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Review

Quantifying energy and nutrient fluxes in coral reef food webs

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The movement of energy and nutrients through ecological communities represents the biological 'pulse' underpinning ecosystem functioning and services. However, energy and nutrient fluxes are inherently difficult to observe, particularly in high-diversity systems such as coral reefs. We review advances in the quantification of fluxes in coral reef fishes, focusing on four key frameworks: demographic modelling, bioenergetics, micronutrients, and compound-specific stable isotope analysis (CSIA). Each framework can be integrated with underwater surveys, enabling researchers to scale organismal processes to ecosystem properties. This has revealed how small fish support biomass turnover, pelagic subsidies sustain fisheries, and fisheries benefit human health. Combining frameworks, closing data gaps, and expansion to other aquatic ecosystems can advance understanding of how fishes contribute to ecosystem functions and services.

Energy and nutrient flux through ecosystems

Surveying and monitoring our planet's biological communities is the bedrock of scientific discovery and conservation. However, the trees, birds, fishes, or insects we count are only the outcomes of dynamic processes, including organismal physiology (e.g., growth, excretion) and ecological interactions (e.g., predation, dispersal). These processes cannot be directly 'seen' in ecological surveys, but they are the pulse of Earth's ecosystems: a hidden metronome dictating the flow of energy and nutrients through food webs, regulating ecosystem functioning and services provided to humanity.

Due to their dynamic nature, understanding of **energy and nutrient flux** (see Glossary) through food webs has long relied on energetic theories of ecological organisation [1,2]. These theories continue to be updated with physiological and biochemical field data [3], explicit consideration of space [4], trophic models [5], and large-scale observational datasets [6]. From early theoretical concepts to today's data-rich analyses, the development of approaches to quantify how individual processes scale up to determine food web structure and functioning through space and time has been a central challenge [7]. This challenge is exacerbated by the ecological complexity of speciose food webs, such as in tropical systems, where effects of biodiversity, habitat connectivity, and human interference on energy flux are difficult to disentangle [8]. Refining approaches to quantify energy and nutrient fluxes in these vulnerable tropical systems is a critical endeavour [9].

Owing to their exceptional biodiversity and connections with other marine and terrestrial ecosystems, tropical coral reefs exhibit complex, open food webs for which pathways of energy and nutrients have remained unresolved. Coral reefs have long been perceived as biodiverse, productive systems that exist in a nutrient-poor ocean seascape [10], supporting millions of people through productive fisheries [11]. Recent advances in biochemical techniques have allowed more nuanced insights into the role of reef fishes –the dominant consumers in reef food webs [12] – in moving and storing energy and provisioning key nutrients for human diets. Several

Highlights

Animal transport of energy and nutrients through food webs and across ecosystem boundaries is highly dynamic in time and space, challenging our ability to quantify ecological processes.

Energy and nutrient flux in individual animals can be measured with data on growth, biochemistry, and trophic ecology, but scaling individual processes up to entire animal communities is inherently difficult.

On coral reefs, new frameworks have been developed to predict growth rates, nutrient cycling, micronutrient concentrations, and energy sources in fishes, helping to uncover ecosystem functions and services.

Filling data gaps and comparing flux frameworks with existing ecosystem tools will improve quantitative predictions and help ecologists trace energy and nutrient flux in other aquatic systems.

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frameworks have been developed that integrate **bioenergetics**, **stoichiometry**, life-history theory, and isotope ecology to measure rates of growth, energy consumption, nutrient cycling, and **biomass production** at the scale of reef fish assemblages. This has enabled the tracing of energetic contributions from pelagic plankton to reef animals [13,14] and their predators, including reef-associated piscivores [15], mobile top predators [16], and people gaining essential dietary **micronutrients** from seafood [17]. Here, we synthesise recent advances in the estimation of energy and nutrient flows in coral reef fishes, identify knowledge gaps, and outline applications to other aquatic systems.

A suite of approaches to quantify coral reef fish energy and nutrient flux

Our improved understanding of energy and nutrient flux on coral reefs is built on combining field data with novel data sources and modelling approaches. From pioneering coral reef scientists of the 1950s [10] to today's global monitoring programmes, underwater observations are a key data source for coral reef ecologists. **Underwater visual surveys (UVS**) provide two core metrics – the abundance and size structure of reef fish species – which are typically used to calculate standing stock biomass. However, standing biomass represents the end point of dynamic ecological processes that unfold over unknown timescales and thus fails to capture the transfer of energy and materials by fish (i.e., the functioning of coral reef food webs) [18]. Integrating reef fish survey data with four complementary approaches – demographic modelling, bioenergetic models, micronutrient analyses, and **CSIA** (Figure 1) – provides new, powerful tools to understand how energy and nutrients move through coral reef food webs and contribute to ecosystem services. As we show later, these advances have already shed light on dynamic processes that have been contemplated for several decades [19].

Demographic modelling

Animals direct energy and nutrients obtained from their prey towards **somatic growth**, metabolic activity, reproduction, and waste. For fish and aquatic invertebrates, individual growth is often modelled by the **von Bertalanffy growth function (VBGF)**, which predicts body size at a given time point based on an individual's expected maximum length and its current age. Although the VBGF has long been used in fisheries science [20], data to estimate its parameters still do not exist for the majority of coral reef fish species (Table S1 in the supplemental information online) [21]. Predictive models based on public data repositories can overcome some of these limitations [22]. For reef fishes, growth rates can be estimated for any species [23] using **out-of-sample predictions** of somatic biomass production and size-based mortality based on simple traits and temperature [24,25].

Bioenergetics and stoichiometry

Nutrient cycling in animals – the ingestion, assimilation, and excretion of elements (carbon, nitrogen, and phosphorus) – can be estimated using metabolic principles, since energetic requirements scale with biomass and temperature [26]. While nutrients ingested by individuals must be assimilated or excreted as waste [27], stoichiometric theory predicts that nutrient cycling will depend on the elemental composition of the fish, its food, and the absorption efficiency [28]. Combining metabolic and stoichiometric models thus allows the prediction of nutrient ingestion, assimilation, and excretion by individuals, and tracing of elemental fluxes in coral reef food webs [29]. Mass-balance models that explicitly incorporate elemental limitations (e.g., nitrogen, phosphorus) can estimate the individual requirements of multiple nutrients for basal metabolic processes and growth, simultaneously predicting reef fish ingestion rates [30]. Complementary to bioenergetic models, empirical estimates of nutrient cycling have revealed strong relationships between nutrient cycling, body size, and taxonomic identity [31,32], affirming the importance of metabolic scaling and phylogeny for individual-based nutrient dynamics.

Glossary

Bioenergetics: study of the transport and storage of elements in biological organisms.
Biomass production: cumulative somatic mass production across individual fishes in a population, trophic group, or assemblage, over a defined time interval.
Compound-specific stable isotope analysis (CSIA): measurement of stable isotope values in individual biochemical compounds (e.g., amino acids, fatty acids) in animal or plant tissue.
Ecosystem connectivity: the movement of energy and nutrients across ecosystems via active or passive movement of materials or individuals.
Energy and nutrient flux: the pathways and rates at which elements (e.g., carbon, iron) and compounds (e.g., carbonate) move through food webs.
Energy sources: organismal pools or organic carbon at the base of energy pathways, such as benthic detritus or pelagic phytoplankton.
Micronutrients: vitamins and minerals required in relatively low concentrations (e.g., calcium, iron, zinc) but that are essential to healthy growth and development in animals.
Out-of-sample prediction: prediction from a statistical model for values beyond the fitted dataset, such as the growth rate of a reef fish species without size and age data.
Somatic growth: assimilation of energy and nutrients by an individual, resulting in tissue growth and a corresponding increase in body size.
Stoichiometry: the study of the balance of energy and multiple chemical elements (e.g., carbon, nitrogen, and phosphorus) in living organisms and systems.
Subsidies: inputs of energy or nutrients transferred from another ecosystem.
Underwater visual surveys (UVS): a common method to census coral reefs, where an observer estimates the abundance and size of individual fish in a given area.
von Bertalanffy growth function (VBGF): equation that describes the rate at which an individual approaches its population asymptotic body size, where parameter *K* is the growth deceleration coefficient. *K* standardised by maximum size (Kmax) is a growth rate parameter that can be compared across species.

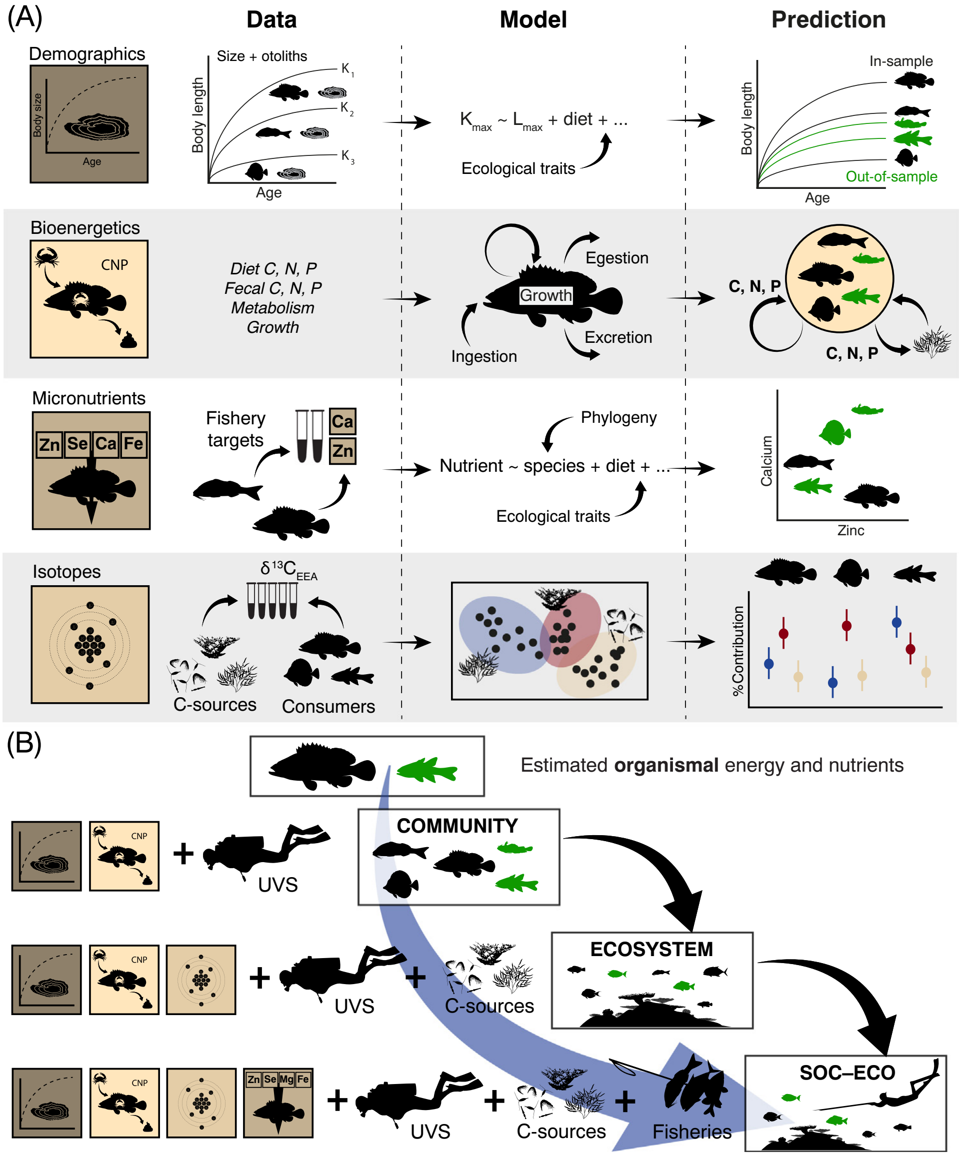

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Figure 1. Advances in modelling of energy and nutrient fluxes on coral reefs. (A) Four frameworks combine field data, biochemical analyses, and ecological traits to build models that predict energy and nutrient flux for data-deficient species. Traits may include diet, body size, trophic level, and other covariates relevant to energy and nutrient flux in fishes. Phylogeny can be modelled according to species' taxonomic hierarchy (e.g., genus, family, class) or using phylogenetic distances. (B) Organismal estimates provide a basis to scale up energy and nutrient fluxes to communities, ecosystems, and socioecological systems. Demographic and bioenergetic models fitted to organism-level data can be combined with field surveys [e.g., fish abundances from underwater visual surveys (UVS)] to estimate community-level processes (e.g., biomass production, excretion rates, nutrient turnover). At the ecosystem level, isotope signatures in carbon-source materials (C-sources) (e.g., algae, corals, phytoplankton) and their consumers (e.g., reef fish) provide information on energy flux within and between ecosystems (e.g., reef–pelagic connectivity). Community- and ecosystem-level approaches can also be combined with socioecological data (e.g., fisheries catch) to quantify critical ecosystem services (e.g., micronutrient availability, dietary health, fisher incomes).

Micronutrients

Besides carbon, nitrogen, and phosphorus, the customary focus of bioenergetic models, fishes assimilate and store numerous other macronutrients (e.g., protein, omega-3 fatty acids) and micronutrients (e.g., iron, zinc, vitamins). These nutrients also flow through food webs and are essential for animal health, although ecological understanding of micronutrient cycling in food webs remains limited [17]. Beyond their movement through food webs, there is growing interest in how elements and molecules such as iron, zinc, or omega-3 fatty acids contribute to healthy growth and development when consumed as seafood [33]. In Seychelles, for example, coral reef fish consumption is associated with higher levels of omega-3 fatty acids [34] in pregnant women. Statistical models fitted to published nutrient content data show that nutrients in marine fish muscle tissue vary with species' traits (e.g., trophic level, body size, diet) [35] and phylogeny [36], enabling out-of-sample predictions for data-deficient reef fish species [37].

Compound-specific stable isotopes

Analysis of stable isotope ratios (predominantly carbon^{13}/carbon^{12} and nitrogen^{15}/nitrogen^{14}) in organismal whole tissues ('bulk' SIA) has been widely used to understand resource use and trophic position in food webs [38,39]. Bulk SIA can determine whether individuals feed within or across distinct **energy sources** (e.g., pelagic or benthic [40]), but lack resolution in highly connected food webs with multiple energy sources. For example, on coral reefs fishes may consume energy from reef sources (algae, coral, detritus) [41,42], the open ocean ('pelagic') [43], or nearby sandy, seagrass, or mangrove habitats [44]. While additional isotopic tracers (e.g., sulfur) can further separate energy sources across another axis [45], bulk SIA have inherent limitations [46].

CSIA, primarily of amino acids, provides novel insights into energy sources and connectivity between coral reef food webs and nearby ecosystems [15,47]. Compounds are directly routed into consumer tissues, so, in contrast to bulk SIA, enrichment of isotopes up the food web (i.e., fractionation) is minimal. Information on resource use and trophic level [48], across multiple amino acid axes, lends analytical power to resolve energy pathways in more complex systems. CSIA of fatty acids can also help to elucidate the complex energy pathways in aquatic systems [49], but has been rarely used on coral reefs to date (but see [50]).

Projecting organismal estimates onto reef fish communities

Collectively, the four aforementioned approaches (Figure 1A) offer estimates of energy and nutrient assimilation and allocation by individual fishes. These can be harnessed for extrapolative structure-to-function frameworks [1] that project organismal estimates onto fish communities. On coral reefs and other coastal ecosystems, decades of UVS provide databases of abundance, species identity, and estimates of size (e.g., length) of individual fishes. UVS can thus be combined with traits and phylogeny databases (e.g., Fishbase, Fishtree) to predict energy and nutrient parameters for species without empirical data, scaled by their size and abundance [51]. For example, growth coefficients predicted for reef fish species using their observed size, maximum body length, and trophic group allow surveyed individual fish to be positioned in their expected growth trajectories, predicting their immediate expected growth. This estimate of the rate of biomass production is easily scaled up to whole reef fish assemblages (Figure 1B) [24]. Similarly, individual ingestion and excretion rates can be calculated by extrapolating a suite of parameters using empirical data, theory, and phylogenetic relationships [51], while ecological traits can be used to predict carbonate excretion rates [31] and micronutrient concentrations [37]. These predictions allow estimates of community-level energy and nutrient flux [51], providing a powerful tool for speciose ecosystems, such as coral reefs, where analytical data are invariably limited to a subset of species.

While scaling of organismal processes to assemblages using out-of-sample prediction helps to resolve coral reef functioning, it is subject to several assumptions. For example, individual age models estimate somatic biomass production in fishes but may not account for biomass lost to predation, population replenishment, or reproductive investment (but see [25]) (Box 1). Similarly,

Box 1. Biomass production beyond individuals

Somatic growth is the physiological process producing endogenous fish community biomass. Age-based frameworks that estimate the cumulative somatic growth of individuals thus offer a framework to measure fish community biomass production, but often do not account for two key processes. (i) Mortality. Many individuals may not survive long enough to contribute to community growth (i.e., they die before they grow). Since mortality is a non-recursive process, high mortality rates will correspond with a low proportion of individuals contributing their expected biomass production from growth. (ii) Recruitment. New individuals may be added to the community and, vice versa, not enough individuals may settle to maintain populations suffering continued mortality.

Upscaling from individual to population and community levels thus requires that investigators consider mortality and recruitment effects, in their capacity both to accrue biomass and to maintain population persistence. First, mortality rates are typically considered to decline exponentially with cohort age and body size (simulating mortality risk). These relationships can be incorporated into community somatic growth estimates either by removing the growth of individuals expected to die (net somatic production) or by estimating the total biomass lost via mortality (net or surplus production) [25]. Second, recruitment dynamics are not easily predicted for open systems such as coral reefs because early life stages of fish predominantly occupy the open ocean, decoupling fish reproduction and settlement. Although recruitment potential has been assessed in other marine systems (e.g., stock-recruitment relationships) and can be gauged by coupling surveys of larval and adult communities [25], this topic remains largely under-investigated for coral reefs. Mortality and recruitment in fishes are also linked with habitat quality [55,94], indicating that habitat–productivity relationships should be considered when estimating reef fish biomass production for fisheries management.

Alternative approaches to estimate fish community biomass production include ecosystem models and stock-production models. Ecosystem models often use size-structured trophic relationships to describe how energy and matter move between producers, prey, and predators, generating fisheries and ecosystem outputs (e.g., surplus biomass production) [55]. Stock-production models, by contrast, quantify intrinsic population dynamics using rates derived from time-series abundance data and thus only implicitly account for biomass incorporated from non-fish sources [95]. Stock-production models require more data inputs than individual age models, potentially limiting their use in data-limited tropical systems such as coral reefs, whereas size-based models are well suited to data-poor systems. Comparative analyses of these different approaches to the estimation of assemblage productivity, and extensions that consider recruitment and mortality, will improve our ability to upscale individual somatic growth to community biomass production.

nutrient cycling model parameters, and data underlying statistical models of growth rates and nutrient content, are usually based on ‘snapshots’ of fish physiology through space and time that are prone to vary among individuals; for example, due to seasonality in ingestion rates or carbonate excretion, or intraspecific variability in metabolic [52] and growth rates [53] (Box 2). Furthermore, there is good evidence for fundamental differences in organismal traits for closely related species, distinct populations of the same species, or even different individuals in the same population [54]. Uncertainty from these unmeasured sources of variability can be propagated using statistical techniques (e.g., Bayesian posteriors), and assessed through comparisons with ecosystem models. For example, size-structured ecosystem models use metabolic scaling relationships and trophic efficiency information to simulate long-term trophodynamics [55] and can account for energetic inputs from connected ecosystems such as mangroves [56]. Integration across approaches to obtain accurate assemblage-level estimates for parameters of interest [25] is critical to empower these emerging techniques.

Ecosystem connectivity

Energy pathways quantified via CSIA are typically assessed at the community level through targeted sampling of representative species rather than out-of-sample predictions. Species of interest are targeted within or across feeding pathways and trophic levels, including consumers with offshore (e.g., Scombridae) and reef-based (e.g., Caesionidae) planktonic sources, fish that derive energy from benthic algae (e.g., Pomacentridae), coral (e.g., Chaetodontidae), and detritus (e.g., Acanthuridae), and higher-order predators (e.g., Lutjanidae, Serranidae), as well as basal energy sources (e.g., plankton, algae, coral) [15,57]. Species-specific CSIA signatures are often obtained for the most abundant species and then used as ‘vignettes’ for key trophic linkages and energy pathways (although even closely related species may differ in their resource use and CSIA signatures). By explicitly targeting non-reef resources (e.g., sand, seagrass, and

Box 2. Overcoming data limitations and model assumptions

Many methods to measure individual processes fit regression models to publicly available datasets (e.g., Fishbase) to estimate key parameters with statistical uncertainty. These approaches are thus highly reliant on existing datasets, often collected for different reasons, limiting our ability to understand sources of uncertainty. Diet, in particular, is a trait used in models predicting growth, bioenergetics, and micronutrients, yet it is known to be highly variable within species. Dietary classifications for coral reef fishes remain contentious [96], partly due to differences in classification methods (e.g., gut contents vs. behavioural observations) as well as a prevalence of ontogenetic and spatial dietary shifts in reef species. Furthermore, there is a general lack of data on the nutrient content of these diets, which is a key parameter in bioenergetic models (see Table S1 in the supplemental information online). Thus, there are inherent risks in applying population- or species-level diets to all individuals, especially when intraspecific behavioural variation can result in large deviations from average values [88]. However, species-level average values remain the best current practice for scaling organismal rates to community and ecosystem scales.

Environmental conditions can also influence pathways of energy and nutrients flowing through food webs, and in turn affect productivity, bioenergetics, and micronutrient content. While certain environmental conditions, such as temperature, are integrated into modelling frameworks (e.g., temperature-dependent growth and metabolic rates), other drivers are masked when using statistical modelling approaches alone. For example, micronutrients such as iron and zinc can be enriched in fish muscle tissue on reefs following a shift in the benthic energy base from corals to algae [37], while the availability of these elements to marine food webs varies at ocean-basin scales [97]. Similarly, pelagic nutrient subsidies to reefs provided by seabirds increase fish growth rates measured *in situ* [14], which could influence assemblage-level productivity when scaling up from pelagic-enriched individuals [71]. Such environmental variation in nutrient availability and growth rates, respectively, have not yet been empirically modelled.

At present, incorporating uncertainty in parameter values (e.g., sampling from Bayesian posteriors [37] or quartile ranges of bootstrapped machine-learning predictions [23,24]) can help to improve estimates of intraspecific and environmental effects, when such data exist. Further *in situ* sampling for analytical data (including reef invertebrates) remains critical in improving current data limitations and testing model assumptions about individual, spatial, and environmental variability.

mangrove production) or mobile-link consumers (e.g., apex predators, roving herbivores), cross-system linkages can be investigated in detail.

Resolving flows in open, connected systems with multiple energy sources remains challenging due to the volatility of isotopic signatures across space and time [58]. Furthermore, the strength and diversity of energy pathways on coral reefs can vary with environmental conditions (e.g., primary productivity, depth) and are disrupted by anthropogenic stressors such as habitat degradation [59] and invasive species [14]. Such spatiotemporal variation in isotope signatures has thus far limited our ability to predict feeding pathways for species without analytical data, as used in other energy and nutrient frameworks. However, global meta-analyses of bulk isotope samples for zooplankton [60] and sharks [61] have used biochemical models to interpret spatial variability. Such frameworks could be tested for CSIA samples from coral reef fishes and then integrated with metrics such as biomass, biomass production, or metabolic rates to quantify the contribution of, for example, offshore pelagic **subsidies** entering reef food webs at large spatial scales. As CSIA is more robust to variation in baseline signatures, has minimal discrimination across trophic levels, and does not vary as strongly over spatial and temporal scales as bulk isotopic values [48], future meta-analyses of CSIA samples might be used to develop predictive models of **ecosystem connectivity**.

Socioecological systems and ecosystem services

Coral reef energy and nutrient fluxes determine ecosystem services that directly affect human well-being through the provisioning of nutritious food and livelihoods. Advances in the tracing of energy and nutrient fluxes in coral reef food webs can therefore help to reveal mechanisms through which fish support ecosystem services, such as fisheries production. For example, estimates of reef fish biomass production in Tonga have shown that areas under fisheries co-management harboured increased biomass production compared with openly fished reefs, despite similar standing biomass [62]. Growth rate predictions have also revealed how turnover of fast-growing fishes can maintain assemblage productivity on fished reefs despite biomass depletion [63], and that this compensatory fisheries production is dependent on the complexity of coral reef habitat [64].

Such empirical analyses of assemblage-level biomass production complement ecosystem models of reef fisheries [55] that can, together, advance efforts to manage their sustainability.

Beyond biomass production, the value of fisheries-derived food to human well-being depends on its nutritional quality [65], especially in remote coastal and indigenous communities with limited access to commercial food sources [66]. Charting the distribution of trace-level elements in reef fish tissues offers a powerful avenue to advance integrative socioecological science, such as contributions of reef fish to healthy diets. As with fish growth rates, assessments of reef fish contributions to nutrient supply must place predictions in the context of fish stock size and catch composition, and other ecosystem services [67]. This can be achieved by integrating species' nutrient concentrations with UVS data to estimate the nutrient yield contained by targeted fish assemblages [37] or with catch records to quantify gear selectivity for nutrients [68].

Novel insights into coral reef ecosystems

Scaling of energy and nutrient flux to reef fish assemblages has advanced our understanding of the roles of the different energy and nutrient pathways in coral reef functioning (Figure 2). For

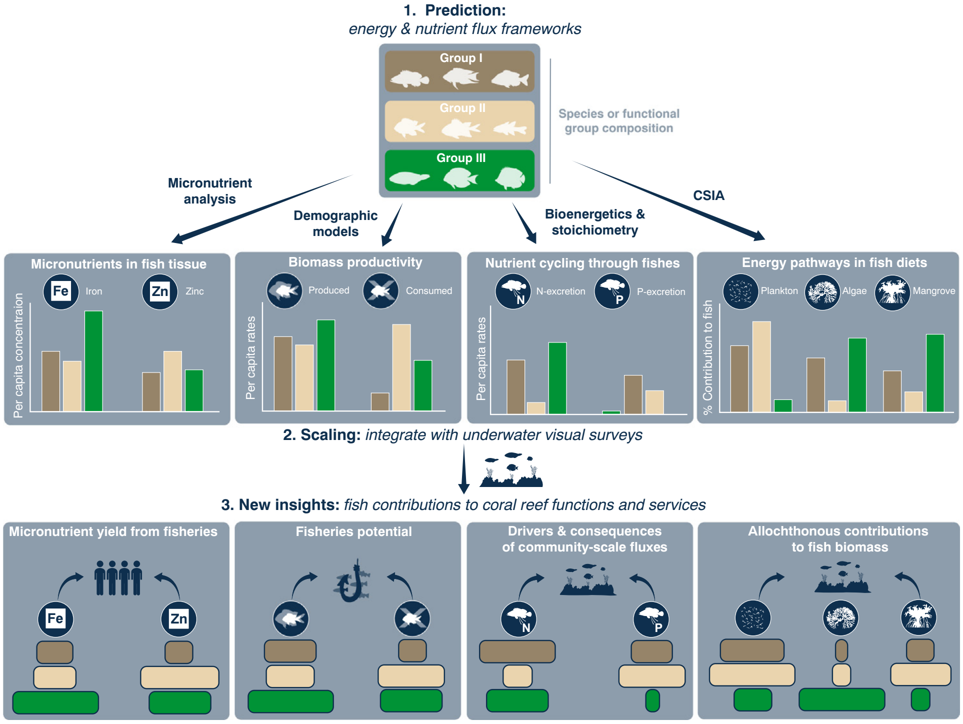

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Figure 2. Applying recent advances in modelling of energy and nutrient fluxes in fish communities. Using reef fish surveys and groupings within these communities (e.g., functional, trophic), the four highlighted frameworks can be used to determine the role of fish groups in energy and nutrient flux. For each approach, estimated values for fish species or groups (vertical bars, 1) can be projected onto entire fish communities and scaled by underwater visual survey (UVS) biomass estimates, revealing fish contributions to ecosystem functioning and services (horizontal bars, 3). For a hypothetical community of three fish groups (1), micronutrient concentrations can yield insights into fish groups that sustain micronutrient yields for human populations. Demographic models can estimate the *per capita* contributions of these groups to biomass production and consumption, revealing how different groups contribute to fisheries potential. Using bioenergetics and stoichiometry, *per capita* rates of nitrogen and phosphorus excretion scaled to fish groups can reveal community-scale trade-offs in reef functioning. With compound-specific stable isotope analysis (CSIA), individual fish samples can quantify the contributions of carbon sources to the different groups of fishes, uncovering the importance of allochthonous contributions to fish biomass. Combining these four methods can provide a more powerful understanding of elemental flux through fishes, in coral reefs and other aquatic ecosystems.

example, modelling species growth rates revealed that planktivorous fishes, particularly species feeding on offshore plankton in forereef habitats, can contribute 41–57% of total fish biomass production in some locations [13,69]. CSIA has similarly uncovered complex roles of pelagic inputs for coral reef food webs, with offshore plankton, rather than reef-associated plankton or benthic energy, as a cryptic dominant component of predatory reef fish diets [15,57]. However, there is seasonality in the quality of plankton subsidies [50] and the importance of benthic versus pelagic energy shifts from inshore (shelf) to offshore (oceanic) reefs [57]. The relative importance of the different energy pathways may explain why, on some reefs, tiny bottom-dwelling 'cryptobenthic' fishes dominate biomass transfer to higher trophic levels – a consequence of their exceptional life-history and demographic dynamics [25]. By contrast, higher trophic levels often dominate phosphorus cycling on coral-dominated reefs [51], suggesting that degradation of coral habitat and structure may alter nutrient cycling in fish communities.

Together, growth rate models and CSIA techniques suggest that the strength of energy and nutrient pathways on coral reefs vary through time and space. Such trophic flexibility reflects both oceanographic and anthropogenic effects on energy pathways, fish community structure, and habitat condition. For example, reefs subject to extreme temperatures may have diminished contributions of cryptobenthic fishes to biomass production and transfer [70], while marine heatwaves can decrease reef fish productivity by reducing fish biodiversity [71]. By contrast, reef–pelagic connectivity may be independent from coral cover, as shown by high reliance on offshore plankton even in low-coral-cover reef systems [50]. Furthermore, cryptobenthic fish communities at one island on the Great Barrier Reef provide stable contributions to biomass flux despite multiple disturbance events and profound compositional changes [72]. Such disturbed reefs can, however, undergo algal overgrowth following coral mortality, resulting in enhanced short-term biomass production by herbivorous fishes, in both fished [73] and protected [74] coral reefs. Size-based models corroborate these observations, predicting that fish productivity can be maintained after coral mortality when habitat complexity is retained, but declines on reefs where habitat structure collapses [55]. Such habitat-mediated shifts in herbivore communities can alter the quantity and composition of nutrients excreted on reefs [75] and enrich fish tissue with some essential dietary nutrients [37].

These approaches to quantify energy and nutrient fluxes on coral reefs also help to test classic ecological theories. One prime example is the role of fish community structure for coral reef functioning, particularly biodiversity–ecosystem functioning relationships [18]. For example, species richness is positively correlated with fish assemblage productivity, both locally in the Chagos Archipelago [71] and globally [51], a pattern previously inferred from standing stock biomass alone [76]. In turn, richness plays a more nuanced role in fish-mediated nutrient cycling on reefs, which is primarily driven by fish standing stock biomass and, at local scales, dependent on a few dominant species [51,77]. For instance, species richness correlates negatively with (biomass-independent) estimates of piscivory, whereas high-diversity assemblages have positive correlations with herbivory [51]. The latter relationship suggests a positive effect of diversity on coral reef herbivory rates, which is empirically supported at local [78], regional [79], and global [80] scales but often subject to criticisms surrounding the confounding role of fish biomass in underpinning this relationship. Such a relationship could be due to resource partitioning among herbivores, which can be identified using CSIA [50]. Although all functions performed by reef fishes scale positively with biomass, bioenergetic modelling has revealed that these relationships are allometric and influenced by community composition, leading to trade-offs among fish-mediated functions [51]. For example, phosphorus excretion rates decrease as fish productivity and herbivory increase, owing to large fish predators that contribute little to productivity or herbivory but have phosphorus-rich diets that result in higher phosphorus excretion rates [51]. Although we are only beginning to develop process-based understanding of linkages between community structure, energy and nutrient flux, and ecosystem functioning [18], the four highlighted approaches hold great power to deepen this knowledge.

Extending and combining approaches

Open access to data and methods is pivotal in ensuring wide application of these frameworks, which typically draw on large-scale UVS monitoring data (e.g., Reef Life Survey) [81], public trait and phylogeny databases, and analytical tools (e.g., *fishflux*, *rfishprod*) [24,30]. Developing these databases and tools in an accessible and curated format will permit stronger, more robust inference into energy and nutrient fluxes on reefs. This includes continued sampling of fishes and their diets across bioregions, ontogenetic stages, and taxonomic groups (Box 2). Extended sampling coverage would also help to generate new insights. For example, UVS chronically ignores (or inadequately surveys) fish that are small bodied [82], nocturnal [83], cryptic [84], or mobile [16] or recruit to non-reef habitats [85], reinforcing the need to systematically accrue and publish surveys of functionally important groups such as cryptobenthic invertebrates [86] and cryptobenthic fishes [25]. Furthermore, while CSIA-focused studies are gaining momentum, there is no dedicated database to deposit isotope values across coral reef fish studies (e.g., IsoBank; https://isobank.tacc.utexas.edu) and no consensus on derivatisation methodologies or reference materials for standards. The initiation of such databases in the nascent field of coral reef CSIA would greatly enhance standardisation, coordination, and the applicability of case studies, stimulating synthesis work using the four approaches. Furthermore, reproductive energy allocation and its consequences for community and fisheries productivity is not currently considered in organismal energy budgets, owing to a paucity of size-fecundity and stock-recruitment data (Box 1), rendering a critical aspect of energy flux unquantified in community- and ecosystem-scale models.

Beyond these methodological and data limitations, the four highlighted approaches can also be extended through research combining growth, nutrient, and isotope techniques. Several studies have integrated bioenergetic models with fine-scale data on individual space use or movement capacity (e.g., acoustic telemetry) to examine the transport of elements across reefscapes. For example, telemetry tracks combined with accelerometery tags, demography, and diet data can reveal the roles of reef-associated top predators in cross-habitat nutrient cycling [16,87] and improve estimates of ecosystem-level energy and nutrient flux [88]. Combining energy flux measures with data collected beyond the reef can also generate insights into reef functioning, such as investigations of how water-borne transport of fish larval phases via ocean currents influence reef systems (e.g., larval dispersal [89], *Sargassum* or flotsam rafts [90]). To date, such large-scale oceanographic processes have rarely been integrated into assessments of coral reef energy flux (but see [91]).

Looking forward, research synergies between energy and nutrient flux approaches will help to paint a more holistic picture of how energy and nutrients move through aquatic food webs (Box 3). This, for instance, could include studies combining growth-based modelling with high-resolution CSIA data to identify the main energy pathways driving biomass production and nutrient flux – not just standing biomass – in specific locations. Similarly, studies integrating macro- or micronutrient composition in fish tissue with bioenergetic models would yield insights into the flux of ‘neglected’ nutrients from fish ingestion, through nutrient cycling in faeces [92] to the health of people consuming reef seafood. Fishers often target species that derive energy from connected habitats such as seagrass, mangroves, and open oceans [85], suggesting that CSIA can improve understanding of how non-reef habitats contribute to fisheries production across tropical seascapes [15]. These links expand the spatial boundaries of reef fisheries, emphasising the importance of ecosystem-scale processes, such as energy subsidies, in supporting ecosystem services. Finally, bioenergetic modelling can be combined with other emerging high-resolution diet data, such as gut-content DNA metabarcoding [93], to understand predator–prey relationships and their role in trophic dynamics on reefs.

Box 3. Applications to other aquatic systems

Approaches scaling individual processes to fish communities were developed for tropical coral reefs, where fish account for the majority of the biomass and thus have a strong influence on energy flux and nutrient cycling. Fish also frequently dominate consumer biomass in kelp forests, temperate rocky reefs, estuaries, lakes, and rivers. These ecosystems share some aspects of trophic ecology with coral reefs, suggesting that energy and nutrient frameworks can be extrapolated to non-reef fish species. Kelp forests and some temperate reefs, for example, are characterised by habitat-forming seaweeds that support speciose fish assemblages, and high levels of benthic energy production [98]. Temperate fish species can thus be classified using the same trait-based frameworks applied to coral reefs, which enabled, for example, estimates of growth rates and biomass production in Western Australia [99]. The trait-based models used to predict micronutrient concentrations were originally developed for marine teleost fishes worldwide [35], leading to analyses of nutrient supplies in global fisheries. Similarly, CSIA has already been used to delineate multiple carbon sources in non-reef systems, advancing understanding of connectivity and energy pathways in rivers, kelp forests, and mangroves (e.g., [100]).

Principles for the measurement of energy and nutrient flux in fish assemblages can also help to guide the conservation and management of threatened aquatic ecosystems. Coastal ecosystems and tropical lakes can support similar types of fisheries to coral reefs, in which fishers target multispecies assemblages, often at high fishing mortality, including lakes and rivers, seaweed reefs, and kelp forests. Many of these ecosystems are shallow and thus also suited to UVS, providing the abundance, size, and assemblage composition data necessary to estimate energy and nutrient flux. However, collecting species and size data in inland, turbid, or deeper ecosystems (e.g., mesophotic reefs) may require alternative techniques such as remotely operated videos, electrofishing, or hydroacoustics. Ultimately, energy and nutrient flux frameworks can be implemented in any ecosystem where fish are a dominant conduit of energy and nutrients and where sufficient data exist to estimate community composition, size structure, and biomass.

Concluding remarks

New frameworks to quantify energy and nutrient flux in coral reef fishes have challenged fundamental ecological assumptions, from the role of fishes in nutrient cycling [92] to the nuanced manifestation of biodiversity–function relationships [71]. At the same time, new isotope techniques have uncovered prevalent pelagic subsidies in coral reef food webs [15] and modelling approaches have revealed critical roles of the smallest fishes in sustaining coral reef productivity [13,25,64]. Many of these tools are now freely available and employ statistical or numerical techniques that allow investigators to scale organismal properties to ecosystems by simply using accessible size, species, and abundance data. Areas for future research may address the influence of intraspecific variation and environmental conditions on energy and nutrient flux, contrast these tools with complementary approaches in ecology and fisheries, and explicitly consider the spatial context in which coral reefs are immersed (see Outstanding questions). Such holistic approaches to the quantification of energy and nutrient flux in fish will continue to transform our understanding of the structure and functioning of ecological communities.

Outstanding questions

How strong is intraspecific variation in life history (e.g., growth, excretion rates) and elemental composition?

How can we incorporate intraspecific variation in species-level statistical models?

Do empirical models of individual processes (e.g., growth, nutrients) agree with outputs from ecosystem models?

Can databases of CSIA mixing models reliably predict energy pathways in reef fish assemblages without *in situ* CSIA samples?

Do oceanographic conditions, such as primary production or temperature, govern the strength of pelagic energy pathways in coral reef ecosystems?

Do specific energy pathways on coral reefs correlate with concentrations of certain micronutrients?

How does habitat structure and composition mediate energy and nutrient fluxes?

What is the role of reproductive investment in governing reef fish biomass production?

How does movement of animals and elements between reef and adjacent ecosystems compare with internal photosynthesis in sustaining biomass production on coral reefs?

What is the spatial variation in the diet stoichiometry of fish species?

How does activity level impact energy and nutrient fluxes?

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Declaration of interests

No interests are declared.

Supplemental information

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