1　Management of scleractinian coral assemblages in temperate non-reefal areas: Insights
2　from a long-term monitoring study in Kushimoto, Japan (33°N)

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Abstract: In this era of global climate change, understanding fundamental mechanisms of coral community maintenance and persistence in temperate non-reefal areas is a high marine conservation priority. To identify mechanisms of community maintenance and persistence via larval supply, we monitored coral settlement over 12 years and investigated the genetic population structure of two major acroporid species at Kushimoto, Wakayama Prefecture, Japan (33° N). From 8 to 30 artificial settlement panel pairs were deployed from May or June to September, October, or November of each year. Recruits on settlement panel pairs were scarce, especially those of acroporids (0 or < 1 recruit per panel pair in most years). As coral cover in the Kushimoto area remained relatively high over a decade, such low recruitment may be sufficient for persistence of acroporid communities in this region. In addition, genetic analysis using 8 or 10 microsatellite markers demonstrated differences in genetic structure between populations of *Acropora hyacinthus*, which is a long-term resident species in this area, and *A. muricata*, a recently arrived species. *Acropora hyacinthus* displayed higher numbers of multilocus genotypes (41 of 43 samples collected) whereas only one multilocus genotype in 30 samples was seen in *A. muricata*. This difference may reflect both the length of time since population establishment and morphology. Consequently, acroporid communities in the Kushimoto area are likely maintained by survival and growth of existing colonies and/or fragmentation, indicating that conservation of established corals should be the first priority to ensure persistence of coral assemblages in such temperate non-reefal areas.

Introduction

Coral assemblages in higher-latitude areas, such as subtropical reefs and temperate non-reefal areas, have attracted enormous attention as potentially important refugia for tropical coral species due to global climate change (Riegl 2003; Riegl and Piller 2003; Beger et al. 2014; Yamano et al. 2011; Baird et al. 2012). Abnormally high summer seawater temperatures have induced coral bleaching events, resulting in substantial mortality and structural shifts in tropical coral communities (Hughes et al. 2018, 2019). Effects of thermal bleaching have been comparatively less severe in many higher-latitude coral communities (Hughes et al. 2018). In addition, rising seawater temperatures are gradually extending the distributional limits of coral species to higher latitudes (Precht and Aronson 2004; Greenstein and Pandolfi 2008; Yamano et al. 2011; Baird et al. 2012; Nakamura and Yokochi 2020). In the Solitary Islands (30° S), Australia, four tropical *Acropora* species have recently been observed for the first time (Baird et al. 2012). In Japan, poleward expansion of distributional ranges of tropical coral species to temperate non-reefal areas has been confirmed, based on records since the 1930's (Yamano et al. 2011). The lesser impact of thermal bleaching and northward range expansion of tropical corals suggest that subtropical reef and temperate non-reefal regions may serve as refugia in this era of global warming (Riegl 2003; Riegl and Piller 2003; Beger et al. 2014; Nakabayashi et al. 2019); hence, coral communities in those regions need to be given high conservation priority. For this reason, understanding fundamental mechanisms of coral community maintenance and persistence is now urgently required in subtropical reef and temperate non-reefal areas.

Recruitment of new individuals is critical for persistence and maintenance of coral communities (Underwood and Fairweather 1989). However, current knowledge of recruitment processes is very limited in subtropical reef and temperate non-reefal areas, and most previous studies were conducted for less than ten years (Table 1). Since recruitment demonstrates spatiotemporal variability due to complex biological and environmental factors (Adjeroud et al. 2017), longer-term data must be gathered to estimate effects of recruitment for community maintenance in these higher-latitude coral populations.

The Kushimoto area of Wakayama Prefecture in Japan supports relatively higher-latitude coral habitat (33° N). These populations are located near the northern limit of coral distribution, and these coral assemblages have maintained relatively high species diversity and high coverage for at least 100 years (Sugiyama 1937; Uchinomi 1966; Marine Parks Center 1970; Nomura et al. 2008; Nomura 2009). Today, they comprise

93 roughly 115 reef coral species (Nomura et al. 2016), and coral cover has remained

94 above 30% on average (Biodiversity Center of Japan, 2019), even though coral

95 communities in the area have experienced severe disturbances, such as large typhoons

96 and predation by rock snails (*Drupella fragum*) and crown-of-thorns starfish

97 (*Achantaster planci*) (Nomura 2009). For these reasons, the area was designated as the

98 first national marine park in Japan in 1970, and efforts have been made to conserve

99 marine life and the environment. These results have been internationally evaluated and

100 the area was designated as a registered wetland under the Ramsar Convention in 2005.

101 Recent genetic studies and community surveys have suggested possible recruitment

102 patterns of acroporid corals in the Kushimoto area. *Acropora hyacinthus* (Dana 1846) is

103 found throughout the Indo-Pacific, including temperate non-reefal regions, such as

104 Kushimoto (Veron 2000), where it has been recorded since 1931 (Sugiyama 1937).

105 Nonetheless, the major genetic lineage in temperate non-reefal populations is distinct

106 from those in sub-tropical populations in Japan (Suzuki et al. 2016; Nakabayashi et al.

107 2019). In contrast, *A. muricata* (Linnaeus 1758) has only been recorded in Kushimoto

108 since 1995, where it has since replaced *A. hyacinthus* throughout much of its preferred

109 habitat (Nomura 2009). These results imply that temperate non-reefal populations of *A.*

110 *hyacinthus* have been locally maintained since its establishment, whereas larval supply

111 of *A. muricata* from subtropical areas occurs somehow in the Kushimoto area. However,

112 sexual recruitment patterns in the Kushimoto area have not been confirmed and quantified

113 using settlement panels or other means.

114 In this study, we observed settlement from 2004–2016 (except 2007) in the Kushimoto

115 area to quantify larval supply in these temperate coral populations. We also assessed

116 genetic population structures of these two acroporid species.

117

118 **Methods**

119 **1. Study site**

120 We selected three sites in the Kushimoto area, two along the coast of Kushimoto (St 1

121 and St 2) and another at Cape Shionomisaki (St 3, Fig 1). Amounts and composition of

122 settlement were investigated at these sites. In addition, genetic diversity of both acroporid

123 species at St 1 and St 2 was investigated.

124

125 **2. Settlement surveys**

126 Assessments of settlement were conducted since 2004 at St 1 (except 2007), and 2008

127 at St 2 and St 3. To assess settlement patterns, 8 to 10 artificial settlement panel pairs (Fig

128　2) were deployed at each site at a depth of approximately 5 m. This was done about one
129　month before the predicted major coral spawning periods, so as to pre-condition the
130　panels. In the Kushimoto area, acroporid communities are reproductively active, as
131　evidenced by observations of spawning from 2003 to 2015. Acroporid corals at
132　Kushimoto spawned from the beginning of June to the middle of August (Table 2).

133　　Artificial settlement panel pairs consisted of a pair of $10 \times 10 \times 0.6$ cm panels made
134　of fiber-reinforced cement. Two panels were fastened one above the other with a 2-cm
135　separation, so that coral larvae can settle between them and most grazers cannot pass
136　between them. Panel pairs were set haphazardly on substrates, at least 1 m apart, using
137　underwater epoxy glue. They were retrieved from September to November, at least 1
138　month after observed spawning of acroporids (Supplementary Table 1). Retrieved panel
139　pairs were bleached with a chlorine solution for one week to eliminate organic matter and
140　then dried for observation under a stereomicroscope. Upper and lower surfaces of both
141　panels were observed; thus, 0.04 m^2 of surface were sampled for each panel pair (no
142　recruits were observed on the sides of the panels). Coral recruits on panels were identified
143　to the family level (Acroporidae, Poritidae, Pocilloporidae, and others) and counted,
144　based on skeletal morphology (Babcock et al. 2003). Annual variations in mean
145　settlement (mean number of recruits per panel pair) of total corals and of each coral family
146　were analyzed using the Kruskal-Wallis test. Results of settlement were compared with
147　percent cover data collected as part of the Monitoring Sites 1000 Project by the Ministry
148　of Environment and the Biodiversity Centre (http://www.biodic.go.jp/moni1000/, in
149　Japanese). Percent cover was estimated using the spot-check method. Changes in % cover
150　at all three sites for 2004 to 2016 are shown in Supplementary Fig 1. To estimate effects
151　of local stocks on settlement, we analyzed whether mean coral settlement of all corals
152　was related to mean % cover at the three sites, using Spearman's rank-order correlation.
153　All analyses were performed in R, version 4.1.0 (R Core Team 2021).

154

3. Genetic diversity

156　　Genetic population structure of the two most abundant coral species in the
157　Kushimoto area, *Acropora hyacinthus* and *A. muricata*, was analyzed to estimate
158　potential sexual recruitment. Forty-three samples of *A. hyacinthus* were collected at 5-m
159　intervals along 50 m of the shore and 15 m from the shore to the near edge of the coral
160　communities. Thirty samples of *A. muricata* were collected every 2 m from a patch of
161　$\geq$16 m along the shore and $\geq$8 m perpendicular to the shore. Specimens were preserved
162　in 99.5% ethanol, and DNA was extracted using a DNeasy Blood & Tissue Kit

163 (QIAGEN) following the standard protocol. Extracted DNA was amplified using

164 multiplex PCR, and four primer sets were added to each PCR tube. Multiplex PCR was

165 performed using a Multiplex PCR Kit (QIAGEN) in a total reaction volume of 10 µL

166 containing about 50 ng of template genomic DNA, $2 \times$ Multiplex PCR Master Mix, and

167 0.2 µM (final concentration) of each of three primers for each locus: a forward primer, a

168 reverse primer with a U19, M13RV, T7, or SP6 tail (*A. muricata*: 846m3/U19,

169 11401m4/M13RV, 441m6/U19, Am01[h]/U19, Am02[h]/M13RV, Am03[h]/T7, Am04[h]/SP6,

170 Am05[h]/U19, Am06[h]/T7, Am07[h]/SP6 from Shinzato et al. 2014 and Goossens 2015; *A.*

171 *hyacinthus*: 8346m6/U19, 11401m4/M13RV, Ac0753/U19, Ac0808/T7,

172 Amil2_002/SP6, Amil_006/U19, Amil2_022/M13RV, Amil2_023/T7 from van Oppen

173 et al. 2007, Concepcion et al. 2010, and Shinzato et al. 2014) labeled with FAM, VIC,

174 NED, or PET, respectively. PCR cycling conditions were 15 min at 95 °C, followed by

175 30 cycles of 30 s at 94 °C, 90 s at 57 °C, and 60 s at 72 °C, with an extension of 30 min

176 at 60 °C in the final cycle. When amplification was insufficient, Ampli Taq Gold 360

177 Master Mix (Thermo Fisher Scientific) was used with the following conditions: 95 °C

178 for 9 min followed by 35 cycles at 95 °C for 30 s, 54 °C for 30 s, 72 °C for 1 min, and a

179 final extension of 5 min at 72 °C. Allelic variations of amplified products were analyzed

180 using a DNA capillary sequencer (3130xl Genetic Analyzer, Thermo Fisher Scientific)

181 and GeneMapper ver. 3.7 (Thermo Fisher Scientific). GenClone ver. 2.0 (Arnaud-Haond

182 and Belkhir 2007) was used to determine clonality in the populations. Clonal replicates

183 were removed according to the results of GeneClone ver.2.0, and GenAlEx ver.6.5

184 (Peakall and Smouse 2006) was used to calculate the probability of identity (PI),

185 number of alleles (Na), observed and expected heterozygosities (Ho and He,

186 respectively), and deviation from Hardy-Weinberg equilibrium (F).

187

188 **Results**

189　　In all, 1086 coral recruits were observed on 278 settlement panel pairs for 2004 – 2016

190 (no data in 2007, Table 3). Total settlement was dominated by the family Poritidae, which

191 accounted for 83.0% (902 recruits) of total settlement. Acroporid and pocilloporid

192 settlements comprised only 6.0% (66 recruits) and 10.9% (119 recruits) of total settlement,

193 respectively.

194　　Each year, >75% of all settlement panel pairs recorded 0-9 coral recruits per panel pair

195 (Fig 3). Notably, for the family Acroporidae, more than 80% of all settlement panel pairs

196 of each year recorded 0 recruits. In 2008 – 2014 and 2016, one to three acroporid recruits

197 per panel pair were observed, except in 2014. In 2014, 29 acroporid recruits were

198   observed in total and one of 25 panel pairs recorded 11 recruits (Table 3, Fig 3). Mean

199   acroporid recruits per panel pair were fewer than 1 in most years (1.16 $\pm$ 0.53, mean

200    $\pm$ SE) in 2014 (Fig 4). For the family Pocilloporidae, proportions of panel pairs with 0

201   and <10 recruits per year were 69.2-100% and 0-42.3%, respectively. However, 21

202   recruits were observed on a panel pair in 2012. As for acroporids, mean pocillporid

203   recruits per panel pair were <1 most years, but 1.92 $\pm$ 0.87 in 2012. Comparatively, the

204   proportion of panels with >10 recruits per pair was 3.5-23.3% (for 2008 – 2014 and 2016)

205   for the family Poritidae. In 2008, 195 poritid recruits were observed on one panel pair.

206   Relatively, mean poritid recruits per panel pair were >1 in most years with 14.0 $\pm$ 6.7

207   in 2008. There was no correlation between mean settlement and mean % cover of total

208   corals (r = -0.02, Spearman's rank correlation, Supplementary Fig 2).

209   Thirty samples taken from a patch of *A. muricata* showed the same genotypes for all

210   10 loci and were therefore considered clones. However, for *A. hyacinthus*, we identified

211   41 genotypes, with 87.5% polymorphic loci, among the 43 samples. There were two

212   clonal groups in *A. hyacinthus* populations, and clonemates within each group were

213   approximately 5 m apart. With multilocus genotypes (G=41), the probability of identity

214   (PI) at the eight loci was 2.4×10^{-4}. The number of alleles ranged from one to nine for

215   eight loci (average 5.1 per locus; Table 4). Mean observed and expected heterozygosities

216   were 0.21±0.08 and 0.39±0.09, respectively. Deviation from Hardy-Weinberg

217   equilibrium ranged from 0.168 to 1.000 for the eight loci.

218

Discussion

220   Recruitment of acroporid corals was low, even though acroporid corals are one of the

221   foundation species in the area. Pocilloporid recruits were also few in number, but poritid

222   corals showed relatively high recruitment and dominated total recruitment in the

223   Kushimoto area. The dominance of poritid corals contrasted with results of similar studies

224   conducted in subtropical reefs and temperate non-reefal areas (>26° N/S latitude), at

225   which pocilloporids tended to dominate recruitment on settlement panels (Table 1).

226   Earlier studies also reported a scarcity of acroporid recruits (Harriott & Banks 1995;

227   Harriott 1999; Nozawa et al. 2006). In the Solitary Islands, low acroporid recruitment has

228   been consistently recorded (Harriott 1999), while coral cover of the area has been stable

229   during the past 10 to 15 years (Dalton & Roff 2013). These results suggest that relatively

230   low larval supply may be sufficient to maintain the populations. Similarly, coral

231   assemblages in the Kushimoto area, mainly composed of acroporid corals, have

232   maintained relatively high cover for over a decade. Coral cover remained >20%, and

233 recently increased more than 30% in the area (Supplementary Fig. 1). This is relatively

234 high coverage compared with that in other regions worldwide, with most showing <25%

235 cover from 1997 to 2004 (Bruno and Selig 2007). The relatively high coral cover in the

236 Kushimoto area may have resulted from asexual growth and low mortality of existing

237 corals because acroporid recruits in the area were 0 or fewer than 1 per panel pair in most

238 years. This suggests that sexual recruitment could be of limited importance for

239 community maintenance in the Kushimoto area. On the other hand, it also implies that

240 relatively low recruitment may be sufficient for community maintenance.

241   Constant low recruitment suggests the possibility that new genotypes are rarely

242 added to the population at Kushimoto. In addition, recently established populations tend

243 to have relatively lower clonal diversity (Nakabayashi et al. 2019). Therefore, instead of

244 the potential for rare recruitment of new genotypes, differences in the length of time

245 since population establishment may affect genetic structure of populations in this area.

246 The tabular acroporid, *A. hyacinthus*, is widely distributed from subtropical reefs to

247 temperate non-reefal areas in Japan (Suzuki et al. 2016; Nakabayashi et al. 2019;

248 Nakamura and Yokochi 2020), including the Kushimoto area, where this acroporid

249 species has been recorded since 1931 (Sugiyama 1937). That is, this population has

250 been maintained for nearly 100 years. *A. hyacinthus* is a long-term resident in the area.

251 Over the years, new recruits, even though few in number, may have intermittently

252 settled in the area, resulting in relatively higher genotypic diversity compared to the

253 recently arrived species, *A. muricata*. A branching acroporid, *A. muricata* was first

254 observed at Kushimoto in 1995. In Kushimoto, the annual average seawater temperature

255 has risen abruptly since the1990s (Fig 5), and colonization of some tropical coral

256 species that had not been seen before, including *A. muricata,* has been observed. After

257 colonization, *A. muricata* began to invade areas covered by *A. hyacinthus* (Nomura

258 2009). Percent coverage of *A. muricata* was only ~5% in 1995, in comparison with

259 approximately 70% for *A. hyacinthus*, but by 2002, both species showed coverage of

260 ~40%, and by the following year, *A. muricata* had achieved approximately 60%

261 coverage. In October 2004, the *A. muricata* population was reduced by a typhoon, and

262 many colonies broke into fragments due to their arborescent growth form. However, re-

263 growth of remnants and fragments was observed in subsequent years (Nomura 2009).

264 That may explain why the observed patch of *A. muricata* consists of only a single

265 genotype. On the other hand, due to limited acroporid recruitment, recently arrived *A.*

266 *muricata* may not have had enough time to establish patches with different genotypes;

267 however, sampling from other patches of *A. muricata* will be necessary to better

268 estimate the genetic structure of the population.

269   When sexual recruitment occurs at low levels, asexual reproduction by clonal growth

270 and fragmentation may allow population persistence. Recovery due to asexual

271 reproduction by fragmentation and reattachment of branches has been observed in

272 branching acroporid corals after hurricanes in the Caribbean (Highsmith 1982). However,

273 while tabular acroporids are considered more vulnerable to physical disturbances, e.g.,

274 wave action during storms or hurricanes, similar to branching corals (Muko et al. 2013),

275 fragments of tabular corals are less likely to survive, because of higher risk of polyp

276 disorientation (Smith and Hughes 1999). In addition, as tabular *A. hyacinthus* at

277 Kushimoto have relatively short stalks and tend to grow close to the substrate (Fig 6),

278 storm-induced fragmentation of tabular *A. hyacinthus* at Kushimoto is less severe than

279 might be expected. This could be one of the reasons that the *A. hyacinthus* population

280 shows less clonality than *A. muricata* in the Kushimoto area.

281   Our findings imply that acroporid communities in the Kushimoto area are likely

282 maintained by survival and growth of existing colonies and/or fragmentation. Even

283 though acroporid corals are reproductively active (Misaki 2017), gametes produced

284 locally may largely be swept away by currents because of the lack of reefs; therefore,

285 sexual recruitment has been low for over a decade. From these findings, if coral

286 assemblages in the Kushimoto area become degraded due to drastic environmental

287 changes, they are unlikely to be resupplied by larvae from either the local area or the

288 upper stream of the Kuroshio Current. Their recovery would depend mainly on asexual

289 growth of remnant colonies.

290   As a designated Wetland of International Importance under the Ramsar Convention,

291 specifically because of coral assemblages in the Kushimoto area, conservation of existing

292 corals should be a top priority for sustainability of marine ecosystems in the area.

293 Moreover, a recent taxonomic study in higher-latitude areas revealed a number of

294 unidentified coral species in the area, suggesting that higher-latitude coral communities

295 may contain a number of unidentified endemic species (Nomura et al. 2020). Because a

296 low level of recruitment is observed at Kushimoto and also in other higher-latitude coral

297 assemblages (Harriott & Banks 1995; Harriott 1999; Nozawa et al. 2006), conservation

298 measures for existing corals should be the first priority to ensure persistence of coral

299 assemblages in these areas, indicating that a re-evaluation of conservation strategies in

300 coral assemblages is now needed.

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424 **Table 1.** Summary of coral recruitment at subtropical marginal reefs and temperate non-reefal areas (>26° N/S latitude)

Area	Site	Latidude	Survey periods	Size of settlement panels/ plates/ tiles	Months of deployment	Number of settlement panels/ plates/ tiles	Total recruits during the survey	Mean recruits	Most abundant family/genus of recruits	Ref
South Africa	Sodwana Bay	27 - 28 °S	1999 to 2002	12 × 12 × 1 cm	1 to 16 months	570 panel pairs	2124 recruits	13.2 per tile for the highest	Pocilloporidae	Glasson et al. 2006
Western Australia	Houtman Abrolhos Islands	28 - 29 °S	2011 to 2013	12 × 12 × 1 cm	5 months	135 tiles		0.4 - 128.8 recruits per tile	Acroporidae	Markey et al. 2016
Eastern Australia	Solitary Islands	30 °S	1992 to 1993	15 × 15 cm	3 to 5 months	120 plate pairs	190 recruits	0.0 - 8.0 recruits per plate pair	Pocilloporidae	Harriott & Banks 1995
			1993 to 1998	15 × 15 cm	5 months	570 panel pairs		0.1 - 20.3 per panel pair	Pocilloporidae	Harriott 1999
Eastern Australia	Lord Howe Island	31 °S	1991	15 × 15 cm	2 to 8 months		585 recruits	3.5 - 48.5 per tile pair	Pocilloporidae	Harriott 1992
Japan	Amakusa	32 °N	2001 to 2003	10 × 10 × 0.4 cm	3 months	200 plates	4 reecruits		*Acropora*/ *Alveopora*	Nozawa et al. 2006
Japan	Southwestern Shikoku	32 °N	2007 to 2008	10 × 10 × 0.5 cm	2 months	400 panel pairs		3.2 -18.0 per panel pair	Pocilloporidae	Watanabe et al. 2009

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Table 2. Summary of spawning patterns of major acroporid corals in the Kushimoto area.

Species	Season of spawning	Days from the full moon		Days from the new moon	
Acropora hyacinthus	The beginning of July to the beginning of August	6.6 ± 2.3	[3~11days]	5.0 ± 1.0	[4 ~ 6 days]
Acropora muricata	The beginning of June to the beginning of July	7.6 ± 1.9 (mean ± SE)	[4~10 days]	13.5 ± 0.7 (mean ± SE)	[13 ~ 14 days]
Acropora solitaryensis	The middle of July to the middle of August	7.5 ± 0.7	[7~8 days]	5.1± 1.8	[2 ~ 8 days]

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Table 3. Total settlement recorded on all settlement panel pairs by family per year. The total number of coral recruits did not correlate with weeks of deployment of settlement panel pairs (r=0.099, Pearson's correlation).

Year	Weeks of deployment	Number of panel pairs	Total	Acroporidae	Pocilloporidae	Poritidae	Others
2004	15 weeks	9	0	0	0	0	0
2005	12 weeks	8	0	0	0	0	0
2006	12 weeks	8	0	0	2	0	0
2007	—	—	—	—	—	—	—
2008	15 weeks	30	436	5	12	419	0
2009	14 weeks	28	93	8	11	74	0
2010	22 weeks	30	78	9	14	55	0
2011	20 weeks	30	132	2	12	117	1
2012	20weeks	26	147	2	50	95	0
2013	23 weeks	28	58	7	6	45	0
2014	22 weeks	25	88	29	4	55	0
2015	15 weeks	30	8	0	0	8	0
2016	18 weeks	26	46	4	8	34	0
Total		278	1086	66	119	902	1

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451 **Table 4.** Population genetic indices for *A. hyacinthus* for 8 loci. Numbers of multilocus genotypes (G), numbers of alleles (Na), observed and
452 expected heterozygosities (Ho and He, respectively), and deviation index from Hardy-Weinberg equilibrium (F). * p <0.001.
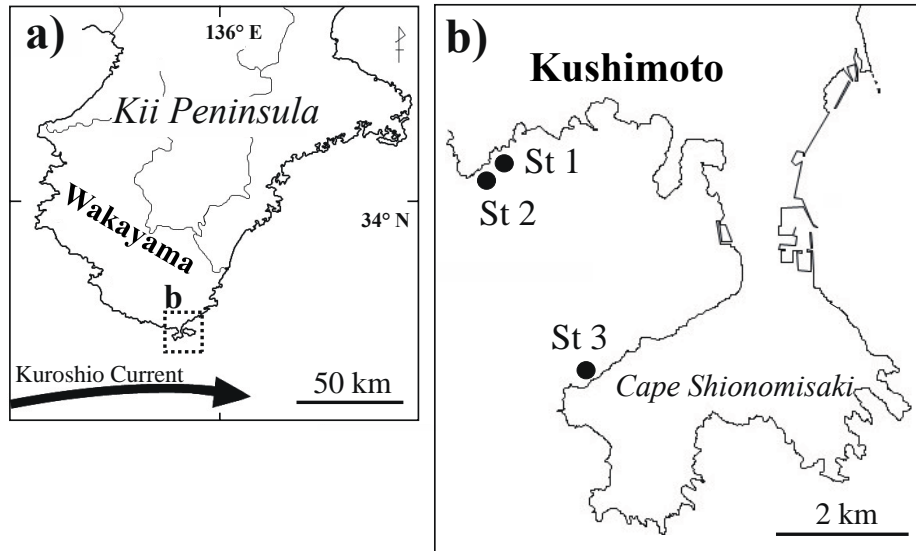
Locus	8346m3	11401m4	Ac0753	Ac0808	Amil2-002	Amil2-006	Amil2-022	Amil2-023	Total (Mean ± SE)
G	41	41	41	41	41	41	41	41	
Na	4	9	2	1	5	7	8	5	5.125 ± 0.990
Ho	0.073	0.610	0.000	0.000	0.293	0.366	0.317	0.000	0.207 ± 0.079
He	0.386	0.802	0.093	0.000	0.389	0.483	0.381	0.621	0.394 ± 0.092
F	0.810*	0.240*	1.000*	—	0.248*	0.243*	0.168*	1.000*	0.530 ± 0.137

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456 **Figures:**

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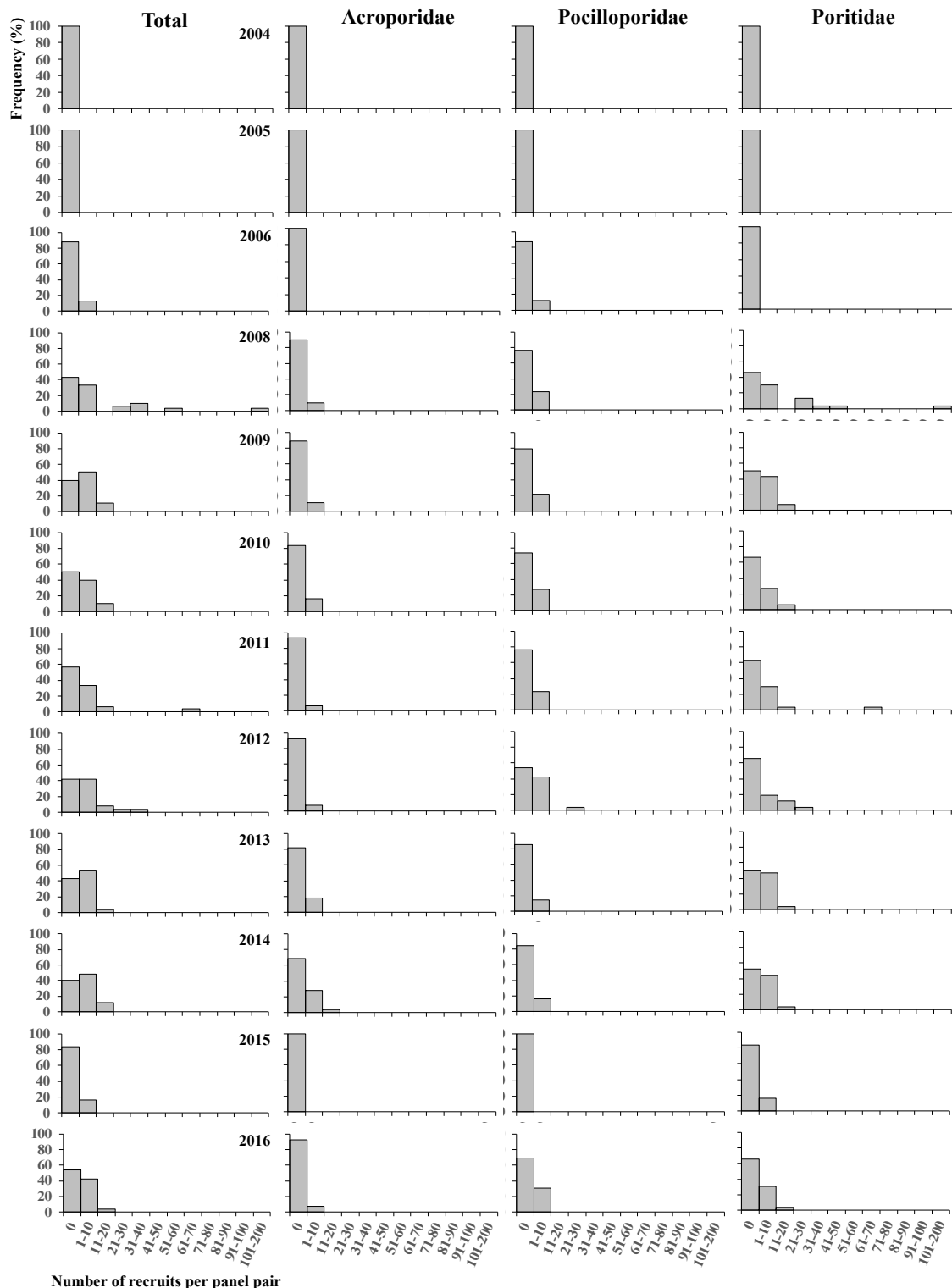458 **Fig. 1** Study sites. a) Wakayama Prefecture in the Kii Peninsula, b) the Kushimoto area.
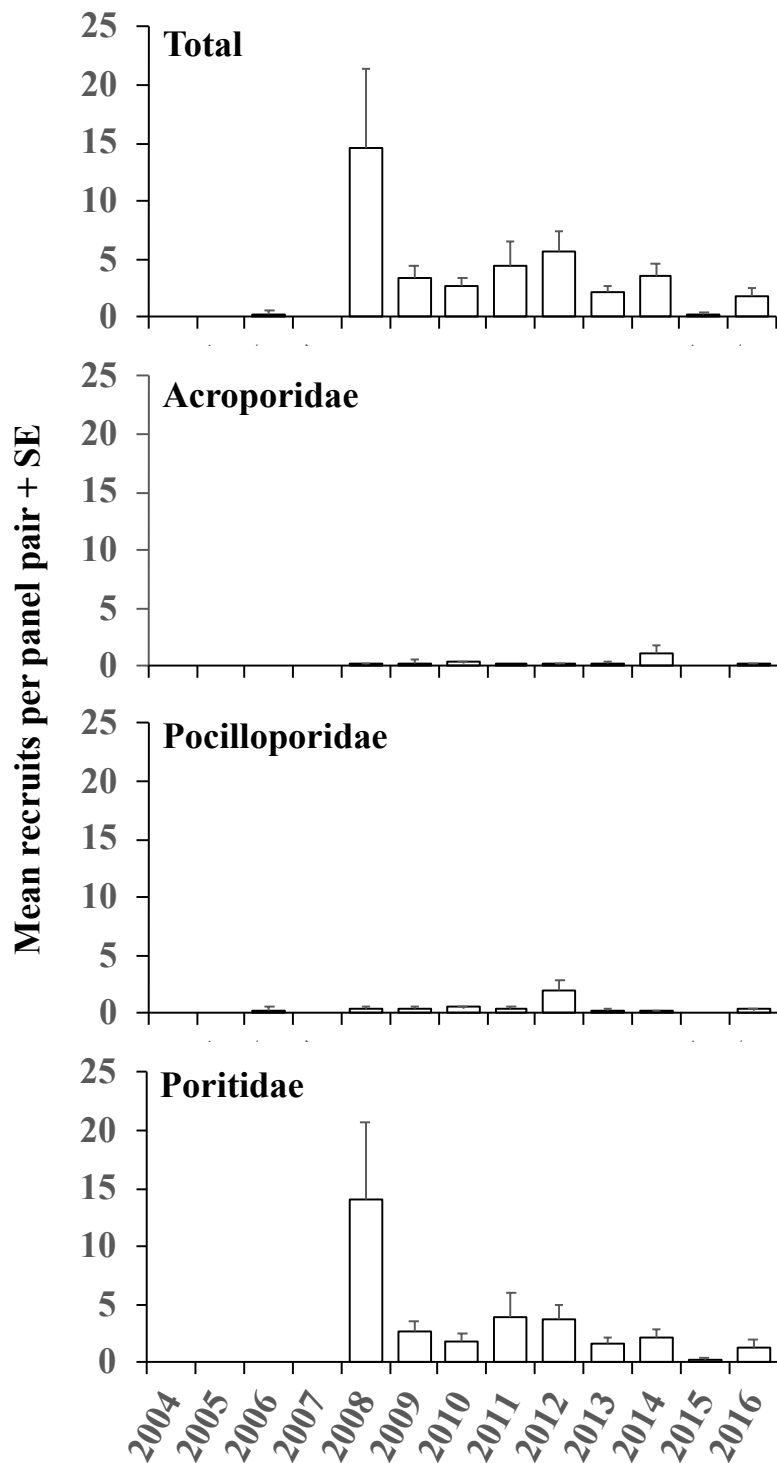
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473 **Fig. 2** Settlement panel pairs, just after deployment.

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Fig. 3 Frequency distributions of numbers of total coral recruits, Acroporidae, Pocilloporidae and Poritidae per panel pair from 2004 to 2016, except 2007 at Kushimoto, Wakayama Prefecture, Japan. Data of the three sites were pooled.
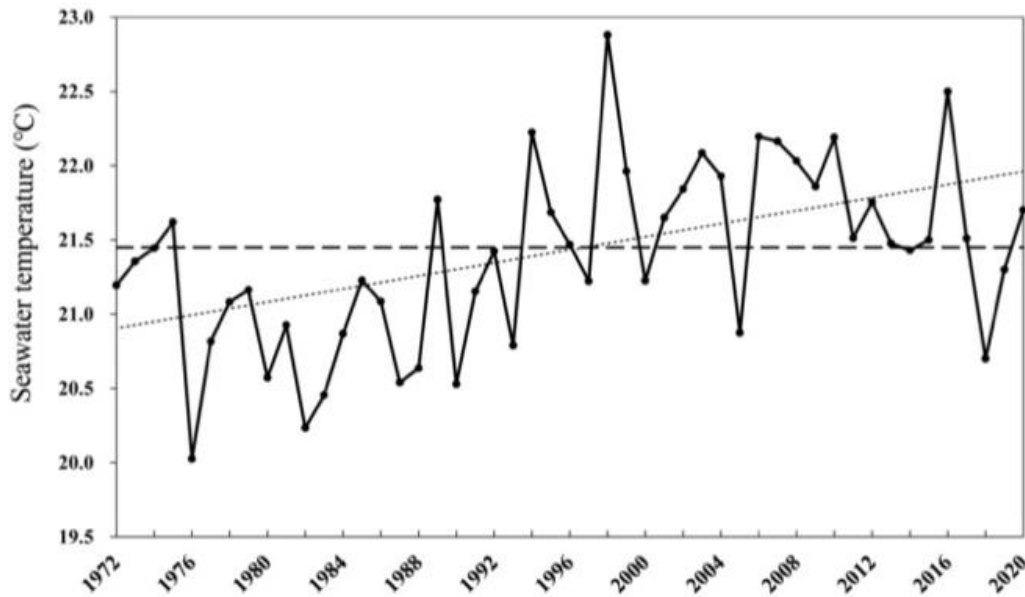
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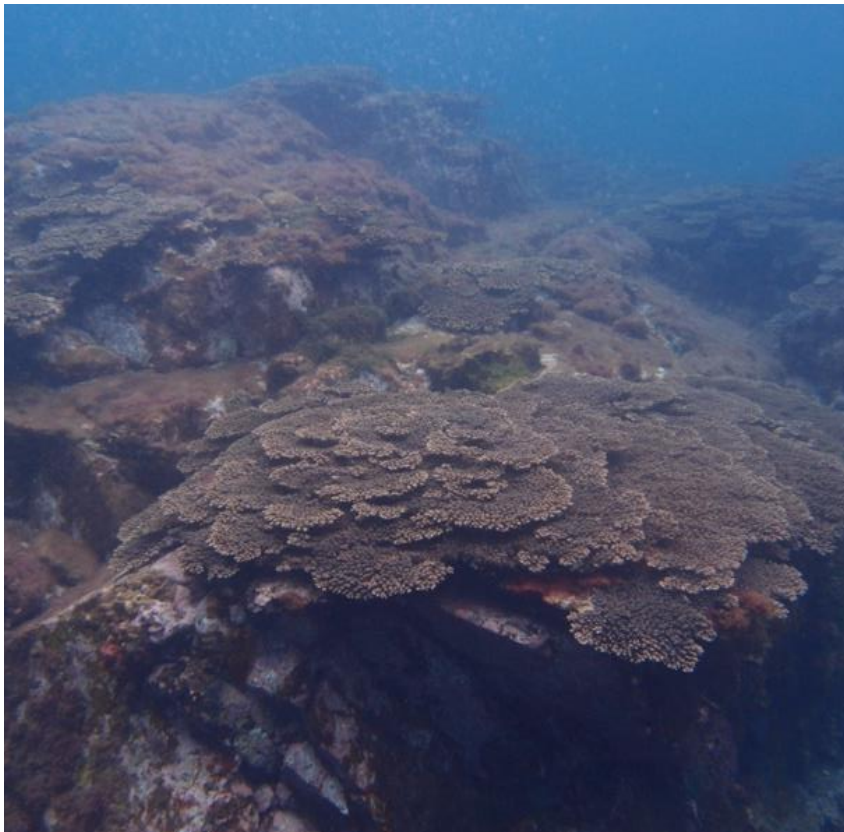**Fig. 4** Annual variation in settlement for 2004-2016 (except 2007) in the Kushimoto area.
Data from three sites were pooled. Mean settlement of all corals and of each coral family
differed significantly among years ($p < 0.05$, Kruskal-Wallis test).

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485 **Fig. 5** Annual average surface water temperature at Kushimoto, Wakayama Prefecture,
486 Japan. Data were recorded at St 1. The mean annual average surface temperature, from
487 1981 – 2010, was 21.45℃, an increase of 1.1℃ over the last 50 years (dashed line). The
488 regression line (y = 0.0209x – 20.2685, r=0.491, p <0.05) is shown as a dotted line.
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491 **Fig. 6** *Acropora hyacinth*us at Kushimoto, Wakayama Prefecture, Japan.

492   Supplementary Tables & Figures

493   **Supplementary Table 1.** Dates of deployment and retrieval of settlement panel pairs.

| Year	Date of Deployment	Date of Retrievement
2004	June 3rd	September 25th
2005	June 18th	September 15th
2006	June 14th	September 14th
2007	—	—
2008	June 8th & 9th	October 3rd
2009	May 30th & 31st	September 17th
2010	May 21st & 22nd	November 2nd
2011	May 25th & 26th	October 24th
2012	May 23rd & 24th	October 22nd
2013	May 22nd & 23rd	November 11th
2014	May 28th & 29th	November 17th
2015	June 17th & 18th	October 6th & 7th
2016	May 14th & 15th	September 30th

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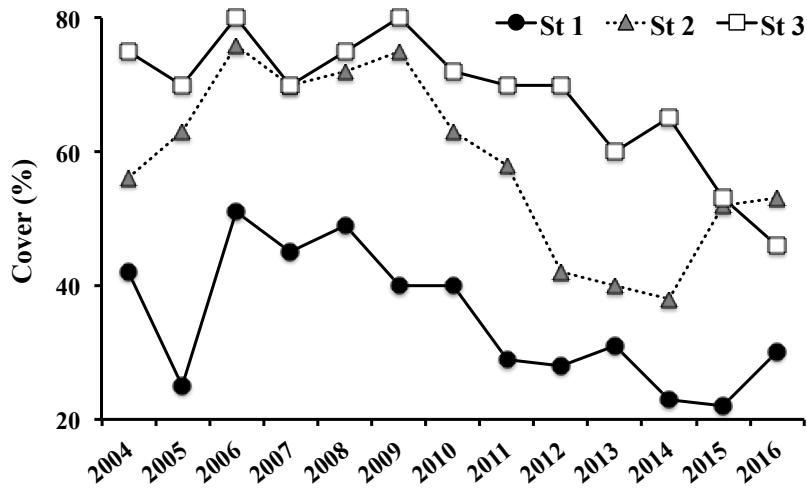
Supplementary Fig. 1 Coral % cover at three sites from 2004-2016 at Kushimoto, Wakayama Prefecture, Japan, estimated using the Spot Check Method. At St 1 and St 2, percent coral cover essentially equated to acroporid % cover, because coral communities at these sites consisted mainly of *Acropora* spp., especially *A. hyacinthus* and *A. muricata*.

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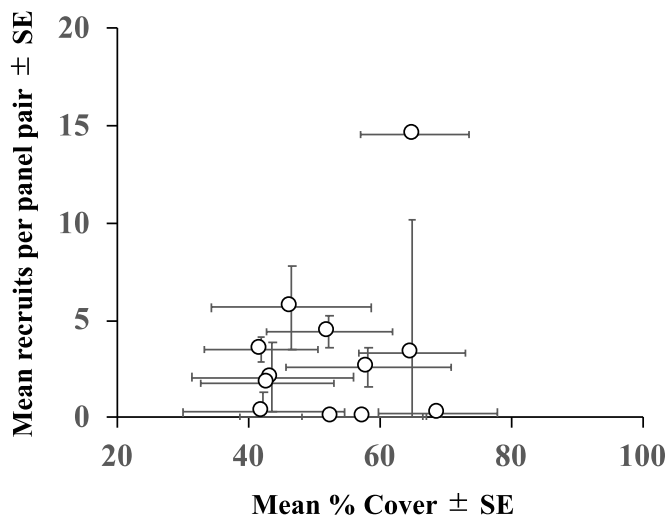
Supplementary Fig. 2 Relationship between mean settlement and mean percent cover of all corals.