High temporal resolution sampling reveals reef fish settlement is highly clustered

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Manuscripts

1   **High temporal resolution sampling reveals reef fish settlement is highly clustered**

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15   **Abstract**

16   Coral reef fish larvae settle on reefs predominantly at night around the new-moon phase, after

17   an early developmental period spent in the pelagic environment. Most sampling is conducted

18   across whole nights, and any studies that have examined the frequency of arrival within

19   nights have typically been limited to coarse sampling time scales of 1–5 hours. Here, we

20   present results for arrival numbers of fish caught between dusk and midnight from light traps

21   sampled every 15 min at an Indonesian coral reef, providing the finest temporal resolution for

22   this type of study to date. A Spatial Analysis by Distance IndicEs (SADIE) analysis, adapted

23   to temporal data, revealed clustering of reef arrival times for many species, with an increase

24   in catches immediately after dusk dropping off towards midnight. Importantly, the timing of

25   clusters differed among species indicating that different factors determine the timing of

26   arrival among taxa. Our results support the hypothesis that larval behaviour influences the

27   timing of arrival at a coral reef for different fish species.

28   **Keywords: Coral reefs; fish larvae; larval behaviour; larval settlement; SADIE analysis; Indo-**
29   **Pacific.**

30   **Introduction**

31   Most coral reef fish spend their early life stage as larvae in the open ocean before returning to reefs to

32   settle (Montgomery *et al.* 2001; Kingsford *et al.* 2002; Leis and McCormick 2002). Settlement stage

33   larvae move onto the reef predominantly at night (Robertson *et al.* 1988; Stobutzki and Bellwood

34   1998), with a few species potentially also settling to the reef during the daytime (e.g. Dufour and

35   Galzin 1993; Kingsford 2001). Settlement is higher around the new and third quarter moon, when

36   moonlight is weak (Milicich 1988; Meekan *et al.* 1993; Milicich and Doherty 1994; Sponaugle and

37   Cowen 1997; Leis and Carson-Ewart 1999; D'Alessandro *et al.* 2007;). Nocturnal settlement has

38   been suggested as a life strategy for avoidance of predators feeding on fish larvae at the reef (Hamner

39   *et al.* 1988), which could otherwise have a significant impact on the already high mortality rate of

40   settlement stage fishes (Almany and Webster 2006; Dytham and Simpson 2007). The high risk of

41   mortality typical of this life stage of demersal reef fishes is also thought to drive other behaviours in

42   larval fish including auditory and olfactory orientation (Atema *et al.* 2002; Simpson *et al.* 2004, 2005)

43   and schooling (Pitcher 1986; Leis 2006; Codling *et al.* 2007; Simpson *et al.* 2013; Irisson *et al.* 2015).

44   Because of the small size of larval fish and their tendency to settle during low-light levels, it is

45   challenging to directly observe larval behaviour *in situ*, which often has to be inferred from controlled

46   environments (e.g. olfactory preference Dixson *et al.* 2008; swimming speed Fisher and Bellwood

47   2003) or *in situ* observations made during the daytime (Dixson *et al.* 2014; Simpson *et al.* 2005; Leis

48   *et al.* 2015). From nocturnal sampling methods that are highly restricted in space and time it should be

49   possible to make informed speculations on the behaviours that drive settlement patterns. However,

50   only a few studies have examined the arrival patterns of fish over single night periods (Dufour *et al.*

51   1996; McIlwain 1997; Wilson 2003), with the highest temporal resolution being used typically in the

52   range of one recording every 1–2 hours. Whilst this can provide us with useful information on when

53   the main settlement peaks occur during the night, it is not sufficient temporal resolution to capture

54   arrival of individual cohorts of fish. In the present study we assessed arrival of fish larvae to

55   Indonesian reefs using light traps sampled every 15 min: a finer temporal resolution than any previous

56   sampling method used in this context. The light trap sampling technique is stage selective, capturing

57   phototactic larval species at a competent settlement stage in high numbers. It does have species

58   sampling biases dependent on the degree of phototactic response and the swimming abilities of the

59   individual larvae (Choat *et al.* 1993). Overall, however, this technique lends itself well to the study of

60   larval settlement, providing large catches and ease of replication (Milichich 1988; Choat *et al.* 1993;

61   Wilson 2001, 2003). The focus of this study was not to examine the arrival rate of settlement stage

62   fish for this region (which would also be of interest), as it does not cover lunar, seasonal, or yearly

63   temporal variation, but to explore at high temporal resolution the arrival of fish within single nights.

64   We hypothesised that: a) settlement stage fish would not arrive at a constant rate in the light traps but

65   would display a high degree of clustering in the catches due to behaviour influencing settlement

66   times; and b) that the arrival rate of different species would follow different arrival patterns if

67   hydrodynamic forces were not the main drivers of clustering patterns.

68   **Materials and Methods**

69   *Sites*

70   Sampling was carried out at two sites offshore from the coral reefs of Hoga Island, Southeast

71   Sulawesi, Indonesia (Fig.1), selected based on their different water flow regimes. Buoy 1 is a site

72   located on the reef in the channel between Hoga Island and Kaledupa Island through which a large

73   body mass of water moves daily with the tides. Buoy 5 is located off the western reef of the island and

74   is relatively sheltered although the large changes in tidal range (~2m) can result in relatively strong

75   water currents during tide flows towards and away from the shore. There were differences in the

76   acoustic composition of the reef sound spectra and some of the coral composition of the reef (Piercy

77   2015), but no other known significant differences between them.
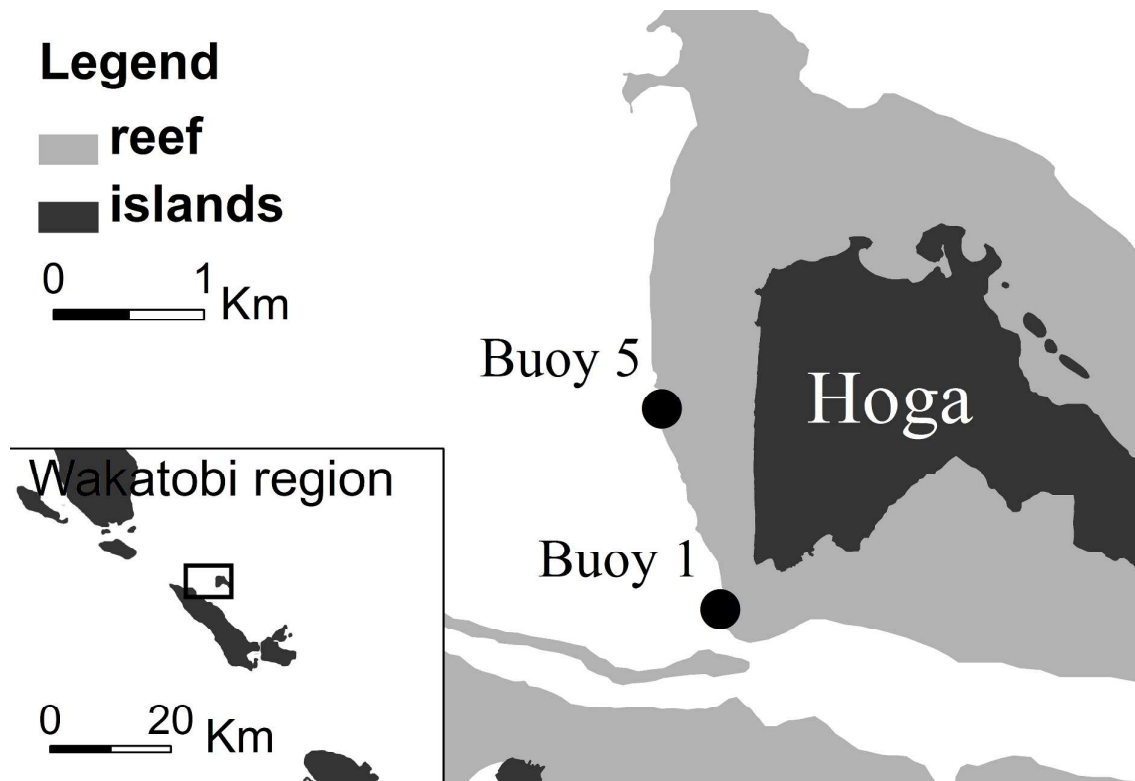
80　Figure 1. Sites of light trap sampling off Hoga Island, Indonesia (5° 28' 20" S; 123° 45' 25" E). Buoy

81　1 is located in the channel between Hoga Island and Kaledupa (bottom left corner of this map) where

82　the water current is strongest. Buoy 5 is located in a central position along the Hoga Island western

83　reef and is dominated by inshore and offshore currents as the reef flat (45º grey bars) fills and drains.

84　*Sampling*

85　Sampling was carried out between the third quarter moon, 24 July 2011, and three days after the new

86　moon, 3 August 2011 (new moon was 31 July 2011) between dusk and midnight (18:00–00:00). The

87　focus of this study was on collecting high temporal resolution data rather than lunar or seasonal

88　changes that have been previously extensively examined (e.g., Robertson *et al.* 1988; Stobutzki and

89　Bellwood 1998; Dufour and Galzin 1993; Kingsford 2001). This "snapshot" approach is

90　representative of a typical new moon recruitment period but may differ in terms of abundance and

91　species composition compared to other times of the year. Throughout the night time period, light

92　levels remained low as the moon had not yet risen with the exception of the last two sampling dates (1

93   and 3 August) when the moon did not set until 19:30 and 21:00 respectively. However, considering

94   the proximity of these dates to the new moon phase the maximum fraction of the moon illuminated

95   was 17.8% (3 August) with the moon at a maximum altitude of 40° (18:15 2011-08-03) estimated

96   using the MoonAngle function in R (package oce, version 0.9-20), with half or more of the sampling

97   time being undertaken in the absence of any moonlight. Buoy 1 was sampled on nights of the 24 July

98   2011, and 1 and 3 August 2011, while B5 was sampled on 26, 28 and 30 July 2011.

99   Sampling was conducted using two Stobutzki and Bellwood (1997) light traps, suspended 1 m below

100   the water surface and fishing alternatively every 15 min throughout the sampling periods. The traps

101   were fitted with a 40 W 12 V fluorescent tube light connected to a 12 V 12 Ah lead acid battery

102   charged to >13 V. A boat was moored to a buoy to which the light trap was attached during

103   deployment at 1.5 m below the sea surface. The boat was attached to the mooring using 30 m of rope

104   to maintain it at a distance from the light trap and mooring and to minimise disturbance to recruiting

105   fish. Every 15 min the boat was hauled closer to the first light trap, and the second light trap was

106   deployed immediately prior to the first one being extracted from the water to maintain a constant light

107   source in the water column. The contents of the first light trap were emptied via a funnel into a

108   10x10x10 cm container with mesh netting openings on the sides and sealed with a mesh netting cap.

109   The operation was carried out within a 20 L bucket containing fresh seawater 10 cm deep to maintain

110   the fish alive and re-capture any escaped fish during the emptying operation. The container was then

111   placed in a fish mesh holder over the side of the boat. Once all 24 samples over the night period had

112   been collected, the mesh containers were placed inside a 100 L polystyrene container filled with fresh

113   seawater, brought back to the shore, and kept aerated using two airstones. The next day, fish from

114   each container were sedated using a mixture of clove oil, 90% ethanol, and sea water in a ratio of

115   1:3:6 respectively (see ethical note in Simpson *et al.* 2008). The fish from each container were spread

116   out on a gridded tray with 1 cm of water and photographed lying on their side using a Samsung S860

117   8.1 MP digital camera (Samsung Electronics Co., Ltd., Suwon, South Korea) and allowed to recover

118   in a 50 L aerated plastic tank containing fresh seawater before being released back onto the reef at

119   dusk. Fish were identified from the photos to family level using the guide by Leis and Carson-Ewart

120   (2000), and to genera and species where feasible. Fish that were difficult to identify were preserved in

121   70% ethanol after being anaesthetised and photographed using a Veho VMS-1 USB microscope with

122   x200 maximum magnification (Veho Electronics, Hampshire, UK). All work was carried out under

123   permits held by D. Smith and issued by the Indonesian Minister for Research and Development.

124   *Clustering analysis*

125   To test for non-randomness and provide indices for the degree of clustering on the temporal

126   distribution of fish counts, the Spatial Analysis by Distance IndicEs (SADIE) methodology (Perry *et*

127   *al.* 1999) was applied using the SADIEShell program (Open Source under GNU General Public

128   License, V3). This analysis is usually used to test for spatial clustering of species in a two-

129   dimensional grid, but can also be applied to one-dimensional data sets such as quadrats positioned in

130   line along a transect (Perry *et al.* 2002). Since the calculation of the indices is based on a "spatial"

131   matrix of count data, to transpose this problem to a one-dimensional (1-D) context an artificial extra

132   dimension was included where units on the x axis were represented by the times of sampling and their

133   position on the y axis was assumed to be a constant (i.e. y = 1; Perry, pers. comm.). Hence, for I =

134   1,…, n cells were of the form $(x_i, 1)$, each containing an observed sample count. This method

135   calculates three indices for the counts of data before testing them against random permutations of the

136   counts to provide the probability *p* of the measures of aggregation against the randomised ones (Perry

137   1998; Perry *et al.* 1999).The first measure is the *index of aggregation* (Perry 1998)*,* which quantifies

138   the degree of effort required for each cell to reach an even distribution across all cells. The index of

139   aggregation, *Ia*, is defined as:

140 $$Ia = D/Ea$$ (1)

141   where *D* is the distance to regularity, defined as the minimum value of the total distance that the *ith*

142   individual sample unit at position $(x_i, 1)$ would have to move, from one unit to the next, so that all

143   units contained an identical count. *Ea* is the arithmetic mean distance to regularity for the randomised

144   samples.

145   The second index is the *distance to crowding index* (Perry 1998), a measure of the minimum effort

146   required for the counts of each cell to move into a single cell. The distance to crowding index, J_a, is

147   defined as

$$J_a = F_a/C \tag{2}$$

149   where C is the distance to crowding, defined as the minimum value of the total distance that the ith

150   individual sample unit at position $(x_i, 1)$ must move so that all are congregated in one unit. F_a is the

151   arithmetic mean distance to crowding for the randomised samples. This index increases in value as the

152   distance to crowding C decreases, (i.e. a high index value indicates a more clustered group, with a

153   lower distance needed for all data to move to the same sampling point). The index is more powerful at

154   detecting a cluster than the index of aggregation I_a but cannot be interpreted correctly if more than one

155   cluster is present.

156   The final measure is the *degree of clustering*. Similar to the distance to regularity, it calculates the

157   effort required for each cell to reach an even distribution among the cells. However, in this case it

158   computes the degree to which each data point influences the overall clustering, by calculating the

159   strength of inflow and outflow from one cell to another in order to reach an even count between cells.

160   For donor unit i, at position $(x_i, 1)$, the outflow to the j of n_i receiver units, $j = 1, \ldots, n_i$, at position $(x_j$

161   , 1), is denoted as v_{ij} . The distance of this flow d_{ij} is

$$d_{ij} = \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2} = |x_i - x_j| \tag{3}$$

163   The average distance of outflow from unit i, weighted by the magnitude of each individual flow, is

164   denoted as Y_i, where $Y_i = \Sigma_j d_{ij} v_{ij} / \Sigma_j v_{ij}$. The same calculation is carried out for inflows.

165   The distances for inflows and outflows need to be standardised in order to obtain the dimensionless

166   clustering indices. For outflows, a standardised and dimensionless index of clustering, v_i, is then given

167   by:

$$v_i = Y_{i\,o}Y / {}_iY_{\,c}Y \tag{4}$$

169   where Y_i is the distance of the flow; $_iY$ is the expected value of the average absolute flow distance for

170   the i unit, assuming a random arrangement of the observed counts among the observed sample units,

171   where the outflows are computed for each count that is randomly assigned to the i Unit. Similarly,

172   instead of following the unit $i,$ through the counts randomised to it, we can follow the count c through

173   its randomisations to different units, where $_cY$ is the expected value of the average flow distance for

174   the observed count c; $_0Y$ is the expected value of the overall average absolute distance of flow for all

175   points and counts in the randomisations. By convention, inflows are given negative scores and

176   outflows positive scores and the average of their absolute values is used as the clustering index. Only

177   taxa for which at least an average of one individual per sampling time was collected on any one day

178   (i.e. > 24 individuals) were included in the analysis.

179   *Association analysis*

180   Temporal association between the arrival rates of different fish taxa was measured using the SADIE

181   association index. This method first calculates the similarity between the clustering indices of the two

182   populations at each time point then averages those similarities to provide an overall measure of

183   association: the correlation coefficient.

184   The measure of local spatial association for unit i is given by:

185    $$\chi_i = \frac{n(z_{i1} - q_1)(z_{i2} - q_2)}{\sqrt{\sum_k (z_{i1} - q_1)^2 \sum_k (z_{i2} - q_2)^2}}$$ (5)

186   where z_{k1} denotes the clustering indices of the first set of data, with mean q_1, and z_{k2} denotes the

187   clustering indices for the second set of data, with mean q_2. The overall spatial association is the mean

188   of these local values:

189    $$X = \Sigma_i \chi_i / n$$ (6)

190   where X is the correlation coefficient between the clustering indices of each set. The correlation is not

191   performed directly on the counts because large count values would contribute disproportionately to

192   the correlation coefficient. The significance of the association or disassociation is calculated by

193   permutation of the counts. Since the randomisation process produces a histogram with the probability

194   for both association and disassociation, the α value to accept or reject the null hypothesis is divided

195   between the two ends of the distribution. Thus α = 0.05 is split between the two extremities so that the

196   null hypothesis is rejected either for p > 0.975 (significant disassociation) or p < 0.025 (significant

197   association).

198   Autocorrelation is a property present in all clustering scenarios and could increase the chance of

199   finding non-existent associations and dis-associations because of the lack of independence of the

200   samples from one another. To minimise this effect and as recommended in Perry *et al.* (2002), a

201   Dutilleul adjustment was applied to account for the degree of autocorrelation and reduce the effective

202   sample size (Dutilleul 1993). To do this, where necessary, the sets were detrended, and the degrees of

203   freedom corrected for correlation, *M*-2, where *M* is the effective sample size. The critical values are

204   inflated by a scale factor of $\sqrt{\frac{M-3}{n-3}}$ and the significance of the randomisation test adjusted accordingly.

205   An extreme example of this would be if all samples are so strongly autocorrelated that we only need

206   one sample in order to estimate the size of all the remaining samples, effectively reducing the sample

207   size to one.

208   **Results**

209   During the 144 light trap deployments and collections a total of 2,187 individual fish were caught,

210   representing 28 families, of which some Pomacentridae, Apogonidae, and Sygnathidae could be

211   identified to genus level and even separated into species. The species themselves could rarely be

212   identified due to lack of guides on species level identification for fish at the larval stage for this region

213   of high biodiversity; therefore some species may have been grouped under the same taxon.

214   No fish were caught during the first sampling period on any night (18:00–18:15) and only one

215   individual fish from the genus *Spratelloides* was caught on the second sampling period (18:15–18:30)

216   over the six sampling days. More fish were caught at B1 (1,656) compared to B5 (531 individuals;

217   Chi-square test, $\chi^2 = 37.8$, p<0.001, d.f. = 2).

218   *Clustering*

219   All taxa that met the inclusion criteria on at least one day (>24 individuals caught on that sampling

220   night), except Gobiidae and Synodontidae, displayed significant temporal clusters for at least one of

221   the measures for clustering (degree of clustering, index of aggregation and distance to crowding;

222   Table 1 and Figs. 2-5). The significance level of the degree of clustering and the index of aggregation

223   was in agreement for all taxa (i.e. they were either both significant or both non-significant). However,

224   the significance level of the distance to crowding index occasionally differed from the other two

225   indices. A significant clustering effect was observed in *Corythoichthys* sp.1 (family Sygnathidae) on

226   24 July 2011, *Abudefduf* sp.1 (family Pomacentridae) on 1 August 2011, and in *Apogon* sp.1 (family

227   Apogonidae), *Apogon* sp.3, *Chromis sp.* (family Pomacentridae) on 3 August 2011 according to the

228   distance to crowding but not the degree of clustering or the index of aggregation (Table 1 and Figs. 2

229   and 3). This is likely due to the greater sensitivity of the former index compared to the latter indices

230   when a single cluster is present. In contrast, the Gobiidae were significantly clustered according to the

231   degree of clustering and the index of aggregation on 30 July 2011 and 1 August 2011, but not

232   according to the distance to crowding index. This is likely due to the fact that the latter index only

233   provides meaningful results in the presence of a single cluster in the data, whilst two or three temporal

234   clusters appear to be present in Gobiidae catches on those days (Figs. 5a, b).

235

236   Table 1. Clustering indices from the SADIE methodology for fish taxa that met the minimum catch requirement (minimum 24 fish of the taxa caught over the

237   sampling night). Significant clustering indices are highlighted in bold with the significance level in brackets below (underlined).

| Species or nearest identifiable taxon	Site	Day	# individuals	Degree of clustering (p)	Index of aggregation (p)	Distance to crowding index (p)
Apogon sp. 1	Buoy 1	2011-08-03	40	1.70 (0.069)	1.72 (0.063)	**1.90 (0.001)**
Apogon sp. 2	Buoy 1	2011-08-03	48	**1.73 (0.012)**	**1.87 (0.032)**	**2.11 (0.001)**
Apogon sp. 3	Buoy 1	2011-08-01	41	**1.99 (0.032)**	**1.93 (0.034)**	**2.11 (<0.001)**
		2011-08-03	52	1.44 (0.143)	1.59 (0.090)	**1.82 (0.003)**
Chromis sp.	Buoy 1	2011-07-24	245	**2.18 (0.015)**	**2.29 (0.010)**	**1.64 (<0.001)**
		2011-08-01	133	**1.97 (0.035)**	**2.07 (0.022)**	**1.87 (<0.001)**
		2011-08-03	133	1.57 (0.097)	1.68 (0.072)	**1.76 (<0.001)**
Gobiidae	Buoy 1	2011-08-01	42	**1.99 (0.025)**	**1.92 (0.026)**	1.20 (0.209)
		2011-08-03	27	0.75 (0.685)	0.77 (0.654)	1.18 (0.173)
	Buoy 5	2011-07-26	63	1.39 (0.101)	1.30 (0.140)	0.96 (0.611)
		2011-07-28	38	1.45 (0.128)	1.58 (0.091)	1.39 (0.061)
		2011-07-30	50	**1.90 (0.021)**	**1.80 (0.035)**	1.36 (0.178)
Holocentridae	Buoy 1	2011-07-24	31	**2.68 (0.002)**	**2.52 (0.002)**	**2.80 (<0.001)**
Pomacentrus sp. 1	Buoy 1	2011-07-24	29	**2.47 (0.005)**	**2.78 (0.001)**	**1.81 (0.001)**
Corythoichthys sp.1	Buoy 1	2011-07-24	105	1.38 (0.140)	1.30 (0.180)	**2.51 (0.001)**
Synodontidae	Buoy 1	2011-07-24	31	0.45 (0.999)	0.51 (0.994)	0.69 (0.920)
Abudefduf sp.1	Buoy 1	2011-07-24	248	**1.742 (0.060)**	**1.93 (0.033)**	**2.10 (<0.001)**
		2011-08-01	53	**2.12 (0.022)**	**2.30 (0.011)**	**2.17 (<0.001)**
	Buoy 5	2011-07-26	27	1.23 (0.233)	1.23 (0.235)	**1.49 (0.011)**

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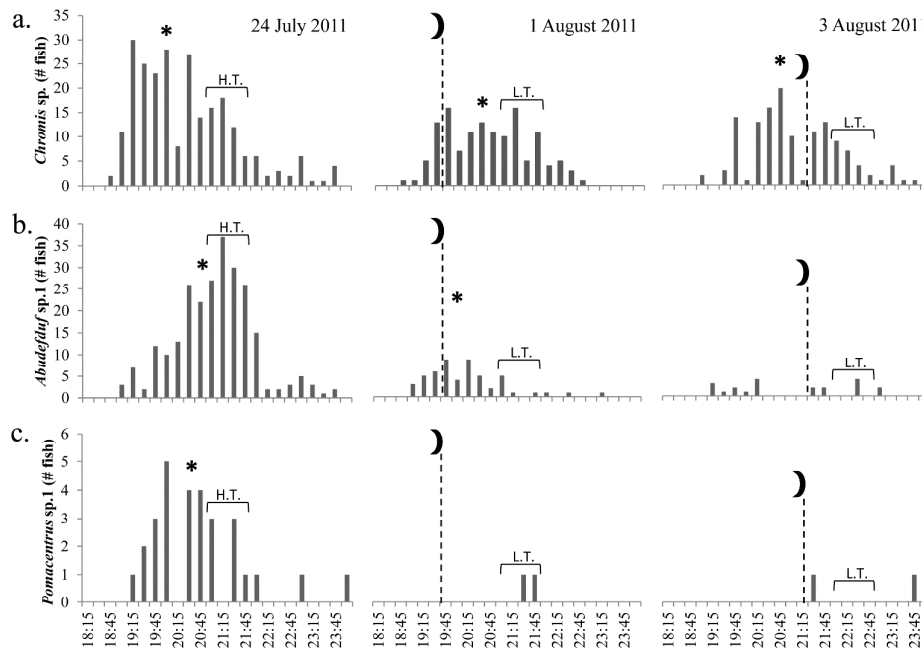
241

242   Figure 2. Arrival numbers of different Pomacentrid taxa at Buoy 1 on three different nights. a) Arrival

243   numbers of *Chromis sp.,* the most abundant taxon; b) *Abudefduf* sp.1*,* the second most abundant

244   taxon; and c) *Pomacentrus* sp.1. The scales for the fish counts vary between panels. The time period

245   of the high (H.T.) and low (L.T) tides are indicated above their respective periods and the time of the

246   moon set is indicated with a dashed line and moon symbol. For 24 July there was no moon in the sky

247   during the sampling period. Nights on which a significant temporal cluster in arrival numbers was

248   present for at least one of the clustering indices presented in Table 1 are indicated by an asterisk (*).

249
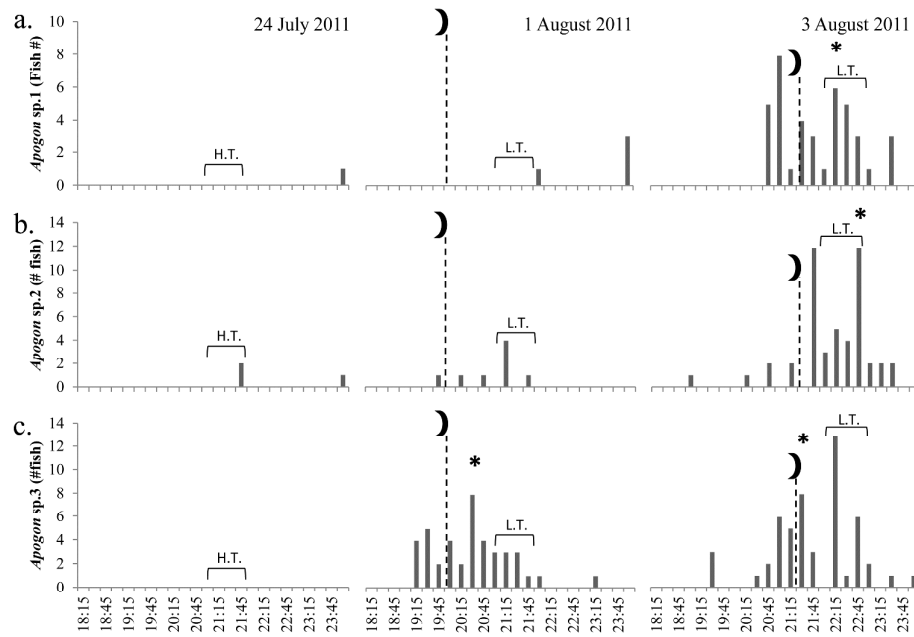
250

251   Figure 3. Arrival numbers of different Apogonid taxa at Buoy 1 on three different nights. a) Arrival

252   numbers of *Apogon* sp.1*;* b) *Apogon* sp.2; and c) *Apogon* sp.3. Explanation of the symbols is given in

253   Fig. 2.
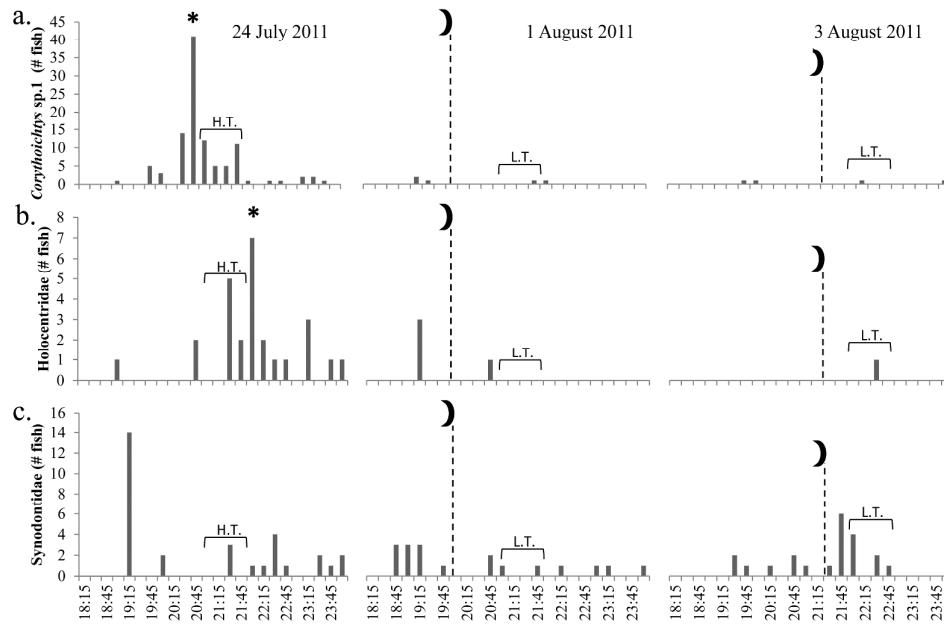
254

255   Figure 4. Arrival numbers of selected taxa at Buoy 1 on three different nights. The taxa presented all
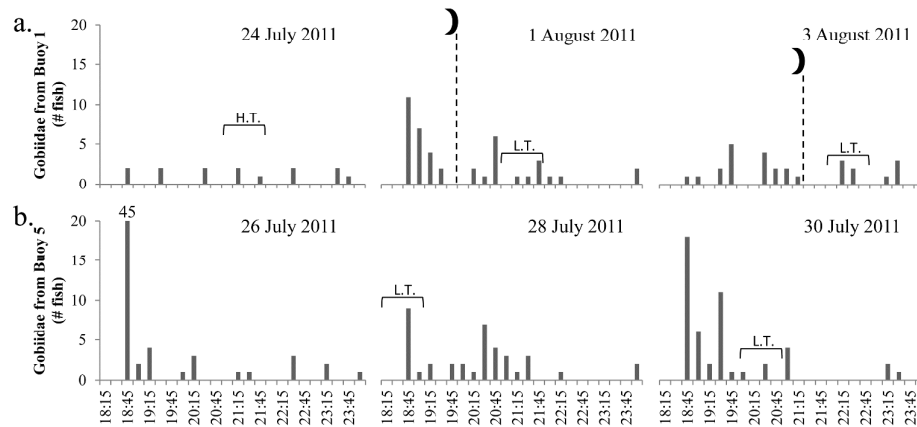
256   met the selection criteria of >24 individuals on a single sampling night: a) *Chorythoichtys* sp.1

257   (Family: Sygnathidae); b) Holocentridae; and c) Synodontidae. Explanation of the symbols is given in

258   Fig. 2

259

260

261

Figure 5. Arrival numbers on six different nights of Gobiidae at: a) Buoy 1; and b) Buoy 5.

Explanation of the symbols is given in Fig. 2. Where >20 individuals were caught at a single sample

point, the number of fish caught is indicated above the bar.

Associations

There were significant associations in the arrival numbers among taxa of the same family (e.g.

Pomacentridae: *Chromis sp.* associated with *Abudefduf* sp.1 and *Pomacentrus* sp.1, and Apogonidae:

Apogon sp.1 associated with *Apogon* sp.3), but also between taxa from different families (e.g.

Chromis sp. associated with *Apogon* sp.1, and *Chromis sp.* associated with Gobiidae; Table 2). Most

association analyses between taxa only met the inclusion criteria for one of the sampling days (both

taxa with >24 individuals caught on the day). Exceptions to this were comparisons between *Chromis*

sp. and *Abudefduf* sp.1 (significantly associated on both days; $X = 0.45$, $p = 0.02$, and $X = 0.68$, $p <$

0.001 on 24 July 2011 and 1 August 2011 respectively), and *Chromis sp.* and Gobiidae, which were

significantly associated on 3 August 2011 ($X = 0.44$, $p = 0.02$) but not on 1 August 2011, when the

Gobiidae arrived in more than one cluster (Fig. 6).

Table 2. Association indices between temporal arrival numbers of different fish taxa. The

comparisons are made only between taxa on days for which both had a total catch of >24 individuals

(i.e. average of >1 individual per sampling period). The symbol N/A denotes where no comparisons

were possible because one species in each pair had fewer than 24 individuals. The date is indicated in

280   the top line of the box, followed by the association index below with its significance level and

281   Dutilleul adjusted sample size in brackets. Significant associations are highlighted in bold.

	Chromis sp.	Apogon sp.1	Apogon sp.2	Apogon sp.3	Abudefduf sp.1	Pomacentrus sp.1	Corythoichthys sp.1	Synodontidae	Holocentridae	Significant associations per testable pairs
Chromis sp.	-	-	-	-	-	-	-	-	-	4 / 9
Apogon sp. *1*	2011-08-03 0.37 (0.092; 24)	-	-	-	-	-	-	-	-	1 / 4
Apogon sp.2	2011-08-03 0.13 (0.56; 21.7)	2011-08-03 0.35 (0.14, 22.9)	-	-	-	-	-	-	-	0 / 4
Apogon sp.3	**2011-08-01 0.71 (<0.001, 24)**	**2011-08-03 0.69 (0.004, 19.8)**	2011-08-03 0.36 (0.16, 19.8)	-	-	-	-	-	-	2 / 4
Abudefduf sp.1	**2011-07-24 0.45 (0.04, 22.8)** **2011-08-01 0.68 (<0.001, 22.9)**	N/A	N/A	N/A	-	-	-	-	-	1 / 6
Pomacentrus sp.1	**2011-07-24 0.45 (0.04, 22.4)**	N/A	N/A	N/A	2011-07-24 −0.12 (0.60, 23.7)	-	-	-	-	1 / 5
Corythoichthys sp.1	2011-07-24 0.26 (0.32, 24)	N/A	N/A	N/A	2011-07-24 0.54 (0.14, 11.1)	2011-07-24 0.01 (0.8, 21.7)	-	-	-	0 / 5
Synodontidae	2011-07-24 0.33 (0.24, 21.2)	N/A	N/A	N/A	2011-07-24- 0.10 (0.64, 21.6)	2011-07-24 −0.29 (0.08, 20.9)	2011-07-24 −0.18 (0.20, 21.7)	-	-	0 / 5
Holocentridae	2011-07-24 0.33 (0.16, 23.8)	N/A	N/A	N/A	2011-07-24 0.58 (0.06, 13)	2011-07-24 0.04 (0.82, 23.3)	2011-07-24 0.45 (0.12, 18.5)	2011-07-24 −0.21 (0.14, 23.1)	-	0 / 5
Gobiidae	2011-08-01 −0.01 (0.98, 19.8) **2011-08-03 0.44 (0.04, 23.9)**	2011-08-03 0.35 (0.14, 22.9)	2011-08-03 −0.14 (0.62, 20.3)	2011-08-01 0.002 (0.90, 24) 2011-08-03 0.15 (0.52, 18.6)	2011-07-26 −0.16 (0.72, 20.2) 2011-08-01 0.001 (0.90, 19.3)	N/A	N/A	N/A	N/A	1 / 5

282

283   **Discussion**

284   To our knowledge, this is the first study to present high temporal resolution arrival numbers of

285   settlement stage fish. In this study clear temporal clustering was widespread among the ten most

286   abundant taxa over single night sampling periods, usually involving a single cluster for taxa identified

287   to genus level. Importantly, the arrival pattern in the light traps across the night often differed among

288   taxa, which suggests that different mechanisms could underlie their settlement timing. For the taxa

289   identified Pomacentridae taxa, 82-90% were caught between 19:00 and 22:00 on all sampling days at

290   Buoy 1, while the three taxa from the next most abundant family, Apogonidae, arrived later in the

291   evening, with 80-85% caught between 21:00 and 23:00 on 3 August but earlier for *Apogonidae* sp.3

292   on 1 August (19:00 – 22:00).

293   The fact that the Gobiidae were present in higher numbers at the site with lower flow could be a

294   strategy to increase their chances of settlement. Indeed, their smaller size compared to other taxa

295   collected is likely to result in slower swimming speeds (reviewed in Leis 2010). This would make

296   active swimming more energetically demanding due to the higher viscosity environment faced by

297   smaller fish (Bellwood and Fisher 2001) and the higher water flow, hence diminishing their settlement

298   success. Although larvae from the Gobiidae family did not appear to arrive at the traps in clusters, this

299   could be a result of the low taxonomic identification level. In fact, an outlier in Fig. 5b where 45

300   individuals (39% of the total Gobiidae caught on that sampling night) were caught in a single 15 min

301   sampling period, hints at possible high levels of clustering in a narrow time frame. A possible

302   explanation for this high catch could be that the Gobiidae were shoaling, as observed in laboratory

303   and field studies for larvae in this family (Breitburg 1989; Breitburg 1991). This may also be true for

304   the arrival of Synodontidae, which displayed no significant pattern of settlement but did recruit in

305   high numbers on a single sampling period on 24 July (Fig. 4c). However, these conclusions remain

306   speculative.

307   Comparisons among species forms an important part of this study. Setting aside taxa identified only to

308   family level, where lack of associations might be due to multiple species composition of the catches,

309   the arrival patterns of *Apogon* sp.2 and *Chorythoichthys* sp.1 were not similar to any of the other taxa.

310   There was also a lack of association between arrival patterns of two Pomacentrid species, *Abudefduf*

311   sp.1 and *Pomacentrus* sp.1.

312   Settlement stage larvae of *Chromis* sp. have been observed to settle in small groups during the

313   daytime (Nolan 1975). *Chromis atripectorialis* improve orientation consistency, are able to more

314   accurately maintain a bearing, and swim faster when they school compared to movement as

315   individuals (Irisson *et al.* 2015). This could provide an important survival advantage to larvae that

316   school as this behaviour would enable them to reach a settlement site faster, therefore reducing the

317   time spent in the pelagic environment where they incur high mortality rates (Houde and Zastroe

318   1993). Persistent aggregations have been found to occur in the splitnose rockfish, *Sebastes diploproa,*

319   where 11.6% of settlement stage larvae were siblings (Ottmann *et al.* 2016). Interactions among group

320   members may play a role in maintaining these aggregations from spawning to settlement and could

321   provide the basis for clustering patterns observed in this study. It is important to note, however, that

322   there are a number of other mechanisms which could drive the observed clustering patterns, including

323   concentration of larvae in particular locations due to mesoscale eddies (Shulzitski *et al.* 2016). It is

324   also unclear how larvae would be able to maintain a school at night without being able to use vision to

325   see other group members, although other senses such as lateral line sensing (Faucher *et al.* 2010) or

326   vocal communication (Staaterman *et al.* 2014) may play a role.

327   There are insufficient sampling days in this study to determine whether different arrival patterns

328   observed among taxa are explained by random arrival of patches of larvae or driven by behaviours

329   aimed at improving settlement for a particular species. Why different taxa have different patterns of

330   arrival could, for example, be due to a trade-off between finding limited suitable settlement habitat

331   and avoiding predators. For *Corythoichthys* sp.1, that is widespread around the island and settle in

332   seagrass habitat between the reef crest and the shore (pers. obs.), avoidance of predators may be a

333   more important factor than limited habitat availability compared to species that recruit to specific

334   coral types like many pomacentrids. If this were the case, it might explain why they recruit only later

335   in the night when no light is available to predators (Johannes 1978; Dytham and Simpson 2007), and

336   the narrower time frame over which the recruitment occurred in this study (Fig.4a). The latter could

337   increase their chances of passing through the "wall of mouths" (Hamner et al. 1988) awaiting them at

338   the reef by achieving safety in numbers according to group theory (Bertram 1978).

339   This study furthers our understanding of the manner in which settlement stage fish recruit to the reef

340   in this critical transition phase, but cannot explain why different species display clustering patterns,

341   whether group behaviour mediates the temporal clustering or how and when the clustering is initiated.

342   Aggregations of larvae prior to settlement have been documented (Patterson *et al.* 2005), however,

343   whether this is due to environmental processes (e.g. eddies) that concentrate larvae in particular

344   locations or whether behaviour mediates the observed clustering patterns, will require further studies

345   that directly observe larvae during this critical life period..

346   **Acknowledgements**

350   **References**

351

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