Reef fish carbonate production assessments highlight regional variation in sedimentary significance

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ABSTRACT

Recent studies show that all marine bony fish produce mud-sized (<63 μm) carbonate at rates relevant to carbonate sediment budgets, thus adding to the debate about the often enigmatic origins of fine-grained marine carbonates. However, existing production data are geographically and taxonomically limited, and because different fish families are now known to produce different carbonate polymorphs—an issue relevant to predicting their preservation potential—these limitations represent an important knowledge gap. Here we present new data from sites in the Western Pacific Ocean, based on an analysis of 45 fish species. Our data show that previously reported production outputs (in terms of rates and family-specific mineralogies) are applicable across different biogeographic regions. On this basis, we model carbonate production for nine coral reef systems around Australia, with production rates averaging 2.1–9.6 g m^{-2} yr^{-1}, and up to 105 g m^{-2} yr^{-1} at discrete sites with high fish biomass. With projected production rates on lower-latitude reefs up to two-fold higher, these outputs indicate that carbonate production rates by fish can be comparable with other fine-grained carbonate-producing taxa such as codiacean algae. However, carbonates produced by Australian reef fish assemblages are dominated by a highly unstable amorphous polymorph; a marked contrast to Caribbean assemblages in which Mg calcite dominates. These findings highlight important regional differences in the sedimentary relevance and preservation potential of fish carbonates as a function of historical biogeographic processes that have shaped the world's marine fish faunas.

INTRODUCTION

Shallow, warm marine carbonate settings are sites of prolific carbonate sediment production and accumulation (Schlager, 2003). The origins of coarse-grained components of these sediments are often readily discernible, and form the basis for interpretations of carbonate depositional histories. However, determining the origins of mud-grade (<63 μm) carbonates can be problematic (Flügel, 2004). Much shallow mud production has been ascribed to post-mortem breakdown of carbonate-secreting taxa (especially codiacean algae and seagrass epiphytes) along with microbially mediated and abiotic precipitation (see Gischler et al., 2013). In addition, evidence has emerged that all bony marine fishes (teleosts) precipitate mud-sized carbonates in their intestines (Walsh et al., 1991), and that these can be excreted at rates relevant to carbonate sediment budgets—especially in habitats with high fish biomass, such as coral reefs (Perry et al., 2011; Salter et al., 2017).

Our understanding of the sedimentary significance of fish carbonates is, however, limited by the small number of taxa studied to date, and the restricted biogeographic range captured by existing research (limited to the Caribbean; Perry et al., 2011; Salter et al., 2012, 2017). The first issue is problematic because different fish families produce different carbonate polymorphs; the discrete solubilities of each having implications for preservation potential (Salter et al., 2017). Though progress is being made in elucidating the controls on precipitation processes (Schauer et al., 2018), a means of predicting the polymorphs produced by any given family remains elusive. Existing data are sufficient to generate relevant production models for Caribbean reef fish assemblages, but differences in fish family compositions among ocean basins (Bellwood, 1997; Kulbicki et al., 2013) have hindered attempts to extend the spatial scale of such models. Furthermore, the applicability of initial findings from Caribbean settings in other biogeographic regions remains to be tested; e.g., are carbonate types consistent within families regardless of geographic location?

Here we address these knowledge gaps by extending the biogeographic range of fish carbonate studies across sub-tropical Western Pacific Ocean locations with surface seawater parameters directly comparable to those of previously used Caribbean locations. We also expand the range of teleost taxa for which production is documented to encompass 67 species (more than a three-fold increase over existing data) and 34 families (more than a two-fold increase). Integrating these new data with fish biomass data sets, we generate production models for nine coral reef systems in Australia.

STUDY LOCATIONS AND METHODS

Carbonate production by 45 Western Pacific members of 27 teleost fish families (Table DR1 in the GSA Data Repository[1]) was quantified at two locations in Queensland, Australia, during April/May 2014 and May 2015: Heron Reef (23°45′S, 151°92′E); and Moreton Bay (27°29′S, 153°24′E). Fish were housed in aquaria at the Heron Island and Moreton Bay Research Stations in locally drawn seawater filtered to 1 μm, and maintained at ambient conditions (mean temperature of 23–25 °C; salinity of 35.1–36.4 PSU). Food was withheld prior to and during sampling to ensure excreted inorganic material comprised only gut carbonates, which were allowed to sink through mesh floors immediately after excretion to prevent further disturbance or ingestion by fish. Carbonates were sampled at 24 h intervals and prepared for subsequent morphological, compositional, and mineralogical characterization using scanning electron microscopy (SEM), energy-dispersive X-ray spectroscopy (EDX), and Fourier transform infrared spectroscopy (FTIR). Relative abundances of the different mineral polymorphs identified from each species were

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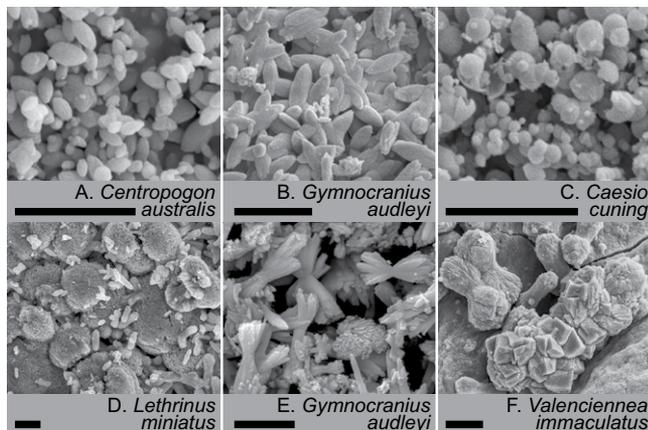
estimated using a combination of these techniques. A production rate–body mass relationship was constructed by quantifying $CaCO_3$ produced by fish of known body mass. Full details of all procedures are described in the Methods section of the Data Repository.

Production data were integrated with fish biomass data from the Reef Life Survey (RLS, https://reeflifesurvey.com) database (Edgar and Stuart-Smith, 2014; see the Data Repository) to generate production models for nine coral reef systems in Australia (Table DR2 in the Data Repository). Because temperature is an important control on fish carbonate production (Wilson et al., 2009), only reef systems with comparable sea-surface temperature (SST) regimes to the sampling locations were modeled. Models were generated by estimating production for each fish recorded in the RLS database based on the production rate–body mass relationship, to which a metabolic scaling factor was applied to reflect 'real-world' production rates when fish are feeding and actively swimming (after Wilson et al., 2009; see the Data Repository). Mineral abundance data were assigned to each fish for which these family-specific data are available; otherwise polymorphs were categorized as 'unknown'. Outputs for individual fish were then summed to generate production estimates for each 500 m² RLS transect. Within each reef system numerous transects (n = 25–534) across multiple discrete locations (n = 10–72) were available, and were averaged to yield overall reef system production outputs.
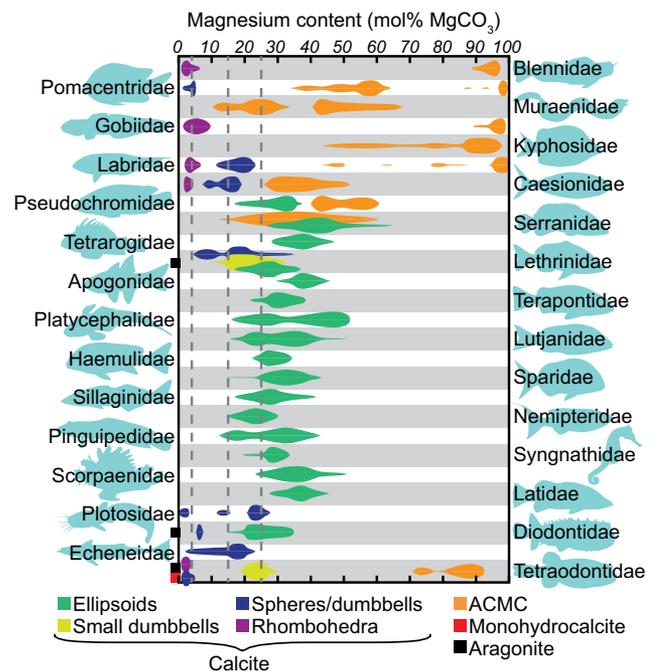
RESULTS AND DISCUSSION

Carbonates from all fish comprised fine-grained (typically <30 μm) particles with distinctive morphologies (Fig. 1), seemingly unique among marine carbonates and similar to those described in earlier fish carbonate studies from The Bahamas (Salter et al., 2012). They are also mineralogically similar, comprising one or more of the following carbonate polymorphs: high-Mg calcite (HMC; >4 mol% $MgCO_3$); low-Mg calcite (LMC; <4 mol% $MgCO_3$); aragonite; Mg-rich amorphous calcium carbonate (ACMC); and monohydrocalcite (Fig. DR1, Tables DR1 and DR3). Consistent morphology–mineralogy–composition relationships (Fig. 2) corroborate data from previous studies and facilitate straightforward assessment of polymorph abundances. For example, all particles with ellipsoidal, rod, and wheat-sheaf morphologies are HMC with typically >20 mol% $MgCO_3$, whereas other calcite morphotypes have lower $MgCO_3$ contents: typically <10 mol% in rhombohedra and 5–20 mol% in dumbbells and spheres.

We further find carbonates to be broadly consistent among members of each fish family studied, including those sampled in both Australia and the

Figure 2. Magnesium content distributions (mol% MgCO₃) of Australian fish-derived low-Mg calcite (LMC), high-Mg calcite (HMC), and Mg-rich amorphous calcium carbonate (ACMC). Family-level results are a composite of data from each member (n = 1–4; see Table DR1 [see footnote 1]). Where products involve a variety of carbonate polymorphs/morphologies (e.g., family: Lethrinidae [emperors]), corresponding histograms are independent and do not show relative abundances.

Figure 1. Electron microscope images showing each of the main carbonate morphologies produced by different fish species. A,B: High-Mg calcite (HMC) ellipsoids. C: Mg-rich amorphous calcium carbonate (ACMC) nanospheres. D,E: Low-Mg calcite (LMC) and HMC spheres and dumbbells. F: LMC rhombohedra. Scale bars are 4 μm.

Caribbean (n = 7 families), providing strong evidence that our findings are relevant at low latitudes globally. For example, all Western Pacific species of Lutjanidae (snappers, n = 4) produced HMC ellipsoids, as did Caribbean members (n = 2). Across both regions, families in which multiple members were sampled total 13, involving 310 individuals of 46 species—40 of which yielded products consistent with their confamilials. Of the other six species (family: Labridae, wrasses and parrotfishes), five yielded consistent products; the exception being the only parrotfish sampled (the Caribbean scarine labrid *Sparisoma chrysopterum*, n = 2 individuals). While this data set is insufficient for robust conclusions, evidence that parrotfishes possess unique gut chemistries due to their $CaCO_3$-rich diets (Smith and Paulson, 1975) provides a potential explanation for their carbonate products being distinct from those of other (non-scarine) labrids. Additional data are needed to clarify this issue, but on this basis, coupled with the available carbonate product data, we consider scarine labrids separately from other labrids. This observation does, however, dictate that the wider assumption of within-family consistency comes with the caveat that there may be exceptions. Nevertheless, the otherwise remarkably high degree of within-family consistency regardless of genus and geographic location suggests this to be a reasonable assumption based on available data.

Production rate data were generated using samples from 180 fish with body masses spanning three orders of magnitude (0.001–2.8 kg). The resultant production rate–body mass relationship is similar to that described previously (Perry et al., 2011), although this is unsurprising given comparable sampling temperatures (23–25 °C). Combining these data sets yields a production rate–body mass relationship based on data from 270 individual fish (Fig. 3); our new data contribute important refinements by incorporating considerably more taxa and numerous data at the previously sparse lower end of the body-mass range.

We summarize reef-fish community production models, generated by integrating these data with RLS biomass data, in Figure 4. Average
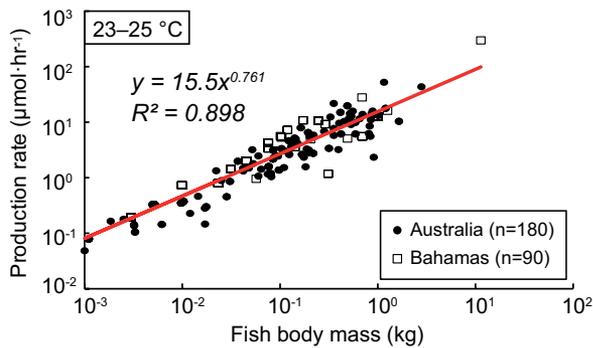
Figure 3. CaCO₃ production rate–body mass relationship at 23–25 °C, based on data from Australia (this study) and the Caribbean (Perry et al., 2011).

carbonate production rates range from 2.1 g m⁻² yr⁻¹ in the subtropical Abrolhos Islands (offshore Western Australia, Indian Ocean), where fish biomass is relatively low (averaging 47 g m⁻²), to 9.6 g m⁻² yr⁻¹ in the more-tropical southern section of the outer Great Barrier Reef (GBR), where biomass is high by comparison (averaging 183 g m⁻²). At 12.5% of the outer GBR sites, production exceeds 20 g m⁻² yr⁻¹, with rates up to 105 g m⁻² yr⁻¹ where fish biomass is highest.

Although average production rates vary among test locations as a function of teleost biomass, overall they are comparable to previous estimates for Bahamian reefs of 6.2 g m⁻² yr⁻¹ (Salter et al., 2017), or ~3.8 g m⁻² yr⁻¹ when revised to match the more-detailed and updated modeling approach used here. Importantly, these rates are almost certainly conservative in the context of being broadly representative of production in contemporary and historical reef systems.

First, this is because our data were derived at SSTs in the range 23–25 °C. Many coral reefs are located in regions with higher annual average SSTs; up to 29–30 °C in large parts of the Indo-Pacific, for example (NOAA Coral Reef Watch, 2000). Because fish carbonate production rates correlate positively and exponentially with temperature, with available data indicating a 2.33× change for every 10 °C (Wilson et al., 2009), rates in the warmest coral reef regions should be up to 2× higher than reported here. Thus, average community production might approach 20 g m⁻² yr⁻¹ in warm reefs with fish biomass comparable to southern parts of the outer GBR.

Second, although many of the modeled Australian reef systems include sites where fishing restrictions are enforced, their average teleost

biomasses (47–183 g m⁻²) are low compared with more-tropical reefs in some of the most effective reserves and/or most remote locations globally. Such reefs—perhaps the best available proxies for pristine historical reefs—frequently support biomasses exceeding 400 g m⁻² (e.g., Graham and McClanahan, 2013). These communities may comprise a greater proportion of less-productive large fishes (Halpern, 2003), but they have the potential to yield considerably more carbonate than our Australian communities.

Collectively, these considerations point to rates in warm and pristine reef systems on the order of 10¹–10² g m⁻² yr⁻¹. By comparison, bio-erosion in these systems typically generates sediment at rates on the order of 10²–10⁴ g m⁻² yr⁻¹ (see Kennedy et al., 2013), meaning the overall contribution by fish to local sediment accumulation will be variable, and in some cases trivial. Nevertheless, they are likely an important source of mud-grade (<63 μm) sediment. In part, this is because much of the fine-grained component of bio-eroded sediment is probably exported off-reef (Bellwood, 1996), whereas fish carbonates have greater potential for incorporation within local sediments because they are excreted as faster-sinking sand-sized (>63 μm) pellets that can remain intact for weeks after excretion (Salter et al., 2014). Their pathway to deposition is thus similar to that of fine-grained aragonite from *Halimeda* algae, which is produced at comparable rates in some reef systems (reported rates span 10¹–10³ g m⁻² yr⁻¹: Drew, 1983; Perry et al., 2016). The significance of fish carbonate will thus vary among reefs; its inclusion within site-specific sediment budgets being necessary to properly elucidate its role.

The high solubilities of some fish carbonate polymorphs are also likely to influence sedimentary significance (Salter et al., 2012; 2017); an especially important consideration here because >50% of production in most Australian test reefs can be attributed to fish families that produce large amounts of highly unstable ACMC (Pomacentridae [damselfishes], Labridae, and Caesionidae [fusiliers]; Fig. 4). This is reflected in our model outputs, which indicate that relatively stable calcites collectively average 16–30% of overall production (29–39% of known products) across all reef systems except Dampier (offshore Western Australia; 52% of known products), whereas ACMC averages at least 24–62% (42–70% of known products). At least some ACMC produced by fish is known to dissolve within a few hours of excretion (Foran et al., 2013), and if such dissolution is pervasive it would result in average losses from our test reefs of at least 0.6–4.6 g m⁻² yr⁻¹, leaving up to 1.2–5.0 g m⁻² yr⁻¹ of more stable fish carbonate (primarily LMC and HMC) to accumulate as sediment. In addition to the evident sedimentary implications, this potential for extensive dissolution raises an intriguing possibility that fish carbonates

Figure 4. Summary of fish carbonate production models for nine coral reef systems in Australia, with outputs averaged across multiple sites in each system. Horizontal box plots show production rate and fish biomass (median values within inter-quartile ranges). Vertical box plots show percent abundance of each carbonate polymorph (median values within inter-quartile ranges), overlaid on a solubility gradient spanning relatively stable low-Mg calcite (LMC) to highly unstable Mg-rich amorphous calcium carbonate (ACMC). For corresponding polymorph codes (see legend), "C X" refers to calcite with X mol% MgCO₃. Pie charts show mean CaCO₃ contributions (as percentages of total production) for each teleost family contributing >5% in any one reef system; less-significant families being grouped as 'others'.
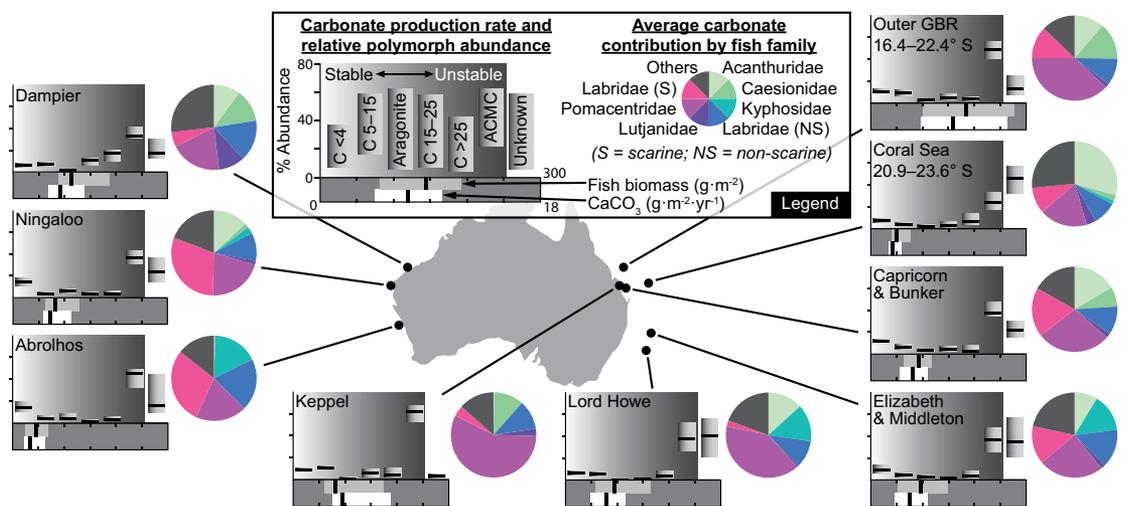
have important roles in the regulation of both sediment pore-water chemistry and diel cycles in coral reef carbonate chemistry (e.g., Albright et al., 2015). However, there are several uncertainties regarding this issue, including (1) the possibility that some ACMC crystallizes to more stable polymorphs (Radha et al., 2010); (2) unknown polymorph components in our test reefs that can exceed 45% of production—though these could be largely resolved with the addition of data from the Acanthuridae (surgeonfishes, tangs, and unicornfishes) and Kyphosidae (sea chubs) (Fig. 4); and (3) with respect to warmer reefs, the possibility that fish carbonate polymorphs will differ across thermal gradients.

Significantly, our polymorph outputs contrast markedly with data from Bahamian reefs, where ACMC accounted for only 4–13% of fish carbonate production, and HMC (55–75%) dominated (Salter et al., 2017); a disparity explained mainly by differences in fish family assemblages. On the Australian study reefs, 60–87% of the teleost biomass for which products have been assessed comprises significant ACMC producers (primarily Caesionidae, Labridae, Pomacentridae), whereas in The Bahamas, 71–90% comprises HMC producers (primarily Haemulidae [grunts] and Lutjanidae; see Fig. DR2). Evidently, fish carbonate products are defined by the fish family assemblage from which they derive, and natural variations in these assemblages mean that patterns of fish carbonate preservation potential and sedimentary significance must be both geographically and temporally variable. Our data nevertheless point to an important overall role for fish in fine-grained carbonate production within shallow marine systems. As our understanding of the processes and products improves, we can begin to more accurately quantify the production rates of different carbonate forms, and thus better predict their partitioning between sediment accumulation and rapid recycling both in the water column and in near-surface sediments.

REFERENCES CITED
Albright, R., Benthuysen, J., Cantin, N., Caldeira, K., and Anthony, K., 2015, Coral reef metabolism and carbon chemistry dynamics of a coral reef flat: Geophysical Research Letters, v. 42, p. 3980–3988, https://doi.org/10.1002/2015GL063488.

Bellwood, D.R., 1996, Production and reworking of sediment by parrotfishes (family Scaridae) on the Great Barrier Reef, Australia: Marine Biology, v. 125, p. 795–800, https://doi.org/10.1007/BF00349262.

Bellwood, D.R., 1997, Reef fish biogeography: Habitat associations, fossils and phylogenies: Proceedings of the 8th International Coral Reef Symposium, Smithsonian Tropical Research Institute, Panama, v. 1, p. 379–384.

Drew, E.A., 1983, Halimeda biomass, growth rates, and sediment generation on reefs in the central Great Barrier Reef province: Coral Reefs, v. 2, p. 101–110, https://doi.org/10.1007/BF02395280.

Edgar, G.J., and Stuart-Smith, R.D., 2014, Systematic global assessment of reef fish communities by the Reef Life Survey program: Scientific Data, v. 1, p. 140007, https://doi.org/10.1038/sdata.2014.7.

Flügel, E., 2004, Microfacies of carbonate rocks: Analysis, interpretation and application. Berlin, Heidelberg: Springer-Verlag, 976 p., https://doi.org/10.1007/978-3-662-08726-8.

Foran, E., Weiner, S., and Fine, M., 2013, Biogenic fish-gut calcium carbonate is a stable amorphous phase in the gilt-head seabream, *Sparus aurata*: Scientific Reports, v. 3, https://doi.org/10.1038/srep01700.

Gischler, E., Dietrich, S., Harris, D., Webster, J.M., and Ginsburg, R.N., 2013, A comparative study of modern carbonate mud in reefs and carbonate platforms: Mostly biogenic, some precipitated: Sedimentary Geology, v. 292, p. 36–55, https://doi.org/10.1016/j.sedgeo.2013.04.003.

Graham, N.A.J., and McClanahan, T.R., 2013, The last call for marine wilderness?: Bioscience, v. 63, p. 397–402, https://doi.org/10.1525/bio.2013.63.5.13.

Halpern, B.S., 2003, The impact of marine reserves: Do reserves work and does reserve size matter?: Ecological Applications, v. 13, p. 117–137, https://doi.org/10.1890/1051-0761(2003)013[0117:TIOMRD]2.0.CO;2.

Kennedy, E.V., et al., 2013, Avoiding coral reef functional collapse requires local and global action: Current Biology, v. 23, p. 912–918, https://doi.org/10.1016/j.cub.2013.04.020.

Kulbicki, M., et al., 2013, Global biogeography of reef fishes: A hierarchical quantitative delineation of regions: PLoS One, v. 8, https://doi.org/10.1371/journal.pone.0081847.

NOAA Coral Reef Watch, 2000. Annual composite of NOAA Coral Reef Watch Operational 50-km Satellite Coral Bleaching monitoring products (2001–2017): Silver Spring, Maryland, National Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch, https://coralreefwatch.noaa.gov/satellite/composites/index.php (accessed March 2018).

Perry, C.T., Salter, M.A., Harborne, A.R., Crowley, S.F., Jelks, H.L. and Wilson, R.W., 2011, Fish as major carbonate mud producers and missing components of the tropical carbonate factory: Proceedings of the National Academy of Sciences of the United States of America, v. 108, p. 3865–3869, https://doi.org/10.1073/pnas.1015895108.

Perry, C.T., Morgan, K.M., and Salter, M.A., 2016, Sediment generation by *Halimeda* on atoll interior coral reefs of the southern Maldives: A census-based approach for estimating carbonate production by calcareous green algae: Sedimentary Geology, v. 346, p. 17–24, https://doi.org/10.1016/j.sedgeo.2016.10.005.

Radha, A.V., Forbes, T.Z., Killian, C.E., Gilbert, P.U.P.A., and Navrotsky, A., 2010, Transformation and crystallization energetics of synthetic and biogenic amorphous calcium carbonate: Proceedings of the National Academy of Sciences of the United States of America, v. 107, p. 16438–16443, https://doi.org/10.1073/pnas.1009959107.

Salter, M.A., Perry, C.T., and Wilson, R.W., 2012, Production of mud-grade carbonates by marine fish: Crystalline products and their sedimentary significance: Sedimentology, v. 59, p. 2172–2198, https://doi.org/10.1111/j.1365-3091.2012.01339.x.

Salter, M.A., Perry, C.T., and Wilson, R.W., 2014, Size fraction analysis of fish-derived carbonates in shallow sub-tropical marine environments and a potentially unrecognised origin for peloidal carbonates: Sedimentary Geology, v. 314, p. 17–30, https://doi.org/10.1016/j.sedgeo.2014.10.005.

Salter, M.A., Harborne, A.R., Perry, C.T., and Wilson, R.W., 2017, Phase heterogeneity in carbonate production by marine fish influences their roles in sediment generation and the inorganic carbon cycle: Scientific Reports, v. 7, https://doi.org/10.1038/s41598-017-00787-4.

Schauer, K.L., Christensen, E.A.F., and Grosell, M., 2018, Comparison of the organic matrix found in intestinal $CaCO_3$ precipitates produced by several marine teleost species: Comparative Biochemistry and Physiology, v. 221, p. 15–23, https://doi.org/10.1016/j.cbpa.2018.03.007.

Schlager, W., 2003, Benthic carbonate factories of the Phanerozoic: International Journal of Earth Sciences, v. 92, p. 445–464, https://doi.org/10.1007/s00531-003-0327-x.

Smith, R.L., and Paulson, A.C., 1975, Carbonic anhydrase in some coral reef fishes: adaptation to carbonate ingestion?: Comparative Biochemistry and Physiology, v. 50, p. 131–134, https://doi.org/10.1016/S0010-406X(75)80214-3.

Walsh, P.J., Blackwelder, P., Gill, K.A., Danulat, E., and Mommsen, T.P., 1991, Carbonate deposits in marine fish intestines: A new source of biomineralization: Limnology and Oceanography, v. 36, p. 1227–1232, https://doi.org/10.4319/lo.1991.36.6.1227.

Wilson, R.W., Millero, F.J., Taylor, J.R., Walsh, P.J., Christensen, V., Jennings, S., and Grosell, M., 2009, Contribution of fish to the marine inorganic carbon cycle: Science, v. 323, p. 359–362, https://doi.org/10.1126/science.1157972.