

Natal philopatry increases relatedness within groups of coral reef cardinalfish

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1 Abstract

2

3 A central issue in evolutionary ecology is how patterns of dispersal influence patterns of
4 relatedness in populations. In terrestrial organisms, limited dispersal of offspring leads to
5 groups of related individuals. In contrast, for most marine organisms, larval dispersal in open
6 waters is thought to minimise kin associations within populations. However, recent molecular
7 evidence and theoretical approaches have shown that limited dispersal, sibling cohesion,
8 and/or differential reproductive success can lead to kin-association and elevated relatedness.
9 Here, we tested the hypothesis that limited dispersal explains small-scale patterns of
10 relatedness in the pajama cardinalfish *Sphaeramia nematoptera*. We used 19 microsatellite
11 markers to assess parentage of 233 juveniles and pairwise relatedness among 527 individuals
12 from 41 groups in Kimbe Bay, Papua New Guinea. Our findings support three predictions of
13 the limited dispersal hypothesis: 1) Elevated relatedness within groups, compared to among
14 groups, and elevated relatedness within reefs compared to among reefs; 2) A weak negative
15 correlation of relatedness with distance; 3) More juveniles than would be expected by chance
16 in the same group and the same reef as their parents. We provide the first example for natal
17 philopatry at the group level causing small-scale patterns of genetic relatedness in a marine
18 fish.

19

20 Key words: Genetic relatedness, kin cohesion, limited dispersal, reproductive sweepstakes,
21 natal philopatry, cardinalfish

22 Introduction

23

24 Linking patterns of genetic structure of populations with larval dispersal is paramount for our
25 understanding of population dynamics and the evolution of social systems. Whether close
26 relatives, such as offspring, parents, siblings or half-siblings, are located nearby has important
27 consequences on individual fitness and population growth (Keller & Waller 2002; Crokarak &
28 Roff 1999). How far offspring disperse and the consequences for the degree of relatedness
29 within and among groups of individuals have important implications for applicability of
30 inclusive fitness theory to the evolution of social systems (Hamilton 1963, 1964; West-
31 Eberhard 1975, Queller 1994). The genetic consequences of dispersal patterns are
32 challenging to discern in environments where dispersive life phases potentially disrupt the
33 interaction of close relatives and offspring cannot easily be tracked. The majority of marine
34 animals have a dispersal larvae phase, and any link between patterns of dispersal and patterns
35 of genetic structure is often assumed to be at spatial scales too large for there to be elevated
36 relatedness within local populations or social groups (Shanks 2009; Als et al. 2011; Selkoe et
37 al. 2014).

38

39 Recently, the paradigm that the dispersal larval phase of most marine organisms leads to the
40 separation of larvae from their parents and siblings (Victor 1984, Leis 1991) has been
41 challenged. A growing body of work utilizing molecular evidence has found fine scale
42 genetic structure in marine populations, showing high proportions of relatives in close
43 proximity (e.g., Grosberg & Quinn 1986, Bernardi et al. 2001, Beheregaray & Sunnuck 2001,
44 James et al. 2002, Iacchei et al. 2013, Morales-Gonzales et al. 2019, Schunter et al. 2019).
45 Additionally, there is now a large number of examples of sibs near each other (e.g., Duffy
46 1996, Selkoe et al. 2006, Buston et al. 2009, Bernardi et al. 2012, Herrera et al. 2016, Selwyn
47 et al. 2016, Riquet et al. 2017) and parent-offspring pairs found on the same reefs or within
48 the same lagoons (e.g., Jones et al. 1999, Swearer et al. 1999, Jones et al. 2005, Patterson &
49 Swearer 2007, Beldade et al. 2012, Saenz-Agudelo et al. 2012, D'Aloia et al. 2013, Salles et
50 al. 2016, Bonin et al. 2016). These patterns raise the possibility that relatedness may be a
51 factor in the formation of social groups and may influence local population dynamics.

52

53 Possible mechanisms for fine scale relatedness structures in marine populations include
54 limited dispersal, sweepstakes reproduction, and sibling cohesion (D'Aloia & Neubert 2018;
55 D'Aloia et al. 2018). Limited dispersal is where high levels of self-recruitment to local

56 populations occurs and leads to close relatives living together or nearby. This has been
57 demonstrated for several marine populations (e.g., Jones et al. 1999, Swearer et al 1999,
58 D'Aloia et al. 2015, Almany et al. 2017). Sweepstakes reproduction describes the hypothesis
59 that differential reproductive success can lead to some cohorts derived from a small number
60 of adults being dominant in a population (Hedgecock 1994, Hedgecock et al. 2011). For this
61 hypothesis, models predict that there should be large differences in relatedness between and
62 within sites, with no spatial patterns in the degree of relatedness (D'Aloia & Neubert 2018).
63 On the other hand, sibling cohesion, observed in marine fishes where siblings are co-located
64 (Selkoe et al. 2006, Buston et al. 2009, Bernardi et al. 2012) leads to high within-site
65 relatedness, but low relatedness among sites, because siblings dispersing together are likely to
66 settle together (D'Aloia & Neubert 2018). The testing of dyad relatedness and the spatial
67 distance among dyads, in conjunction with parentage analyses, provides a means of
68 distinguishing among these three possible mechanisms (D'Aloia & Neubert 2018; D'Aloia et
69 al. 2018), and crucially requires empirical tests. Indeed, studies of fine scale relatedness
70 structures within populations and evidence for the mechanisms leading to this structuring still
71 require empirical evidence for most marine taxa.

72

73 The overall aim of this study was to describe spatial patterns of relatedness and test potential
74 mechanisms for those patterns in a population of pajama cardinalfish, *Sphaeramia*
75 *nematoptera*. *S. nematoptera* form pairs within small social groups of 2-35 individuals
76 (Rueger et al. 2016). While most pairs are monogamous for at least one breeding cycles,
77 examples of multiple paternity as well as multiple maternity have been found (Rueger et al.
78 2019). *S. nematoptera* are mouthbrooders and the males orally incubate eggs for about 8 days
79 (pers. obs). Once hatched offspring have a larval dispersal duration of 24-25 days (Fisher &
80 Bellwood 2003), but larval dispersal distances are unknown. Several species of cardinalfish
81 have shown potential for genetic population differentiation at the scale of 12 km (Hoffman et
82 al. 2005, Gerlach et al. 2007a). Our study is conducted on inshore reefs in Kimbe Bay, Papua
83 New Guinea, which provide a unique opportunity to study relatedness and dispersal of *S.*
84 *nematoptera* at smaller spatial scales (0-4 km).

85

86 We specifically addressed 3 predictions derived from the hypothesis that local patterns of
87 relatedness will be caused by limited dispersal, rather than sweepstakes reproduction or
88 sibling cohesion: 1) Relatedness within groups and reefs will be higher than relatedness
89 among groups and reefs; 2) There will be an inverse relationship between average relatedness

90 and distance between pairs of individuals; 3) More larvae than expected by chance will return
91 to the same group and the same reef as their parents.

92

93 Methods

94

95 *Study location and sample collection*

96

97 The study was conducted on inshore reefs near Mahonia Na Dari Research and Conservation
98 Centre, Kimbe Bay, Papua New Guinea (5°30'S, 150°05'E), from October 2012 to
99 September 2014 (Figure 1). All work was conducted using SCUBA at depths of up to 18m. A
100 total of 41 social groups of pajama cardinalfish, *Sphaeramia nematoptera*, were
101 comprehensively sampled from nearshore reefs and along a fringing reef (Figure 1). The
102 whole population was sampled as well as possible with the means available, during two years
103 and more than 500 hours of surveying.

104

105 A total of 527 *S. nematoptera* were caught using hand nets and diluted clove oil as a mild
106 anaesthetic (Munday & Wilson 1997). Each fish was measured underwater (Standard Length
107 SL) and a fin clip was taken from the caudal fin. Tissue samples were preserved in 99%
108 ethanol for genetic analysis. All fish were categorized as either adult (≥ 38 mm SL), subadult
109 (33-37mm SL) or juvenile (< 33 mm SL), with categories assessed by gonad histology (Rueger
110 et al. 2016).

111

112 *Genetic analyses and locus characteristics*

113

114 Genomic DNA was extracted from ~ 2 mm² of fin tissue collected from each individual and
115 screened at 23 microsatellite markers in four multiplexes (Rueger et al. 2015). DNA
116 extractions were performed following procedures described in the Nucleospin-96 Tissue kit
117 (Macherey-Nagel, Germany). Selected primer pairs were combined in a primer premix for in-
118 reaction concentrations ranging from 0.02 to 0.06 μ M, adjusted for even amplification. All
119 four multiplex reactions were performed using the QIAGEN Microsatellite Type-it kit
120 (QIAGEN, Germany) in a total volume of 10 μ l containing 5 μ l of QIAGEN Multiplex
121 Master Mix (2x), 1 μ l QIAGEN Q-solution, 1 μ l of distilled water, 2 μ l of primer premix, and
122 1 μ l template DNA. PCR products were screened on an ABI 3370xl DNA Analyzer (Applied

123 Biosystems) with the GeneScan 500 LIZ (Applied Biosystems) internal size standard
124 following a 1:15 dilution. Individual genotypes were scored in GENEMAPPER v4.0 and unique
125 alleles were distinguished using marker specific binsets in MSATALLELE (Alberto 2009).

126

127 Allele frequencies, linkage disequilibrium and deviation from Hardy-Weinberg equilibrium
128 were estimated with Genepop (Raymond and Rousset, 1995) and the data was checked for
129 the presence of null alleles with Microchecker (van Oosterhout et al 2004). Genotyping error
130 was assessed using repeat samples from 43 individuals and calculated as the ratio between
131 mismatches in alleles and the number of replicated alleles (Pompanon et al. 2005). For further
132 analysis, we used the 19 markers with the lowest genotyping error, <6%. Marker specific
133 summary statistics are provided in Supplemental Material Table 1 (adapted from Rueger et al.
134 2015).

135

136 *Pairwise relatedness at different spatial scales*

137

138 The relatedness of any two of sampled individuals was assessed using the relatedness
139 moment-based estimator described by Queller & Goodnight (1989) calculated by
140 COANCESTRY (Wang 2011). To test accuracy, we first simulated 1000 individuals from the
141 estimated allele frequencies at each locus. The rate of missing allele was set to 0.01 for all
142 loci and locus-specific genotyping error rates were used. The correlation with the true values
143 for the Queller & Goodnight moment-based estimator (1989) was high (Pearson's $r = 0.941$,
144 $p < 0.001$).

145

146 With the aim of studying whether pairwise relatedness estimates change with spatial scale, a
147 mixed model was fitted with relative location of a given dyad as a fixed factor (both
148 individuals in the same social group; both on the same reef but in separate social groups; both
149 on separate reefs) and individual tags of both dyad members were used as random terms to
150 account for nonindependence of relatedness values involving the same individuals. Statistical
151 significance was assessed with a likelihood ratio test.

152

153 *Relationship between pairwise relatedness and distance*

154

155 Distance was calculated using the Cartesian coordinates of each social group (Grant et al.
156 2006). With the aim of determining whether pairwise relatedness estimates change with

157 distance, an analysis of variance was performed with mean dyad relatedness as response
158 variable, and distance categorized in five bins (0m, 0-200m, 200-400m, 400-600m, >600m)
159 as predictor variable. To account for possible positive autocorrelation between dyad samples,
160 we randomly sampled 10 dyads from each bin without replacement and calculated the mean
161 (Kraemer et al. 2016). We replicated each set 100 times. All statistical analyses were
162 performed using R version 3.6.1. (R core team 2019).

163

164 *Natal philopatry*

165

166 To determine whether natal philopatry at the scale of the group or reef occurred, we used the
167 same 19 microsatellites (Rueger *et al.* 2015, Appendix D) to match juveniles and subadults to
168 potential parents. Parentage was assessed with COLONY, with the following parameters;
169 Full likelihood, medium likelihood precision, long run. As per Harrison et al. (2014), these
170 parameters were shown to yield a very high overall accuracy for this marker set identifying
171 true parent-offspring pairs (99.9%; type-I error 0.1%, type-II error 0%) (see Rueger et al.
172 2019 for details of the simulation).

173

174 To assess whether there was a statistical bias towards natal philopatry, the juveniles that
175 returned to their natal reef and natal group were identified. We tested whether the number of
176 juveniles that were found on the same reef and the same group as their assigned parents was
177 different than expected by chance with a Chi-squared test of independence. Expected
178 frequencies were calculated by establishing the possible recruitment trajectories in our
179 population leading to natal philopatry (recruitment to the same group as the parents), self-
180 recruitment (recruitment to the same reef but not the same group as the parents) or
181 recruitment to neither the same group nor reef as the parents (see example in Figure 2). The
182 expected frequencies were then compared to the observed frequencies of natal philopatry,
183 self-recruitment and those recruitment events that represented neither. In a population with 41
184 social groups there are $41^2=1681$ possible recruitment trajectories.

185

186 Results

187

188 *Patterns of relatedness within and among reefs and social groups*

189

190 The prediction that relatedness within groups and within reefs should be higher than
191 relatedness among groups and among reefs was supported by the study. There was a
192 significant effect of spatial scale on the pairwise relatedness estimates in *S. nematoptera* ($\chi^2_{(2)}$
193 = 23.05, $p < 0.001$). Dyads on the same reef had higher relatedness than those not on the
194 same reef ($>0.0013 \pm 0.0008$). Within reefs, dyads in the same group were more related
195 than dyads across different groups ($>0.0075 \pm 0.001$) (Figure 4).

196

197 *Relationship between relatedness and distance*

198

199 The prediction that there should be an inverse relationship between average relatedness and
200 distance between pairs of individuals was supported by the study. Mean pairwise relatedness
201 differed significantly with distance category in the inshore population of *S. nematoptera* in
202 Kimbe Bay ($df=4$, $F=5.43$, $p<0.001$) (Figure 4).

203

204 *Natal philopatry*

205

206 The prediction that more larvae than would be expected by chance should return to their natal
207 groups and reefs was supported by the study. Out of 233 juveniles and subadults, 34 could be
208 assigned either to a single parent ($N=27$), or to a parent pair ($N=7$) within the sampling area.
209 Out of the assigned individuals, three were found in the same social group as their parents,
210 eight were found on the same reef but not the same group as their parents, and 23 were found
211 on different reefs from their parents. Four full sibling pairs were detected in the population
212 through parentage analysis, all of them found on different reefs from each other. Twelve half
213 sibling pairs were found in the same groups, twelve on the same reefs, and 72 on different
214 reefs as each other. All parents that half siblings had in common were inferred by COLONY
215 and were not part of the sampled population.

216

217 Within the population, recruitment patterns were found to be dependent on spatial scale, with
218 more recruits assigned to the same social group or the same reef as their parents than
219 expected by chance ($\chi^2_{(2)} = 7.51$, $p = 0.022$).

220

221 Subdivision of the χ^2 showed that the likelihood of natal philopatry to groups and self-
222 recruitment to reefs were not significantly different from each other ($\chi^2 = 0.66$, $p=0.415$), but
223 together they were more likely to occur than was dispersal to different reefs ($\chi^2 = 3.93$,

224 p=0.047, Figure 5). The likelihood of self-recruitment to reefs and dispersal to different reefs
225 were not significantly different from each other ($\chi^2=1.67$, p=0.196), but together they were
226 marginally significantly less likely to occur than was natal philopatry to groups ($\chi^2=3.18$,
227 p=0.075, Figure 5). Finally, the recruitment patterns to natal groups were significantly
228 different to those to non-natal reefs ($\chi^2=3.93$, p=0.047, Figure 5).

229

230 Discussion

231

232 Our study links natal philopatry to reefs and social groups and small-scale patterns of
233 relatedness for the inshore population of *S. nematoptera* in Kimbe Bay. All three predictions
234 based on the limited dispersal hypothesis were supported by the data: 1) We detected elevated
235 relatedness within groups and reefs; 2) The relatedness values were negatively correlated
236 with distance; 3) Parentage analysis revealed more larvae than expected by chance returning
237 to the same social group and the same reef as their parents. Limited dispersal was confirmed
238 as a likely mechanism for the spatial pattern in relatedness by the direct evidence of
239 recruitment varying with spatial scale. Thus, our study provides empirical evidence for
240 elevated relatedness at the scale of the group and demonstrates natal philopatry as the cause
241 in a coral reef fish.

242

243 Relatedness in the population was low overall but higher within social groups compared to
244 among social groups and higher within reefs than among reefs, supporting predictions based
245 on limited dispersal. This finding contributes to a growing body of work howing that small
246 scale population structures are possible in marine organisms in general (Beheragaray &
247 Sunnucks 2001, Morales-Gonzales et al. 2019) and specifically coral reef fishes (Hoffman et
248 al. 2005, Kolm et al. 2005, Gerlach et al. 2007a, Buston et al. 2009). In some coral reef fish
249 species, small effective population sizes and high levels of natal philopatry may increase the
250 risk of inbreeding (Shields 1982, Purcell et al. 2006). However, Salles et al. (2016) showed
251 using pedigree analysis that despite close relatives sometimes being found in the same group
252 in *Amphiprion percula*, successful inbreeding was rare and did not impair local population
253 persistence. In contrast to the strict group structure with only one monogamous breeding pair
254 in *A. percula*, in *S. nematoptera* groups encompass several breeding pairs and some
255 individuals mate polygamously (Rueger et al. 2019). This may further reduce the risk of
256 elevated inbreeding despite the presence of some close relatives. Thus, any benefits of
257 settling close to kin might outweigh potential costs.

258

259 The observation of elevated relatedness at small spatial scales demands explanation. There
260 are three plausible alternative hypotheses: limited dispersal; kin cohesion; sweepstakes
261 reproduction. The correlation between pairwise relatedness values and spatial distance
262 supports the limited dispersal hypothesis for *S. nematoptera*. Based on theoretical models, the
263 prediction for limited dispersal are a strong spatial effect both within and between sites, since
264 the probability of dispersal should decrease as a function of distance (D'Aloia & Neubert
265 2018). This is similar to what we found for *S. nematoptera*. The negative relationship
266 between relatedness and dyad distance was significant but weak, with most of the dyads
267 showing very low relatedness values. Relatedness and distance are correlated in many taxa,
268 including e.g., arthropods (Beye et al. 1998), birds (Foerster et al. 2006, Shanahan et al.
269 2011) and mammals (McEachern et al. 2007). Limited dispersal in the form of natal
270 philopatry is often identified as the cause of such patterns (Waser & Jones 1983,
271 Weatherhead & Forbes 1994, Sutherland et al. 2000).

272

273 Direct evidence of self-recruitment to social groups and reefs confirms limited dispersal as
274 the cause of relatedness patterns observed in *S. nematoptera*. In our study, within a very small
275 area (max distance ~3.6km, average distance ~0.5km), 15% of the juveniles were assigned to
276 sampled adults. In another cardinalfish, *Ostorhincus doederleini*, approximately 60% of
277 juveniles were assigned to the population in a small study area (~12km) (Gerlach et al.
278 2007a). High levels of self-recruitment have also been recorded in other coral reef fishes,
279 such as butterflyfish and anemonefish (Jones et al. 1999, 2005, Almany et al. 2007, Planes et
280 al. 2009, Bonin et al. 2016). Settling near close relatives has the potential benefits of
281 increases in reproductive output, social group stability, reduced competition and more
282 effective cooperation (Hamilton 1964, Milinski 1987, Ward & Hart 2003, Frommen &
283 Bakker 2004, Gerlach et al. 2007b).

284

285 Limited dispersal alone is sufficient to explain the patterns observed in *S. nematoptera*. In
286 contrast, sweepstakes reproduction and/or sibling cohesion alone cannot explain the patterns
287 observed for *S. nematoptera*. However, sibling cohesion and sweepstakes reproduction
288 cannot be ruled out as possible co-contributing mechanisms. That is to say, it is possible that
289 several mechanisms are at work at the same time (D'Aloia & Neubert 2018). Evidence of
290 siblings or closely related individuals of similar size settling together after a pelagic larval
291 stage has been described for the damselfishes *Dascyllus aruanus* (Buston et al. 2009) and *D.*

292 *trimaculatus* (Bernardi et al. 2012). Though with the benefit of hindsight, these results may
293 also be explained by limited dispersal. In *S. nematoptera*, we do not have direct evidence for
294 sibling cohesion, since the number of markers utilized does not allow us to identify full or
295 half sibs with confidence (D'Aloia et al. 2018). Parentage analysis detected some full
296 siblings, all found on different reefs from each other. Future research may employ a much
297 larger marker set to reliably identify full and half siblings in the population and explore
298 sibling cohesion as a contributing factor to the relatedness patterns we describe (D'Aloia et
299 al. 2018). To rule out or confirm sweepstakes reproduction in future studies will require
300 comprehensive data on temporal and spatial patterns of larval dispersal and recruitment
301 (Hedgecock & Pudovkin 2011). Based on the available evidence, limited dispersal is
302 sufficient to explain the small-scale patterns of relatedness that we observe in this population.
303

304 *Conclusion*

305

306 Empirical studies linking limited dispersal and fine scale genetic structure in a marine
307 population are scarce. Dispersal kernels showing dispersal declining with distance have been
308 demonstrated empirically for the reef fishes *Elacatinus lori* (D'Aloia et al. 2015) and
309 *Amphiprion percula* (Almany et al. 2017) and these may be linked to spatial genetic structure
310 at the scale of the reef or region (D'Aloia et al. 2014, 2020; Pinsky et al. 2017). However,
311 these studies do not link limited dispersal directly to relatedness structures at the scale of the
312 group or patch reef.

313

314 In our study we found a clear link between natal philopatry to different spatial scales and
315 patterns of genetic relatedness within a population of *S. nematoptera*. Individuals within
316 groups and reefs were more closely related than between groups and reefs. These relatedness
317 patterns were most readily explained by the limited dispersal patterns found in the population.
318 Thereby we provide one of only very few examples of empirical evidence for the cause of
319 fine scale genetic structure within marine populations, and the first example at such a small
320 spatial scale. More empirical evidence for small scale genetic structures and their links to
321 dispersal patterns is needed to fully understand the population dynamics, individual fitness
322 and social evolution of marine organisms.

323

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330 for granting access to their reefs for this study.

331

332 Data accessibility

333 – DNA sequences for microsatellite markers: GenBank accessions KP790099- KP790121

334 – Genotypes, relatedness, parentage, natural history parameters and simulated distances:

335 Dryad, doi: 10.5061/dryad.cz8w9gj0q

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515

516

517 **Figure 1.** Map of sampling area in Kimbe Bay, Papua New Guinea, near Mahonia Na Dari
 518 Research and Conservation Center. Outlines and names of seven sampled inshore reefs are
 519 provided. Grey shading indicates land. Sizes of black circles indicate the size of 41 social
 520 groups of *Sphaeramia nematoptera*, with all fish that were observed sampled.

521

522 **Figure 2.** Recruitment trajectories in a hypothetical population with three groups of fish each
 523 on three reefs. Blue arrows represent all possible trajectories leading to natal philopatry at the
 524 group level (N=9), orange arrows represent self-recruitment to the natal reef (N=18) and

525 black arrows represent trajectories leading to neither natal philopatry nor self-recruitment
526 (N=54).

527

528 **Figure 3.** Density distribution of pairwise relatedness estimates for dyads of *Sphaeramia*
529 *nematoptera* in Kimbe Bay: dark grey, both individuals on separate reefs; grey, both
530 individuals on the same reef but in separate groups; light grey, both individuals in the same
531 group. Pairwise relatedness values were assigned to bins with width $r = 0.05$.

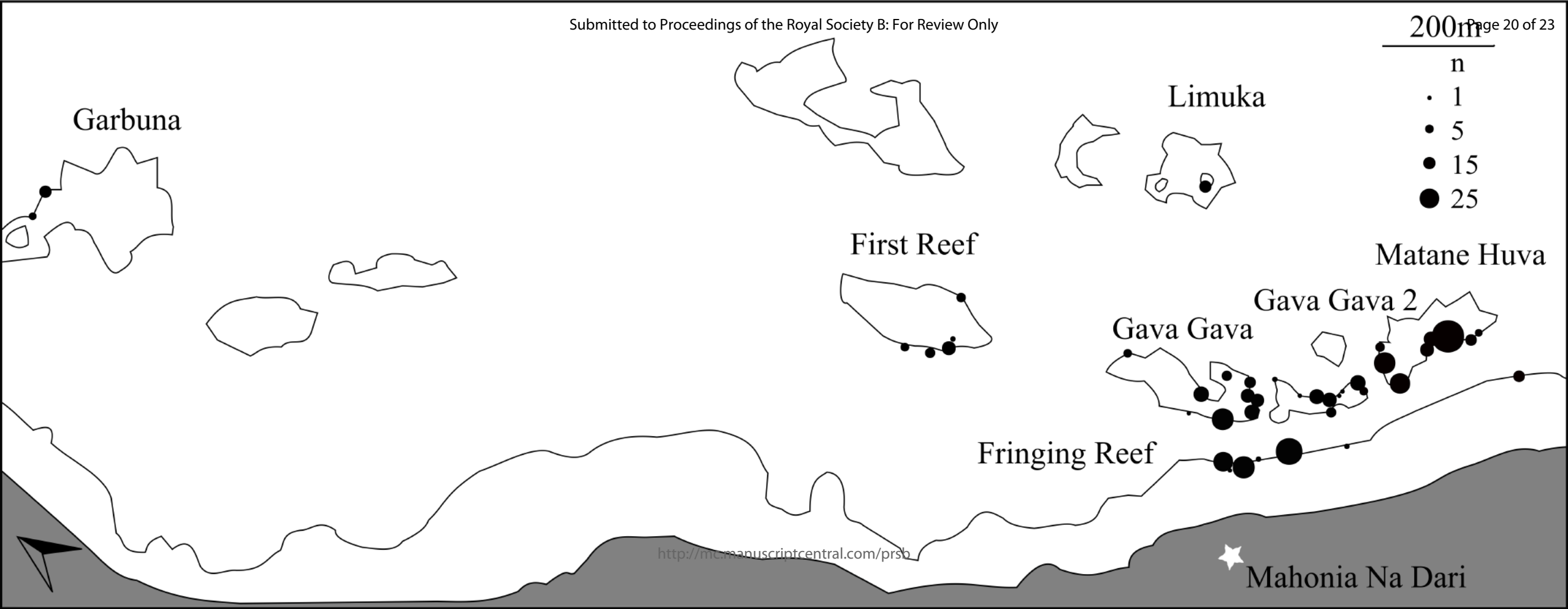
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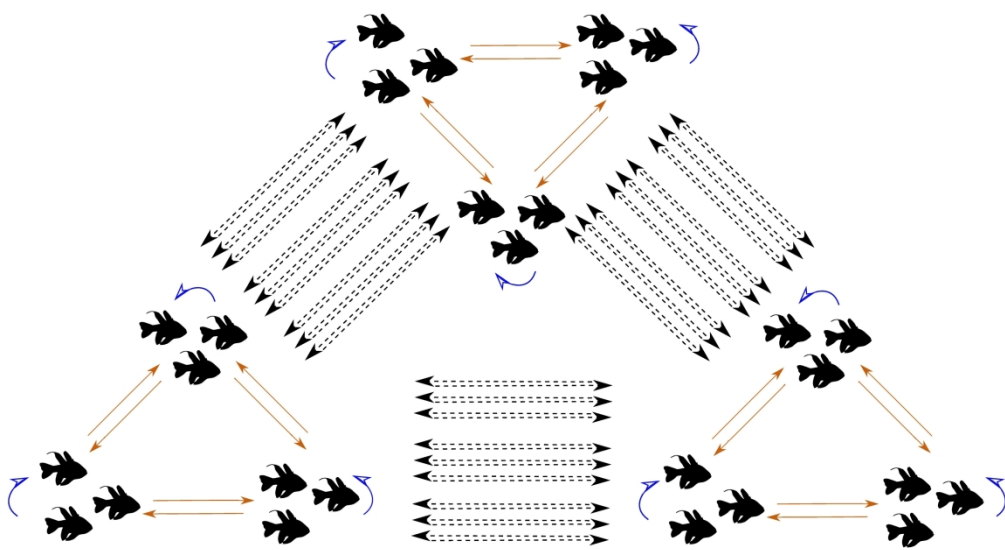
533 **Figure 4.** Mean relatedness (Queller & Goodnight moment-based estimator +/- Standard
534 Error (SE)) by distance of dyads. Dyad pairs (N=10) were randomly sampled without
535 replacement 100 times from five distance categories (0m, 0-200m, 200-400m, 400-600m,
536 >600m).

537

538 **Figure 5.** Recruitment events in a metapopulation of *Sphaeramia nematoptera* at different
539 spatial scales. Observed events (black) were determined by tracing juveniles and subadults
540 back to their parents within the metapopulation (n=34), expected events (white) were
541 determined by calculating possible recruitment trajectories in the metapopulation (n=1681,
542 scaled to n=34). Comparisons of distributions were done using subdivided χ^2 goodness of fit
543 tests. N.S. $p > 0.05$; * $p < 0.05$.

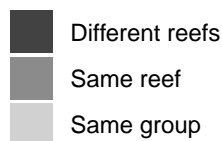
544





291x155mm (300 x 300 DPI)

Dyad location



Density

3

2

1

0

-0.6

-0.3

0.0

0.3

0.6

Relatedness (QG estimator)

<http://mc.manuscriptcentral.com/prsb>

