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# Demographic dynamics of the smallest marine vertebrates fuel coral-reef ecosystem functioning

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**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.**

How coral reefs maintain high diversity and productivity in oligotrophic tropical oceans – often termed "Darwin's paradox" – remains poorly understood (*1*–*3*). Both pelagic subsidies (*2*) and internal energy and nutrient cycling (*3*) have been put forward as drivers of productivity on reefs, but their relative importance is not resolved.

Fishes form the largest reservoir of consumer biomass on reefs and are involved in most internal energy and nutrient fluxes (*4*), but they also bridge the pelagic-reef interface during their larval development (*5*) and may therefore subsidize reefs with pelagic productivity (*6*). Over the past two decades, larval dispersal pathway reconstruction (*7*, *8*) has revealed the importance of larval dynamics for reef-fish ecology, evolution, and conservation (*9*–*11*). However, the role of larval stages in coral-reef ecosystem functioning remains virtually unknown.

Integrating published surveys of coral-reef fish larvae, new data on adult reef-fish communities, and a theoretical population model (*12*), we demonstrate that cryptobenthic reef fishes (a group of 17 reef-associated fish families characterized by species <50mm in length (*12*, *13*)) play a previously unrecognized, but critically important role in coral-reef ecosystem functioning, which hinges on their unique larval dynamics, rapid growth, and extreme mortality.

Cryptobenthic larvae greatly outnumber large reef-fish larvae near coral reefs (Fig. 1) despite limited adult reproductive outputs. As more gametes produce more larvae, family-specific larval abundance predictably increases with gamete output for both cryptobenthic and large reef fishes (calculated from adult densities, fecundity, and spawning frequency (*12*, *14*)). However, the respective slopes differ drastically, with the relationship for cryptobenthics being over an order of magnitude steeper than for large reef fishes (Fig. 2 and table S1), which is consistent across locations (Australia, Belize, and French Polynesia). We found no statistical evidence for effects of pelagic larval duration (i.e., the time larvae spend in the plankton) or broadcast (i.e., eggs released into the water column) versus benthic clutch spawning (i.e., distinct clutches of guarded eggs) on larval supply (Table S2) despite the high prevalence of benthic clutch spawning in cryptobenthics. Furthermore, the difference in slopes was robust to variability in the input data, including increases in spawning frequency for cryptobenthics (fig. S2 and tables S3 and S4) and uncertainties in the body-mass fecundity relationship, adult densities, and larval composition (figs. S3 to S5). Thus, cryptobenthics are disproportionally more successful at converting adult gametes into larval supply, which likely underpins their extreme abundance in the nearshore ichthyoplankton.

The abundance of cryptobenthic larvae, despite limited gamete output, may provide the continuous (*15*) and copious inflow of larvae that is assumed necessary for adult population maintenance in small, short-lived reef fishes (*16*). Our results show that this, in turn, forms the basis of a critical energy and nutrient pump that operates across the reef-pelagic interface and may help explain the enigmatic productivity of coral-reef ecosystems (Fig. 3). Using a demographic model that simulates the daily arrival, 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 macroevolutionary 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.

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**SUPPLEMENTARY MATERIALS**

science.sciencemag.org/cgi/content/full/science.aav3384/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S6
Tables S1 to S6
References (*38*–*95*)
Raw Data and Code

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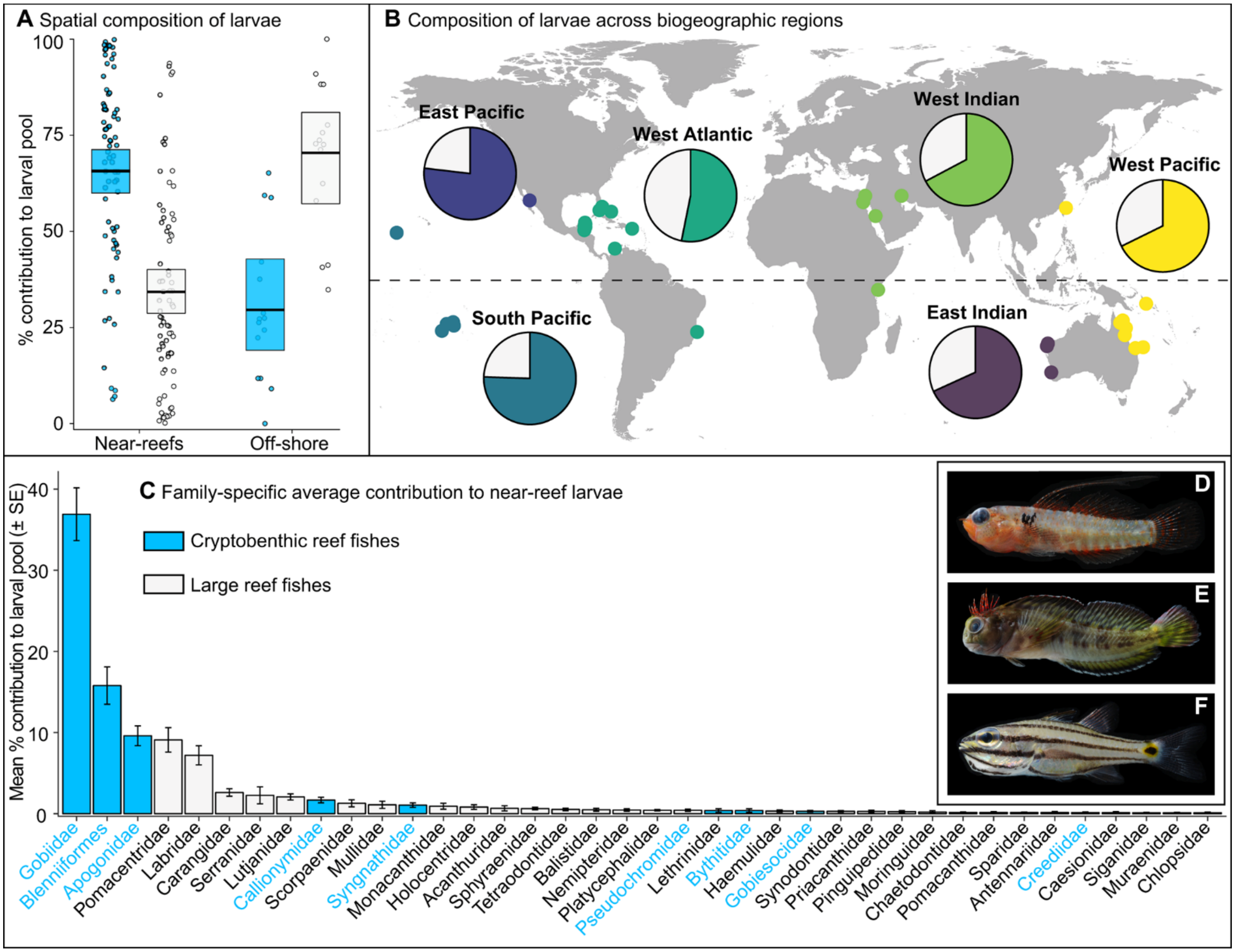


**Fig. 1. Global dominance of cryptobenthic reef fishes in the near-reef ichthyoplankton.** (**A**) Cryptobenthic larvae (blue) account for two-thirds (65.7%) of the larval reef-fish pool <10km from reefs, while large reef-fish larvae (light grey) dominate >10 km from reefs. Crossbars represent predicted 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* (Blenniiformes–Blenniidae), and *Cheilodipterus quinquelineatus* (Apogonidae). Families contributing <0.1% were omitted for clarity.

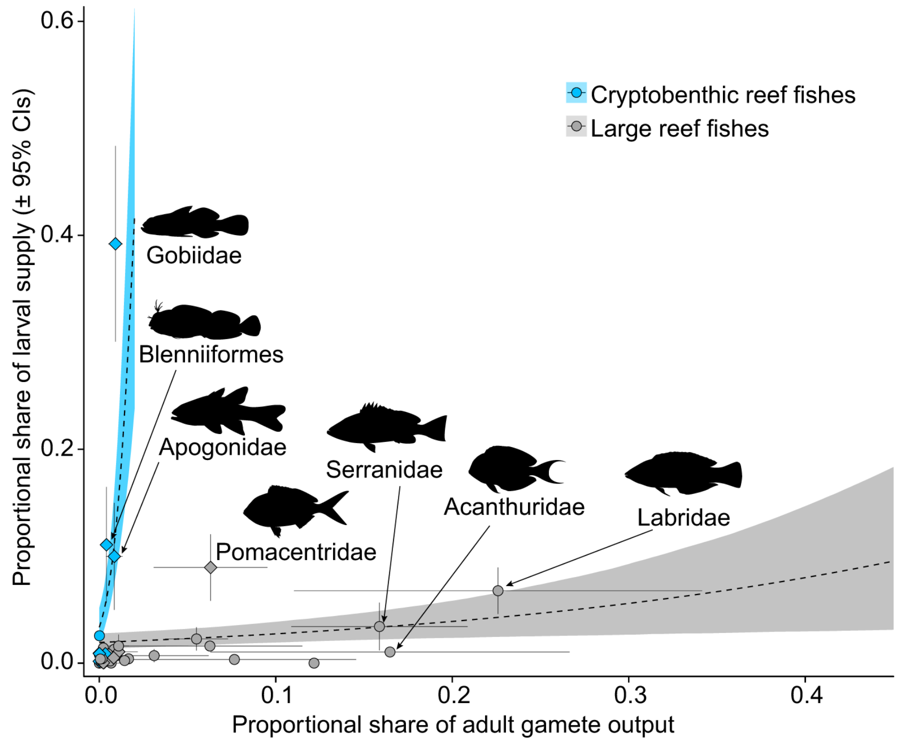


**Fig. 2. Differences in the relationship between larval supply and adult gamete output for cryptobenthic and large reef fishes.** Dashed lines and ribbons represent predicted fits from a Bayesian beta-regression model (± 95% credible intervals); circles (broadcast spawners) and diamonds (demersal brooders) represent raw data averaged across three sampling locations (± standard errors [SE]). Both axes represent proportional shares.

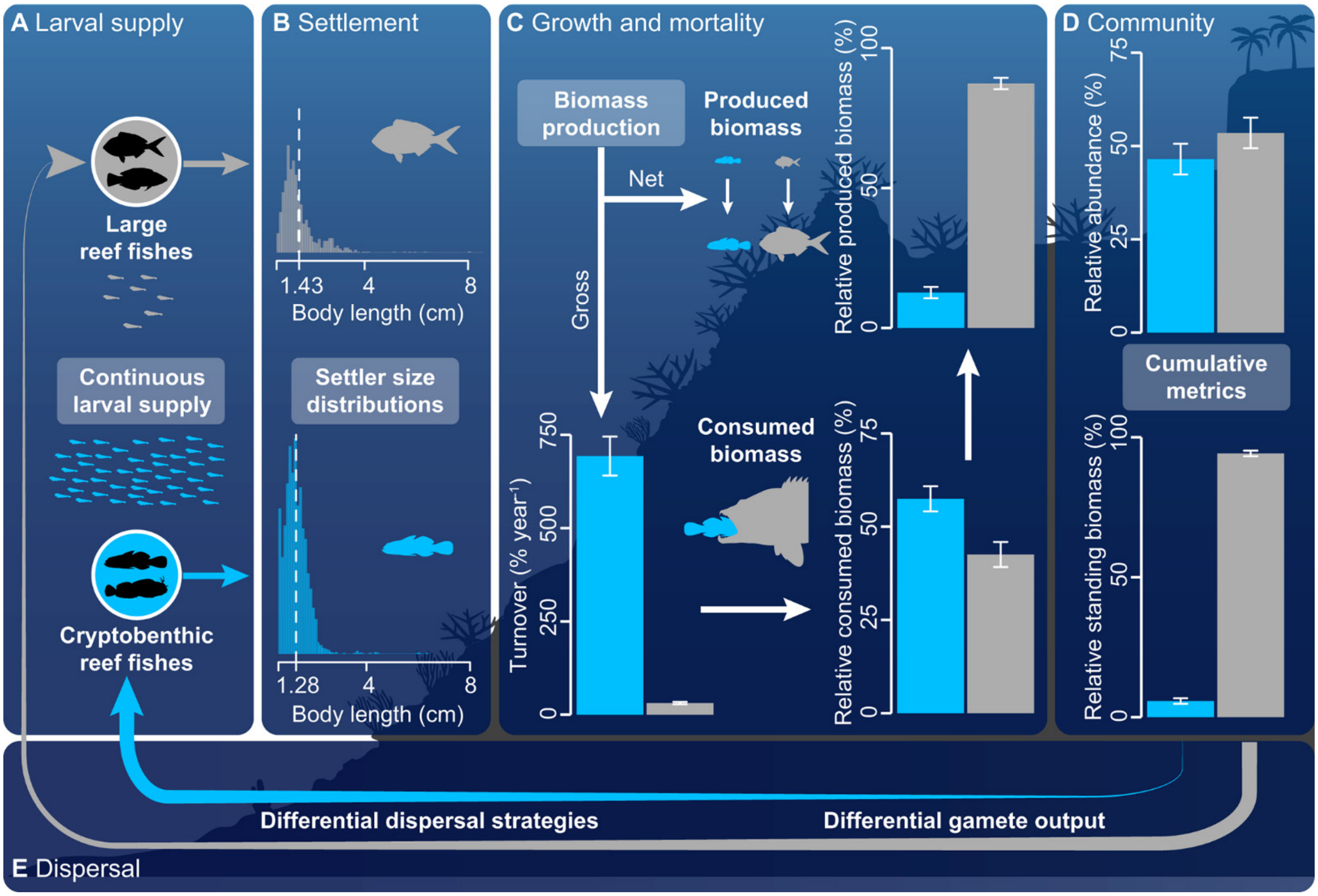


**Fig. 3. Ecosystem-scale effects of the demographic dynamics of cryptobenthic reef fishes.** (**A**) Cryptobenthics far outnumber large reef fishes in cohorts of larvae that recruit to reefs. (**B**) At settlement, large reef-fish recruits are, on average, slightly larger than cryptobenthics. (**C**) 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.

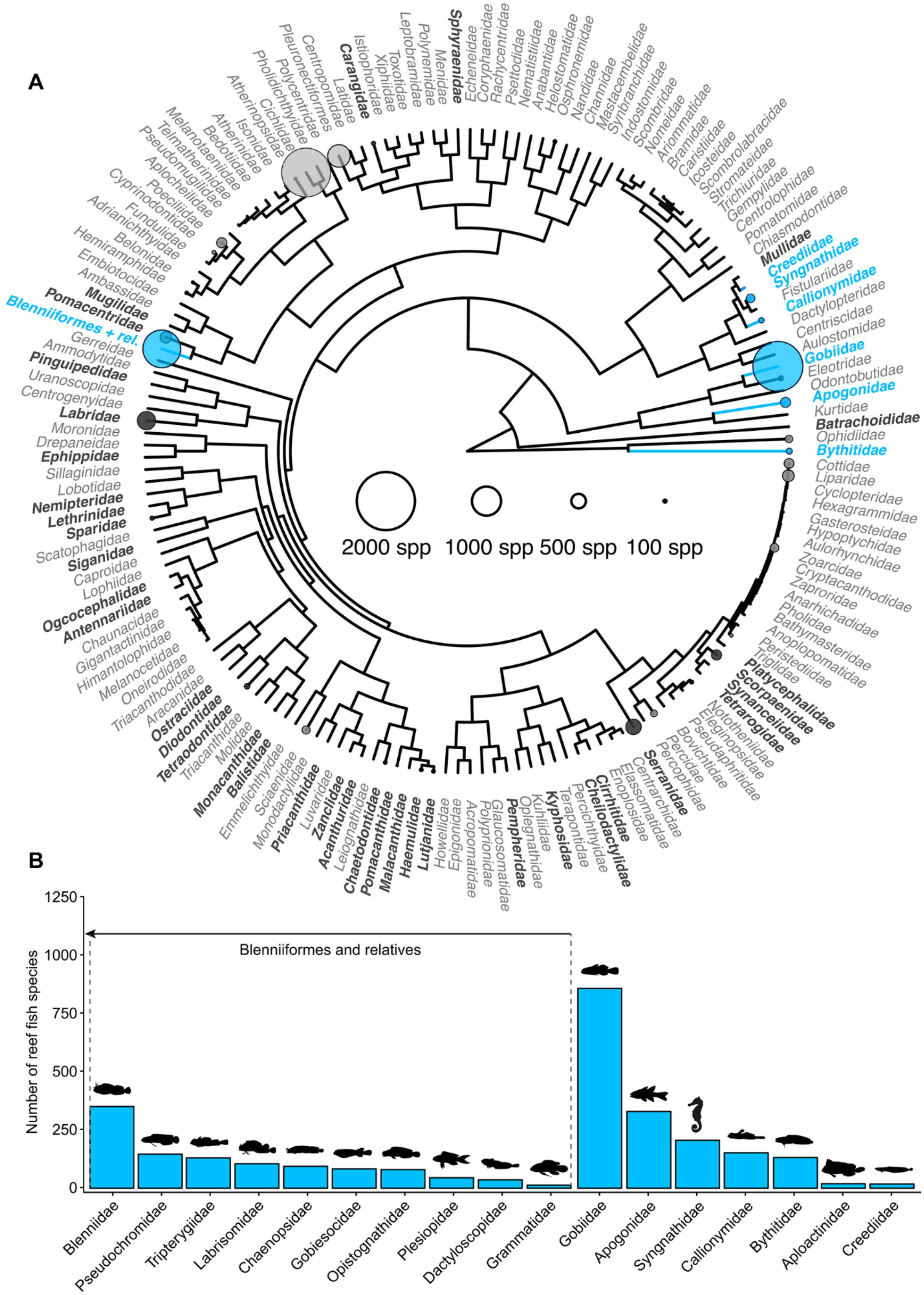
A
Atherinopsidae
Isonidae
Atherinidae
Bedotiidae
Melanotaeniidae
Telmatherinidae
Pseudomugilidae
Aplocheilidae
Cyprinodontidae
Poeciliidae
Fundulidae
Adrianichthyidae
Belonidae
Hemiramphidae
Embiotocidae
Ambassidae
Mugilidae
Pomacentridae
Blenniiformes + rel.
Gerreidae
Ammodytidae
Pinguipedidae
Uranoscopidae
Centrogenyidae
Labridae
Moronidae
Drepaneidae
Ephippidae
Sillaginidae
Lobotidae
Nemipteridae
Lethrinidae
Sparidae
Scatophagidae
Siganidae
Caproidae
Lophiidae
Ogcocephalidae
Antennariidae
Chaunacidae
Gigantactinidae
Himantolophidae
Melanocetidae
Oneirodidae
Triacanthodidae
Aracanidae
Ostraciidae
Diodontidae
Tetraodontidae
Triacanthidae
Molidae
Monacanthidae
Balistidae
Emmelichthyidae
Sciaenidae
Monodactylidae
Priacanthidae
Luvaridae
Zanclidae
Acanthuridae
Leiognathidae
Chaetodontidae
Pomacanthidae
Malacanthidae
Haemulidae
Lutjanidae
Howellidae
Epigonidae
Acropomatidae
Polyprionidae
Glaucosomatidae
Pempheridae
Oplegnathidae
Kuhliidae
Kyphosidae
Terapontidae
Percichthyidae
Cirrhitidae
Cheilodactylidae
Enoplosidae
Elassomatidae
Centrarchidae
Serranidae
Percophidae
Percidae
Bovichtidae
Pseudaphritidae
Eleginopsidae
Nototheniidae
Tetrarogidae
Synanceiidae
Scorpaenidae
Platycephalidae
Triglidae
Peristediidae
Anoplopomatidae
Bathymasteridae
Pholidae
Anarhichadidae
Zaproridae
Cryptacanthodidae
Zoarcidae
Aulorhynchidae
Hypoptychidae
Gasterosteidae
Hexagrammidae
Cyclopteridae
Liparidae
Cottidae
Bythitidae
Ophidiidae
Batrachoididae
Kurtidae
Apogonidae
Odontobutidae
Eleotridae
Gobiidae
Aulostomidae
Centriscidae
Dactylopteridae
Callionymidae
Fistulariidae
Syngnathidae
Creediidae
Mullidae
Chiasmodontidae
Pomatomidae
Centrolophidae
Gempylidae
Trichiuridae
Stromateidae
Scombrolabracidae
Icosteidae
Caristiidae
Bramidae
Ariommatidae
Nomeidae
Scombridae
Indostomidae
Synbranchidae
Mastacembelidae
Channidae
Nandidae
Osphronemidae
Helostomatidae
Anabantidae
Nematistiidae
Psettodidae
Rachycentridae
Coryphaenidae
Echeneidae
Sphyraenidae
Menidae
Polynemidae
Leptobramidae
Toxotidae
Xiphiidae
Istiophoridae
Carangidae
Latidae
Centropomidae
Pleuronectiformes
Polycentridae
Cichlidae
Pholidichthyidae
2000 spp
1000 spp
500 spp
100 spp
B
Number of reef fish species
1250
1000
750
500
250
0
Blenniiformes and relatives
Blenniidae
Pseudochromidae
Tripterygiidae
Labrisomidae
Chaenopsidae
Gobiesocidae
Opistognathidae
Plesiopidae
Dactyloscopidae
Grammatidae
Gobiidae
Apogonidae
Syngnathidae
Callionymidae
Bythitidae
Aploactinidae
Creediidae

**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.