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# Linking animal contests and community structure using rockpool fishes as a model system

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# Linking animal contests and community structure using rockpool fishes as a model system

## Abstract

Competition for limiting resources is a fundamental and well-established driver of niche partitioning, which in turn promotes species coexistence and biodiversity. Although contests are a well-known behavioural mechanism by which organisms compete over limiting resources, there has been surprisingly little application of contest theory to understanding interspecific interactions, niche partitioning, species coexistence and biodiversity. We investigated the link between contest dynamics and community structure using two intertidal rockpool fishes, *Bathygobius cocosensis* (Gobiidae) and *Lepidoblennius haplodactylus* (Tripterygiidae), as model species. We assessed the abundance and distribution of the two species on intertidal rocky shores of South-East Australia, and whether distribution patterns were related to abiotic variables. We then conducted interspecific contest experiments between pairs of *B. cocosensis* and *L. haplodactylus* of varying size and sex under high and low dissolved oxygen levels to assess the competitive dominance of the species. To relate these results to community structure, we quantified temporal patterns of rockpool fidelity of each species in situ. Field surveys revealed that *B. cocosensis* was most prevalent in rockpools with higher dissolved oxygen, and *L. haplodactylus* was most prevalent in rockpools that contained no *B. cocosensis*. Contest experiments revealed that *B. cocosensis* displayed higher resource holding power than *L. haplodactylus* regardless of size asymmetry, sex or dissolved oxygen concentration, although contest intensity was influenced by relative body size of competing individuals. Furthermore, the microhabitat preference of *L. haplodactylus* was modulated in the presence of *B. cocosensis*. In the field, *B. cocosensis* displayed higher rockpool fidelity than *L. haplodactylus*. In light of these findings, we propose that *B. cocosensis* is the superior competitor but persistence of both species is likely facilitated by low-cost contest resolution strategies, plasticity in microhabitat preference, negative spatial co-variation and interspecific variation in dispersal and corresponding home range sizes. By using contest theory to understand the dynamics of interspecific contests, insight has been gained into how habitat is partitioned, species coexist and ultimately how biodiversity is maintained. A lay summary is available for this article.

## Disciplines

Medicine and Health Sciences | Social and Behavioral Sciences

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1 Fish Contests and Community Structure

2

3 **LINKING ANIMAL CONTESTS AND COMMUNITY STRUCTURE**

4 **USING ROCKPOOL FISHES AS A MODEL SYSTEM**

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## 24 **Summary**

- 25 **1.** Competition for limiting resources is a fundamental and well established driver of  
26 niche partitioning, which in turn promotes species coexistence and biodiversity.  
27 Although contests are a well-known behavioral mechanism by which organisms  
28 compete over limiting resources, there has been surprisingly little application of  
29 contest theory to understanding interspecific interactions, niche partitioning, species  
30 coexistence and biodiversity.
- 31 **2.** We investigated the link between contest dynamics and community structure using  
32 two intertidal rockpool fishes, *Bathygobius cocosensis* (Gobiidae) and *Lepidoblennius*  
33 *haplodactylus* (Tripterygiidae), as model species. We assessed the abundance and  
34 distribution of the two species on intertidal rocky shores of South East Australia, and  
35 whether distribution patterns were related to abiotic variables. We then conducted  
36 interspecific contest experiments between pairs of *B. cocosensis* and *L. haplodactylus*  
37 of varying size and sex under high and low dissolved oxygen levels to assess the  
38 competitive dominance of the species. To relate these results to community structure,  
39 we quantified temporal patterns of rockpool fidelity of each species *in situ*.
- 40 **3.** Field surveys revealed that *B. cocosensis* was most prevalent in rockpools with higher  
41 dissolved oxygen, and *L. haplodactylus* was most prevalent in rockpools that  
42 contained no *B. cocosensis*. Contest experiments revealed that *B. cocosensis* displayed  
43 higher resource holding power than *L. haplodactylus* regardless of size asymmetry,  
44 sex or dissolved oxygen concentration, although contest intensity was influenced by  
45 relative body size of competing individuals. Furthermore, the microhabitat preference  
46 of *L. haplodactylus* was modulated in the presence of *B. cocosensis*. In the field, *B.*  
47 *cocosensis* displayed higher rockpool fidelity than *L. haplodactylus*.

- 48       **4.** In light of these findings we propose that, *B. cocosensis* is the superior competitor but  
49           persistence of both species is likely facilitated by low-cost contest resolution  
50           strategies, plasticity in microhabitat preference, negative spatial co-variation and  
51           interspecific variation in dispersal and corresponding home range sizes.
- 52       **5.** By using contest theory to understand the dynamics of interspecific contests, insight  
53           has been gained into how habitat is partitioned, species coexist and ultimately how  
54           biodiversity is maintained.

55

56   **Key Words:** Assessment strategy, Asymmetrical competition, Community Ecology,  
57   Coexistence, Contest theory, Gobiidae, Rockpool fishes, Tripterygiidae.

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## 59   **Introduction**

60   One of the most fundamental and well-established mechanisms by which biodiversity is  
61   maintained is via competition for limiting resources. Interspecific competition over resources  
62   is suggested to drive niche partitioning (Dawkins & Krebs 1979) which in turn facilitates  
63   species coexistence and biodiversity (Connell 1961; Pianka 1976; Schluter 1994; Schoener  
64   1974; Vandermeer 1972; Volterra 1926). Competition over limiting resources can be  
65   symmetric or asymmetric. If competition is symmetric, in other words when the competitive  
66   ability of competing species is equal and the outcome of competitive interactions is  
67   unpredictable (Dawkins & Krebs 1979), the coexistence of species may be determined, for  
68   example by arrival time (Munday 2004). If competition is asymmetric, the competitive ability  
69   of one species is greater than the other and the outcome of competitive interactions is more  
70   predictable (Dawkins & Krebs 1979). In these cases, a key question arises – how do inferior  
71   competitors persist given their inherent disadvantage?

72       A range of mechanisms have been proposed to explain coexistence of superior and inferior

73 competitors, including competition colonisation trade-offs (Tilman 1994), the intermediate  
74 disturbance hypothesis (Connell 1978; Sousa 1979), microhabitat partitioning (Denno,  
75 Mcclure & Ott 1995) and complex behaviors generating the formation of hierarchies among  
76 species (e.g. Geange, Adrian & Jeffery 2013). One behavioral mechanism by which  
77 individuals compete over limiting resources and generate such species hierarchies is via  
78 aggressive contests (Austad 1989; Smith & Price 1973). Despite its prevalence in behavioral  
79 ecology literature (Arnott & Elwood 2009; Briffa & Elwood 2009; Elwood & Arnott 2012;  
80 Hardy & Briffa 2013), contest theory has rarely been employed to investigate the coexistence  
81 of competing species. This is surprising given that contest theory provides a framework for  
82 understanding how fighting ability is assessed during the course of a contest, and hence the  
83 behavioral mechanisms by which animals resolve contests over limiting resources (Austad  
84 1989; Smith & Parker 1976; Smith & Price 1973).

85       According to contest theory, an individual's assessment of its opponent's fighting ability,  
86 termed Resource Holding Power (RHP) (Parker, 1974) and its own RHP has significant  
87 implications for the extent to which a contest will escalate and hence the cost associated with  
88 that contest (Arnott & Elwood 2009; Koops & Grant 1993). The extent to which a contest  
89 escalates is typically measured in terms of contest intensity and duration. Three main models  
90 of RHP assessment have been proposed (Arnott & Elwood 2009) (Table 1) based on variation  
91 in contest duration and intensity, which are termed pure self-assessment, cumulative  
92 assessment (Payne 1998) and mutual assessment (Arnott & Elwood 2009; Briffa & Elwood  
93 2009; Elwood & Arnott 2012). According to Arnott & Elwood (2009), the mutual assessment  
94 model is superior to pure self-assessment and cumulative assessment because it provides the  
95 most energy efficient mechanism by which opponents can resolve a contest. However,  
96 because these assessment models are based largely on studies of intraspecific interactions, it  
97 is also important to consider the possibility of no-assessment when investigating interspecific

98 interactions, which is equivalent to a null model. This is because we would expect that  
99 different species may have evolved different contest strategies (Smith & Price 1973) (Table  
100 1).

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119 **Table 1:** Four models of Resource Holding Power (RHP) assessment and identifiers of each  
 120 assessment model including a null model of no assessment (summarised from Arnott &  
 121 Elwood 2009 and Elwood, & Arnott 2012).

<b>Model</b>	<b>Description</b>	<b>Identifiers</b>
No assessment	The outcome of a contest is reached without either contestant assessing RHP.	The contestant with the higher RHP wins.
Pure self-assessment	Each contestant only has information about its own ability to win a fight and fails to gather information about its opponent's ability. Hence the weaker contestant gives up when it has reached its physiological limit.	Contest duration and intensity are correlated solely with the inferior competitors RHP. The higher the RHP of the inferior contestant, the longer and more intense a contest will be.
Cumulative assessment	Similarly to pure self-assessment, in cumulative assessment each individual does not initially gather information about its opponent's ability to win a fight. However, unlike pure self-assessment costs associated with an opponent's actions inform a contestant and hence influence its decision to withdraw from a contest.	Contest duration and intensity are related to both contestants RHP.
Mutual assessment	Both contestants gain information regarding their own RHP and their opponent's RHP. This allows the contestants to estimate the relative fighting ability of their opponent and therefore costs associated with continued conflict.	The losers RHP is positively related, and the winners RHP negatively related to contest duration.

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132 In addition to contest dynamics, contest theory provides a framework with which to  
133 investigate the predictors of contest outcome (Hammerstein 1981). The most commonly  
134 identified and often most easily investigated predictors are relative body size, prior residency,  
135 prior experience and sex (e.g. Briffa & Dallaway 2007; Davies 1978; Draud & Lynch 2002).  
136 The relative size of competing individuals has obvious implications for contest outcomes as  
137 body size is typically associated with strength and the ability to inflict injury (Archer 1988).  
138 For example, Draud & Lynch (2002) investigated contests between monogamous pairs of  
139 convict cichlids (*Archocentrus nigrofasciatum*) and found that a size difference of 15-25%  
140 was a clear predictor of contest outcome. Sex has also been shown to have significant  
141 influence on contest outcome. For example, inter-sexual contests between hermit crabs  
142 (*Pagurus bernhardus*) revealed males were superior competitors compared to females  
143 regardless of body size asymmetries (Briffa & Dallaway 2007).

144 Although contest theory has a distinctly individual-level focus, the dynamics and outcome  
145 of contests as explained by contest theory can shed important insights into community  
146 composition, niche partitioning, species coexistence and biodiversity within ecosystems  
147 (Dugatkin & Reeve 1998; Tinbergen 1952; 1963). However, in order to be useful at higher  
148 levels of ecological organisation, a greater focus on applying contest theory to understanding  
149 the dynamics, predictors and outcome of interspecific contests is required, since the  
150 prevailing emphasis has been on intraspecific contests. Evaluating the usefulness of contest  
151 theory for understanding the dynamics and outcome of interspecific interactions can not only  
152 provide detailed insight into how interspecific competition shapes community structure and  
153 species coexistence, but also provides an important test of the generality of contest theory  
154 (e.g. Arakaki & Tokeshi 2012; Riechert & Hammerstein 1983).

155 Natural systems rich in species with close taxonomic affinities and life history traits  
156 provide interesting systems with which competitive interactions and their importance as

157 drivers of community composition and biodiversity can be explored (Yoshiyama 1981). For  
158 this reason, intertidal rockpool fish communities are an ideal model for investigating the  
159 impact of interspecific contests on community structure and biodiversity. This is because  
160 there is significant spatial overlap of multiple fish species on intertidal rocky shores (Griffiths  
161 2003a), rockpool fishes have been found to exhibit aggressive interactions (Arakaki &  
162 Tokeshi 2005), rockpool fishes exhibit size and sex based variations in dispersal (Arakaki &  
163 Tokeshi 2012; Tavalga 1954) and these species are well suited to experimental studies within  
164 aquaria due to their tolerance for abiotic variability and confined space (Ford, Tibbetts &  
165 Carseldine 2004). In addition, rockpools have distinct microhabitat types within a contained,  
166 small scale and observable habitat (Arakaki & Tokeshi 2005), and are easily accessible *in situ*  
167 (Griffiths 2002).

168 In the current study, two common rockpool fishes along the SE coast of NSW, Australia,  
169 *Bathygobius cocosensis* (Gobiidae) and *Lepidoblennius haplodactylus* (Tripterygiidae)  
170 (Griffiths 2002) were chosen as models to investigate how interspecific contest dynamics  
171 relate to community structure. These species are permanent residents of intertidal rockpools  
172 and possess specialised adaptations to intertidal life (Griffiths 2002) (Fig. 1). *B. cocosensis*  
173 and *L. haplodactylus* are highly abundant in SE Australia, exhibit spatial overlap on intertidal  
174 rocky shores (Griffiths 2002; 2003a) and both value shelter (rocks) as a limiting resource  
175 (Griffiths, Davis & West 2006; White, Hose & Brown 2014). Specifically, we investigated  
176 the abundance and spatial distribution of intertidal fish communities in relation to biotic and  
177 abiotic factors by sampling multiple sites along the SE coast of NSW. Having quantified  
178 spatial distributions, we performed aquarium-based contest experiments with rock shelters as  
179 a limiting resource, to determine the relative influence of body size, sex and dissolved oxygen  
180 on contest dynamics and outcome between individuals of *B. cocosensis* and *L. haplodactylus*.  
181 Finally, we assessed the temporal dynamics and site fidelity of the two species to relate

182 interspecific contest behaviors to observed temporal patterns of space use and occurrence of  
183 the two species *in situ*. Although temporal dynamics in these species has been previously  
184 investigated (Griffiths 2003a; White & Brown 2013), our study extends from these by taking  
185 into consideration multiple possible predictors of fish movement in addition to body size,  
186 namely sex and pool volume.

187 Our study is split into three related parts – investigating abundance and spatial variation,  
188 contest dynamics and temporal rockpool fidelity. For abundance and spatial variation, we  
189 predicted that: 1) biotic factors, namely interspecific competition, would lead to negative  
190 spatial co-variation of *B. cocosensis* and *L. haplodactylus*; and 2) abiotic factors, including  
191 temperature, dissolved oxygen, pH, rugosity and pool elevation, would also influence  
192 abundance and spatial patterns of occurrence of both species. For contest dynamics, we  
193 predicted that: 3) one species would win the majority of contests over a key limiting resource;  
194 4) size asymmetry, sex and dissolved oxygen would influence the outcome, duration and  
195 intensity of contests, 5) Contest dynamics would align either with no assessment because  
196 different species are contesting, or with predictions of low cost assessment strategies –  
197 namely mutual assessment or cumulative assessment, 6) microhabitat utilisation of the  
198 inferior competitor would change in the presence of the superior competitor. For temporal  
199 site fidelity, we predicted that: 7) the superior competitor would show higher rockpool  
200 fidelity over time than the inferior competitor, and 8) individual characteristics (size and sex)  
201 would influence temporal rockpool fidelity for both species.

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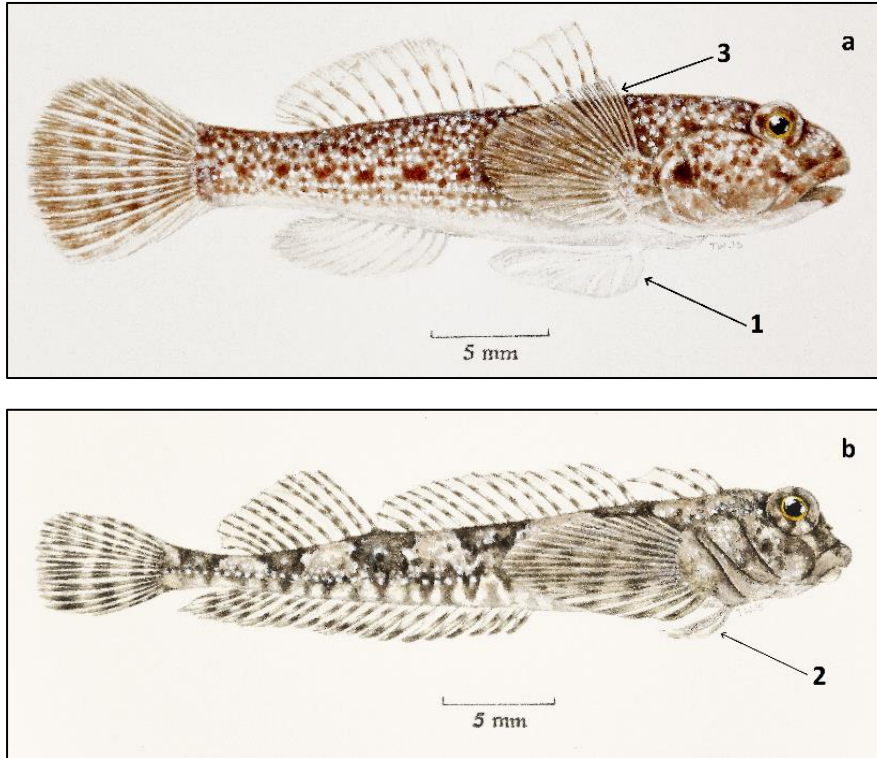
## 203 **Materials and Methods**

### 204 STUDY SPECIES AND LOCATION

205 This study was conducted in SE Australia between March 2014 and September 2015 on five  
206 intertidal rocky shores, separated by sandy beaches, between 34.246S/150.977E and

207 34.421S/150.909E. Aquarium-based contest experiments were conducted at the Ecological  
208 Research Centre (ERC) located at the University of Wollongong, NSW, Australia.

209



212 **Figure 1:** **a.** *Bathygobius cocosensis* (Gobiidae) and **b.** *Lepidoblennius haplodactylus*  
213 (*Tripterygiidae*) are both highly adapted to life in the intertidal zone. This is evident due to a  
214 series of morphological features: firstly, cryptic coloration and the ability to change skin tone  
215 and markings to rapidly match the substrate. Secondly, negative buoyancy and eyes  
216 positioned on the top of the head characterise a benthic dwelling life history. Thirdly, both  
217 species possess pelvic fins adapted to allow adhesion to the substrate. *B. cocosensis* has a  
218 suction cup like fused pelvic fin common to the *Gobiidae* family (1) and *L. haplodactylus* a  
219 pair of finger like pelvic fins that allow them to “grip” the substrate (2). Another feature to  
220 note is the fine elongate fin rays on the upper pectoral fins of *B. cocosensis* (3) which have  
221 been suggested to act as extra gill filaments, possibly increasing the ability of *B. cocosensis*  
222 to tolerate limited dissolved oxygen levels (Tavolga 1954). Illustrations © Tilley Wood.

223

224 DRIVERS OF SPATIAL VARIATION IN DISTRIBUTIONS AND ABUNDANCE

225 Rockpools (N = 15) were randomly sampled at each location by laying three 40m transects  
226 greater than 20m apart from low tide level to the upper shore. A random number table was  
227 used to select 5 points on each transect. From each of these points another random number  
228 was used to select a perpendicular line to the left or right. The closest suitable rockpool  
229 within 1 m either side of the selected line was then sampled. Having located a rockpool, final  
230 rockpool selection was based on several criteria: 1) rockpools must contain fish (determined  
231 via a 5-minute visual search prior to sampling), 2) rockpools must not be connected to other  
232 rockpools and 3) rockpools must be no larger than 500 litres (due to sampling time  
233 constraints imposed by the tides).

234 For each rockpool, the elevation of the surface of the rockpool above the low tide level  
235 was measured to the nearest 5cm at low tide using a measuring staff, stringline and spirit  
236 level. The elevation was then calculated by adding the measured elevation to the height above  
237 absolute low of the low tide that day (methods adapted from Griffiths 2002). pH, temperature  
238 (°C), dissolved oxygen (mg/L) and salinity (PSS) were measured using a Hydrolab water  
239 quality monitoring system (HACH). Once the rockpool was empty (see below), the percent  
240 cover of algae was visually estimated. Rockpool rugosity (heterogeneity) was measured by  
241 taking three evenly spaced length measurements (cm) across the pool's length and width  
242 (totaling 6 measurements). Each of these 6 measurements was compared to the length of a  
243 chain that followed the same line but was laid over the substrate. The ratio of the straight  
244 length to the chain length gave a number between 0-1, 1 being a flat surface and any number  
245 approaching 0 representing high heterogeneity. The 6 values were averaged to give an  
246 'average rugosity ratio' measure for each pool (methods adapted from Luckhurst &  
247 Luckhurst 1978).

248 Once the water quality and elevation data was collected for a given rockpool, the pool was  
249 emptied by pumping water out into a large plastic graduated container (for volume  
250 measurement) using a bilge pump. Once empty, all fish were captured using dip nets, making  
251 sure to thoroughly search all algal fronds and crevices. Any loose pebbles or boulders were  
252 removed temporarily during the search. Once all fish were captured, water was pumped back  
253 into the pool so as to minimise disturbance. All fish were identified, photographed, measured  
254 to standard length (to the nearest 0.1mm using hand-held callipers), and weighed using a  
255 Scout Pro SPU123 digital balance (Ohaus Corporation, USA) to the nearest 0.01g, before  
256 being returned to their original rockpool.

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## 258 CONTEST DYNAMICS

### 259 *Housing and contest arenas*

260 *B. cocosensis* (total N = 42) and *L. haplodactylus* (total N = 42) were captured from  
261 rockpools using the same methods as those described above. Fish were transported  
262 immediately to the ERC and housed singly in glass aquaria (60x30x30 cm) within a re-  
263 circulating saltwater aquarium system. Each aquarium was lined with natural coarse gravel  
264 and contained a single larger rock to act as shelter. During the entirety of the experiment,  
265 salinity was maintained at 37ppt and temperature at 21-22 °C, conditions that would typically  
266 be encountered by rockpool fishes at that time of year (Griffiths 2003b). After an initial  
267 acclimation period of two days, fish were weighed and measured as described previously, and  
268 then tagged and sexed. To tag fish, fish were lightly anaesthetised by placing them into a  
269 solution of clove oil anaesthetic (Griffiths 2000). A small spot of fluorescent elastomer  
270 (Northwest Marine Technology Inc.) was injected subcutaneously into their dorsal  
271 musculature (Malone, Forrester & Steele 1999). To sex fish, anaesthetised fish were  
272 observed under a dissecting microscope to note the shape of the genital papilla (see below for

273 verification of this method). Fish were then placed back into their aquaria and allowed to  
274 acclimatise for a further two days prior to behavioral observations. Fish were fed daily with a  
275 combination of frozen brine shrimp, bloodworms and pink coralline algae.

276 Contest arenas were created by dividing an aquarium (60x30x30cm, LxHxD) into three  
277 compartments using opaque mesh partitions, with each compartment measuring 19x30x30cm  
278 (Fig. 2). The mesh partitions allowed water to flow but inhibited paired fish from seeing or  
279 interacting with each other prior to contests. In the center of each compartment, a shelter was  
280 introduced consisting of a single rock elevated by small tiles, allowing the fish to hide under  
281 it (Fig. 2).

282 All behavioral observations were made via recordings using GoPro™ cameras mounted  
283 directly above the aquarium compartments (Fig. 2). Fish were recorded for 20 minutes and all  
284 observations were conducted at least 12 hours after fish had fed. During behavioral  
285 observations researchers remained outside the room.

286





303 of male and female *B. cocosensis* were assigned (N = 7 fish per sex) to each of the 3 size  
304 asymmetry treatments. Then, to investigate the effect of dissolved oxygen (DO) on contest  
305 behavior, each assigned pair of contestants was tested twice; once under standard DO levels  
306 (7.0mg/L), reflecting the dissolved oxygen level naturally occurring in recirculating aquarium  
307 systems, and once under reduced DO conditions (5.9mg/L), reflecting the lowest naturally  
308 observed dissolved oxygen level measured in pools containing fish (Griffiths 2003b).  
309 Repeated measures were independent (see Appendix S1 in supporting information for tests of  
310 order effects).

311 Once fish had been assigned to a contestant pair, each fish was initially recorded whilst  
312 solitary in either end compartment of the aquarium (compartments 1) (Fig. 2) so that  
313 preferred microhabitat utilisation could be scored (see below). Having recorded each fish in  
314 isolation, a contest trial began when the partitions were lifted, enabling both fish to move  
315 from the side compartments (1) into the central compartment (2) (Fig. 2).

316 To record the behavior of each pair of contestants under reduced dissolved oxygen  
317 conditions, dissolved oxygen levels were reduced when fish were still in compartments 1.  
318 This was done by circumventing the recirculating flow of water away from the test aquarium,  
319 removing the air stone supplied to each aquarium and bubbling pure nitrogen gas into the  
320 aquarium. Dissolved oxygen levels were simultaneously monitored using a hand-held water  
321 quality monitor (HACH). Once the dissolved oxygen had dropped to 5.9mg/L, the nitrogen  
322 gas bubbler was removed from the aquarium and a contest initiated as previously described.  
323 In order to make sure the repeated DO contests were independent of each other, contestant  
324 fish were separated for at least 48 hours between the two dissolved oxygen level contests.  
325 Further, the order with which pairs of contestants were tested was randomized.

326

327 *Behavioral analysis*

328 Once each fish had been recorded under solitary conditions, and then under paired conditions  
329 of both standard and reduced dissolved oxygen levels, videos were analysed to quantify  
330 contest dynamics and microhabitat utilisation. To quantify contest dynamics, contest  
331 intensity, duration and outcome of each contest was analysed. Aggressive actions displayed  
332 by each individual fish (Table 2) were tallied using JWatcher © version 1.0. The total number  
333 of aggressive actions displayed by each fish was then calculated by summing all chases (with  
334 and without heterospecific flees) and displacements (Reddon *et al.* 2011) (Table 2). An  
335 intensity score was then calculated for each contest by summing the total aggressive action  
336 scores for both fish together. Contest outcome was defined as the first fish to spend ten  
337 seconds or more under or on the rock shelter (Szabo 2002). Initial observations suggest that  
338 rock crevices are the preferred microhabitat for these species. Results confirm this  
339 assumption, with identified winners spending on average six times more time utilising the  
340 rock shelter than losers (ANOVA:  $F = 33.56_{1,118}$   $P < 0.001$ ). Finally, contest duration was  
341 defined as the time it took before a fish was classified as the winner (i.e. spent at least ten  
342 seconds under or on the rock shelter) (Reddon *et al.* 2011).

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349 **Table 2:** Ethogram showing recorded behaviours and how those behaviours were defined and  
350 identified by the researchers.

<b>Behaviour</b>	<b>Description</b>
Chase with heterospecific flee	An accelerated and directed movement towards the heterospecific resulting in the heterospecific fleeing.
Chase without heterospecific flee	An accelerated and directed movement towards the heterospecific without the heterospecific fleeing.
Displacement	Heterospecific fleeing as a result of an approach without any apparent chase.

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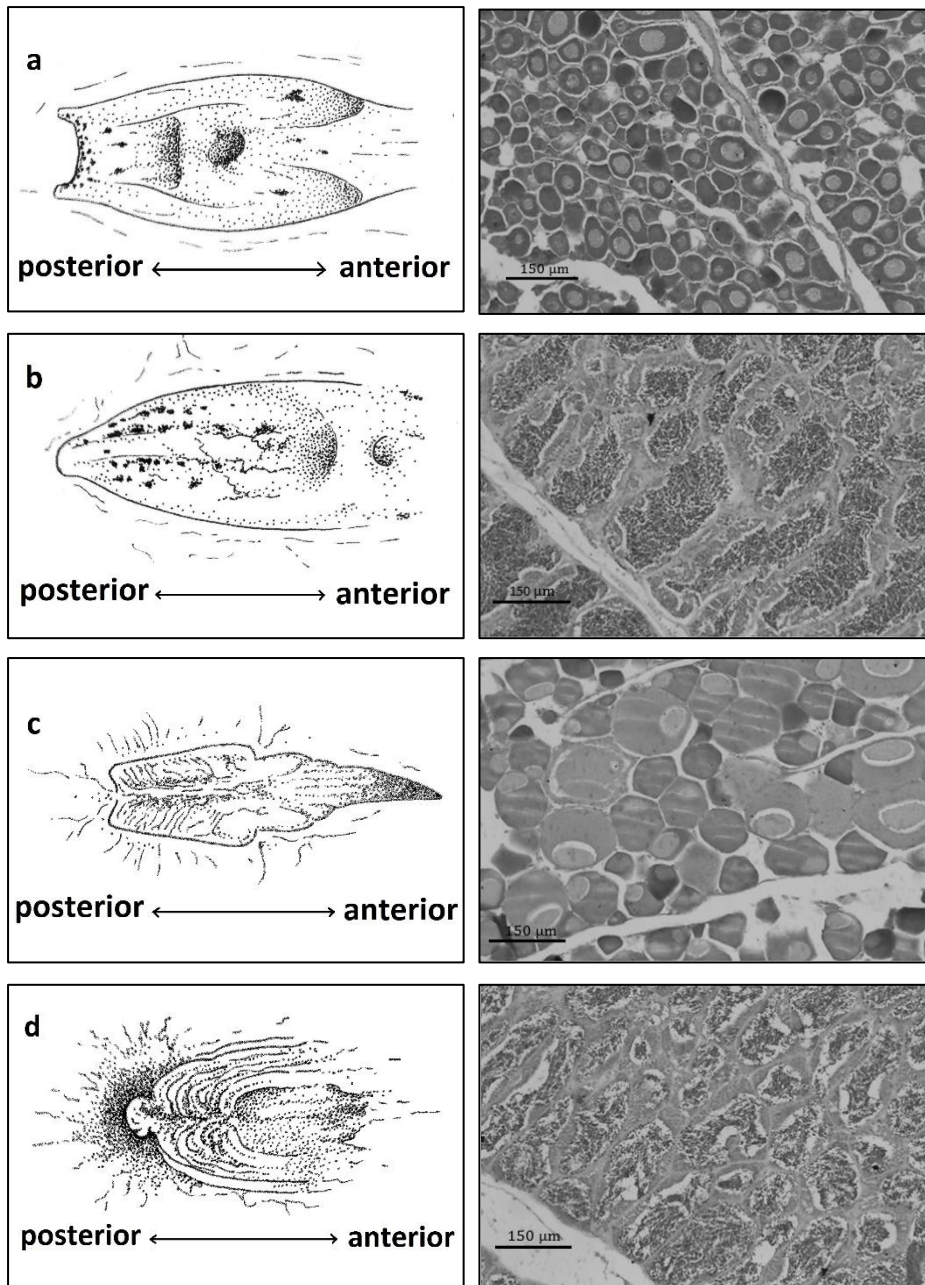
364

365 From the solitary videos as well as contest videos, microhabitat utilisation patterns over a  
366 20-minute period were scored for each fish using JWatcher © version 1.0. To do this, the  
367 aquarium compartments were divided into three microhabitat categories: gravel, wall, and  
368 rock (Fig. 2).

369

#### 370 SEX DETERMINATION

371 To confirm the sex of both *B. cocosensis* and *L. haplodactylus* as determined via external  
372 observation of the genital papilla, a subset of fish (N = 20 per species) were euthanized and  
373 processed to remove the visceral mass. The visceral mass of each fish was processed in a  
374 tissue processor (Leica – ASP200S brand), embedded in paraffin wax, transverse sectioned at  
375 5µm using a rotary microtome, mounted onto glass slides and stained with Mayer’s alum  
376 haemotoxylin and Young’s eosin-erythrosin. Thin sections were then viewed by light  
377 microscopy. Females were identified based on the categories defined by West (1990), from  
378 the presence of oocytes. Males were identified based on the categories as defined by Cole  
379 and Hoese (2001) from the presence of spermatocytes and spermatozoa. Female *B.*  
380 *cocosensis* had a flattened end on their genital papillae, often associated with a distinct line of  
381 melanophores across the end of the genital papillae. Male *B. cocosensis* had pointed genital  
382 papillae often associated with melanophores over the entire papillae. In contrast, female *L.*  
383 *haplodactylus* had “frilly” or filamentous features covering the genital papillae whilst male *L.*  
384 *haplodactylus* had distinctly smaller genital papillae than females, with a pointed end feature  
385 on the papillae (Fig. 3).



386

387 **Figure 3:** illustrations of the genital papillae and photographs of associated sectioned

388 gonads of: **(a)** female *Bathygobius cocosensis*, **(b)** male *B. cocosensis*, **(c)** female

389 *Lepidoblennius haplodactylus* and **(d)** male *L. haplodactylus*. Images of genital papillae are

390 magnified 20 times. Illustrations © Tilley Wood.

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392

393 SHORT-TERM TEMPORAL DYNAMICS

394 Rockpools (N = 36) were repeatedly sampled over nine day periods. Pools were carefully  
395 selected to ensure that the sampling procedure caused minimal disturbance to fish fauna  
396 during the repeated sampling period. This was done by selecting “pothole” rockpools, defined  
397 as those with few crevices or overhangs where fish could lodge themselves, and from where  
398 the collection of fish was not a highly disruptive procedure. The selection of such rockpools  
399 was considered representative and unbiased as the initial investigation into the drivers of fish  
400 distributions and abundance suggested that both *B. cocosensis* and *L. haplodactylus* inhabit  
401 all pool types regardless of pool substrate complexity (rugosity) (Appendix S2).

402 On the first day of sampling (day 1), the location of a selected rockpool was recorded with  
403 a GPS (GARMIN Etrex 10). The rockpool was then emptied and fish were captured and  
404 placed in aerated containers using methods described previously. Once all *B. cocosensis* and  
405 *L. haplodactylus* were captured, the rockpool was refilled and rocks were carefully replaced  
406 from where they were taken. Fish were measured, weighed and tagged as described  
407 previously, and sexed via observation of the genital papillae under a cordless field  
408 microscope (WILD HEERBRUGG). All fish were then released back into their original  
409 rockpool and each rockpool was re-sampled every two days for the next nine days in order to  
410 determine the number and identity of tagged fish present.

411

412 STATISTICAL ANALYSIS

413 *Spatial variation*

414 In order to analyse the drivers of fish distributions and abundance, abiotic and biotic drivers  
415 for: 1) the presence of *B. cocosensis*, 2) *B. cocosensis* abundance, and 3) *L. haplodactylus*  
416 abundance within rockpools were analysed using Generalized Linear Models (GLM).

417 Elevation, temperature, dissolved oxygen, pH, algal cover, and rugosity were included as  
418 predictors in all models, however salinity and rockpool volume were excluded due to  
419 multicollinearity with other predictors (determined using Pearson correlation coefficients -  
420 methods described in Quinn & Keough (2002) and Field (2010)) (Appendix S3). For the  
421 model of *L. haplodactylus* abundance, *B. cocosensis* presence was also included as a  
422 predictor variable because *B. cocosensis* has been previously hypothesised to be a significant  
423 driver of heterospecific distributions (Griffiths 2002).

424

#### 425 *Contest dynamics*

426 To assess the predictors of contest intensity and duration, size asymmetry, dissolved oxygen  
427 level, *B. cocosensis* sex, *L. haplodactylus* sex, *B. cocosensis* body size and *L. haplodactylus*  
428 body size were included as predictors in GLM's. Contest intensity displayed a normal  
429 distribution and was therefore analysed using a General Linear Model. For contest duration  
430 the vast majority of winners either won within the first twenty seconds or after one hundred  
431 seconds, therefore contest duration was analysed as a binomial response variable with two  
432 levels: Instant (winner identified within twenty seconds) and Prolonged (winner identified  
433 after twenty seconds). Note that the predictors of contest outcome could not be analysed in  
434 this way, owing to the paucity of contests won by *L. haplodactylus* (6 out of 84 contests).

435 To determine whether the total number of aggressive actions displayed by fish varied  
436 between species, a GLM was performed with all main effects plus two-way species  
437 interaction terms (species\*sex, species\*size asymmetry, species\*body size and  
438 species\*dissolved oxygen treatment).

439 To examine changes in microhabitat utilisation patterns of *B. cocosensis* or *L.*  
440 *haplodactylus* in the absence and presence of each other, GLM's were used to investigate the

441 predictors of three response variables: 1) the amount of time (s) that fish spent on the wall ,2)  
442 the amount of time (s) fish spent on the gravel and 3) the amount of time (s) fish spent under  
443 and on the rock shelter. Context (solitary or paired contest), species, sex, body size and two-  
444 way species interaction terms (species\*context, species\*sex, species\*body size) were  
445 included in the models as predictor variables. The body size\*context interaction term was  
446 also included as body size was found to have a significant influence on microhabitat  
447 utilisation (current study).

448

#### 449 *Temporal dynamics*

450 In order to analysis the temporal dynamics of *B. cocosensis* and *L. haplodactylus*, predictors  
451 of the presence or absence of tagged fish were analysed using a repeated measures  
452 Generalized Estimating Equation (GEE). A repeated measures GEE was used because it  
453 allowed for the construction of a model with a binomial response variable (presence/absence  
454 of fish) and a temporally auto-correlated repeated measures predictor variable (day) (Zuur *et*  
455 *al.* 2009). Day, location, rockpool volume, species, sex and body size were all entered as  
456 predictor variables, and two-way interaction terms (species\*day, species\*rockpool volume,  
457 species\*sex and species\*body size) were included to identify any interactive species effects.

458 All statistical analysis was conducted using SPSS 21. For all models, Normality of  
459 response variables was assessed via inspection of plotted residuals and transformations were  
460 conducted where necessary to conform to the assumption of normality. backwards-stepwise  
461 elimination was conducted in order to identify significant predictors (following methods  
462 described by Wong *et al.* 2008), and significant interaction terms were explored using  
463 Tukey's post hoc comparisons.

464



465 **Results**

466 SPATIAL VARIATION IN DISTRIBUTIONS AND ABUNDANCE

467 A total of 207 fish from 11 species from 7 families were recorded from all sites that were  
468 sampled (Appendix S4). The rockpools sampled lay between 30 and 145 cm elevation above  
469 absolute low tide and ranged from 2 to 404 L in volume. *B. cocosensis* and *L. haplodactylus*  
470 were the most abundant species, comprising 40.6% and 49.3% of the total recorded fish  
471 respectively. None of the predictor variables (elevation, temperature, dissolved oxygen, pH,  
472 algal cover and rugosity) varied significantly between locations, except for rugosity which  
473 was significantly lower at Sandon point than at Bellambi and North Wollongong (ANOVA:  
474  $F_{2,42} = 4.29, P = 0.02$ ) (Appendix S5).

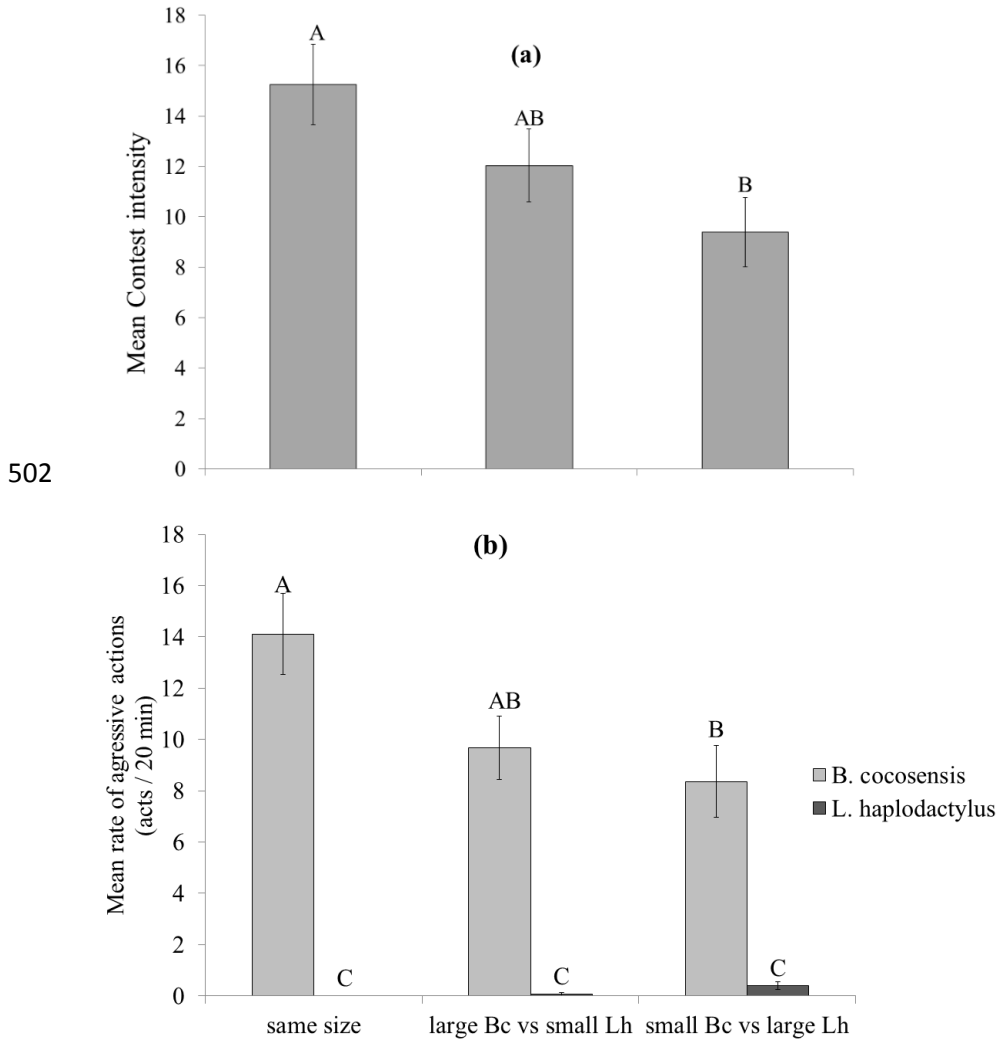
475 Dissolved oxygen was significantly higher in rockpools where *B. cocosensis* was present  
476 (average 10.7 mg/L) compared to rockpools where *B. cocosensis* was absent (average 9.0  
477 mg/L) (GLM:  $Wald X^2_1 = 5.62, P = 0.02$ ), however dissolved oxygen did not significantly  
478 predict *B. cocosensis* abundance (GLM:  $F_{1,29} = 3.2, P = 0.08$ ). For *L. haplodactylus*  
479 abundance the presence of *B. cocosensis* was a significant predictor of abundance ( $F_{1,41} =$   
480  $11.07, P = 0.002$ ). *L. haplodactylus* was on average 2.7 times more abundant in rockpools  
481 where *B. cocosensis* was absent. There were trends towards a significant effect of elevation  
482 ( $F_{1,41} = 4.23, P = 0.05$ ) and algal cover ( $F_{1,41} = 4.02, P = 0.05$ ) on *L. haplodactylus*  
483 abundance.

484

485 CONTEST OUTCOME, DURATION AND INTENSITY

486 In terms of contest outcome, *B. cocosensis* won 93% of all contests (78 out of a total of 84  
487 contests). None of the predictor variables, namely size asymmetry (GLM  $F_{2,52} = 0.42, P =$   
488  $0.66$ ), dissolved oxygen level ( $F_{1,58} = 0.08, P = 0.78$ ), *B. cocosensis* sex ( $F_{1,57} = 2.09, P =$   
489  $0.15$ ), *L. haplodactylus* sex ( $F_{1,55} = 1.99, P = 0.16$ ), *B. cocosensis* body size ( $F_{1,56} = 1.94, P =$

490 0.17) or *L. haplodactylus* body size ( $F_{1,54} = 1.66$ ,  $P = 0.20$ ) were significant predictors of  
491 contest duration. However, contestant size asymmetry did influence contest intensity;  
492 specifically, the intensity of contests was greater during contests between equal sized fish  
493 compared to contests between small *B. cocosensis* and large *L. haplodactylus* (Tukey's post-  
494 hoc:  $P = 0.03$ ), although, there was no significant difference in contest intensity between  
495 equal sized fish and between large *B. cocosensis* and small *L. haplodactylus* ( $P = 0.33$ ) (Fig.  
496 4a). The increased intensity of contests between equal sized contestants was driven by the  
497 fact that *B. cocosensis*, but not *L. haplodactylus*, was significantly more aggressive when  
498 paired with an equal sized versus unequal sized heterospecific (*B. cocosensis*,  $P = 0.02$ ; *L.*  
499 *haplodactylus*,  $P = 0.19$ ). In fact, analysis of the aggressive behaviors displayed by individual  
500 fish revealed that *B. cocosensis* was on average 70 times more aggressive than *L.*  
501 *haplodactylus* (Fig. 5b).



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#### 511 MICROHABITAT UTILISATION

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513

**Figure 4:** Mean ( $\pm$ SE) (a) contest intensity during interspecific contests between *Bathygobius cocosensis* and *Lepidoblennius haplodactylus*, and (b) number of aggressive actions displayed by *Bathygobius cocosensis* and *Lepidoblennius haplodactylus* during interspecific contests. Pairs of fish were grouped into three size asymmetry treatments (N=14 contests per treatment). Bc = *Bathygobius cocosensis*, Lh = *Lepidoblennius haplodactylus*. Bars not connected by the same letter are significantly different.

The amount of time that individual fish spent in each of the three microhabitats when solitary versus when paired with a heterospecific varied with species and social context (GLM:

514 Species\*Context; Time on wall,  $F_{1,163} = 39.43$ ,  $P < 0.01$ ; Time on gravel,  $F_{1,163} = 11.41$ ,  $P <$   
515  $0.01$ ; Time under and on rock,  $F_{1,164} = 15.71$ ,  $P < 0.01$ ). For *L. haplodactylus*, the percentage  
516 time spent on the wall was significantly higher when paired with *B. cocosensis* compared to  
517 when solitary (Tukey's post hoc:  $P < 0.001$ ). For *B. cocosensis* however, the percentage time  
518 spent on the wall was not influenced by the presence of *L. haplodactylus* ( $P = 0.99$ ).  
519 Furthermore, *L. haplodactylus* spent a significantly greater percentage of time under and on  
520 the rock when solitary compared to when paired with *B. cocosensis* ( $P < 0.001$ ). For *B.*  
521 *cocosensis* however, the percentage time spent under and on the rock was not influenced by  
522 the presence of *L. haplodactylus* ( $P = 0.92$ ) (Fig. 5). In addition, the body size of fish  
523 predicted patterns of microhabitat utilisation. Larger fish spent less time on the wall than  
524 smaller fish (GLM Size,  $F_{1,163} = 19.78$ ,  $P < 0.01$ ) and larger fish spent more time on the  
525 gravel than smaller fish (Size,  $F_{1,163} = 13.72$ ,  $P < 0.01$ ), regardless of species or social  
526 context.

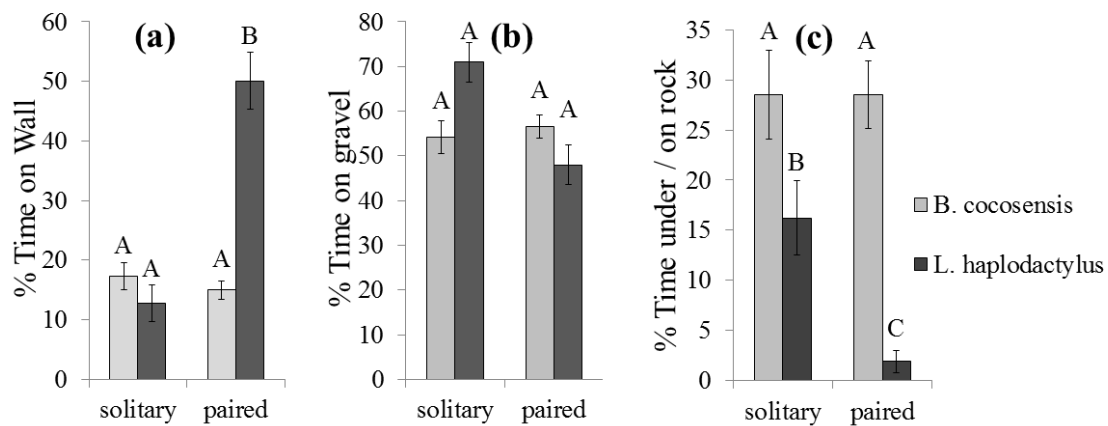
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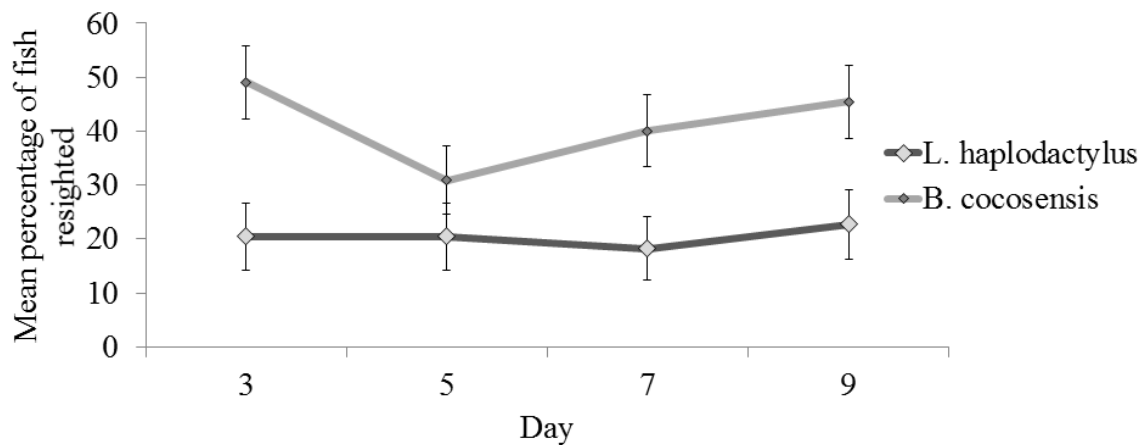
533 **Figure 5:** The mean ( $\pm$ SE) percentage of time spent (a) on the wall, (b) on the gravel and (c)  
 534 under / on the rock in aquarium compartments by *Bathygobius cocosensis* and  
 535 *Lepidoblennius haplodactylus* whilst solitary and during interspecific contests under standard  
 536 dissolved oxygen conditions.

537

#### 538 TEMPORAL DYNAMICS

539 The presence or absence of tagged *B. cocosensis* and *L. haplodactylus* in their rockpool of  
 540 original capture was unrelated to body size (GEE:  $Wald X^2_1 = 1.41$ ,  $P = 0.25$ ), sex ( $Wald X^2_1$   
 541  $= 0.59$ ,  $P = 0.44$ ) or number of days past since original capture ( $Wald X^2_3 = 3.82$ ,  $P = 0.28$ ).  
 542 Instead, presence or absence differed significantly between the species ( $Wald X^2_1 = 9.21$ ,  $P <$   
 543  $0.01$ ), with *B. cocosensis* being re-sighted significantly more frequently (41% of re-sampling  
 544 days) than *L. haplodactylus* (20% of re-sampling days) (Fig. 6).

545



546

547 **Figure 6:** Mean ( $\pm$ SE) percentage of *Bathygobius cocosensis* and *Lepidoblennius*  
 548 *haplodactylus* resighted in their rockpool of original capture 3, 5, 7 and 9 days after being  
 549 tagged.

550

## 551 Discussion

552 The aim of this study was to investigate the important yet poorly understood link between  
 553 contest dynamics and community structure. By undertaking individual level contest  
 554 experiments and interpreting results within the context of quantitative community level  
 555 investigations, the present study provides a novel application of contest theory. Our  
 556 investigation into the drivers of rockpool fish abundance and distribution revealed two  
 557 important results: firstly; *B. cocosensis* exhibited an apparent competitive dominance,  
 558 limiting the distribution of *L. haplodactylus*, and secondly *B. cocosensis* were more prevalent  
 559 in pools with elevated dissolved oxygen levels. In line with these findings, contest  
 560 experiments revealed that competition between *B. cocosensis* and *L. haplodactylus* was  
 561 asymmetric, with *B. cocosensis* being competitively superior and more aggressive. Further, *L.*  
 562 *haplodactylus* altered its microhabitat preference when in the presence of *B. cocosensis*. In  
 563 addition, short-term temporal field investigations suggested that *B. cocosensis* exhibits

564 stronger site fidelity and is therefore likely to possess a smaller home range than *L.*  
565 *haplodactylus*, although further quantification of home range sizes of both species is required  
566 to confirm this possibility.

567 *L. haplodactylus* was less abundant in pools where *B. cocosensis* was present compared to  
568 pools where *B. cocosensis* was absent, however the abundance of *L. haplodactylus* was  
569 unaffected by the abundance of *B. cocosensis*. This result suggests that the mere presence of  
570 *B. cocosensis* in a rockpool, regardless of its abundance, is sufficient to reduce the abundance  
571 of *L. haplodactylus*. In support of this finding, mesocosm experiments have demonstrated  
572 that the occupation of adjacent distinct habitats by two species of competing fish that would  
573 otherwise occupy the same habitat is a result of competitive dominance and exclusion by one  
574 species (Chargulaf, Burfeind & Tibbetts 2013, Keller & Brown 2008). A similar mechanism  
575 may be driving the patterns identified in this study. Given that *B. cocosensis* and *L.*  
576 *haplodactylus* have similar habitat and microhabitat preferences (White and Brown 2015;  
577 current study), it is likely that the distribution patterns identified are a result of *L.*  
578 *haplodactylus* actively avoiding pools or being aggressively excluded from pools where *B.*  
579 *cocosensis* is present.

580 In support of aggressive exclusion, contest experiments demonstrated that *B. cocosensis*  
581 possesses a higher RHP than *L. haplodactylus*, irrespective of the degree of size asymmetry  
582 between the contestants. This result was surprising, as size asymmetry is the most commonly  
583 identified predictor of contest outcome in intraspecific contests (Archer 1988; Hammerstein  
584 1981). In interspecific contests, size asymmetry has also been shown to predict contest  
585 outcome. For example, Berger and Mayr (1992) found that size asymmetry between  
586 contestants during interspecific competition between two rockpool fishes (*Forsterygian*  
587 *nigripenne robustum* and *Acanthoclinus fuscus*) predicted contest outcome in 74% of contest  
588 trials. In contrast, the present study suggests that for interspecific contests, species is more

589 important than relative body size in predicting contest outcome. Similarly, Anthony,  
590 Wicknick & Jaeger (1997) reported that species was the most important predictor of  
591 interspecific contest outcome between sympatric salamanders (*Plathodon ouachitae* and *P.*  
592 *albagula*) irrespective of size asymmetry. This discrepancy between studies show that species  
593 specific RHP can vary in importance relative to body size asymmetry depending on the study  
594 system. This variability is likely due to the evolution of different systems of niche  
595 partitioning (Berec, Krivan & Berec 2006). In cases where contest outcome is associated with  
596 species specific RHP, superior and inferior species will occupy their fundamental and  
597 realised niches respectively On the other hand, if contest outcome is determined by size  
598 asymmetry, niche partitioning will occur based on body size rather than species identity (e.g.  
599 French and Smith 2005).

600       Given that competition between *B. cocosensis* and *L. haplodactylus* was largely  
601 asymmetric, how is co-habitation by these two species achieved on intertidal rocky shores?  
602 At the level of individual rockpools, it is likely that individuals are using assessment  
603 strategies to minimize the costs associated with aggressive interactions (see Arnott & Elwood  
604 2009) (Table 1). The finding that contests of greater intensity occurred between equal sized  
605 fish compared to contests between small *B. cocosensis* and large *L. haplodactylus* provides  
606 support for the mutual assessment model (Arnott & Elwood 2009) (Table 1). However,  
607 contest intensity didn't vary between the size matched treatment and the large *B. cocosensis* -  
608 small *L. haplodactylus* treatment. This finding, along with the finding of no effects on contest  
609 duration, is in contradiction to the mutual assessment model (Table 1). Therefore, a more  
610 appropriate explanation is that these species do not assess each other during a contest (i.e. the  
611 no assessment model – Table 1), but rather have inherently different contest strategies as  
612 explained by the hawk-dove model (Smith & Price 1973). Both the aggressive hawk and  
613 passive dove strategies of contest behaviour are considered to be evolutionarily stable



614 strategies, providing effective means of contest resolution. It is likely that the aggressive  
615 strategy of *B. cocosensis* and the passive strategy of *L. haplodactylus* promote their  
616 cohabitation of rockpools by minimizing the occurrence of aggressive interactions.

617 It was also predicted that sex would have an effect on contest dynamics, based on  
618 observed distinct differences in aggression between males and females of a congeneric  
619 species, *Bathygobius saporator* (Tavolga 1954). However, there was no effect of sex on  
620 aggression. It is possible that differences in aggression between males and females are  
621 associated with reproductive events and therefore most prevalent during breeding seasons.  
622 Griffiths (2002) suggested that both *B. cocosensis* and *L. haplodactylus* recruit to rocky  
623 shores (and therefore breed) in spring and early summer. As fish were collected for the  
624 present study outside of breeding season, this could potentially explain why aggression did  
625 not vary with sex. Furthermore, variation in aggression with sex may only be evident during  
626 intraspecific social interactions. Therefore, future research should incorporate contests  
627 performed both within and outside of the breeding season to rigorously investigate the  
628 existence of sex differences in interspecific contest behavior.

629 Field surveys demonstrated that *B. cocosensis* was more likely to be found in rockpools  
630 with elevated dissolved oxygen. Therefore, it was predicted that *B. cocosensis* would place  
631 higher value on rock shelters under standard compared to reduced dissolved oxygen  
632 conditions and would be more aggressive and motivated to win contests under those  
633 conditions. Contrary to expectations, *B. cocosensis* did not display any differences in  
634 aggression between dissolved oxygen treatments. There are at least three possible  
635 explanations for this result: 1) it may be that the inherently aggressive nature of *B. cocosensis*  
636 is exhibited regardless of metabolic costs, particularly given that contests were generally  
637 resolved very quickly; 2) the methods used, whereby dissolved oxygen was reduced in  
638 aquaria immediately prior to contest initiation, may not have allowed sufficient time for

639 metabolic costs to be incurred and subsequently affect behavior; and 3) *B. cocosensis* may  
640 not have placed differing value on the rock shelter under high and low dissolved oxygen  
641 levels, and hence exhibited no differences in aggression. To examine these possibilities,  
642 future research should investigate the influence of varying dissolved oxygen concentrations  
643 on metabolic rate and associated behavior in both species, both prior to and after contests.

644 Plasticity in microhabitat use has also been shown to facilitate the co-occurrence of  
645 species within a specific habitat (e.g. Denno, McClure & Ott 1995; Kimura & Chiba 2010).  
646 When solitary, *L. haplodactylus* displayed a preference for the gravel and rock shelter,  
647 however microhabitat usage abruptly changed when in the presence of *B. cocosensis*, with *L.*  
648 *haplodactylus* spending on average four times more time on the wall. In contrast,  
649 *B. cocosensis* also preferred the rock/gravel but showed no shift in microhabitat use in the  
650 presence of *L. haplodactylus*, likely reflecting its overall competitive superiority and  
651 subsequent exclusion of *L. haplodactylus* from its preferred microhabitat. Similarly, Arakaki  
652 & Tokeshi (2011; 2012) found contest outcomes and associated microhabitat preference for  
653 three rockpool fishes (*Bathygobius fuscus*, *Chaenogobius annularis* and *C. gulosus*) was  
654 largely dependent on species identity and the identity of heterospecifics present. Specifically,  
655 *B. fuscus* showed very little variation in microhabitat preference when solitary compared to  
656 when paired with either *C. annularis* or *C. glosus*, whilst both *C. annularis* and *C. glosus*  
657 showed large variations in microhabitat preference when paired with *B. fuscus* compared to  
658 when solitary. In contrast, Nakamura (1976) found that two species of rockpool sculpins  
659 (*Oligocottus maculosus* and *O. snyderi*) had distinctly different microhabitat preferences  
660 regardless of the presence or absence of heterospecifics. However, fish in the study by  
661 Nakamura (1976) never displayed interspecific aggressive behaviors and hence did not  
662 compete with each other. Fish in the present study and those examined by Arakaki & Tokeshi  
663 (2011; 2012) have overlapping microhabitat preferences and hence aggressively compete for

664 the common resource. As such, plasticity in microhabitat use is likely to be another  
665 mechanism by which within-rockpool coexistence of competing *B. cocosensis* and *L.*  
666 *haplodactylus* is facilitated (Arakaki & Tokeshi 2012).

667 Microhabitat preference was also found to vary with absolute body size. Similarly,  
668 Arakaki & Tokeshi (2005) showed that body size influenced the microhabitat preference of  
669 intertidal goby species irrespective of contest interactions. Size-based variation in  
670 microhabitat preference may reflect intraspecific competition (Polis 1984), ontogenetic shifts  
671 in habitat preference related to dietary shifts or the ability of different sized fish to  
672 camouflage effectively in different microhabitats (Rojas & Ojeda 2010) - These hypotheses  
673 would be intriguing to test in future studies.

674 Both *B. cocosensis* and *L. haplodactylus* displayed a stable level of rockpool fidelity over  
675 the short term (9 days) and also longer term (6 weeks) (White & Brown 2013), suggesting  
676 that both species do show site fidelity and possess a home range in which they reside over  
677 significant periods of time. However, *B. cocosensis* displayed significantly higher rockpool  
678 fidelity than *L. haplodactylus*, with approximately double the re-sight rate of *L. haplodactylus*  
679 (41% versus 20% respectively). There are at least two possible mechanisms generating this  
680 pattern. First, it could be that *B. cocosensis* has a smaller home range (~2-3 rockpools -  
681 inferred from the finding that *B. cocosensis* had a resight rate 41% in rockpool of original  
682 capture), whereas *L. haplodactylus* has a larger home range (~5 pools - inferred from a  
683 resight rate of 20% in rockpools of original capture). In order to test this hypothesis, it would  
684 be useful to quantify home range sizes of both species by tagging and following individuals  
685 over time and space. Alternatively, the differences in rockpool fidelity may simply be a  
686 function of differing activity levels of *B. cocosensis* and *L. haplodactylus*. For instance, for a  
687 given home range size, *B. cocosensis* may show less activity and hence appear to occupy a  
688 smaller subset of rockpools, whilst *L. haplodactylus* may show higher activity and hence

689 move between a larger subset of pools, possibly due to exclusion by *B. cocosensis*. In any  
690 case, species-specific variation in home range size and/or activity within a home range may  
691 also contribute towards the coexistence of the two species, at the between-rockpool spatial  
692 scale (Hanski 1981).

693 Contrary to expectations, sex had no impact on rockpool fidelity for either species,  
694 suggesting that both sexes of each species display similar movement patterns. The lack of sex  
695 effect was surprising, given that strong sex effects on movement have previously been  
696 documented in a range of fishes (Jarvi-Laturi *et al.* 2007; Stiver *et al.* 2007). For example,  
697 Stiver *et al.* (2007) showed, through genetic studies of the population structure of an African  
698 Great Lakes Cichlid (*Neolamprologus pulcher*), that large males were more related to large  
699 males in other subpopulations than they were to other fish in their own subpopulation and had  
700 therefore dispersed over larger distances than females. To conclusively demonstrate a lack of  
701 sex effect, future studies should attempt to quantify temporal rockpool fidelity of males and  
702 females during reproductive as well as non-reproductive seasons, as sex may be differentially  
703 important depending on reproduction (Griffiths 2003b). *B. saporator* males for example are  
704 known to maintain and look after nests, making them relatively less mobile than females  
705 during reproductive seasons (Tavolga 1954).

706

## 707 CONCLUSIONS

708 Contest experiments revealed that *Bathygobius cocosensis* was more aggressive and  
709 displayed higher resource holding power than *Lepidoblennius haplodactylus*. These results  
710 indicate that *B. cocosensis* is competitively dominant and that the competitive dynamics  
711 between *B. cocosensis* and *L. haplodactylus* are asymmetric. In light of these findings the  
712 present study provides several possible explanations for the coexistence of these competing  
713 species under asymmetric competition. Findings suggest that there are mechanisms operating

714 at both within- and between-rockpool levels that facilitate the cohabitation of rocky shores by  
715 the two numerically dominant species. Within rockpools, coexistence may be facilitated by  
716 variations in contest behaviours between the two species. Additionally, flexibility in  
717 microhabitat use within rockpools, particularly by the weaker competitor in the presence of  
718 heterospecifics, promotes coexistence. At the between-rockpool level, variations in the  
719 degree of site fidelity, territoriality and possibly home range size of *B. cocosensis* and *L.*  
720 *haplodactylus* may facilitate co-occurrence at larger spatial scales.

721 The present study provides evidence for interspecific competition being a significant  
722 driver of South East Australian rockpool fish community structure. Further, this study has  
723 demonstrated that by using contest theory to understand the dynamics of interspecific  
724 contests between competing species, insight can be gained into how those species coexist and  
725 potentially how habitat is partitioned and biodiversity is maintained. More broadly, this study  
726 has highlighted the applicability of contest theory for investigations of community ecology  
727 and has demonstrated the possible application of contest experiments for investigations into  
728 the drivers of community dynamics across a wide range of ecological systems.

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746

747 All procedures were approved by and in accordance with guidelines specified by the

748 University of Wollongong animal ethics committee (#AE 14/34) and the NSW DPI Scientific

749 Collection permit (#P14/0005-1.2).

750

751 Data accessibility - All data used in this manuscript is accessible via figshare online data

752 archiving - <https://dx.doi.org/10.6084/m9.figshare.4292921.v1>

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## 919 **Supporting Information**

920 Additional supporting information may be found in the online version of this article.

921

922 Appendix S1: Results of statistical tests showing there is no order effect of repeated measures  
923 dissolved oxygen treatments on response variables.

924 Appendix S2: Results of Generalized Linear Models showing predictors of *Bathygobius*  
925 *cocosensis* abundance, *Lepidoblennius haplodactylus* abundance and the presence or absence  
926 of *Bathygobius cocosensis* in rockpools.

927 Appendix S3: Correlation matrix of variables used to construct models of fish distributions.

928 Appendix S4: Fish species caught from 45 rockpools across 3 locations on the South East  
929 coast of Australia.

930 Appendix S5: Results of ANOVA's testing for variation of continuous predictor variables  
931 between three locations.

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