge

101   intruders, what are their chances of survival? (3) How does the growth rate of dislodged limpets,

102   subsequent to dislodgement, compare to that of undisturbed conspecifics?

103   METHODS

104   Mason et al. (2018) compared the hydrostatic lift force required for a wave to wash off

105   individuals of *L. gigantea* engaged in different agonistic behaviors to the calculated lift forces of

106   local wave action in order to estimate wash-off risk of behaving limpets. Here, we employed

107   variations of these methods to compare the maximum shear forces exerted by limpets during

108   their territorial response to the ability of intruding limpets to resist such shear forces.

109   *Risk of dislodgement*

5

110   During negative daytime low-low tides (< 0.0 m), we identified prospective territorial

111   limpets, i.e., limpets > 15 mm larger than their largest neighbor within 0.5 m. Onto the top of

112   each of these limpets we glued a permanent numbered tag using water-proof two-part epoxy

113   ("Splash Zone", Z-spar Inc). To enable later measurement of the strength of their territorial

114   thrust (see below), we also glued a screw eye to the posterior part of each limpet's shell (Fig. 1).

115   We measured the longest length of each limpet to the nearest 0.3 mm using digital calipers. We

116   also identified prospective retreater limpets. A prospective retreater has one or more neighbors

117   (within less than 0.5 m), whose shell lengths are at least 15 mm longer than its own. We tagged,

118   and measured prospective retreaters, as above.

119   Field observations of limpet behavior were conducted June through September 2012, and

120   July 2014–January 2015, near Corona del Mar, California (33.591413°N, 117.872104°W),

121   mainly after dark when predicted high-low tidal heights were 0.4–0.6 m above mean lower-low

122   water. We found such high-low tides to be high enough to consistently wet most limpets, and at

123   the same time low enough to allow unobstructed observation of behavior. During these

124   observations, we identified foraging subject limpets by the presence of anterior cephalic tentacles

125   extended beyond their shell (Wright 1982; Mason et al. 2018).

126   *Thrust capacity*

127   Upon identifying a foraging limpet with a tag and a posterior screw eye, we first induced

128   territorial behavior by contacting the head/tentacles, mantle or foot of a recently removed

129   conspecific "bait" limpet to the cephalic tentacles of the prospective territorial subject (Fig. 1).

130   Once the subject's territorial response was initiated (movement of more than one shell length in

131   less than 90 sec in pursuit of the bait limpet), we connected a line from the attached screw-eye on

132   the subject limpet to a spring scale with a maximum reading pointer, all the while maintaining

133   contact of the bait limpet to the cephalic tentacles of the subject. Once the line was taut, the

134   spring scale was held steady to measure the maximum force exerted by the subject as it moved in

135   pursuit of the bait limpet (see Fig. 1).

136   *Resistance to thrust force*

137   To measure resistance to thrust force, we first placed a bait limpet in front of a limpet foraging

138   near a larger conspecific (Fig. 2). As the subject limpet turned away from the bait limpet, we

139   maintained contact of the soft parts of the bait and subject limpets (Fig. 2, top panels), first

140   touching the bait limpet to the tentacles of the subject limpet, and, upon the subject turning

141   farther than 90° from its initial orientation, shifting the bait-limpet contact to more posterior parts

142   of the subject's mantle and foot. Limpets were defined as "retreating" if they moved more than

143   90° away from the point of contact within 90 sec. Once a subject had retreated 1–3 shell lengths

144   we measured its resistance to shear force (Fig. 2, top panels) by dragging an empty limpet shell

145   (ca 55 mm), with a line attached to a spring scale with a maximum reading pointer, up against

146   the retreating subject limpet. We continually held the anterior end of the empty limpet shell

147   lightly against the substratum, while pulling the spring scale-line-shell across the subject limpet

148   with a constant velocity approximating that of moving territorial limpets (5–20 cm·min⁻¹, Wright

149   1982; Mason et al. 2018) until the subject was dislodged (Fig. 2, upper right panel). Note that

150   this meant that the actual force applied by the dragged shell across the subject necessarily

151   increased, sometimes substantially, over the 1–2 sec of contact with the empty shell, until the

152   subject was dislodged, at which point the maximum reading pointer would register this "force to

153   dislodge." In this way, we measured and recorded the thrust force required by this model of a

154   territorial resident to dislodge an actively retreating intruder. Some subject limpets did not

155   retreat in response to intraspecific contact, but, instead, simply continued foraging. We tested

156 the dislodgement force of these limpets as well (Fig. 2, lower panels). Many of the limpets on

157 which thrust resistance was measured were not previously tagged. Such limpets were retained

158 after dislodgement to allow measurement of their shell length to the nearest 0.3 mm with digital

159 calipers.

160 *Effect of dislodgement on mortality and growth rate*

161 Some of the dislodged limpets had been previously tagged and measured. These limpets were

162 not retained when they were dislodged, but instead allowed to be taken by the waves. On four

163 separate occasions, we performed multiple (8–20) such dislodgements on different tagged

164 limpets. Two weeks after each of those occasions (30 July, 24 October, 22 and 23 December

165 2014; 21 January 2015) we returned to the same intertidal region to search for survivors among

166 these dislodged limpets.

167   On the first of those occasions (30 July 2015), we remeasured shell length of survivors,

168 as well as the shell length of many additional limpets that had been tagged, but not previously

169 dislodged (most were not moving during the high-low tide 2 weeks before). This "undislodged"

170 group comprised a control against which the growth of the dislodged limpets could be compared.

171 We then returned to the intertidal 5.3 months later (7 January 2015) to measure shell length, and

172 thereby growth rate of both dislodged (seven of the nine survivors still had their tags) and

173 untouched control limpets. Note that limpet growth in shell length represents the net sum of

174 shell added and shell eroded (Wright 1985; Shanks & Wright 1986) and can thus be negative,

175 indicating that the limpet has accreted less shell material than has been eroded.

176   All statistical tests of significance (t-tests, correlation, regression slopes, analysis of

177 covariance) are 2-tailed. We report averages ± standard error of means. We plot scattergrams,

178 and report Pearson's R^2 (and two-tailed *P*-value) for generated Thrust Force vs Shell Length. To

179   understand the functional relationships of Thrust resistance to combinations of Shell Length and

180   Behavior and their interaction, we performed a full interaction general linear model (lm: Thrust

181   Resistance ~ Shell Length + Behavior + Shell Length:Behavior; R-project) on the data.

<center>RESULTS</center>

183   *Thrust capacity*

184   We found wide variation in the capacity of territorial limpets to generate thrust force (1.8-6.7 N,

185   mean = 4.6 ± 0.3), and much of this variation was correlated with shell length (Fig. 3; $R^2 = 0.43$,

186   n = 27, $P = 0.0002$).

187   *Resistance to thrust*

188   The full linear model of thrust resistance as a function of shell length, behavior, and their

189   interaction ($F_{3,30} = 64$, $P < 0.0001$), revealed significant main effects of shell length ($P < 0.0001$)

190   and behavior ($P = 0.002$) on thrust resistance (Fig. 4): thrust resistance was positively correlated

191   with shell length for both retreaters (Fig. 4, gray symbols, $R^2 = 0.36$, N = 26, $P = 0.001$) and

192   continued foragers (Fig. 4, open symbols, $R^2 = 0.66$, N = 8, $P = 0.014$), and limpets that

193   continued foraging resisted thrust more effectively (6.6–61.2 N, mean = 35.3 ± 7.2 N, Fig. 4,

194   white symbols) than did limpets that retreated (0.2–16 N, mean = 4.7 N ± 0.8, Fig. 4, gray

195   symbols), and in addition, there was a highly significant interaction between shell length and

196   behavior in predicting thrust resistance ($P < 0.0001$), reflecting the clear pattern that thrust

197   resistance ascended much more steeply with increased shell length (slope = 1.8 N • mm^{-1}) in

198   limpets that continued foraging than it did in limpets that retreated (slope = 0.27 N • mm^{-1}).

199

200   *Thrust capacity vs resistance*

201   In Fig. 5, results from Fig. 3 are plotted with those from Fig. 4 to visualize which limpets are

<center>9</center>

202 vulnerable to being dislodged by territorial limpets. Also shown is the window of vulnerability

203 (grey area); its height represents the maximum thrust-force (6.7 N), observed from a territorial

204 limpet. Thrust resistance of retreating limpets was dangerously weak: 20 of 26 limpets (77%)

205 were dislodged by less than 6.7 N, thus putting them in the window of vulnerability. By contrast

206 the resistance of only one of eight limpets (13%) that continued slow foraging in response to the

207 bait limpet was vulnerable to dislodgement. These data indicate that limpets that continued slow

208 foraging in response to intraspecific contact were unlikely to be dislodged by a thrusting

209 territorial limpet, whereas the reduced tenacity of those that chose to retreat, especially those

210 smaller than 40 mm, made them more vulnerable to such thrusts.

211 *Survival/growth of dislodged limpets*

212 On four different dates, we baited tagged subject limpets into agonistic (retreat or territorial)

213 behavior, and upon their beginning rapid agonistic behavior, dislodged them (see Methods). The

214 survivorship of limpets dislodged during these semi-natural behavioral interactions was

215 surprisingly high (average of each of the four dates: 0.446 ± 0.068, Fig. 6). We did not estimate

216 survival of limpets that were dislodged during continued foraging because their likelihood of

217 dislodgement by a territorial limpet was so low (see previous paragraph).

218　　　Growth of limpets following dislodgement during "chase behavior" (territorial limpets

219 combined with retreat limpets, Fig. 7, $N = 7$) was similar to that of untouched control limpets

220 over the same period ($N = 54$), although the growth of the two limpets dislodged after retreat

221 behavior trended higher than expected.

222　　　　　　　　　　　　　　　　DISCUSSION

223　　　This field comparison of potency of territorial defense to the resistance of intruders to

224 that defense is the first evidence among territorial limpets that their territorial thrusting can

225   dislodge and thereby eliminate small intruders from future competitive interactions. To the

226   extent that residents have opportunities to successfully deploy this behavior, it can significantly

227   reduce their future competitive costs: Each intruder removed in this way would reduce the

228   number of subsequent territorial responses required, thereby reducing energy expended on

229   territory defense. It would also reduce the risk of wash-off by waves during subsequent

230   territorial chase of the same intruder (Mason et al. 2018). Finally, it would also increase

231   availability of future algal food, which would otherwise be exploited by the persistent intruder

232   (Shanks 2002). Such an effective weapon against the efficient exploitation of territorial gardens

233   by small intruding limpets (Stimson 1970; Shanks 2002) contributes, perhaps critically, to the

234   economics of territoriality in this limpet species. If *L. gigantea* did not have this dislodging

235   territorial behavior, but could instead only manage slow, steady displacement of intruders to the

236   territory perimeter, displaced intruders would likely re-invade, incurring additional costs for the

237   resident that might well outweigh the benefits of territorial behavior.

238   Given this measured danger level of a resident's thrusting territorial response, it is

239   perhaps surprising that small conspecifics so readily intrude onto the territories of larger limpets

240   (Stimson 1970; Wright 1982, 1985, 1989; Wright & Shanks 1984; Shanks 2002; Schroeder

241   2011). *Lottia gigantea* is a long-lived species (9–8 years; Wright 1989; Fenberg & Roy 2012),

242   and compounding risky behavior in the first few years of life by daily exposure to a mortal threat

243   seems counter-intuitive. Previous studies explicitly (Boulding & Van Alstyne 1993; Denny 1995;

244   Trussell 1997) or implicitly (Denny 1985, 1995; Denny & Blanchette 2000; Gaylord et al. 2003)

245   assumed dislodgement to be tantamount to death, although Miller et al. (2007) demonstrated

246   high survival of littorine snails after wash off. Our measurements of relatively high survival and

247   no reduction in growth of intruders following dislodgement during their active responses to

248 intraspecific contact suggest that dislodgement is not nearly as drastic of a life-history crisis as

249 previously assumed. Our estimate of survival after dislodgement in the course of a retreat or

250 territorial response (44%) is likely an underestimate, since it is based on finding tagged limpets

251 in a large area 2 weeks after dislodgement. These survival and growth data from dislodged

252 limpets shift our understanding of the ecological role of dislodgement of small limpets from a

253 major life-history crisis to a risky inconvenience, and thereby help explain the persistence of

254 intrusion behavior of small limpets onto well-defended territories. This, combined with the

255 ability of small limpets to dodge territorials (Wright 1982) and the demonstrated rich resources

256 to be had on a resident's territory (Shanks 2002), likely contributes to making territorial intrusion

257 a consistently adaptive strategy.

258   Previous research by one of us (W.G. Wright) and colleagues (Shanks et al. 1986; Wright

259 & Shanks 1995) has documented limpets actively releasing their grip on a substratum that is

260 rolling around in the sea. This release seems at first glance to further belie the contention that

261 dislodgement is very dangerous; however the realization that such rolling substratum is

262 comprised nearly exclusively of dislodged mussels to which limpets are attached, led us to

263 propose that this "bail-out" behaviour reduces the chances that a limpet will be swallowed along

264 with its mussel substratum by an anemone, a common fate of dislodged mussels (Sebens 1981).

265 Dislodged limpets regain their footing orders of magnitude more quickly than do mussels large

266 enough to host epifaunal limpets (Shanks et al. 1986; Wright & Shanks 1995). Thus, bail out

267 from, not adhesion to, a rolling mussel is likely the safer of these two very dangerous situations.

268   Related to the question of the adaptive value of intrusion is an unknown, but potentially

269 significant, contribution of intrusion directly to reproductive success. In particular, the

270 protandric hermaphroditism of *L. gigantea* (Lindberg & Wright 1985; Wright 1989), combined

12

271   with the observation (Wright 1989) that only 6% (N = 64) of evading limpets were females,

272   means that small intruding limpets are nearly exclusively male. This raises the possibility that

273   one function of the intrusion of small limpets that respond with retreat behavior is to be near the

274   spawn of the resident, which has a good chance (52%, N = 71, Wright 1989) of being female.

275   This proximity is very likely to give such an intruding male a competitive fertilization advantage

276   over less bold male intruders. Inasmuch as spawning occurs over no more than a few days every

277   winter (based on suddenly depleted gonad indices, Daly 1975), and has yet to be directly

278   observed, such a scenario will be difficult to illuminate with field observations, and must remain

279   a distant possibility at best.

280   It is worthy of note that the surprisingly benign prospects for the dislodged intruder are

281   unlikely to diminish the adaptive advantage to the resident of its dislodging thrust behavior. This

282   is because reattachment of dislodged limpets almost always occurs several to many meters away

283   from the site of dislodgement, making future exploitation of the original territory by the same

284   intruder quite unlikely. Thus, the resident will likely reduce its local conspecific competition

285   with this thrust behavior.

286   The above considerations paint a picture of a dynamic system of two dueling adaptive

287   behaviors: (1) explosive territorial defense capable of removing a small intruder from any future

288   intrusions, and (2) persistent intrusions by small limpets onto territories to forage on the rich

289   algal resources and dodge the territorial efforts of the resident until luck runs out and they are

290   dislodged, at which time they have a fair chance of surviving and growing in a different location.

291   An alternative, not mutually exclusive, interpretation of the strong territorial response

292   shown by *L. gigantea* residents, is that its function is to train or "punish" intruders (Stamps 1994;

293   Stamps & Krishnan 1999; Hinsch & Komdeur 2017a). Indeed, Wright and Shanks (1993)

294   demonstrated that agonistic experience of territorial defeats increases the subsequent likelihood

295   that *L. gigantea* foragers engage in retreat behavior in response to conspecific contact. Wright

296   and Shanks (1993) did not vary the intensity of defeats, e.g., the force of the pushing during

297   training. A reasonable prediction is that more forceful pushing would make intruders more likely

298   to retreat in response to subsequent contact than would weaker pushing; and perhaps decrease the

299   frequency of their intrusions.

300   Although we have not directly tested the resistance of other co-occurring limpet species,

301   such heterospecific limpets (5–30 mm) can be found on territories of *L. gigantea*, where they

302   show well-developed retreat behavior in response to limpet contact (W.G. Wright, pers.

303   observation). These limpets are all as small or smaller than retreating *L. gigantea*, and are thus

304   likely at risk for dislodgement.

305   The fact that *L. gigantea* is most commonly found on vertical habitats with high wave

306   energy (Abbot 1956; Ricketts et al. 1992; Denny & Blanchette 2000) is likely to amplify the

307   effectiveness of this territorial thrust behavior. Breaking the seal of an intruder's foot with the

308   substratum does the resident little good if the encounter occurs on a horizontal substrate in calm

309   seas (see online video), thus giving the intruder time to re-adhere to the substratum as it is

310   shoved to the edge of the territory.

311   This consideration of the distribution of territoriality supports the idea that wave wash

312   may amplify the effectiveness of the territorial response. The well-studied risk of dislodgement

313   by waves in *Lottia gigantea* (Denny 1995; Denny & Blanchette 2000; Mason et al. 2018) is quite

314   likely to interact, perhaps critically, with the ability of territorial residents to rid themselves of

315   exploitative intruders. In particular, removal of intruders from the substratum generally requires

316   both dislodgement by the territorial thrusting, as well as wash-off due to a breaking wave. Thus,

317   the interaction of territorial behavior with ocean waves may be key. Because we can only

318   observe staged interactions in relatively benign conditions, we do not know if territorial behavior

319   of residents, or retreat behavior of intruders, is different in rougher seas. However, we do know

320   that limpets are loath to move during peak tides when wave heights are above 1.5 m (Wright &

321   Nybakken 2007).

322   Adaptive considerations suggest that the evolution of a feeding territory requires that

323   territory defense be sufficiently profitable. If the behavior of the territorial resident cannot

324   sufficiently reduce the cost incurred by intruding limpets, territoriality will not persist (Hinsch &

325   Komdeur 2010). We suggest that the possibility, explicitly identified here, that an intruder that is

326   removed, not just to the perimeter of the territory, but from the entire rocky substratum, can

327   increase the benefit of the resident's territorial behavior by eliminating small intruders from

328   future competitive interactions, thereby increasing future algal food that would be otherwise be

329   exploited by such intruders (Shanks 2002). This suggests that the evolution of the relatively

330   complex thrust-and-follow behavior, which not only enables displacement, but also dislodgement

331   of intruders, may be a necessary requirement for the evolution and persistence of territorial

332   behavior.

333   Conversely, as potentially dangerous as this thrust response is from the perspective of

334   small intruders, its realized ecological effect on them is reduced by their effective retreat

335   behavior, which has significantly shorter latency that the territorial response of residents (Wright

336   1982). This difference in response time results in the observation that most of the directly

337   observed natural contacts between small intruders and residents end with the intruder retreating

338   before the resident responds (Wright 1982). Nevertheless, the explosive thrusting behavior so

339   commonly observed in staged encounters has also been observed in several natural encounters

340 (Wright 1982; W.G. Wright pers. observation); thus, its use is unlikely to be an artifact of the

341 baiting method used to elicit territorial behavior.

342   Owl limpets also respond with similar territorial thrusting to intrusions by at least two

343 different co-occurring limpet species (primarily *Lottia digitalis* and *L. scabra*) placed in front of

344 moving territorial residents (Stimson 1970). Although we have observed retreat behavior by

345 both species from limpet contact while foraging on *L. gigantea* territories, we do not yet know

346 the latency or speed of these behaviors. Thus, the dangerous dislodging component of the

347 territorial thrust response may be also, or even primarily, useful against hetero-specific intruders,

348 whose exploitation of territories would otherwise take a competitive toll on territorial residents

349 (Stimson 1973).

350   To conclude, these measurements and observations suggest that the evolutionary

351 persistence of the territorial ecology of *L. gigantea* is attributable to two different somewhat

352 surprising characteristics: (1) Exuberant territorial response: rapid pursuit, agile directional

353 tracking, and thrust behavior, give a territorial resident the potential to dislodge small intruders,

354 permanently removing them from further competitive interactions with the resident. (2) Low-cost

355 intrusion: exploitation of this apparently dangerous territory remains adaptive, partly because

356 such intruders are quicker to respond (Wright 1982), but also because, if dislodged, they stand a

357 reasonable chance of surviving and continuing to grow in a new location. Thus, we suggest that

358 the "win-win" ethological setting manifested by these two characteristics together contribute to

359 the robust territorial ecology of *L. gigantea*.

360

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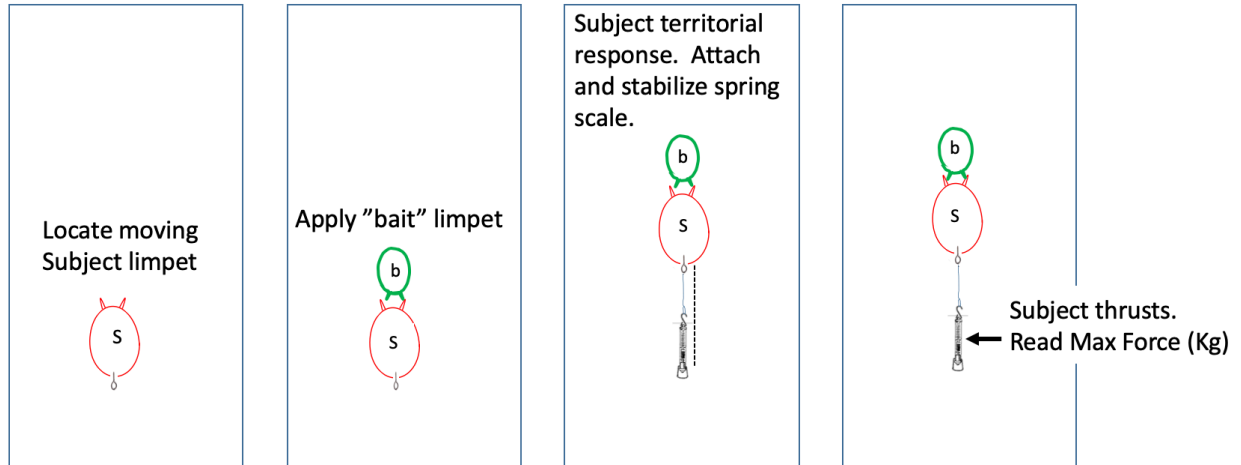
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474 **Figures:**
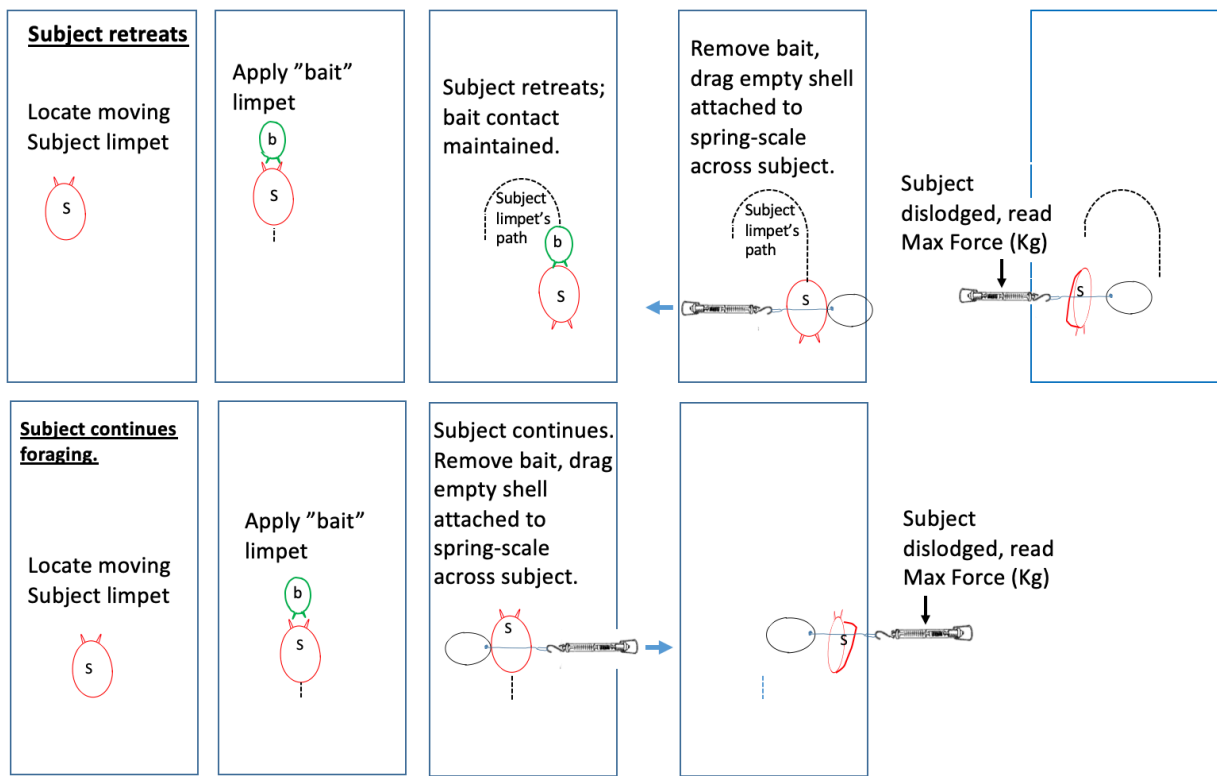
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Measuring thrust force

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477 Fig.1. — Measurement of maximum thrust in territorial limpet. Limpet with ring attached to

478 posterior shell is "baited" into a territorial response. A light line is attached to the ring, and to a

479 spring scale with a maximum reading pointer. The spring scale is stabilized while the line comes

480 taut behind territorial limpet. Maximum thrust force is measured.
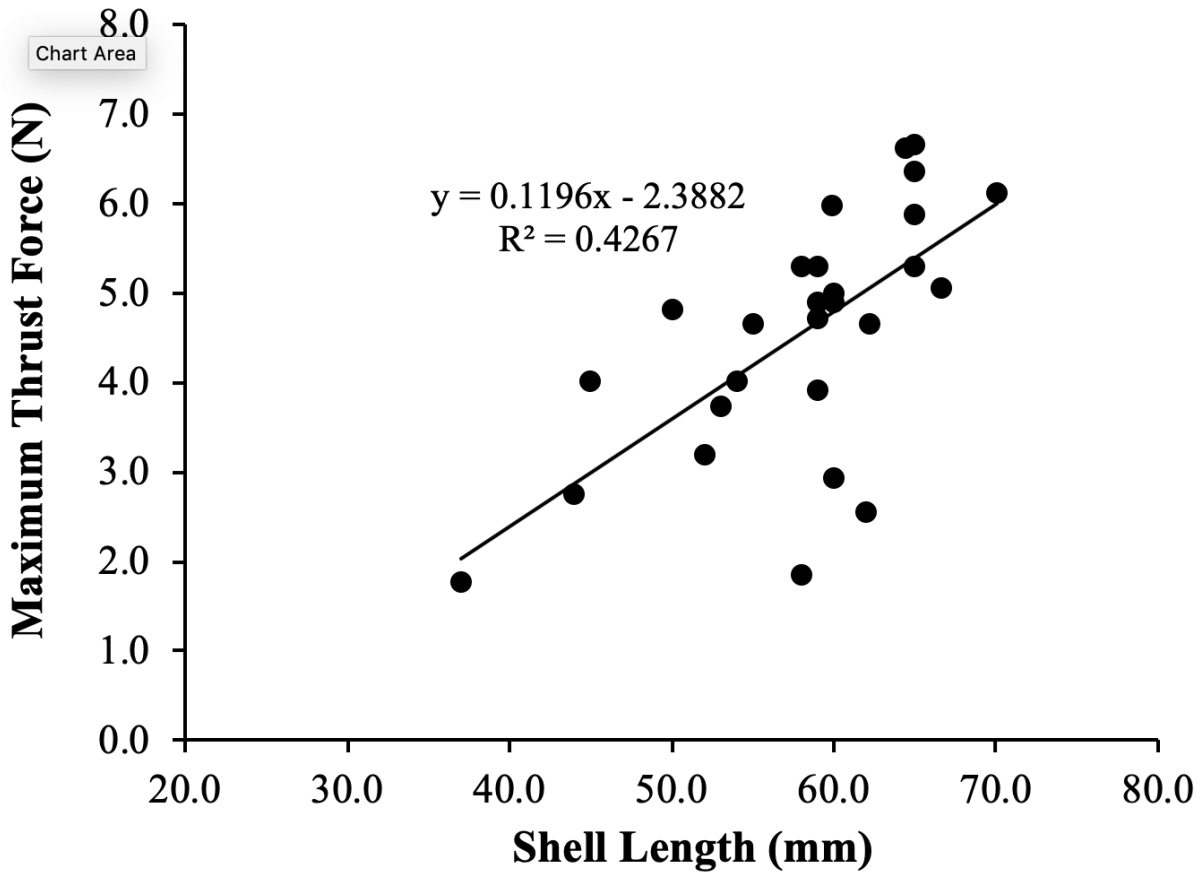
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Measuring thrust-force resistance.

Subject retreats

Locate moving Subject limpet

Apply "bait" limpet

Subject retreats; bait contact maintained.

Remove bait, drag empty shell attached to spring-scale across subject.

Subject dislodged, read Max Force (Kg)

Subject continues foraging.

Locate moving Subject limpet

Apply "bait" limpet

Subject continues. Remove bait, drag empty shell attached to spring-scale across subject.

Subject dislodged, read Max Force (Kg)

Fig. 2. — Measurement of resistance to thrust force in chasing limpets. Subject limpets (red) are "baited" (using a conspecific limpet (green) removed from a different area) into either retreat (above) or territorial (below) behavior. Once a behavioral response is established; either retreat (upper panel), territorial (lower panel), or no response (not shown); an empty shell (no shading) attached to a line and spring scale with maximum pointer is slowly dragged against the limpet until the subject limpet's seal with the substratum is broken. The maximum force exerted until dislodgement is recorded.

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The chart shows Maximum Thrust Force (N) on the y-axis (ranging 0.0 to 8.0) versus Shell Length (mm) on the x-axis (ranging 20.0 to 80.0). A "Chart Area" label appears near the top left. The regression equation is:
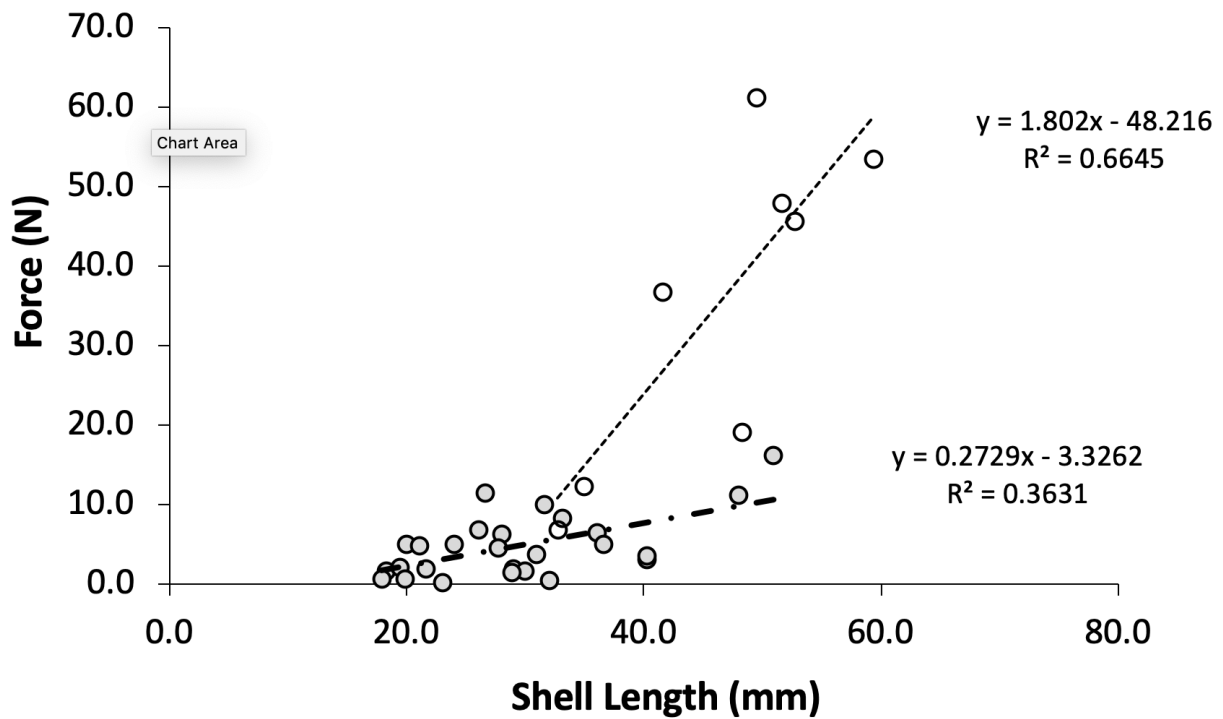
$$y = 0.1196x - 2.3882$$
$$R^2 = 0.4267$$

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501 Fig. 3. — Thrust force is significantly correlated with shell length. Maximum thrust force

502 produced in territorial limpets (Fig. 1) in response to an introduced bait limpet is shown as

503 function of shell length ($R^2 = 0.43$, n = 27, $P = 0.0002$).

504

Fig. 4. — Resistance to shear force is greater and more sensitive to shell length in limpets that continued slow foraging than in limpets that showed retreat behavior.   Shear force resistance (vertical axis) versus shell length (horizontal axis) for limpets engaged in either retreat behavior (grey circles) or continued foraging (open circles).

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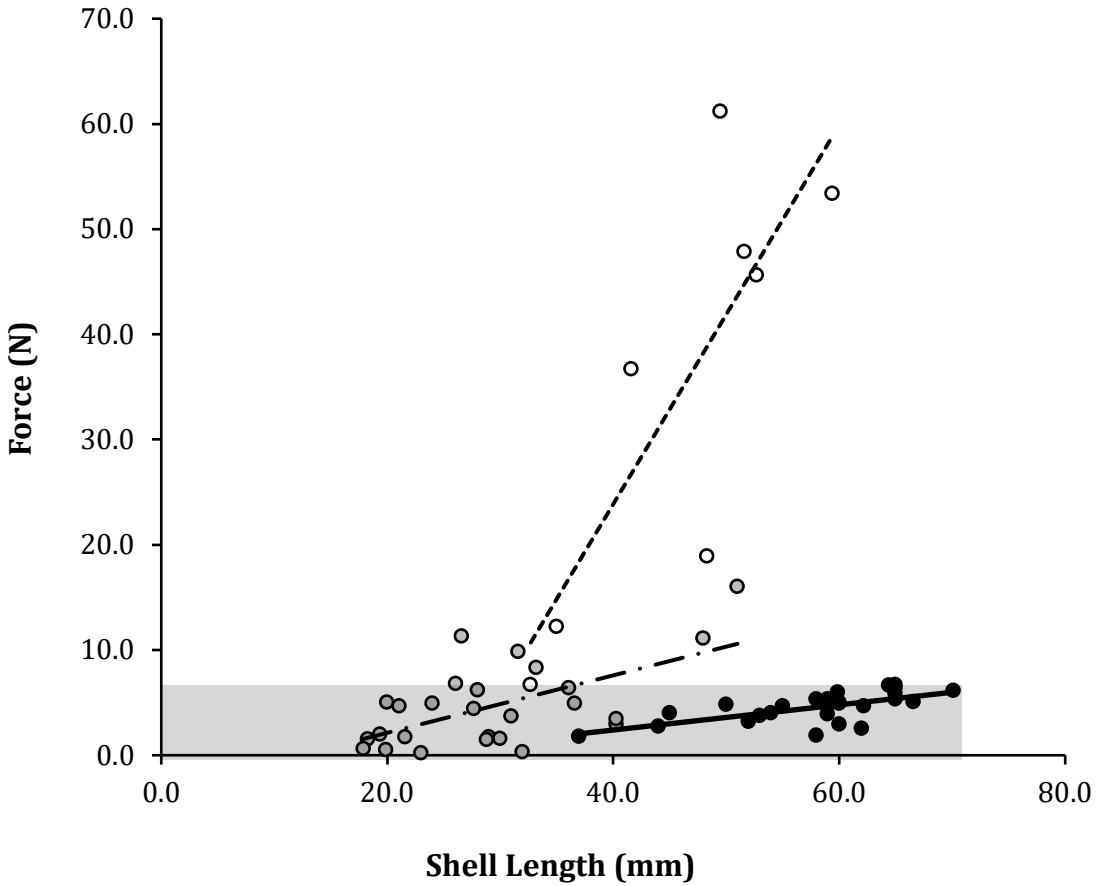
Fig. 5. — Maximum thrust force is greater than resistance to thrust for most retreating limpets.

In this figure, results from Fig.3 are plotted with those from Fig. 4 to directly compare thrust

force of territorials to the resistance of moving limpets. Force to remove (grey circles retreating

limpets, open circles limpets that continued foraging; Fig. 4) and maximum thrust force (solid

circles; from Figure 3) are shown as a function of shell length. The grey area, or "danger zone"

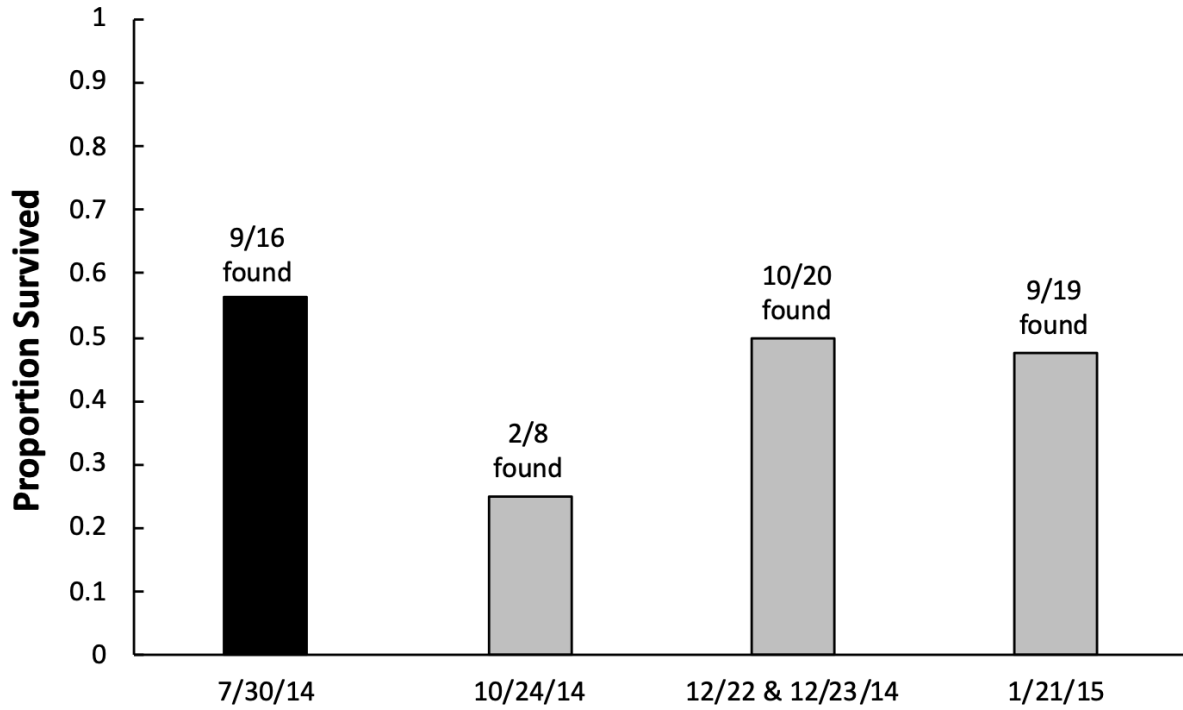(≤ 6.7 N) represents the maximum thrust force observed, and is greater than the resistance of

most retreating limpets (grey circles).

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528   Fig. 6. — Survival of dislodged limpets was surprisingly high (0.25-0.56, average = 0.474 ±

529   0.068). Number found/number dislodged shown above each bar. Dates represent when survivors

530   were found. Seven of the nine survivors from 30 July 2014 (dark bar on left) were measured on

531   that date and 5.3 months later for growth measurement (Fig. 7).
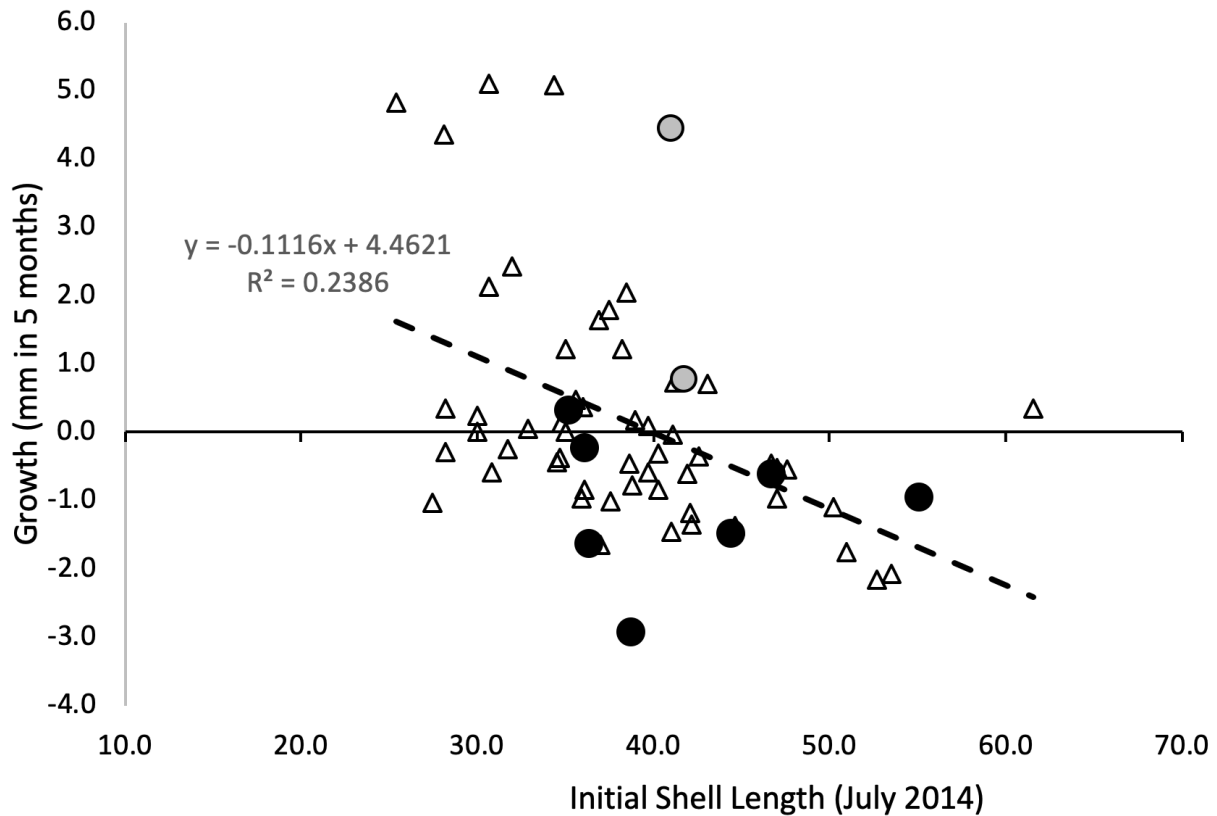
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542   Fig. 7. — Growth of chasing (retreat and territorial) limpets following dislodgement (circles, N =

543   7) was not different than that of undisturbed limpets in same habitat (triangles and dashed line, N

544   = 54). Scattergram shows shell length growth (mm) from late July 2014 to early January 2015,

545   as a function of initial shell length (mm). Regression line depicts undisturbed limpets (triangles).

546   There was no significant difference between residuals of washed-off territorials vs undisturbed

547   limpets (*P* = 0.37).

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