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7 **Running head:** Fish and coral larvae as nutrient subsidies

8 **Estimates of fish and coral larvae as nutrient subsidies to coral reef ecosystems**

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18 **Abstract**

19   Nutrient subsidies are essential for the functioning of many ecosystems. A long-standing

20 conundrum in coral reef ecology is how these systems can be among the most productive

21 globally, but persist in nutrient poor conditions. Here, we investigate the importance of larvae of

22 fishes and corals and gametes of corals as nutrient subsidies for coral reefs. We provide evidence

23 that fish larvae may be an ecologically important source of exogenous nutrients. We found that at

24 the high end of mean estimates of fish larval supply rates, larvae can replace the nutrients in the

25 entire fish community (estimated from Caribbean coral reefs) in 28 and 434 days for nitrogen

26 (N) and phosphorus, respectively. Coral larvae, on the other hand, appear to represent only a

27 fraction of the nutrients supplied by the larval fish community. In contrast, coral gametes provide

28 substantial pulses of recycled nutrients during synchronous spawning events. Within a single

29 night, gametes from coral spawning events can produce nutrient fluxes that represent 13 and 64

30 times the amount of N and carbon, respectively, stored in coral reef fish communities. Our

31 analysis suggests that larvae and/or gametes of fishes and corals may represent an important, but

32 previously underappreciated, source of nutrients to coral reefs that warrant inclusion in to models

33 of nutrient dynamics and ecosystem function.

34 **Key words:** Caribbean, ecosystem ecology**,** Florida Keys, French Polynesia, Great Barrier Reef,

35 Moorea, nitrogen, phosphorus, subsidy, vector.

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Introduction

38 Nutrient subsidies often have important repercussions for the function and structure of

39 ecological communities (Polis et al. 1997). Subsidies provide sources of energy and material that

40 ultimately augment endogenous production in the recipient ecosystem. Subsidies can be highly

41 variable in quality and across space and time, with this variability often impacting how

42 efficiently they are integrated into a food web (Polis et al. 1997). Highly bioavailable subsidies,

43 such as animal waste, can readily be taken up by primary producers, whereas subsidies bound in

44 the tissues of live or dead animal or plant tissue, have to first be integrated into the food web

45 through trophic processes. These subsidies can represent a consistent press or be highly pulsed

46 (Yang et al. 2008). For example, on islands where birds roost in significant numbers, nutrient

47 subsidies from guano represent a consistent daily flux of marine-derived material that can

48 substantially increase primary production relative to islands without roosting populations

49 (Anderson and Polis 1999). In contrast, migratory fishes such as salmonids, represent a seasonal

50 subsidy that can be so extensive that it can enhance tree production throughout entire watersheds

51 (Naiman et al. 2002).

52 Coral reefs are among the most productive ecosystems on the planet (Odum and Odum

53 1955). This high level of productivity is enigmatic because coral reefs often persist in nutrient-

54 poor tropical oceans that typically receive relatively little exogenous nutrient inputs from

55 physical processes such as riverine transport of nutrients or deep-water upwelling (Muscatine

56 and Porter 1977, Szmant 2002). As such, the high rates of productivity on reefs have been

57 largely attributed to efficient internal recycling among the biotic constituents, such as corals,

58 seaweeds, fishes and invertebrates (Hatcher 1988). But coral reefs are not closed systems

59 (Hughes et al. 2000, Pineda et al. 2007) and should, to some extent, be subsidized by exogenous

60 biotic material, e.g., coral or fish larvae—although the extent to which this occurs is unknown.

61 Coral reef nutrient dynamics are being altered worldwide from anthropogenically derived

62 nutrient enrichment (D'Angelo and Wiedenmann 2014) and overfishing (Allgeier et al. 2016).

63 Improving our understanding of nutrient subsidies for coral reefs (and thus improving

64 understanding of coral reef ecosystem nutrient dynamics as a whole) is essential if we are to

65 effectively mitigate the negative effects of these widespread stressors.

66   Most previous research on coral, fish and invertebrate larvae dynamics on coral reefs has

67 focused largely on population dynamics and connectivity via the dispersal (Roberts 1997, Sale

68 2004, Andrello et al. 2015). Here, we explore the importance of fish and coral larvae as

69 ecologically relevant nutrient subsidies to coral reef ecosystems. For corals, we also consider

70 nutrient input and recycling from gametes (spawning material) that are synchronously released in

71 mass spawning events. Specifically, we draw on case studies of fish and coral larval supply and

72 mass spawning events from the wider Caribbean, French Polynesia, and the Great Barrier Reef in

73 Australia, to provide estimates of net nutrient supply rates. We draw comparisons of these

74 estimates with other known nutrient supply rates to reefs and other ecosystems to show their

75 potential importance for coral reefs.

76 **Methods**

77   We estimated nutrient supply rates per unit area per unit time (mg m^{-2} day^{-1}) to coral

78 reefs from fish and coral larval as well coral spawning material. We define coral larvae as the

79 free-swimming planulae that have the potential to settle, and coral spawning material as coral

80 gametes and or remnants of decomposing unfertilized coral gametes from a spawning event. We

81 reviewed the literature to find: (1) estimates of supply rates of fish larvae, coral larvae, or coral

82 spawning material (supply of individuals or biomass per day) to reefs, and (2) estimates of

83 nutrient content of these groups. Studies were found by searching ISI Web of Knowledge and

84 Google Scholar with various combinations of the terms: fish larvae, coral larvae, coral spawning,

85 mass spawning, nutrients, nitrogen, phosphorous, dispersal, supply and input.

86   While our searches revealed a relatively rich literature on larval supply to coral reefs, we

87 found a relative paucity of direct estimates of supply rates of fish and coral larvae - presumably

88 due to the extremely difficult and labor-intensive nature of quantifying such processes. Little

89 data was available for nutrient content of fish (Pfeiler et al. 1998, Coombs et al. 1999) or coral

90 larvae (Wild et al. 2004, Padilla-Gamiño et al. 2013). For these reasons, we focus our study on

91   three regions in which the most data were available: The Florida Keys and the Caribbean, French

92   Polynesia, and The Great Barrier Reef (Table 1).

Estimating fish larvae supply rates and nutrient content

94   Estimates of supply rates were taken from studies that include two methods of collection:

95   light traps and crest nets (Table 1). Light traps, the only method used in The Florida Keys and

96   the Caribbean, use a light to attract fish larvae to a floating trap near the surface of the water.

97   Traps are deployed at night and larvae are collected from the trap by morning (Doherty 1987).

98   Crest nets, used exclusively in studies from French Polynesia, are passive nets that trap larvae

99   passing over the reef crest (Dufour et al. 1996).

100   Data from published studies was reported as number of individuals per trap (maximum,

101   minimum, and mean), which we subsequently converted to biomass (Table 2). The body size of

102   each larva was not available, so we generated a body-size distribution for the reported larval

103   communities through iteratively sampling from a published body-size distributions of larvae

104   supply (Pepin 1995). These size distributions were then converted to mass using a published

105   length-weight regression for larvae (weight = a * length^{b}; where −3.25 was used for the scaling

106   coefficient a and 3.085 was for the shape coefficient b; Pepin 1995). Total larval community

107   biomass was then generated by summing across individuals within a given sample. Total nutrient

108   supply rate per fish larval community was generated by multiplying community biomass by the

109   percent nutrient contents to generate grams of nutrients per total larval community biomass.

110   Larval nutrient content was estimated by taking the average from 5 different studies that

111   quantified carbon (C), nitrogen (N), and phosphorus (P) per unit body mass for various species

112   of fish larvae, only two of which were marine (Appendix S1).

113   Estimates of C, N and P supply (mg m^{-2} day^{-1}) from fish larvae were calculated

114   differently for the two larvae collection methods. In the Caribbean, we assumed that the light

115   traps attracted fish within a 50 m radius of the device (*pers coms* S. Sponaugle), providing the

116   estimated area of ~3.14*50^{2} = 7850 m^{2} that was used to convert supply per unit trap (mg C, N, P

117   trap^{-1} day^{-1}) to supply rates (mg C, N, P m^{-2} day^{-1}). In comparison to light traps, crest nets are a

118   more quantitative and accurate measure of larvae supply (Nolan and Danilowicz 2008). Crest

119   nets, used in French Polynesia, filter a specific area of the water column, typically extending

120   from the top of the reef crest to the top of the water column (Dufour et al. 1996, Nolan and

121   Danilowicz 2008). As such, the raw trap data was scaled to the linear distance of the reef crest

122   around a given island, e.g., ~48,710 m for Moorea, and then converted to m^2 of reef by dividing

123   by the total m^2 of the backreef complex—providing an estimate of C, N, P supply m^{-2} day^{-1}.

124   Both the linear distance of the reef crest and area of back reef were quantified using Google

125   Earth.

126   We acknowledge that these estimates have several potential sources of error, and a few

127   caveats are important to highlight. First, for the Caribbean data, we assume that supply rates are

128   uniform and that the light traps represent a truly random location on the reef – and thus is

129   representative of anywhere along the reef continuum. Light traps are not traditionally considered

130   quantitative measures, but represent some of the only available data to quantify fish larval supply

131   to reefs (*pers coms* S. Sponaugle). Second, Rangiroa, in French Polynesia, is an atoll, unlike the

132   mountainous island of Moorea, with minimal back reef complex making it difficult to calculate

133   areal input rates (supply m^{-2} day^{-1}). To maximize use of limited data and make generalizable

134   comparisons, we applied the crest net data from Rangiroa to the areal extent of the back reef

135   complex in Moorea, providing a rough estimate of the how larvae supply rates from Rangiroa

136   would distribute nutrients across a reef complex the size of Moorea. Given the paucity of data on

137   fish larval densities these data are useful for helping to place into context the potential magnitude

138   of nutrient subsidies by larval fishes.

139   *Coral larvae supply rates and nutrient content*

140   Coral larvae supply rates have not been quantified empirically, presumably because their

141   small size and relative infrequency make them extremely difficult to separate from other

142   organisms captured in traditional zooplankton sampling methods. Instead, we used data from

143   coral recruitment studies to estimate a minimum coral larvae supply rate. Coral recruitment is

144   measured by deploying artificial settlement tiles on the reef, which are then collected and

145   examined with a microscope to quantify recruitment. These data reflect larval supply, settlement,

146   and post-settlement survival, and underestimate the true supply rate of coral larvae to a given

147   reef making our estimates (likely considerably) conservative. We selected studies that used

148   terracotta or unglazed ceramic settlement plates (the most common methods) to quantify coral

149   recruitment. Studies were restricted to Moorea (the most well-studied island in French Polynesia;

150   Gleason 1996, Edmunds et al. 2010), the Florida Keys (van Woesik et al. 2014) and the Great

151   Barrier Reef (Hughes et al. 1999), because these studies each provided the best replication over

152 the geographic range of the region (Table 1). All recruitment estimates were we converted to

153 individuals m^{-2} day^{-1} (Table 1).

154   Coral recruitment can be highly pulsed, e.g., annual spawning events in the GBR, or

155 more consistent throughout the reproductive season, as is more typical in the Caribbean

156 (Humanes and Bastidas 2015). Tile deployment duration can vary substantially from short time

157 scales for studies estimating recruitment events around the time of spawning (Hughes et al. 1999,

158 van Woesik et al. 2014) to longer scales used to estimate recruitment independent of spawning

159 (Adjeroud et al. 2007, Edmunds et al. 2010). Because tiles deployed for longer periods of time

160 have a larger window for recruit mortality we estimated the original number of settled corals

161 from each study using a published relationship between recruit age (a proxy for tile deployment

162 time) and percent survival (y = −0.4499x+57.561) following Humanes and Bastidas (2015).

163   The mean dry mass of a single coral larva (μg dry mass) was estimated as the average of

164 four species of coral eggs and larvae (μg dry mass) from the literature (Harii et al. 2007). Egg

165 dry mass values were included in the estimate of larval dry mass because (1) there is little

166 available data on the dry mass of coral larvae. We acknowledge that it is possible for coral larvae

167 to change mass during the planktonic phase. For example, some larvae lack symbionts (i.e., are

168 lecithotrophic) and therefore loose mass as energy reserves are depleted (Figueiredo et al. 2012),

169 whereas other species contain symbionts and may receive nutritional input from their

170 photosynthesizing symbionts, however evidence suggests this input is minimal (Kopp et al.

171 2016). The percent nutrient content (C and N) per dry mass of coral eggs and larvae was

172 determined by averaging three species (Wild et al. 2004). Only one estimate was available for

173 percent nutrient content of phosphorus (Padilla-Gamiño et al. 2013; Appendix S2). The mean

174 nutrient content of a single coral larva (μg dry mass larva^{-1}) was then estimated as the product of

175 percent nutrient content and mean dry mass. Finally, the supply rate of nutrients via coral

176 larvae (μg dry mass m^{-2} day^{-1}) for each location was calculated as the product of the supply rate

177 of coral larvae (larvae m^{-2} day^{-1}) and nutrient content of a single coral larva (μg dry mass

178 larva^{-1}).

179 **Results**

180   Our study provides compelling support for the importance of fish larvae and coral

181 gametes as an ecologically relevant source of nutrients to coral reef ecosystems. For example,

182 fish larvae import ~0.02–55.3 mg N m^{-2} day^{-1} and ~0.01–5.48 mg P m^{-2} day^{-1} across the

183 Caribbean and French Polynesia, respectively (Table 2). The difference among systems are

184 substantial and are likely a product of factors such as reef type (patch vs. crest, respectively),

185 sampling methodology (light traps vs. crest nets, respectively), and conversion factors used to

186 estimate the dispersal of these nutrients across the reef complex (see *Methods*).

187   In contrast to fish larvae, coral larvae inputs are substantially lower per unit time, but in

188 some regions are highly pulsed due to reef-scale broadcast spawning events that occur once or

189 twice per year. On a daily basis, coral larvae input is only a small fraction of the fish larvae-

190 derived nutrients, but input also varies substantially across systems. Coral larvae import an

191 estimated ~0.0004–0.16 mg N m^{-2} day^{-1} and ~ 0.00002–0.0091 mg P m^{-2} day^{-1} across the

192 Florida Keys and the Great Barrier reef, respectively (Table 2). Synchronous mass spawning can

193 stimulate greater pulses of nitrogen and carbon. Wild et al. (2004) estimate that corals in the

194 genus *Acropora* release 11.7 g C and 0.7 g N m^{-2} of coral surface in the form of eggs at Heron

195 Island in the Great Barrier Reef, which is equivalent to 7.1 g C and 0.4 g N m^{-2} of reef when

196 corrected for coral cover (Wild et al. 2004).

197 **Discussion**

198   Animals are now recognized as a primary driver of the storage and recycling of nutrients

199 on coral reefs (Allgeier et al. 2017), and for their roles in translocating nutrients from adjacent

200 ecosystems, e.g., seagrass beds, to coral reefs (Meyer et al. 1983, Shantz et al. 2015). Here we

201 provide support for the idea that immigrating fish and coral larvae, as well as coral gametes, are

202 likely an important, but underappreciated, component to coral reef nutrient budgets. Both fish

203 and coral larvae represent nutrients bound in animal material, and thus have distinctly different

204 implications for coral reef ecosystems when compared to the more traditionally considered

205 bioavailable forms of nutrients that are supplied by upwelling, terrestrial runoff, or animal

206 excretion. Labile forms of nutrients are readily taken up by primary producers and either

207 retained, remineralized, or enter the food web through trophic interactions. Nutrients entering via

208 the tissue of fish or coral larvae have two primary fates: (1) they enter the food web first via

209 trophic interactions, i.e., direct consumption or detrital pathways, or (2) they settle and

210 themselves begin to incorporate food web-derived nutrients.

211   From an ecosystem ecology perspective, where a primary goal is to understand these

212 processes in the context of an ecosystem nutrient budget, the manner in which these nutrients are

213 sequestered by the ecosystem is less important (DeAngelis 1992). In this context, the net effect

214   these nutrient sources have on the nutrient budget is determined by the manner in which they

215   alter the nutrient capacity of the ecosystem. In other words, how do these nutrients contribute to,

216   or detract from, the total nutrient pool including water column nutrients and the nutrients stored

217   in living and dead tissue (DeAngelis 1992, Allgeier et al. 2016)?

218   Given that coral gametes appear to largely represent recycled forms of nutrients from the

219   same reef complex, they may have little effect on coral reef nutrient capacity in terms of gains or

220   losses. In contrast, fish larvae may have substantial implications for nutrient capacity. The

221   majority of coral reef fish larvae have significant pelagic larval durations, allowing them to be

222   dispersed over substantial distances ranging from 10s to 100s of km (Roberts 1997, Sale 2004).

223   Coral larvae also have a dispersive pelagic phase that lasts from hours to over 100 days

224   (Connolly and Baird 2010) and have the potential to travel 100s of kilometers (Wilson and

225   Harrison 1998). Thus, while some coral and fish larvae are retained near their natal reefs (Miller

226   and Mundy 2003, Sale 2004), many are exported from one reef as a loss of nutrients and

227   imported to another as gain of nutrients. Conceptually speaking this fish and coral larvae

228   conveyor belt could possibly represent a zero-sum game if the number of larvae entering the

229   system are equivalent to the larvae produced in the system. However, it is noteworthy that a

230   substantial portion of larval growth occurs in the pelagic stage and thus a substantial portion of

231   the nutrients within larvae entering a coral reef system is transferred from the pelagic region.

232   Further, in the case of fish larvae, if some of the larval species entering the coral reef complex

233   have origins in other ecosystems, e.g., pelagic ocean, seagrass or mangrove ecosystems, then

234   nutrients bound in fish larvae would represent a net positive gain.

235   An important finding in our study was that a significant proportion of the larval fish

236   community were of non-coral reef origin. For example, Sponaugle et al. (2003) found 29% of the

237   larval community consisted of non coral-associated families (e.g., Atherinidae, Clupeidae,

238   Engraulidae), Grorud-Colvert and Sponaugle (2009) found they accounted for 47% in the Florida

239   Keys, and Valles et al. (2001) found that clupeids alone accounted for 96.6% of their catches in

240   St. Lucia. In French Polynesia, the proportion of the catch from non-reef origin was substantially

241   lower but still represented ~15% of the total abundance of fish larvae (Lo-Yat et al. 2006). It is

242   possible that the difference between the Caribbean and French Polynesia represents differential

243   selectivity in the different methods (light traps vs. crest nets) for clupeids. Nonetheless, these

244 estimates suggest that a substantial proportion of the annual supply of nutrients from fish larvae

245 may come from other ecosystems entirely, representing important allocthonous subsidies.

246   Across relatively unimpacted coral reef ecosystems in the Caribbean, the mean standing

247 biomass of the entire fish community can store ~ 2,800 mg N and 950 mg P m^{-2} (Allgeier et al.

248 2014; Fig. 1)—unfortunately no similar data exist for Indo-Pacific reefs. In comparison, the

249 mean estimated nutrients imported into these systems from fish larvae on a yearly basis ranges

250 from ~1,883 to 36,281 mg N m^{-2} year^{-1}, and ~40 to 799 mg P m^{-2} year^{-1}. Using the higher end

251 of mean larval supply rates across studies for comparison purposes, these data suggest that this

252 subsidy can replace the nutrients stored by the entire coral reef fish community in ~28 and 434

253 days (0.3 and 1.3 years) for N and P, respectively. Importantly, fish larval abundance oscillates

254 relative to lunar cycles more than longer seasonal cycles (Sponaugle and Cowen 1996),

255 suggesting fish larvae may represent a relatively continuous nutrient influx throughout the entire

256 year. Further, in these same Caribbean fish communities, Allgeier et al. (2014) report that fishes

257 recycle nutrients via excretion at rates of ~ 3–20 mg N m^{-2} day^{-1} and ~ 0.3–2.2 mg P m^{-2} day^{-1}

258 (Figure 1). For further comparison, atmospheric deposition of N in the form of rainwater has

259 been found to be ~0.308 mg N m^{-2} day^{-1} (Barile and Lapointe 2005), representing only a small

260 fraction of either the inputs of N from the fish community. Though these later estimates represent

261 nutrients in form that are immediately available for biological uptake, it is still notable that fish

262 larvae provide very similar amounts of nutrients to the system as community-level fish excretion

263 on a daily basis.

264   In contrast to the amount of nutrients supplied by fish larvae, nutrient input from coral

265 larvae is relatively small and likely has little effect on the nutrient capacity of the system.

266 However, synchronous coral spawning events still represent massive pulses of (primarily)

267 recycled nutrients that have important ecological consequences. Coral gametes and spawning

268 material make their way into the food web nearly immediately through consumption by fish and

269 other reef organisms (Pratchett et al. 2001) and through rapid degradation in the water column

270 and sediment (Wild et al. 2004, 2008). Coral spawning can cause elevations in particulate

271 organic matter in the water column and sediment for weeks following the spawning event,

272 highlighting the strength of their effect on nutrient dynamics in these systems (Eyre et al. 2008,

273 Wild et al. 2008).

274   The magnitude of the nutrient pulse generated by coral spawning events will likely

275   depend on the number of species that spawn at a given time and their abundance on the benthos.

276   For example, Wild et al. (2004) demonstrated that in a relatively small spawning event on the

277   Great Barrier Reef one species of *Acropora* alone released 11,600 mg C m^{-2} and 700 mg N m^{-2}

278   coral surface in the form of coral eggs. Assuming that the coral community is mostly composed

279   of various *Acropora* species that release a similar number of eggs, they further estimated that

280   community-level spawning event resulted in a pulse of 7000 mg C and 400 mg N m^{-2} reef in the

281   form of coral eggs (Wild et al. 2004). These numbers represent 64% and 13% of the total C and

282   N, respectively, stored in fish, which are considered to be one of, if not the, primary pools of

283   nutrients, on an average Caribbean reef (10,988 mg C m^{-2} and 3,122 mg N m^{-2}; Allgeier et al.

284   2014, 2015). Further, applied to the whole reef area (26.4 km^2), a spawning event at Heron

285   Island may result in a pulse of 310 t C and 18 t N as coral eggs (Wild et al. 2004). This

286   tremendous pulse of nutrients is substantial compared to examples of what are thought to be

287   extreme animal-derived nutrient pulses in other ecosystems. For example, wildebeest mass-

288   drowning events input an estimated 107 ± 51 t C, 25 ± 12 t N, and 13 ± 6 t P to the Mara River in

289   Kenya nearly annually (Subalusky et al. 2017). Although coral spawn represents recycling of

290   nutrients within the same ecosystem, unlike the wildebeest example, the extreme quantity of

291   nutrients produced by these events warrants recognition as a critically important nutrient

292   pathway in coral reef ecosystems.

293   Our study represents an initial foray to investigate the potential importance of exogenous

294   sources subsidizing the nutrient budgets of coral reefs. Despite obvious limitations in data and

295   potential issues associated with types of methodologies, our findings reveal that fish larvae may

296   represent an important nutrient subsidy to these systems and that coral spawning provides a

297   significant pulse of locally recycled nutrients. The relevance of quantifying nutrient inputs from

298   coral and fish larvae has direct implications for conservation of these imperiled ecosystems.

299   Human activities are altering the nutrient budgets of coral reefs worldwide, through myriad

300   ways, but the mechanisms that underlie these interactions remain poorly understood (Szmant

301   2001). Recent research is improving understanding of coral-nutrient interactions at the organism-

302   level (e.g., Wiedenmann et al. 2013; Ferrier-Pages et al. 2016), but we still know relatively little

303   about how these processes transcend to the ecosystem-scale. To improve understanding of these

304 process at larger scales of organization, exhaustive knowledge of all the components that

305 underpin a coral reef nutrient budget is needed.

306 **Acknowledgments**

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442 **Table 1.** Literature and locations used in our study.

Citation	Region	Location	Organismal grouping	Method of collection	Purpose of study	Collection timing
Lo-Yat et al. 2011	Pacific	Rangiroa	total community >5 mm	crest net	quantify larvae input in El vs La Nina years	10 days (new moon–peak period of sampling)
Dufour 1993	Pacific	Moorea	total community >5 mm	crest net	quantify ambient larval input	replicated 10 minute sets
Grorud-Colvert & Sponaugle 2009	Caribbean	FL Keys	total community >5 mm	light trap	compare MPA vs non MPA	monthly for ~ 1 year
Valles et al. 2001	Caribbean	St. Lucia	total community >5 mm	light trap	compare MPA vs non MPA	3 month sampling period
Sponaugle & Cowen 1996	Caribbean	Barbados	total community >5 mm	light trap	quantify ambient larval input	multiple months 1991–1992

Edmunds et al. 2010	Pacific	Moorea	all coral recruits	coral settlement plates†	quantify recruitment at 10 sites around Moorea	biannual scoring over 2 year period
Adjeroud et al. 2007	Pacific	Moorea	all coral recruits	coral settlement plates†	quantify recruitment at 9 sites around Moorea	scored 4 times per year for two years
Gleason 1996	Pacific	Moorea	all coral recruits	coral settlement plates‡	quantify recruitment on forereef and backreef	scored 3 times per year
Van Woesik et al. 2014	Caribbean	Florida Keys	all coral recruits	coral settlement plates†	quantify recruitment— upper and lower FL Keys @ 3 depths	deployed around coral spawning period (mean of 137 days)
Hughes et al. 1999	Pacific	GBR	all coral recruits	coral settlement plates§	compare recruitment across regions	deployed 10 days before spawning, retrieved 56 days later

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444 † unglazed terracotta tiles

445 ‡ unglazed ceramic tiles

446 ‡ unglazed tiles (unspecified)

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449 **Table 2.** Estimates for number of individuals, biomass and nutrient supply of fishes and corals

450 (mg m^{-2} day^{-1}).

Category	Location	Estimate	No. ind.	Biomass	C	N	P	Units
Fish	Moorea	min	10	1.17	0.58	0.13	0.01	mg m^{-2} day^{-1}
		max	1200	507.30	249.09	55.30	5.48	mg m^{-2} day^{-1}
		mean	240	101.20	49.69	11.03	1.09	mg m^{-2} day^{-1}
	Rangiroa	min	129	56.23	27.61	6.13	0.61	mg m^{-2} day^{-1}
		max	1080	455.71	223.75	49.67	4.92	mg m^{-2} day^{-1}
		mean	470	202.41	99.38	22.06	2.19	mg m^{-2} day^{-1}
	FL Keys	min	2	0.17	0.08	0.02	0.00	mg m^{-2} day^{-1}
		max	400	170.59	83.76	18.59	1.84	mg m^{-2} day^{-1}
		mean	28	13.15	6.46	1.43	0.14	mg m^{-2} day^{-1}
	St. Lucia	min	3	3.10	1.52	0.34	0.03	mg m^{-2} day^{-1}
		max	196	88.62	43.51	9.66	0.96	mg m^{-2} day^{-1}
		mean	22	10.51	5.16	1.15	0.11	mg m^{-2} day^{-1}
	Barbados	min	6	6.53	3.21	0.71	0.07	mg m^{-2} day^{-1}

		max	250	101.25	49.71	11.04	1.09	mg m^{-2} day^{-1}
		mean	66.3	29.97	14.71	3.27	0.32	mg m^{-2} day^{-1}
Coral	Moorea	min		0.006	0.010	0.001	0.000	mg m^{-2} day^{-1}
	FL Keys	min		0.011	0.006	0.000	0.000	mg m^{-2} day^{-1}
	GBR	min		4.555	2.788	0.161	0.009	mg m^{-2} day^{-1}
Coral Spawn	GBR coral surface area			19±15†	11.6†	0.7†		g m^{-2}
	reef area				7.1†	0.4†		g m^{-2}
	whole island				310†	18†		t

451 *Notes:* For fish, estimates are reported in minimum, maximum and mean values as

452 determined from the literature (Table 1). Coral larval-derived nutrient estimates from these

453 recruitment data represent a minimum estimate because coral recruitment data do not represent

454 the proportion of the larval community that enters a given reef ecosystem but does not recruit.

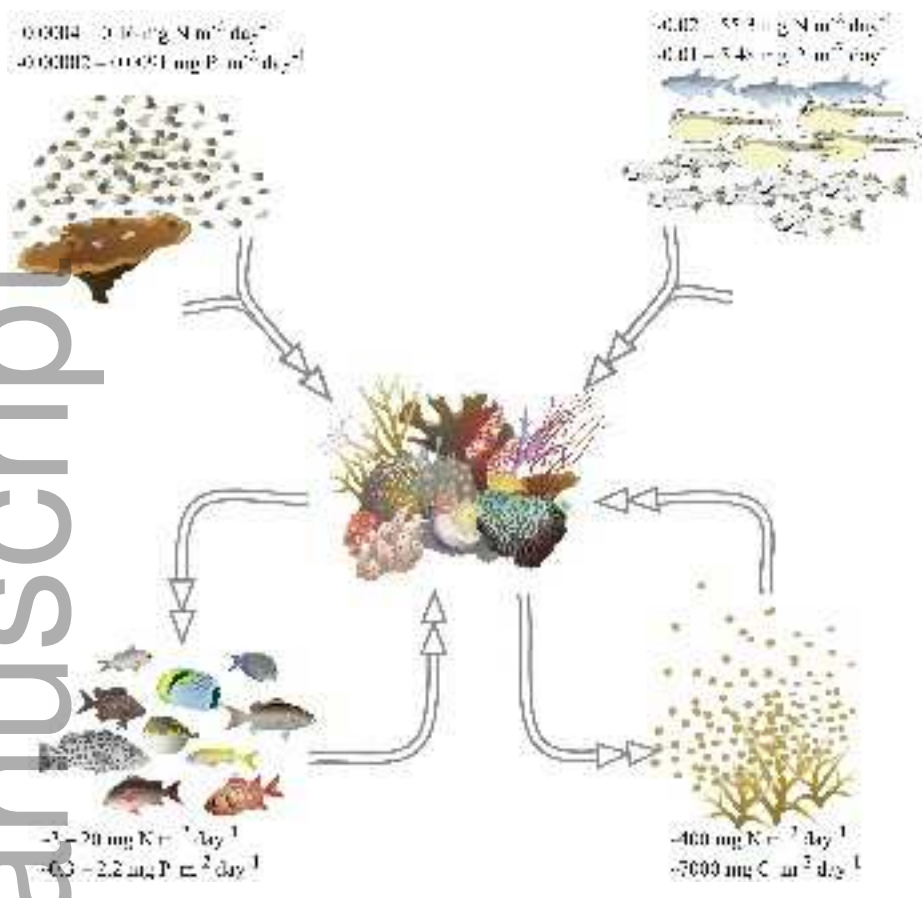455 † Coral spawn data (released as eggs) from Wild et al. (2004).

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459 **Figure 1.** Conceptual figure illustrating nutrient supply from fish and coral larvae (top images),

460 and recycled by the fish community (bottom left) and recycled via synchronous coral spawning

461 events (bottom right).

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