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

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Abstract. Nutrient subsidies are essential for the functioning of many ecosystems. A long-standing conundrum in coral reef ecology is how these systems can be among the most productive globally, but persist in nutrient-poor conditions. Here, we investigate the importance of the larvae of fishes and corals and gametes of corals as nutrient subsidies for coral reefs. We provide evidence that fish larvae may be an ecologically important source of exogenous nutrients. We found that at the high end of mean estimates of fish larval supply rates, larvae can replace the nutrients in the entire fish community (estimated from Caribbean coral reefs) in 28 and 434 d for nitrogen (N) and phosphorus, respectively. Coral larvae, on the other hand, appear to represent only a fraction of the nutrients supplied by the larval fish community. In contrast, coral gametes provide substantial pulses of recycled nutrients during synchronous spawning events. Within a single night, gametes from coral spawning events can produce nutrient fluxes that represent 13 and 64 times the amount of N and carbon, respectively, stored in coral reef fish communities. Our analysis suggests that larvae and/or gametes of fishes and corals may represent an important, but previously underappreciated, source of nutrients to coral reefs that warrant inclusion into models of nutrient dynamics and ecosystem function.

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INTRODUCTION

Nutrient subsidies often have important repercussions for the function and structure of ecological communities (Polis et al. 1997). Subsidies provide sources of energy and material that ultimately augment endogenous production in the recipient ecosystem. Subsidies can be highly variable in quality and across space and time, with this variability often impacting how efficiently they are integrated into a food web (Polis et al. 1997). Highly bioavailable subsidies, such as animal waste, can readily be taken up by primary producers, whereas subsidies bound in the tissues of live or dead animal or plant tissue have to first be integrated into the food web through trophic processes. These subsidies can represent a consistent press or be highly pulsed (Yang et al. 2008). For example, on islands where birds roost in significant numbers, nutrient subsidies from guano represent a consistent daily flux of marine-derived material that can substantially increase primary production relative to islands without roosting populations (Anderson and Polis 1999). In contrast, migratory fishes such as salmonids represent a seasonal subsidy that can

be so extensive that it can enhance tree production throughout entire watersheds (Naiman et al. 2002).

Coral reefs are among the most productive ecosystems on the planet (Odum and Odum 1955). This high level of productivity is enigmatic because coral reefs often persist in nutrient-poor tropical oceans that typically receive relatively little exogenous nutrient inputs from physical processes such as riverine transport of nutrients or deep-water upwelling (Muscatine and Porter 1977, Szmant 2002). As such, the high rates of productivity on reefs have been largely attributed to efficient internal recycling among the biotic constituents, such as corals, seaweeds, fishes, and invertebrates (Hatcher 1988). But coral reefs are not closed systems (Hughes et al. 2000, Pineda et al. 2007) and should, to some extent, be subsidized by exogenous biotic material, for example, coral or fish larvae—although the extent to which this occurs is unknown. Coral reef nutrient dynamics are being altered worldwide from anthropogenically derived nutrient enrichment (D'Angelo and Wiedenmann 2014) and overfishing (Allgeier et al. 2016). Improving our understanding of nutrient subsidies for coral reefs (and thus improving understanding of coral reef ecosystem nutrient dynamics as a whole) is essential if we are to effectively mitigate the negative effects of these widespread stressors.

Most previous research on coral, fish, and invertebrate larvae dynamics on coral reefs has focused largely on population dynamics and connectivity via the dispersal (Roberts 1997, Sale 2004, Andrello et al. 2015). Here, we explore the importance of fish and coral larvae as ecologically relevant nutrient subsidies to coral reef ecosystems. For corals, we also consider nutrient input and recycling from gametes (spawning material) that are synchronously released in mass spawning events. Specifically, we draw on case studies of fish and coral larval supply and mass spawning events from the wider Caribbean, French Polynesia, and the Great Barrier Reef in Australia, to provide estimates of net nutrient supply rates. We draw comparisons of these estimates with other known nutrient supply rates to reefs and other ecosystems to show their potential importance for coral reefs.

METHODS

We estimated nutrient supply rates per unit area per unit time ($mg \cdot m^{-2} \cdot d^{-1}$) to coral reefs from fish and coral larval as well coral spawning material. We define coral larvae as the free-swimming planulae that have the potential to settle, and coral spawning material as coral gametes and/or remnants of decomposing unfertilized coral gametes from a spawning event. We reviewed the literature to find (1) estimates of supply rates of fish larvae, coral larvae, or coral spawning material (supply of individuals or biomass per day) to reefs and (2) estimates of nutrient content of these groups. Studies were found by searching ISI Web of Knowledge and Google Scholar with various combinations of the terms: fish larvae, coral larvae, coral spawning, mass spawning, nutrients, nitrogen, phosphorous, dispersal, supply, and input.

While our searches revealed a relatively rich literature on larval supply to coral reefs, we found a relative paucity of direct estimates of supply rates of fish and coral larvae—presumably due to the extremely difficult and labor-intensive nature of quantifying such processes. Little data were available for nutrient content of fish (Pfeiler et al. 1998, Coombs et al. 1999) or coral larvae (Wild et al. 2004, Padilla-Gamiño et al. 2013). For these reasons, we focus our study on three regions in which the most data were available: The Florida Keys and the Caribbean, French Polynesia, and The Great Barrier Reef (Table 1).

Estimating fish larvae supply rates and nutrient content

Estimates of supply rates were taken from studies that include two methods of collection: light traps and crest nets (Table 1). Light traps, the only method used in The Florida Keys and the Caribbean, use a light to attract fish larvae to a floating trap near the surface of the water. Traps are deployed at night, and larvae are collected from the trap by morning (Doherty 1987). Crest nets, used exclusively in studies from French Polynesia, are passive nets that trap larvae passing over the reef crest (Dufour et al. 1996).

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

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 d (new moon–peak period of sampling)
Dufour and Galzin (1993)	Pacific	Moorea	Total community >5 mm	Crest net	Quantify ambient larval input	Replicated 10 min sets
Grorud-Colvert and Sponaugle (2009)	Caribbean	FL Keys	Total community >5 mm	Light trap	Compare MPA vs. non MPA	Monthly for ~1 yr
Valles et al. (2001)	Caribbean	St. Lucia	Total community >5 mm	Light trap	Compare MPA vs. non MPA	3-month sampling period
Sponaugle and 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-yr period
Adjeroud et al. (2007)	Pacific	Moorea	All coral recruits	Coral settlement plates†	Quantify recruitment at nine sites around Moorea	Scored four times per year for two years
Gleason (1996)	Pacific	Moorea	All coral recruits	Coral settlement plates‡	Quantify recruitment on forereef and backreef	Scored three times per year
van Woesik et al. (2014)	Caribbean	Florida Keys	All coral recruits	Coral settlement plates†	Quantify recruitment—upper and lower FL Keys at three depths	Deployed around coral spawning period (mean of 137 d)
Hughes et al. (1999)	Pacific	GBR	All coral recruits	Coral settlement plates§	Compare recruitment across regions	Deployed 10 d before spawning, retrieved 56 d later

†Unglazed terracotta tiles.
‡Unglazed ceramic tiles.
‡Unglazed tiles (unspecified).

minimum, and mean), which we subsequently converted to biomass (Table 2). The body size of each larva was not available, so we generated a body-size distribution for the reported larval communities through iteratively sampling from a published body-size distribution of larvae supply (Pepin 1995). These size distributions were then converted to mass using a published length–weight regression for larvae (weight = $a \times \text{length}^b$; where −3.25 was used for the scaling coefficient a and 3.085 was for the shape coefficient b; Pepin 1995). Total larval community biomass was then generated by summing across individuals within a given sample. Total nutrient supply rate per fish larval community was generated by multiplying community biomass by the percent nutrient contents to generate grams of nutrients per total larval community biomass. Larval nutrient content was estimated by taking the average from five different studies that quantified carbon (C), nitrogen (N), and phosphorus (P) per unit body mass for various species of fish larvae, only two of which were marine (Appendix S1).

Estimates of C, N, and P supply ($\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) from fish larvae were calculated differently for the two larvae collection methods. In the Caribbean, we assumed that the light traps attracted fish within a 50 m radius of the device (S. Sponaugle, *personal communications*), providing the estimated area of ~3.14 × 50^2 = 7850 m^2 that was used to convert supply per unit trap (mg C, N, $\text{P} \cdot \text{trap}^{-1} \cdot \text{d}^{-1}$) to supply rates (mg C, N, $\text{P} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$). In comparison with light traps, crest nets are a more quantitative and accurate measure of larvae supply (Nolan and Danilowicz 2008). Crest nets, used in French Polynesia, filter a specific area of the water column, typically

Table 2. Estimates for number of individuals, biomass, and nutrient supply of fishes and corals (mg·m^{-2}·d^{-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}·d^{-1}
		Max	1200	507.30	249.09	55.30	5.48	mg·m^{-2}·d^{-1}
		Mean	240	101.20	49.69	11.03	1.09	mg·m^{-2}·d^{-1}
	Rangiroa	Min	129	56.23	27.61	6.13	0.61	mg·m^{-2}·d^{-1}
		Max	1080	455.71	223.75	49.67	4.92	mg·m^{-2}·d^{-1}
		Mean	470	202.41	99.38	22.06	2.19	mg·m^{-2}·d^{-1}
	FL Keys	Min	2	0.17	0.08	0.02	0.00	mg·m^{-2}·d^{-1}
		Max	400	170.59	83.76	18.59	1.84	mg·m^{-2}·d^{-1}
		Mean	28	13.15	6.46	1.43	0.14	mg·m^{-2}·d^{-1}
	St. Lucia	Min	3	3.10	1.52	0.34	0.03	mg·m^{-2}·d^{-1}
		Max	196	88.62	43.51	9.66	0.96	mg·m^{-2}·d^{-1}
		Mean	22	10.51	5.16	1.15	0.11	mg·m^{-2}·d^{-1}
	Barbados	Min	6	6.53	3.21	0.71	0.07	mg·m^{-2}·d^{-1}
		Max	250	101.25	49.71	11.04	1.09	mg·m^{-2}·d^{-1}
		Mean	66.3	29.97	14.71	3.27	0.32	mg·m^{-2}·d^{-1}
Coral	Moorea	Min		0.006	0.010	0.001	0.000	mg·m^{-2}·d^{-1}
	FL Keys	Min		0.011	0.006	0.000	0.000	mg·m^{-2}·d^{-1}
	GBR	Min		4.555	2.788	0.161	0.009	mg·m^{-2}·d^{-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

Notes: For fish, estimates are reported in minimum, maximum, and mean values as determined from the literature (Table 1). Coral larval-derived nutrient estimates from these recruitment data represent a minimum estimate because coral recruitment data do not represent the proportion of the larval community that enters a given reef ecosystem but does not recruit.

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

extending from the top of the reef crest to the top of the water column (Dufour et al. 1996, Nolan and Danilowicz 2008). As such, the raw trap data were scaled to the linear distance of the reef crest around a given island, for example, ~48,710 m for Moorea, and then converted to m^2 of reef by dividing by the total m^2 of the backreef complex —providing an estimate of C, N, P supply·m^{-2}·d^{-1}. Both the linear distance of the reef crest and area of back reef were quantified using Google Earth.

We acknowledge that these estimates have several potential sources of error, and a few caveats are important to highlight. First, for the Caribbean data, we assume that supply rates are uniform and that the light traps represent a truly random location on the reef—and thus is representative of anywhere along the reef continuum. Light traps are not traditionally considered quantitative measures, but represent some of the only available data to quantify fish larval supply to reefs (S. Sponaugle, *personal communications*). Second, Rangiroa, in French Polynesia, is an atoll, unlike the mountainous island of Moorea, with

minimal back reef complex making it difficult to calculate areal input rates (supply·m^{-2}·d^{-1}). To maximize the use of limited data and make generalizable comparisons, we applied the crest net data from Rangiroa to the areal extent of the back reef complex in Moorea, providing a rough estimate of how larvae supply rates from Rangiroa would distribute nutrients across a reef complex the size of Moorea. Given the paucity of data on fish larval densities, these data are useful for helping to place into context the potential magnitude of nutrient subsidies by larval fishes.

Coral larvae supply rates and nutrient content

Coral larvae supply rates have not been quantified empirically, presumably because their small size and relative infrequency make them extremely difficult to separate from other organisms captured in traditional zooplankton sampling methods. Instead, we used data from coral recruitment studies to estimate a minimum coral larvae supply rate. Coral recruitment is measured by deploying artificial settlement tiles on the reef, which are then collected and examined

with a microscope to quantify recruitment. These data reflect larval supply, settlement, and post-settlement survival, and underestimate the true supply rate of coral larvae to a given reef, making our estimates (likely considerably) conservative. We selected studies that used terracotta or unglazed ceramic settlement plates (the most common methods) to quantify coral recruitment. Studies were restricted to Moorea (the most well-studied island in French Polynesia; Gleason 1996, Edmunds et al. 2010), the Florida Keys (van Woesik et al. 2014), and the Great Barrier Reef (Hughes et al. 1999), because these studies each provided the best replication over the geographic range of the region (Table 1). All recruitment estimates were converted to individuals$\cdot$m$^{-2}\cdot$d^{-1} (Table 1).

Coral recruitment can be highly pulsed, for example, annual spawning events in the great barrier reef (GBR), or more consistent throughout the reproductive season, as is more typical in the Caribbean (Humanes and Bastidas 2015). Tile deployment duration can vary substantially from short time scales for studies estimating recruitment events around the time of spawning (Hughes et al. 1999, van Woesik et al. 2014) to longer scales used to estimate recruitment independent of spawning (Adjeroud et al. 2007, Edmunds et al. 2010). Because tiles deployed for longer periods of time have a larger window for recruit mortality, we estimated the original number of settled corals from each study using a published relationship between recruit age (a proxy for tile deployment time) and percent survival ($y = -0.4499x + 57.561$) following Humanes and Bastidas (2015).

The mean dry mass of a single coral larva (μg dry mass) was estimated as the average of four species of coral eggs and larvae (μg dry mass) from the literature (Harii et al. 2007). Egg dry mass values were included in the estimate of larval dry mass because (1) there is little available data on the dry mass of coral larvae. We acknowledge that it is possible for coral larvae to change mass during the planktonic phase. For example, some larvae lack symbionts (i.e., are lecithotrophic) and therefore loose mass as energy reserves are depleted (Figueiredo et al. 2012), whereas other species contain symbionts and may receive nutritional input from their photosynthesizing symbionts; however, evidence

suggests this input is minimal (Kopp et al. 2016). The percent nutrient content (C and N) per dry mass of coral eggs and larvae was determined by averaging three species (Wild et al. 2004). Only one estimate was available for percent nutrient content of phosphorus (Padilla-Gamiño et al. 2013, Appendix S2). The mean nutrient content of a single coral larva (μg dry mass/larva) was then estimated as the product of percent nutrient content and mean dry mass. Finally, the supply rate of nutrients via coral larvae (μg dry mass$\cdot$m$^{-2}\cdot$d^{-1}) for each location was calculated as the product of the supply rate of coral larvae (larvae$\cdot$m$^{-2}\cdot$d^{-1}) and nutrient content of a single coral larva (μg dry mass/larva).

Results

Our study provides compelling support for the importance of fish larvae and coral gametes as an ecologically relevant source of nutrients to coral reef ecosystems. For example, fish larvae import ~0.02–55.3 mg N$\cdot$m$^{-2}\cdot$d^{-1} and ~0.01–5.48 mg P$\cdot$m$^{-2}\cdot$d^{-1} across the Caribbean and French Polynesia, respectively (Table 2). The difference among systems is substantial and is likely a product of factors such as reef type (patch vs. crest, respectively), sampling methodology (light traps vs. crest nets, respectively), and conversion factors used to estimate the dispersal of these nutrients across the reef complex (see *Methods*).

In contrast to fish larvae, coral larvae inputs are substantially lower per unit time, but, in some regions, are highly pulsed due to reef-scale broadcast spawning events that occur once or twice per year. On a daily basis, coral larvae input is only a small fraction of the fish larvae-derived nutrients, but input also varies substantially across systems. Coral larvae import an estimated ~0.0004–0.16 mg N$\cdot$m$^{-2}\cdot$d^{-1} and ~0.00002–0.0091 mg P$\cdot$m$^{-2}\cdot$d^{-1} across the Florida Keys and the Great Barrier Reef, respectively (Table 2). Synchronous mass spawning can stimulate greater pulses of nitrogen and carbon. Wild et al. (2004) estimate that corals in the genus *Acropora* release 11.7 g C and 0.7 g N/m^2 of coral surface in the form of eggs at Heron Island in the Great Barrier Reef, which is equivalent to 7.1 g C and 0.4 g N/m^2 of reef when corrected for coral cover (Wild et al. 2004).

Discussion

Animals are now recognized as a primary driver of the storage and recycling of nutrients on coral reefs (Allgeier et al. 2017), and for their roles in translocating nutrients from adjacent ecosystems, for example, seagrass beds, to coral reefs (Meyer et al. 1983, Shantz et al. 2015). Here, we provide support for the idea that immigrating fish and coral larvae, as well as coral gametes, are likely an important, but underappreciated, component to coral reef nutrient budgets. Both fish and coral larvae represent nutrients bound in animal material and thus have distinctly different implications for coral reef ecosystems when compared to the more traditionally considered bioavailable forms of nutrients that are supplied by upwelling, terrestrial runoff, or animal excretion. Labile forms of nutrients are readily taken up by primary producers and either retained, remineralized, or enter the food web through trophic interactions. Nutrients entering via the tissue of fish or coral larvae have two primary fates: (1) They enter the food web first via trophic interactions, that is, direct consumption or detrital pathways, or (2) they settle and themselves begin to incorporate food web-derived nutrients.

From an ecosystem ecology perspective, where a primary goal is to understand these processes in the context of an ecosystem nutrient budget, the manner in which these nutrients are sequestered by the ecosystem is less important (DeAngelis 1992). In this context, the net effect these nutrient sources have on the nutrient budget is determined by the manner in which they alter the nutrient capacity of the ecosystem. In other words, how do these nutrients contribute to, or detract from, the total nutrient pool including water column nutrients and the nutrients stored in living and dead tissue (DeAngelis 1992, Allgeier et al. 2016)?

Given that coral gametes appear to largely represent recycled forms of nutrients from the same reef complex, they may have little effect on coral reef nutrient capacity in terms of gains or losses. In contrast, fish larvae may have substantial implications for nutrient capacity. The majority of coral reef fish larvae have significant pelagic larval durations, allowing them to be dispersed over substantial distances ranging from 10s to 100s of km (Roberts 1997, Sale 2004). Coral larvae also have a dispersive pelagic phase that lasts from hours to over 100 d (Connolly and Baird 2010) and have the potential to travel 100s of kilometers (Wilson and Harrison 1998). Thus, while some coral and fish larvae are retained near their natal reefs (Miller and Mundy 2003, Sale 2004), many are exported from one reef as a loss of nutrients and imported to another as gain of nutrients. Conceptually speaking, this fish and coral larvae conveyor belt could possibly represent a zero-sum game if the number of larvae entering the system is equivalent to the larvae produced in the system. However, it is noteworthy that a substantial portion of larval growth occurs in the pelagic stage, and thus, a substantial portion of the nutrients within larvae entering a coral reef system is transferred from the pelagic region. Further, in the case of fish larvae, if some of the larval species entering the coral reef complex have origins in other ecosystems, for example, pelagic ocean, seagrass, or mangrove ecosystems, then nutrients bound in fish larvae would represent a net positive gain.

An important finding in our study was that a significant proportion of the larval fish community were of non-coral reef origin. For example, Sponaugle et al. (2003) found 29% of the larval community consisted of non-coral-associated families (e.g., Atherinidae, Clupeidae, Engraulidae), Grorud-Colvert and Sponaugle (2009) found they accounted for 47% in the Florida Keys, and Valles et al. (2001) found that clupeids alone accounted for 96.6% of their catches in St. Lucia. In French Polynesia, the proportion of the catch from non-reef origin was substantially lower but still represented ~15% of the total abundance of fish larvae (Lo-Yat et al. 2006). It is possible that the difference between the Caribbean and French Polynesia represents differential selectivity in the different methods (light traps vs. crest nets) for clupeids. Nonetheless, these estimates suggest that a substantial proportion of the annual supply of nutrients from fish larvae may come from other ecosystems entirely, representing important allocthonous subsidies.

Across relatively unimpacted coral reef ecosystems in the Caribbean, the mean standing biomass of the entire fish community can store ~2800 mg N and 950 mg P/m^2 (Allgeier et al. 2014, Fig. 1)—unfortunately no similar data exist for Indo-Pacific reefs. In comparison, the mean estimated nutrients imported into these systems

$\sim 0.0004 - 0.16$ mg N·m^{-2}·day^{-1}
$\sim 0.00002 - 0.0091$ mg P·m^{-2}·day^{-1}

$\sim 0.02 - 55.3$ mg N·m^{-2}·day^{-1}
$\sim 0.01 - 5.48$ mg P·m^{-2}·day^{-1}

$\sim 2 - 20$ mg N·m^{-2}·day^{-1}
$\sim 0.3 - 2.2$ mg P·m^{-2}·day^{-1}

~ 400 mg N·m^{-2}·day^{-1}
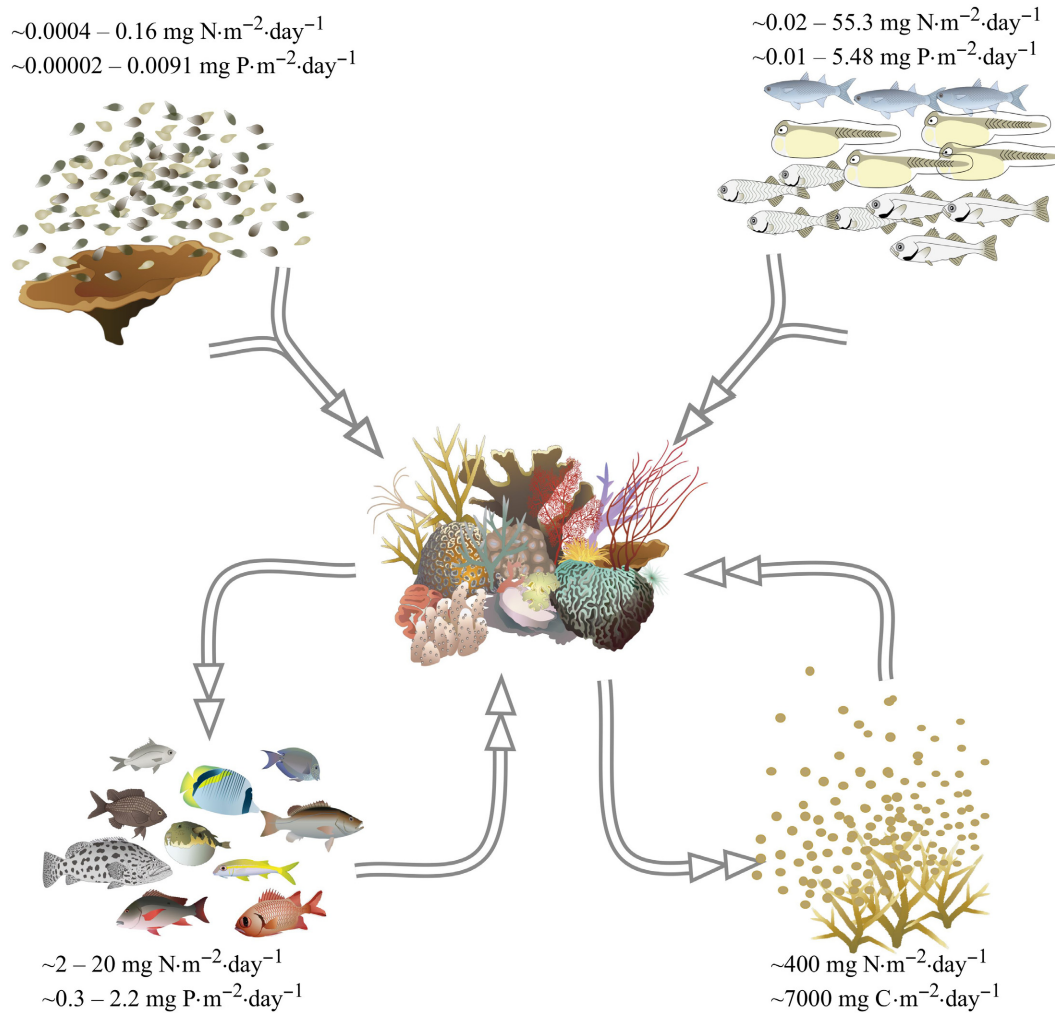~ 7000 mg C·m^{-2}·day^{-1}

Fig. 1. Conceptual figure illustrating nutrient supply from fish and coral larvae (top images), and nutrients recycled by the fish community (bottom left), and via synchronous coral spawning events (bottom right).

from fish larvae on a yearly basis ranges from ~ 1883 to 36,281 mg N·m^{-2}·yr^{-1}, and ~ 40 to 799 mg P·m^{-2}·yr^{-1}. Using the higher end of mean larval supply rates across studies for comparison purposes, these data suggest that this subsidy can replace the nutrients stored by the entire coral reef fish community in ~ 28 and 434 d (0.3 and 1.3 yr) for N and P, respectively. Importantly, fish larval abundance oscillates relative to lunar cycles more than longer seasonal cycles (Sponaugle and Cowen 1996), suggesting fish larvae may represent a relatively continuous nutrient influx throughout the entire year. Further, in these same Caribbean fish communities, Allgeier et al. (2014) report that fishes recycle

nutrients via excretion at rates of ~ 3–20 mg N·m^{-2}·d^{-1} and ~ 0.3–2.2 mg P·m^{-2}·d^{-1} (Fig. 1). For further comparison, atmospheric deposition of N in the form of rainwater has been found to be ~ 0.308 mg N·m^{-2}·d^{-1} (Barile and Lapointe 2005), representing only a small fraction of the inputs of N from the fish community. Though these later estimates represent nutrients in form that are immediately available for biological uptake, it is still notable that fish larvae provide very similar amounts of nutrients to the system as community-level fish excretion on a daily basis.

In contrast to the amount of nutrients supplied by fish larvae, nutrient input from coral larvae is relatively small and likely has little effect on the

nutrient capacity of the system. However, synchronous coral spawning events still represent massive pulses of (primarily) recycled nutrients that have important ecological consequences. Coral gametes and spawning material make their way into the food web nearly immediately through consumption by fish and other reef organisms (Pratchett et al. 2001) and through rapid degradation in the water column and sediment (Wild et al. 2004, 2008). Coral spawning can cause elevations in particulate organic matter in the water column and sediment for weeks following the spawning event, highlighting the strength of their effect on nutrient dynamics in these systems (Eyre et al. 2008, Wild et al. 2008).

The magnitude of the nutrient pulse generated by coral spawning events will likely depend on the number of species that spawn at a given time and their abundance on the benthos. For example, Wild et al. (2004) demonstrated that in a relatively small spawning event on the Great Barrier Reef, one species of *Acropora* alone released 11,600 mg C/m^2 and 700 mg N/m^2 coral surface in the form of coral eggs. Assuming that the coral community is mostly composed of various *Acropora* species that release a similar number of eggs, they further estimated that community-level spawning event resulted in a pulse of 7000 mg C/m^2 and 400 mg N/m^2 reef in the form of coral eggs (Wild et al. 2004). These numbers represent 64% and 13% of the total C and N, respectively, stored in fish, which are considered to be one of, if not the, primary pools of nutrients, on an average Caribbean reef (10,988 mg C/m^2 and 3122 mg N/m^2; Allgeier et al. 2014, 2015). Further, applied to the whole reef area (26.4 km^2), a spawning event at Heron Island may result in a pulse of 310 t C and 18 t N as coral eggs (Wild et al. 2004). This tremendous pulse of nutrients is substantial compared to examples of what are thought to be extreme animal-derived nutrient pulses in other ecosystems. For example, wildebeest mass-drowning events input an estimated 107 ± 51 t C, 25 ± 12 t N, and 13 ± 6 t P to the Mara River in Kenya nearly annually (Subalusky et al. 2017). Although coral spawn represents recycling of nutrients within the same ecosystem, unlike the wildebeest example, the extreme quantity of nutrients produced by these events warrants recognition as a critically important nutrient pathway in coral reef ecosystems.

Our study represents an initial foray to investigate the potential importance of exogenous sources subsidizing the nutrient budgets of coral reefs. Despite obvious limitations in data and potential issues associated with types of methodologies, our findings reveal that fish larvae may represent an important nutrient subsidy to these systems and that coral spawning provides a significant pulse of locally recycled nutrients. The relevance of quantifying nutrient inputs from coral and fish larvae has direct implications for conservation of these imperiled ecosystems. Human activities are altering the nutrient budgets of coral reefs worldwide, through myriad ways, but the mechanisms that underlie these interactions remain poorly understood (Szmant 2002). Recent research is improving understanding of coral-nutrient interactions at the organism-level (Wiedenmann et al. 2013, Ferrier-Pages et al. 2016), but we still know relatively little about how these processes transcend to the ecosystem scale. To improve understanding of these processes at larger scales of organization, exhaustive knowledge of all the components that underpin a coral reef nutrient budget is needed.

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LITERATURE CITED

Adjeroud, M., L. Penin, and A. Carroll. 2007. Spatio-temporal heterogeneity in coral recruitment around Moorea, French Polynesia: implications for population maintenance. Journal of Experimental Marine Biology and Ecology 341:204–218.

Allgeier, J. E., D. E. Burkepile, and C. A. Layman. 2017. Animal pee in the sea: consumer-mediated nutrient dynamics in the world's changing oceans. Global Change Biology 23:2166–2178.

Allgeier, J. E., C. A. Layman, P. J. Mumby, and A. D. Rosemond. 2014. Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. Global Change Biology 20:2459–2472.

Allgeier, J. E., C. A. Layman, P. J. Mumby, and A. D. Rosemond. 2015. Biogeochemical implications of biodiversity loss across regional gradients of

coastal marine ecosystems. Ecological Monographs 85:117–132.

Allgeier, J. E., A. Valdivia, C. Cox, and C. A. Layman. 2016. Fishing down nutrients on coral reefs. Nature Communications 7:1–5.

Anderson, W. B., and G. A. Polis. 1999. Nutrient fluxes from water to land: Seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118:324–332.

Andrello, M., D. Mouillot, S. Somot, W. Thuiller, and S. Manel. 2015. Additive effects of climate change on connectivity between marine protected areas and larval supply to fished areas. Diversity and Distributions 21:139–150.

Barile, P. J., and B. E. Lapointe. 2005. Atmospheric nitrogen deposition from a remote source enriches macroalgae in coral reef ecosystems near Green Turtle Cay, Abacos, Bahamas. Marine Pollution Bulletin 50:1262–1272.

Connolly, S. R., and A. H. Baird. 2010. Estimating dispersal potential for marine larvae: dynamic models applied to scleractinian corals. Ecology 91:3572–3583.

Coombs, S. H., D. V. P. Conway, S. A. Morley, and N. C. Halliday. 1999. Carbon content and nutritional condition of sardine larvae (*Sardina pilchardus*) off the Atlantic coast of Spain. Marine Biology 134:367–373.

D'Angelo, C., and J. Wiedenmann. 2014. Impacts of nutrient enrichment on coral reefs: new perspectives and implications for coastal management and reef survival. Current Opinion in Environmental Sustainability 7:82–93.

DeAngelis, D. L. 1992. Dynamics of nutrient cycling and food webs. Chapman and Hall, London, UK.

Doherty, P. 1987. Light-traps: selective but useful devices for quantifying the distributions and abundances of larval fishes. Bulletin of Marine Science 41:423–431.

Dufour, V., and R. Galzin. 1993. Colonization patterns of reef fish larvae to the lagoon at Moorea Island, French Polynesia. Marine Ecology Progress Series 102:143–152.

Dufour, V., E. Riclet, and A. Lo-Yat. 1996. Colonization of reef fishes at Moorea Island, French Polynesia: temporal and spatial variation of the larval flux. Marine and Freshwater Research 47:413.

Edmunds, P. J., J. J. Leichter, and M. Adjeroud. 2010. Landscape-scale variation in coral recruitment in Moorea, French Polynesia. Marine Ecology Progress Series 414:75–89.

Eyre, B. D., R. N. Glud, and N. Patten. 2008. Mass coral spawning : a natural large-scale nutrient addition experiment. Limnology and Oceanography 53: 997–1013.

Ferrier-Pages, C., C. Godinot, C. D'Angelo, J. Wiedenmann, and R. Grover. 2016. Phosphorus

metabolism of reef organisms with algal symbionts. Ecological Monographs 86:262–277.

Figueiredo, J., A. H. Baird, M. F. Cohen, J.-F. Flot, T. Kamiki, T. Meziane, M. Tsuchiya, and H. Yamasaki. 2012. Ontogenetic change in the lipid and fatty acid composition of scleractinian coral larvae. Coral Reefs 31:613–619.

Gleason, M. G. 1996. Coral recruitment in Moorea, French Polynesia: the importance of patch type and temporal variation. Journal of Experimental Marine Biology and Ecology 207:79–101.

Grorud-Colvert, K., and S. Sponaugle. 2009. Larval supply and juvenile recruitment of coral reef fishes to marine reserves and non-reserves of the upper Florida Keys, USA. Marine Biology 156:277–288.

Harii, S., K. Nadaoka, M. Yamamoto, and K. Iwao. 2007. Temporal changes in settlement, lipid content and lipid composition of larvae of the spawning hermatypic coral *Acropora tenuis*. Marine Ecology Progress Series 346:89–96.

Hatcher, B. G. 1988. Coral reef primary productivity – A beggars banquet. Trends in Ecology & Evolution 3:106–111.

Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschaniwskyj, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 1999. Patterns of recruitment and abundance of corals along the Great Barrier Reef. Nature 397:59–63.

Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschaniwskyj, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 2000. Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. Ecology 81:2241.

Humanes, A., and C. Bastidas. 2015. In situ settlement rates and early survivorship of hard corals: a good year for a Caribbean reef. Marine Ecology Progress Series 539:139–151.

Kopp, C., I. Domart-Coulon, D. Barthelemy, and A. Meibom. 2016. Nutritional input from dinoflagellate symbionts in reef-building corals is minimal during planula larval life stage. Science Advances 2:e1500681.

Lo-Yat, A., M. Meekan, J. Carleton, and R. Galzin. 2006. Large-scale dispersal of the larvae of nearshore and pelagic fishes in the tropical oceanic waters of French Polynesia. Marine Ecology Progress Series 325:195–203.

Lo-Yat, A., S. D. Simpson, M. Meekan, D. Lecchini, E. Martinez, and R. Galzin. 2011. Extreme climatic events reduce ocean productivity and larval supply in a tropical reef ecosystem. Global Change Biology 17:1695–1702.

Meyer, J. L., E. T. Schultz, and G. S. Helfman. 1983. Fish schools – an asset to corals. Science 220: 1047–1049.

Miller, K., and C. Mundy. 2003. Rapid settlement in broadcast spawning corals: implications for larval dispersal. Coral Reefs 22:99–106.

Muscatine, L., and J. W. Porter. 1977. Reef corals – mutualistic symbiosis adapted to nutrient-poor environments. BioScience 27:454–460.

Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399–417.

Nolan, C. J., and B. S. Danilowicz. 2008. Advantages of using crest nets to sample presettlement larvae of reef fishes in the Caribbean Sea. Fisheries Bulletin 106:213–221.

Odum, H. T., and E. P. Odum. 1955. Trohic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecological Monographs 25:291–320.

Padilla-Gamiño, J. L., et al. 2013. Are all eggs created equal? A case study from the Hawaiian reef-building coral *Montipora capitata*. Coral Reefs 32:137–152.

Pepin, P. 1995. An analysis of the length-weight relationship of larval fish: limitations of the general allometric model. Fishery Bulletin 93:419–426.

Pfeiler, E., V. A. Lindley, and J. J. Elser. 1998. Elemental (C, N and P) analysis of metamorphosing bonefish (*Albula* sp.) leptocephali: relationship to catabolism of endogenous organic compounds, tissue remodeling, and feeding ecology. Marine Biology 132:21–28.

Pineda, J., J. Hare, and S. Sponaugle. 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography 20:22–39.

Polis, G. A., W. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:289–316.

Pratchett, M. S., N. Gust, G. Goby, and S. O. Klanten. 2001. Consumption of coral propagules represents a significant trophic link between corals and reef fish. Coral Reefs 20:13–17.

Roberts, C. M. 1997. Connectivity and management of Caribbean coral reefs. Science (New York, N.Y.) 278:1454–1457.

Sale, P. F. 2004. Connectivity, recruitment variation, and the structure of reef fish communities. Integrative and Comparative Biology 44:390–399.

Shantz, A. A., M. C. Ladd, E. Schrack, and D. E. Burkepile. 2015. Fish-derived nutrient hotspots shape coral reef benthic communities. Ecological Applications 25:2142–2152.

Sponaugle, S., and R. Cowen. 1996. Nearshore patterns of coral reef fish larval supply to Barbados, West Indies. Marine Ecology Progress Series 133:13–28.

Sponaugle, S., J. Fortuna, K. Grorud, and T. Lee. 2003. Dynamics of larval fish assemblages over a shallow coral reef in the Florida Keys. Marine Biology 143:175–189.

Subalusky, A. L., C. L. Dutton, E. J. Rosi, and D. M. Post. 2017. Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. Proceedings of the National Academy of Sciences of the USA 114:7647–7652.

Szmant, A. M. 2002. Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? Estuaries 25:743–766.

Valles, H., S. Sponaugle, and H. A. Oxenford. 2001. Larval supply to a marine reserve and adjacent fished area in the Soufrière Marine Management Area, St Lucia, West Indies. Journal of Fish Biology 59:152–177.

van Woesik, R., W. J. Scott, and R. B. Aronson. 2014. Lost opportunities: Coral recruitment does not translate to reef recovery in the Florida Keys. Marine Pollution Bulletin 88:110–117.

Wiedenmann, J., C. D'Angelo, E. G. Smith, A. N. Hunt, F. E. Legiret, A. D. Postle, and E. P. Achterberg. 2013. Nutrient enrichment can increase the susceptibility of reef corals to bleaching. Nature Climate Change 3:160–164.

Wild, C., C. Janzen, U. Struck, O. Hoegh-Guldberg, and M. Huettel. 2008. Biogeochemical responses following coral mass spawning on the Great Barrier Reef: pelagic–benthic coupling. Coral Reefs 27:123–132.

Wild, C., R. Tollrian, and M. Huettel. 2004. Rapid recycling of coral mass-spawning products in permeable reef sediments. Marine Ecology Progress 271:159–166.

Wilson, J. R., and P. L. Harrison. 1998. Settlement-competency periods of larvae of three species of scleractinian corals. Marine Biology 131:339–345.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses? Ecology 89:621–634.

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