How coral reefs survive as oases of life in low-productivity oceans has puzzled scientists for centuries. The answer may lie in internal nutrient cycling and/or input from the pelagic zone. Integrating meta-analysis, field data, and population modelling, we show that the ocean’s smallest vertebrates, cryptobenthic reef fishes, promote internal reef-fish biomass production through exceptional larval supply from the pelagic environment. Specifically, cryptobenthics account for two-thirds of reef-fish larvae in the near-reef pelagic zone, despite limited adult reproductive outputs. This overwhelming abundance of cryptobenthic larvae fuels reef trophodynamics via rapid growth and extreme mortality, producing almost 60% of consumed reef fish biomass. While cryptobenthics are commonly overlooked, their unique demographic dynamics may make them a cornerstone of ecosystem functioning on modern coral reefs.
growth, and death of larval recruits from all reef-fish families over one year (fig. S6), we estimate that juvenile and adult cryptobenthics provide most (57.5 ± 0.1% SE) of the consumed fish biomass on reefs. However, due to extreme mortality rates and small sizes, cryptobenthics appear to make negligible contributions to net productivity and standing fish biomass (Fig. 3C), which mirrors empirical evidence (17). Standing biomass is the most commonly quantified metric of ecosystem functioning on reefs (18). Yet, it does not capture the striking turnover in cryptobenthic populations (693.1 ± 2.7% SE, annually) that is enabled by their extraordinary demographic dynamics. Thus, cryptobenthics represent the ‘dark productivity’ of coral reefs, which fuels reef-fish biomass production but is rarely perceived because it is consumed almost as quickly as it is produced.

This role of cryptobenthics is empirically reflected in their extreme mortality (up to 70% per week (19, 20) and their consumption by virtually any predator capable of eating them (20, 21). While the community-wide representation of cryptobenthics in fish diets frequently appears lower than the ~58% identified herein (22), their true contribution to coral reef trophodynamics may be obscured by (i) rapid digestion, precluding reliable visual identification (23), (ii) predation on cryptobenthics by invertebrates (21), which are fed on by larger fishes, and (iii) predation on cryptobenthics by juvenile predatory fishes (e.g., cryptobenthics comprise up to 88.6% of fish prey for juvenile groupers (24, 25), which are rarely included in community-wide dietary analyses.

The key to the unique demographic dynamics of cryptobenthics and their productivity might be a shift away from long-range dispersal toward retention of larvae in the immediate vicinity of natal (home) reefs. Four lines of evidence, along with our findings, support this hypothesis. First, larval dispersal models show that larval supply easily maintains adult populations in large-bodied, long-lived reef fishes (7). Conversely, small-bodied, short-lived taxa appear unable to sustain local populations, even when active swimming by larvae is considered (7); yet, cryptobenthic populations persist. Near-complete retention of cryptobenthic larvae close to natal reefs may solve this paradox. Second, driven by olfactory and auditory cues, cryptobenthic larvae show stronger natal homing than similarly sized large reef fishes (26) and can have very short dispersal distances (27). Third, cryptobenthic larvae have limited yolk sacs and ingest prey immediately after hatching, indicating dependence on resource-rich, near-reef environments (8, 28). Finally, remaining close to natal reefs during development should result in fine-scale genetic structuring. With few exceptions (29), this is observed in cryptobenthic fishes (10, 26, 30). Collectively, this suggests that the ‘pelagic’ larvae of most cryptobenthics remain close to their natal reefs (31), resulting in prodigious near-reef abundances and a unique role of cryptobenthics for coral-reef ecosystem functioning.

Larval retention may lead to two evolutionary consequences: (i) rapid speciation through micro-allopatry, arising from restricted gene flow among populations and frequent reproductive isolation (10, 32, 33), and (ii) a higher risk of extinction than commonly assumed for small marine fishes (34), since populations can easily become ephemeral and disappear following stochastic environmental changes (35). If these processes scale up to macro-evolutionary levels, cryptobenthics should be phylogenetically rare but species-rich. Indeed, this is the case. Few reef-fish families have successfully adopted cryptobenthic lifestyles and there are only two major diversification events (Fig. 4): the larger Blenniiformes and the Gobiaria (gobies and apogonids). Nevertheless, these lineages are among the most rapidly-diversifying clades of actinopterygian fishes (36) and cryptobenthics collectively account for almost half (44.5%) of total reef-fish biodiversity (Fig. 4) (13).

In summary, through their extraordinary larval dynamics, rapid growth, and extreme mortality, the hyperdiverse consortium of abundant, tiny, and short-lived cryptobenthic species appears to be a critical functional group on coral reefs. The ‘dark productivity’ provided by cryptobenthics underpins reef-fish biomass production and supports the characteristic fast-paced dynamics of modern coral reefs.

REFERENCES AND NOTES

Author contributions: SJB, CHRG, LT, DRB conceived the study; SJB, JMC, CHRG, VP, RAM, CCB, NMDS collected data; SJB, RAM, NMDS, LT analyzed the data; SJB wrote the first draft and all authors contributed. Competing interests: None. Data availability: Data and code will be available on Zenodo (DOI: 10.5281/zenodo.2575005) upon publication (37).

SUPPLEMENTARY MATERIALS

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Materials and Methods

Supplementary Text

Figs. S1 to S6

Tables S1 to S6

References (38–95)

Raw Data and Code

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Fig. 1. Global dominance of cryptobenthic reef fishes in the near-reef ichthyoplankton. (A) Cryptobenthic larvae (blue) account for two-thirds (65.7%) of the larval reef-fish pool <10 km from reefs, while large reef-fish larvae (light grey) dominate >10 km from reefs. Crossbars represent predicted medians (± 95% credible intervals) from a Bayesian beta-regression model; circles represent the raw data (12). (B) The high proportion of cryptobenthics (colored pie slices) in the near-reef ichthyoplankton is consistent across major biogeographic coral reef regions. Dots represent separate studies. (C) Average contribution of reef-fish taxa to global near-reef ichthyoplankton. The three highest contributing taxa are cryptobenthic, represented by photographs of adult *Eviota infulata* (Gobiidae), *Scartella cristata* (Blenniformes–Blenniidae), and *Cheilodipterus quinquelineatus* (Apogonidae). Families contributing <0.1% were omitted for clarity.
Fig. 2. Differences in the relationship between larval supply and adult gamete output for cryptobenthic and large reef fishes. Dashed lines and ribbons represent predicted fits from a Bayesian beta-regression model (± 95% credible intervals); circles (broadcast spawners) and diamonds (demersal brooders) represent raw data averaged across three sampling locations (± standard errors [SE]). Both axes represent proportional shares.
Fig. 3. Ecosystem-scale effects of the demographic dynamics of cryptobenthic reef fishes. (A) Cryptobenthics far outnumber large reef fishes in cohorts of larvae that recruit to reefs. (B) At settlement, large reef-fish recruits are, on average, slightly larger than cryptobenthics. (C) Cryptobenthics contribute little (~13%) to net biomass production but produce almost 60% of consumed reef-fish biomass via exceptionally high turnover. (D) Standing stock biomass of large reef fishes far outweighs that of cryptobenthics, although adult abundances are approximately even. (E) Despite higher gamete output from large reef fishes, cryptobenthic larvae dominate the near-reef ichthyoplankton. This restarts the ‘crypto-pump’ through rapid replenishment of consumed individuals. Uncertainty estimates are based on 100 iterations of the full model.
Figure A: Phylogenetic tree showing the relationships among different fish families, highlighting the Blenniiformes and relatives. The tree is composed of various branches representing different families of fish, with the number of species in each group indicated.

Figure B: Bar graph depicting the number of reef fish species belonging to different families. The x-axis represents different fish families, and the y-axis shows the number of species.
Fig. 4. Phylogenetic positioning and species richness in cryptobenthic and large reef fishes. (A) Cryptobenthic reef fishes (blue) have few independent origins, but account for almost half of all reef-fish species (2,799 species). Black = reef fish taxa; Grey = non-reef fish taxa (following (13)). Bubble sizes (A) and bars (B) represent species richness within all taxa and cryptobenthic families specifically. Arrow in (B) indicates cumulative richness in the Blenniiformes.
Demographic dynamics of the smallest marine vertebrates fuel coral-reef ecosystem functioning


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