Comment on “Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning”

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Brandl et al. (Reports, 21 June 2019, p. 1189) report that cryptobenthic fishes underpin coral reef ecosystem function by contributing ~60% of “consumed fish” biomass and ~20% of production. These results are artifacts of their simulation. Using their data and model, we show that cryptobenthic species contribute less than 4% to fish production, calling into question the extent to which they contribute to the high productivity of coral reefs.

A long-standing question in coral reef ecology is “How can reefs be so productive while residing in such nutrient-poor environments?” Brandl et al. (1) estimated the contribution of cryptobenthic fishes, an elusive and underappreciated group, for total coral reef fish production. They provide interesting and novel perspectives on the unique life history characteristics of cryptobenthics, showing that they have disproportionately high reproductive and larval supply rates, but also high mortality, relative to other major reef fishes. On this basis, the authors suggest that cryptobenthics may help to fuel the rapid nutrient- and energy-recycling rates that typify coral reefs (2, 3). Their main finding was that as a result of this high mortality rate, cryptobenthic fishes contribute ~60% of the “consumed fish” biomass in coral reefs (and ~20% of fish production), and thereby represent a large and previously unknown source of energy that supports coral reef fish production.

We applaud the authors for bringing to light these important life history traits, but we argue that their estimates of the contribution of cryptobenthic fish to fish production are an artifact of their analyses. Brandl et al. used a numerical simulation of larval supply and growth to calculate the relative production of cryptobenthic species after a single year. In doing so, they neglect the contributions of fish that live more than 1 year, thus vastly overestimating the contributions of cryptobenthic fishes to fish production on coral reefs.

The stated goal of the study was to estimate the extent to which cryptobenthic fish species “promote internal reef fish biomass production” (i.e., secondary production). Instead of focusing on the contribution of cryptobenthics to secondary production, defined as the biomass accumulated by a population per unit time (4), Brandl et al. focused primarily on quantifying their contribution to “consumed biomass,” which they define as all biomass lost to mortality (i.e., all fish that die are consumed) (1). Consumed biomass is an inherent component of production, as it represents biomass produced in previous time steps that, once eaten, will not continue to produce biomass. But it is not a good proxy for production. Consider a population with a new cohort of three individual recruits that die over time (Fig. 1A). At time $t_1$, the contribution to production by all individuals is the same; only the black individual has died and thus contributes 100% to consumed biomass. By $t_3$, the red individual contributes much more to production because it has not died, but has contributed nothing to consumed biomass. When all fish die, production and consumed biomass are equal. This conceptual figure illustrates two things: (i) Consumption is not a good proxy for production because fish that are not consumed still contribute to secondary production, and (ii) the timing at which estimates are measured is critical to estimates of both production and consumption.

To quantify the importance of cryptobenthic fish to coral reef fish production, Brandl et al. used a numerical simulation in which cohorts of 3000 larvae (~65% of which are cryptobenthic species on average) recruit to a reef every day for 365 days [supplementary materials of (1)] (Fig. 1B, blue box). Using family-level growth and mortality rates, Brandl et al. summed the new biomass produced and the consumed biomass (assuming all fish that are consumed) of all individuals in their simulation over the first 365 days. Using this model, they found that cryptobenthics represent ~60% of the consumed biomass (i.e., fish that died) and contribute ~20% of total fish production in this first year (with the re-
main percentages contributed by non-cryptobenthic species).

An important finding of Brandl et al. is the high mortality of cryptobenthic fishes, relative to non-cryptobenthic fishes, that occurs in the first year. However, by calculating consumed biomass and production after only 365 days, they ignored all production that occurs from larval recruits that survived past the first year (predominantly non-cryptobenthic fishes). In essence, their model is populating a reef with larval recruits that is otherwise devoid of fish, under the assumption that the recruits are the only fish that can contribute to production. As such, calculating consumed biomass and production after only the first year is tantamount to making this calculation at t0, assuming that the black and blue fish are cryptobenthics (Fig. 1A)—that is, they represent the majority of larval recruits (I). The stated goal of the study was to estimate the contribution of larval recruits to “reef fish biomass production.” Without including surviving individuals in their model, the contribution of cryptobenthics to fish production or consumed biomass is overestimated. To avoid these issues, estimating production by recruits requires that cohorts are tracked over longer time horizons, so as to account for differential mortality rates among species (Fig. 1A).

Using the authors’ published code and parameters [supplementary materials of (I)], we recalculated production and consumed biomass in two ways. First, we tracked 8000 individual cohorts until <1% of individuals remaining in each. The average contribution of cryptobenthic fish to total fish production across all cohorts after 2, 3, 10, and 20 years was 3.3%, 2.2%, 1.1%, and 1.0%, respectively (28.4%, 19.0%, 7.7%, and 6.0% for “consumed biomass”; Fig. 2, A and C). Note that extending the simulations by only 1 to 2 years markedly reduces the estimated contribution of cryptobenthics to fish production, thereby demonstrating that the high levels of production from non-cryptobenthic species are not reliant on long-lived, large individuals. Applying a second community-level approach where a new cohort was added per day following Brandl et al., but extending the simulation until <1% of the individuals in the initial cohorts remained (19 to 20 years; Fig. 1B), we found a similar result: Cryptobenthics contribute 1.0% to produced biomass and 6.4% to consumed biomass.

The key mechanism provided by Brandl et al. for the importance of cryptobenthic fishes is their high turnover. To calculate turnover, Brandl et al. divided the “consumed biomass” by standing biomass, essentially providing a measure of how fast the cohort of cryptobenthics was consumed in the first year—a measure that is circular to their model with implicitly high mortality rates for cryptobenthics. Turnover is typically quantified as production divided by biomass (Brandl et al. call this “net turnover”), which provides an important measure of how fast biomass is being replaced via production. In their supplementary materials, Brandl et al. themselves show that turnover (i.e., production/biomass) is greater for non-cryptobenthic fish.

We applaud the contribution of this study for highlighting the unique life history characteristics of these poorly understood fishes, and much of the information generated by Brandl et al. is important. We also recognize that in many cases Brandl et al. use conservative approaches to estimate the contribution of cryptobenthic fish to fish production. But we disagree that cryptobenthic species “underpin reef fish biomass production” as stated by Brandl et al., and we show here that their contribution is likely much lower than the estimates reported by these authors.

REFERENCES
Fig. 1. Conceptual models illustrating the importance of timing for calculating secondary production. (A) Calculating secondary production (i.e., the production of new biomass) following individual cohorts through to death. X indicates when an individual dies; O indicates that it is alive and included in production. The inset shows the total biomass produced and consumed, as well as the percent contributions of each individual to produced and consumed biomass per time step [Prod/Cons (%)]. This illustrates the importance of allowing all individuals to die before calculating production and highlights that considering only those individuals that die at certain time steps is not a useful proxy for production. (B) Calculating secondary production following multiple cohorts until all individuals from the initial cohort die. At each time step, a new cohort enters the system (represented by different rows, with the size of the circle indicating the number of individuals remaining over time). The colored portions of each circle represent the proportion of individuals belonging to cryptobenthic (blue) and non-cryptobenthic (orange) fishes. The proportion of cryptobenthic fishes (blue) diminishes rapidly because of their high mortality rate. Brandl et al. (1) calculated production for the first year only (blue box). Doing so inflates the production of cryptobenthics because it omits the additional contribution to production by all other cohorts in the community that survive beyond that time period. In essence, their model assumes that the larval recruits are the only fishes on a reef that contribute to production, as if there were no fish present starting at day 0 in their simulation. This has a greater effect on inflating consumed biomass because of the disproportionate amount of cryptobenthic larvae that die shortly after settlement (death is assumed to be by consumption).
Fig. 2. Production and consumed biomass of cryptobenthic and non-cryptobenthic species using the data and model from Brandl et al. carried out to 20 years (<1% of individuals remaining). (A and C) Average cumulative production (A) and consumption (C) of cryptobenthic (blue) and non-cryptobenthic (orange) species across 8000 stochastic cohorts. Vertical dashed lines represent the percent contribution of cryptobenthic species to production (or consumed biomass) at 1, 3, 5, and 10 years. Brandl et al. calculated the mean contribution to consumed biomass and production by averaging proportions, which can only be done when the denominator used to calculate each proportion is the same (not the case here). We calculated proportions by summing the production (or consumed biomass) of cryptobenthic species (black) and dividing by the sum of the total fish production (or consumed biomass) for each time step across all 8000 simulated cohorts. (B and D) Histograms of the cumulative production (B) and consumption (D) of cryptobenthic species after 20 years for all 8000 simulations. The x axis for non-cryptobenthic species is truncated to better show the distribution shape (<1% of simulations are omitted).
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