RESEARCH REVIEW

Animal pee in the sea: consumer-mediated nutrient dynamics in the world's changing oceans

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Abstract

Humans have drastically altered the abundance of animals in marine ecosystems via exploitation. Reduced abundance can destabilize food webs, leading to cascading indirect effects that dramatically reorganize community structure and shift ecosystem function. However, the additional implications of these top-down changes for biogeochemical cycles via consumer-mediated nutrient dynamics (CND) are often overlooked in marine systems, particularly in coastal areas. Here, we review research that underscores the importance of this bottom-up control at local, regional, and global scales in coastal marine ecosystems, and the potential implications of anthropogenic change to fundamentally alter these processes. We focus attention on the two primary ways consumers affect nutrient dynamics, with emphasis on implications for the nutrient capacity of ecosystems: (1) *the storage and retention* of nutrients in biomass, and (2) *the supply* of nutrients via excretion and egestion. Nutrient storage in consumer biomass may be especially important in many marine ecosystems because consumers, as opposed to producers, often dominate organismal biomass. As for nutrient supply, we emphasize how consumers enhance primary production through both press and pulse dynamics. Looking forward, we explore the importance of CDN for improving theory (e.g., ecological stoichiometry, metabolic theory, and biodiversity–ecosystem function relationships), all in the context of global environmental change. Increasing research focus on CND will likely transform our perspectives on how consumers affect the functioning of marine ecosystems.

Keywords: biodiversity loss, ecological stoichiometry, eutrophication, excretion, fish, food web, nitrogen, overfishing, phosphorus

Introduction

A classic dichotomy in ecology is whether primary production is regulated primarily through top-down (consumers) or bottom-up (resource availability) mechanisms (Polis, 1999). It is now widely acknowledged that this is an oversimplified view, in part because the traditional perspective of the top-down role of consumers focuses only on consumer–prey interactions (Vanni, 2002; Schmitz *et al.*, 2010). Yet, the bottom-up role of consumers in mediating nutrient dynamics may be an equally or more important control on primary production and community dynamics in many ecosystems. The importance of consumers for mediating nutrient dynamics has a long history in many terrestrial (McNaughton *et al.*, 1988) and freshwater ecosystems (Kitchell *et al.*, 1979). However, the historical perspective in many marine systems is that animals are unimportant relative to microbes for biogeochemical cycling (Pomeroy, 1974). Improving our understanding of

consumer-mediated nutrient dynamics in the marine environment is an important step to better understand how global change drivers will impact ecosystem function in the decades to come.

One of the most pervasive human impacts on ecosystems is the widespread reduction and redistribution of animal biomass (Jackson *et al.*, 2001; Estes *et al.*, 2011). This phenomenon, driven primarily by direct extraction and habitat degradation (Lotze *et al.*, 2006), has been ongoing for centuries leading to the sixth mass-extinction event currently underway (Barnosky *et al.*, 2011). Until recently, the majority of human-driven change occurred in terrestrial ecosystems, whereas impacts now increasingly are associated with large-scale harvest of marine fauna (Jackson, 2008; Doughty *et al.*, 2015; McCauley *et al.*, 2015). Today's rates of extraction of non-domesticated animal biomass are orders of magnitude greater in the oceans than on land (Worm, 2015).

Much research has focused on the impacts of removing consumers on community dynamics and ecosystem function via direct consumptive and indirect mechanistic pathways (Paine, 1966; Estes, 1995; Power *et al.*, 1996). A classic example is exploitation of sea otters in

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the North Pacific, which led to release of a primary prey item, herbivorous sea urchins, resulting in runaway herbivory on kelp and decimation of entire kelp forests (Estes *et al.*, 1998). These cascading effects of consumers are pervasive in the ocean, including rocky intertidal, coral reef, seagrass, and pelagic ecosystems (Estes *et al.*, 2011). Understanding these "top-down" dynamics has been foundational for the field of ecology and has provided the basis for establishing important ecological theory that has been extended broadly for conservation and management (Terborgh, 2015).

In addition to influencing top-down interactions, animals can be important mediators of biogeochemical cycles through "bottom-up" processes of storage (in tissues) and supply (through excretion and egestion) of nutrients (Elser & Urabe, 1999; Sterner & Elser, 2002; Vanni, 2002). The importance of consumer-mediated nutrient dynamics (herein CND) has been widely recognized by ecologists, with pioneering work taking place in terrestrial (McNaughton *et al.*, 1988), freshwater (Kitchell *et al.*, 1979), and pelagic marine ecosystems (Pomeroy *et al.*, 1963). These early studies highlighted the important role of animals such as wildebeest, lacustrine fishes, and zooplankton in providing a fundamental source of limiting nutrients that fuels primary production. Despite this early work, and the substantial body of research on the importance of CND for ecosystem function that followed (Elser *et al.*, 1988; Frank *et al.*, 1994; Vanni, 2002; Vanni *et al.*, 2002; Evans-White & Lamberti, 2006; Hall *et al.*, 2007; McIntyre *et al.*, 2007; Hernandez-Leon *et al.*, 2008; Schmitz *et al.*, 2010; Turner, 2015), only recently have ecologists begun to extend this line of thinking toward coastal marine ecosystems (with an important earlier exception, e.g., Meyer *et al.*, 1983). Thus, the "bottom-up" role of consumers may provide an alternative perspective through which to better understand the ecology of coastal marine ecosystems, particularly in the context of rapid and expanding human exploitation in these ecosystems.

The open ocean is a system in which coupled consumer–producer dynamics regulate globally significant biogeochemical cycles. Biological production in oligotrophic open ocean depends mostly on nutrient dynamics within the euphotic zone, with only a small fraction supported from exogenous nutrient sources (Falkowski *et al.*, 1998). Nitrogen, phosphorus, and iron limit primary production in these areas (Howarth, 1988), and supply of these nutrients by zooplankton plays a large role in mediating primary production (Nugraha *et al.* 2010). Species vertical migration patterns (e.g., diel vertical migration of zooplankton is the largest migration on the planet; Steinberg *et al.*, 2000; Hannides *et al.*, 2008; Davison *et al.*, 2013), feeding ecology, stoichiometry, and primary producer demand

interact in determining the system-specific role of CND in enhancing primary production, factors too complex to adequately review herein. Yet from a general perspective, the importance of this CND supply is profound. Excretion by the global community of mesozooplankton in the upper 200 m of the oceans, integrated over all latitudes, accounts for ~1.8×10^{12} kg N yr^{-1} (Hernandez-Leon *et al.*, 2008; Table 1). This nutrient regeneration is estimated to be in the range of 12–23% of the total global oceanic requirements for phytoplankton and bacterial production (Hernandez-Leon *et al.*, 2008). The pelagic realm of the ocean has been extensively studied in the context of CND (Pomeroy *et al.*, 1963; Buitenhuis *et al.*, 2006; Hernandez-Leon *et al.*, 2008; Turner, 2015). Accordingly, we focus our review on those ecosystem types that have received less attention.

Here, we review consumer impacts on nutrient dynamics in marine ecosystems with a particular focus on coastal ecosystems. First, we begin by discussing the basic ecology of CND. We then focus attention on the two primary ways consumers affect nutrient dynamics: (1) *the storage and retention* of nutrients in tissues, and (2) *the supply* of nutrients via excretion and egestion. Throughout, we provide examples of anthropogenically driven change on these processes. We conclude by discussing the current and future challenges for empirical research in CND and emerging theory in the context of global change.

The ecology of CND

There are two primary factors that determine the relative importance of CND for ecosystem function: the donor – the entity (individual, population or community) that drives dynamics, and the recipient – the direct and indirect beneficiaries of these dynamics (Fig. 1). From the donor perspective, a complex suite of factors combine to determine the rate and magnitude by which individuals, populations, and communities store and recycle nutrients. At the individual level, combinations of species-level traits, such as stoichiometry and metabolism, are principle factors that govern CND (Fig. 1; Sterner, 1990; Sterner & Elser, 2002; Villeger *et al.*, 2012; Allgeier *et al.*, 2015a; Vanni & McIntyre, 2016). For example, the proportion of boney material that makes up an individual has important implications for the amount of P stored in total biomass and thus relates to the amount recycled back to the environment (Elser & Urabe, 1999; Sterner & George, 2000; Sterner & Elser, 2002; Hood *et al.*, 2005). Trophic ecology of individuals is also critical for CND, as the nutrient composition of an animal's food resource determines the quality (e.g., nutrient content) and rate

Table 1 Estimates of stored and supplied nitrogen (gigagrams of N)

	Gg N	Citation
Storage		
Standing crop		
Human population (global)	2380	Walpole *et al.* (2012)*
Fish (global)	233 480	Jennings *et al.* (2008)
Krill (Antarctic)	8308	Atkinson *et al.* (2009)†
Removal		
Seabird harvest – fish (global)	1820	Brooke (2004)‡
Human harvest – fish (global)	2072	FAO‡
Human harvest – fish (fed to livestock)	564	FAO‡
Supply (rate per year)		
Consumer driven		
Zooplankton (global)	1 780 000	Hernandez-Leon *et al.* (2008)
Tot fish community (global reefs)	1167	Allgeier *et al.* (2014)§
Abiotic		
Reactive N created by humans	140 000	Galloway & Cowling (2002)
Atmospheric Fixation (global ocean)	110 000	Codispoti *et al.* (2001)
Upwelling (Southern Ocean)	196 000	Pollard *et al.* (2006)
Anthropogenic		
Riverine export (Atlantic Ocean)	10 000	Maranger *et al.* (2008)
Fertilizer to golf courses (US)	92	Golf Course Environmental Profile (2009)
Total manure from ag. (global)	92 000	Bouwman *et al.* (2013)¶

*Human biomass was generated from this citation. N content was calculated based on Lukaski *et al.*, 1981.
†Krill N content calculated based on Huntley *et al.* (1994).
‡Biomass generated from this citation. N content was calculated based on Maranger *et al.*, 2008.
§Reef area taken from World Atlas of Coral Reefs.
¶Excluding NH3 released from animal houses.

at which the individual stores and recycles nutrients (Fig. 1; Sterner, 1990; Elser & Urabe, 1999; Sterner & Elser, 2002). Additionally, attributes that are less constrained by the taxonomic identity of an individual can influence CND. For instance, behavioral characteristics, such as increased activity, can elevate the rate of nutrient recycling due to higher metabolism, that is, a fish swimming would excrete more N relative to a fish of the same species at rest. This complex of traits accumulates through the hierarchy of biological organization from individuals to communities, ultimately determining the rates and ratios at which consumers supply nutrients (Fig. 1).

The amount of nutrients an organism has stored within its tissue is proportional to the relative demand of these nutrients for physiological processes, such as growth, maintenance, and reproduction (Sterner & Elser, 2002). An organism's metabolism largely regulates the rate at which these processes occur and thus the turnover of nutrients within an organism (i.e., production). Nutrients acquired through an organism's diet are appropriated to these processes, and the remainder is released into the environment as waste products via either excretion or egestion (Schreck & Moyle, 1990). Dietary products assimilated into the blood stream, but not taken up by tissue, are released as excretion – typically as biologically available compounds (e.g., ammonium; NH_4^+, and phosphate; PO_4^-; Anderson, 2001). Egestion is the by-product of material that was ingested, but not assimilated, and released as less bioavailable, organically bound, material (such as feces) that contains a variety of forms of N and P (Schreck & Moyle, 1990; Walsh & Wright, 1995). Excreta and egestion are the transient phases of nutrients that are available to both primary producers and microbes (Elser & Urabe, 1999).

From the perspective of the recipient, the amount and type of nutrients supplied by the donor is only significant in light of relative demand (Elser *et al.*, 1988; Evans-White & Lamberti, 2006; Vanni *et al.*, 2006; Wilson & Xenopoulos, 2011). For example, autotrophs in oligotrophic environments (such as coral reefs) may rely heavily on CND, compared to more eutrophic environments (such as temperate coastal shelves) where nutrients are supplied by other sources. Yet, even in ecosystems with high ambient availability of nutrients, consumers may play important roles in mediating nutrient availability through alternative pathways such as: (1) the mediation of trace nutrients (e.g., iron; Falkowski *et al.*, 1998; Roman & McCarthy, 2010), (2)
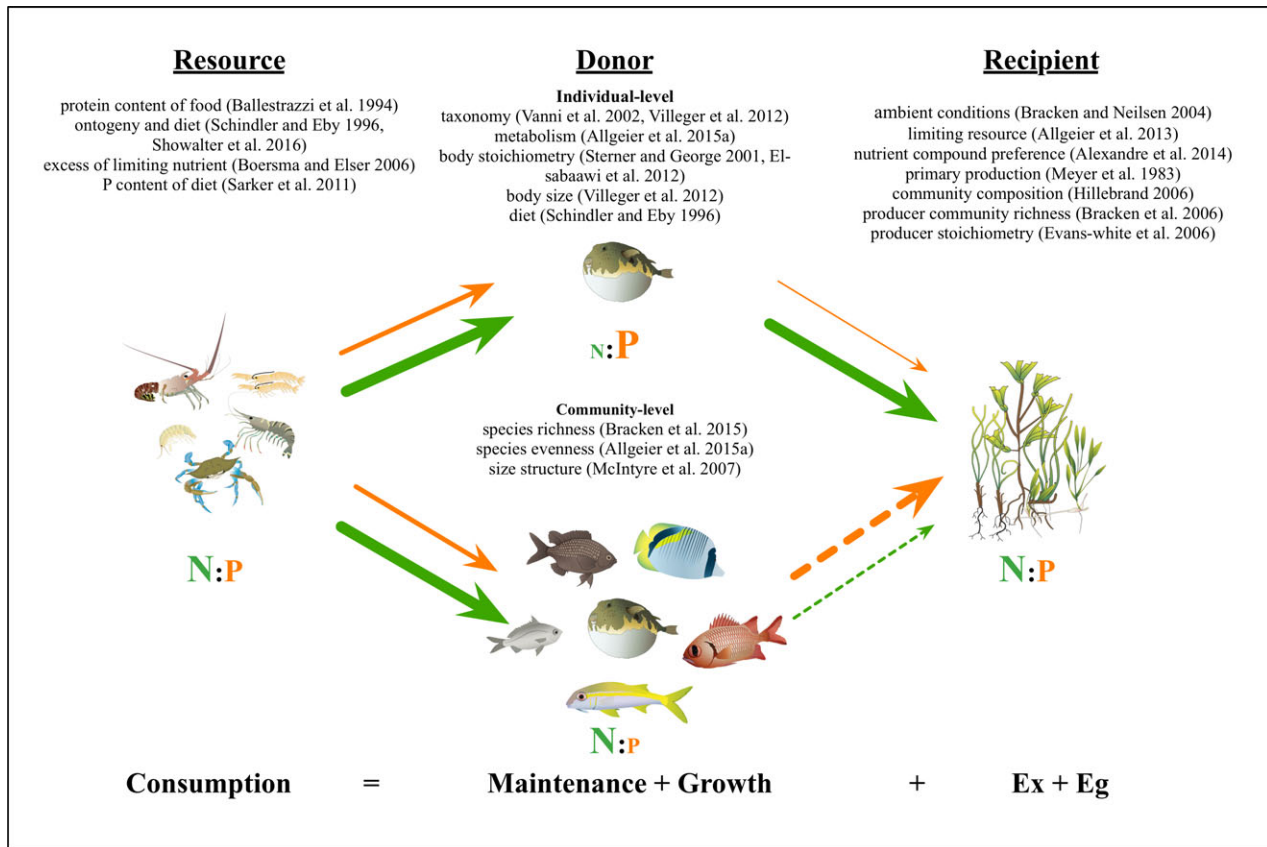
Fig. 1 Conceptual representation of consumer-mediated nutrient dynamics from an ecosystem perspective (i.e., resource, donor and recipient; top of panel) and from a mass-balance perspective (lower panel, whereby Ex and Eg represent excretion and egestion, respectively). Each arrow (N = green, P = orange) represents a respective nutrient pathway, and the size of the arrow indicates the amount of that nutrient. The size of the letter (N or P) below the organism, assemblage of organisms, or producer indicates the relative demand for that nutrient. For example, the puffer fish has a high demand for P and low demand for N. If it feeds on a resource with high N relative to P, then it will excrete large amounts of that excess N and small amounts of P. Citations provide examples of studies associated with the different factors from both freshwater and marine ecosystems.

supplying nutrients at particular ratios that are optimal for primary producers (Sterner, 1990; Evans-White & Lamberti, 2006; Allgeier *et al.*, 2014), (3) supplying nutrients at temporal or spatial scales that complement abiotic sources (Meyer *et al.*, 1983; Devine & Vanni, 2002; Holbrook *et al.*, 2008; McIntyre *et al.*, 2008; Pfister *et al.*, 2014), and/or (4) cycling nutrients through the food web via trophic interactions (DeAngelis, 1992; Kitchell *et al.*, 1994; Hawlena *et al.*, 2012; Fig. 2).

Productivity of many ecosystems depends on the capacity at which nutrients are stored and cycled between the constituents of the system, herein 'nutrient capacity'. Abiotic sources that affect nutrient capacity include upwelling events, riverine inputs, weathering of rock, and atmospheric fixation (Howarth, 1988; Falkowski *et al.*, 1998; Tyrrell, 1999; Fig. 2). Yet, CND can be the primary driver of nutrient capacity in many marine ecosystems, largely because animals may represent the largest pool of biomass – as opposed to many terrestrial

ecosystems where most of the biomass is typically in grasses, shrubs, and trees (DeAngelis, 1992; Valiela, 1995; Chapin, 2002). As such, if animals account for a primary pool of stored nutrients within an ecosystem, they are also important in dictating the rate at which nutrients are cycled internally. An analogous example can be found in tropical rain forests. In these ecosystems, the largest pool of nutrients can be found in vegetation biomass (storage). This pool of nutrients in turn mediates nutrient cycling through supply of dead vegetation which is the basis of nutrient remineralization through decomposition (supply; Vitousek, 1982; Tiessen *et al.*, 1994). The concept of nutrient capacity is rooted in ecosystem ecology theory (see DeAngelis, 1992) and has been significant in calling to attention the importance of CND in ecology (He *et al.*, 1993; Kitchell *et al.*, 1994; Vanni *et al.*, 2013). We structure the next sections around these two components (i.e., supply and storage) of nutrient capacity in marine ecosystems.
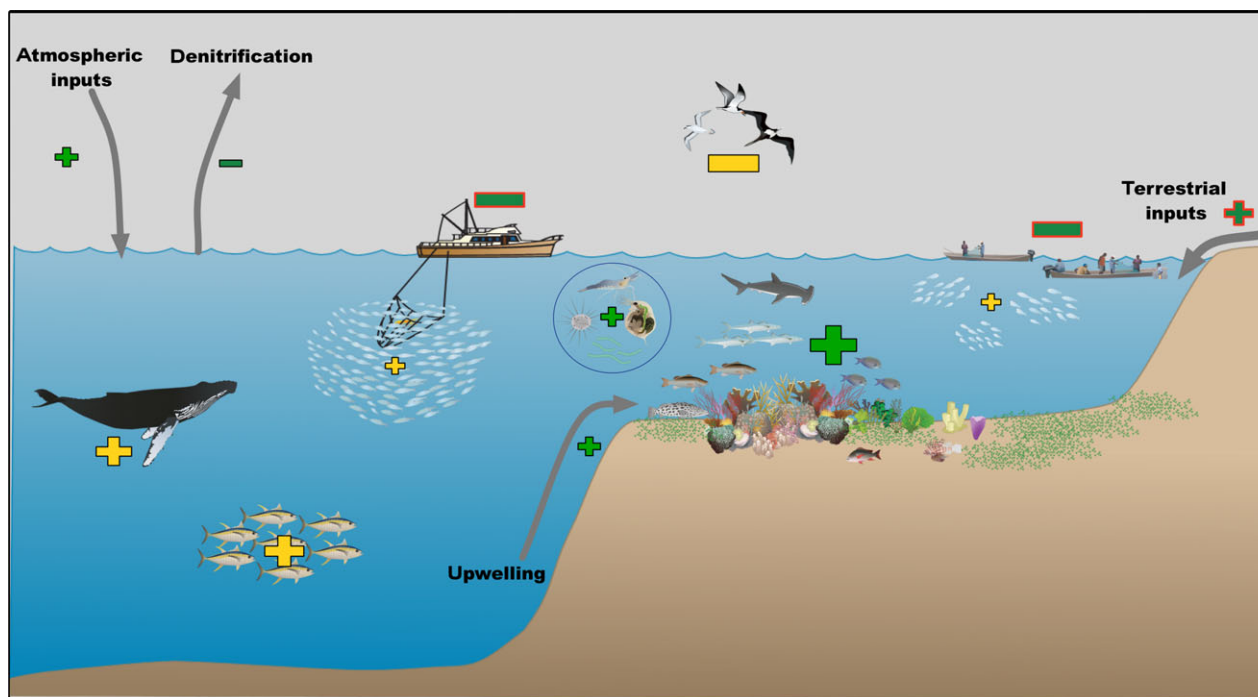
Fig. 2 Schematic of nutrient inputs in oligotrophic marine ecosystems. Plus and minus signs indicate inputs and reductions in nutrients due to various factors. Symbols with red borders indicate anthropogenically altered inputs and losses. For example, fishing represents an important factor that reduces consumer-mediated nutrient dynamics through the removal of animal biomass. In contrast, oceanic upwelling represents a major source of nutrients to coastal ecosystems. Colors indicate temporal context of nutrient inputs whereby green = press inputs (operating on times scales of days to months), yellow = pulse (operating on timescales of minutes to hours). For example, the periodic movement of large animals, such as whales and pelagic fishes, into nearshore systems would likely represent pulses of nutrients. In contrast, fishes that are residents on coral reefs would likely represent consistent (press) sources of nutrients. More details on all nutrient pathways are provided in the text.

Nutrient storage

Consumer-mediated nutrient storage (Carpenter *et al.*, 1992) at the ecosystem scale is an additive function of all individuals in that community. Thus, variation in the body nutrient content of individuals is central to community-wide patterns of nutrient storage. The amount of nutrients stored by an individual is best predicted by biomass (Sterner & George, 2000), as well as the identity of the species (Vanni *et al.*, 2002), although more data are needed to confirm this, particularly in marine ecosystems (see *Future Directions* section below). In contrast, body size or functional (trophic) group are often relatively poor predictors, contrary to expectations from theory and mass-balance physiology (Sterner & George, 2000; Fagan *et al.*, 2002; Vanni *et al.*, 2002; Lemoine *et al.*, 2014). Describing how these factors scale from the individual- to the community-level represents an important challenge, particularly with respect to identifying the ecological consequences of anthropogenically driven changes to community structure in marine environments. Our current understanding of which explanatory variables (e.g., community-level biomass, size structure, biodiversity) best explain nutrient storage in marine ecosystems is largely limited to fish communities in the Caribbean. In these communities, species richness and the biomass of the communities explained the vast majority of variation in community-level nutrient storage across coral reef, seagrass, and mangrove ecosystems (Allgeier *et al.*, 2015b).

Coral reefs offer a prime example in which the nutrients stored in animal biomass strongly regulate within-ecosystem nutrient dynamics (Pomeroy, 1974; DeAngelis, 1992). Because coral thrive best in nutrient-poor environments, coral reefs develop almost exclusively in regions that lack large abiotic nutrient sources such as upwelling or riverine inputs (Szmant, 2002; Atkinson, 2011). Despite this, coral reefs are among the most productive ecosystems on the planet, due to the efficiency with which nutrients cycle among different pools of biomass (e.g., algae, coral, fishes; Hatcher, 1988, 1990). On coral reefs, animals may represent the largest pool of biomass, especially when excluding

carbonate coral skeletons (Sorokin, 1995; Newman *et al.*, 2006). On some coral reefs in the Caribbean, fish biomass alone can exceed 400 g m^{-2} (Newman *et al.*, 2006). In comparison, area-corrected animal biomass in terrestrial systems is often much lower. Even when considering places such as the Serengeti Ecosystem or Ngorongoro Crater, with abundant wildebeest, zebra, and other ungulates, biomass reaches only 8–10 g m^{-2} (Sinclair & Arcese, 1995). Thus, the tremendous amount of nutrients stored in animal biomass in coral reef communities appears to be a principle process that regulates nutrient capacity in these systems.

In contrast, the relative importance of nutrient storage for ecosystem function is considerably different in more eutrophic ecosystems that receive substantial exogenous nutrient inputs (Evans-White & Lamberti, 2006; Vanni *et al.*, 2006; Wilson & Xenopoulos, 2011; Spooner *et al.*, 2013). In these systems, high rates of nutrient delivery from abiotic sources fuel high levels of primary production and reduce the relative contribution of animals for ecosystem nutrient capacity. Instead, a principle role of consumers for nutrient dynamics is the mediation of nutrient capacity through trophic pathways (as opposed to directly fueling primary production via excretion). Nutrients stored in animal biomass are transferred throughout the food web through trophic interactions with two primary fates: (1) They are retained within the same ecosystem after being consumed by other resident animals – thus maintaining ecosystem nutrient capacity (Carpenter *et al.*, 1992; Kitchell *et al.*, 1994; Vanni *et al.*, 2013), or (2) they are redistributed to other areas via movement (Doughty *et al.*, 2015) or removal by transient consumers (Anderson & Polis, 1999; Rex & Petticrew, 2008).

The redistribution of this biomass via trophic interactions or migrations can fundamentally impact the nutrient capacity of both donor and recipient ecosystems (Deangelis *et al.*, 1989). Seabirds, which are important predators of marine fishes, are an important vector of nutrients moving out of marine ecosystems. Global seabird populations consume 70 billion kg of marine fish each year, representing 1963 × 10^6 kg of stored N, just less than the 80 billion kg harvested by humans (Brooke, 2004; Table 1). Migration of consumers also represents an important process that affects nutrient storage of ecosystems. Few examples of this type of translocation of nutrients are more well studied than the migration of salmon (e.g., Doughty *et al.*, 2015). Anadromous salmon typically spend 2–5 years in the marine environment, feeding, and amassing nutrients before they depart for their natal rivers to spawn and die. It is estimated from historical records that migrating salmon exported from the marine environment as much as 6 854 000 kg N and 810 000 kg P per year in

the Pacific Coast of the continental USA alone, a number that has been reduced by ~93% in modern times (Gresh *et al.*, 2000).

The large-scale extraction of consumer biomass from ecosystems by human exploitation may have extensive, long-term, consequences for CND. As an example, whales are increasingly recognized for their important role in marine biogeochemical cycles (Roman & McCarthy, 2010; Roman *et al.*, 2014). Many species of whales spend the summer months in high-latitude, nutrient-rich, feeding grounds where they gain biomass in preparation for the long migration to low-latitude, nutrient-poor, coastal waters where they birth and nurse calves (Roman *et al.*, 2014). Such migrations represent a massive transport of nutrients between these regions, provisioning the nutrient-poor tropical waters with nutrients via excretion and egestion. Further, deposition of whale carcasses following mortality (whale falls), and the subsequent decomposition of animal tissue, is an important but often overlooked fate of nutrients (Roman *et al.*, 2014). Recent evidence has shown that during peak historical whale densities, whale falls translocated ~190 million kg of carbon (C) yr^{-1} to the deep sea, a rate threefold greater than is found today. The reduction in translocated carbon due to historic whaling has been compared in magnitude to the hypothetical Fe-fertilization (climate engineering) projects proposed to mitigate anthropogenic climate change (Roman *et al.*, 2014). The amount of nutrients humans are removing from the world's oceans is increasingly acknowledged (Doughty *et al.*, 2015; Maranger *et al.* 2008; Table 1), yet the implications of this reduced nutrient capacity at a global scale are little known.

Nutrient supply

The supply of nutrients via excretion and egestion is the second primary means through which consumers affect ecosystem nutrient capacity. In some cases, supply represents a continuous press of nutrients, whereby consumption, excretion, and egestion are tightly coupled spatially and temporally, and typically occur at localized scales, for example, fishes feeding and sheltering within kelp beds (Bray *et al.*, 1986). In other situations, supply is more pulsed, whereby consumers translocate nutrients across habitat or ecosystem boundaries by feeding in one area and redistributing nutrients to another. For example, some coral reef fishes make daily nocturnal feeding migrations over tens to hundreds of meters and then aggregate around reefs during the day, which serves to concentrate nutrient supply locally (Meyer *et al.*, 1983). An example at larger scales is the annual migration of whales from temperate

feeding grounds to spawning areas in the tropics, resulting in nutrient redistributions that span hundreds of kilometers (Roman *et al.*, 2014).

At the press end of the continuum are examples where constituent animal- and plant-driven processes are tightly coupled. In these cases, consumer-mediated nutrient supply can drive reciprocal mutualisms where consumers supply limiting nutrients to foundation species (e.g., kelps, corals; *sensu* Bruno & Bertness 2001) that provide habitat for other species, thereby creating a self-reinforcing feedback cycle. One example of this is found in the vast *Sargassum* spp. mats of the western North Atlantic Ocean, constituting a primary producer biomass of perhaps $6–9 \times 10^9$ kg (Butler & Stoner, 1984). As foundation species, *Sargassum* spp. form the basis for an entire ecosystem that supports hundreds of fish and invertebrate species (Lapointe *et al.*, 2014). Fish within the *Sargassum* matrix supply nutrients derived from food gathered within the matrix and the adjacent open water column. These nutrients mediate the growth and overall biomass of the mats and thereby improve the habitat quality (e.g., additional refugia, higher prey densities) for the consumers (Lapointe *et al.*, 2014). Such self-reinforcing feedback cycles between plants and animals have been termed "whole community mutualisms" (Bracken *et al.* 2007), with examples in seagrass beds (Allgeier *et al.* 2013; Layman *et al.* 2013), coral reefs (Holbrook *et al.*, 2008), oyster reefs (Hoellein & Zarnoch, 2014), and temperate rocky intertidal ecosystems (Bracken *et al.* 2007).

Press and pulse CND dynamics both can contribute to productivity within the same system. As an example of press dynamics, on coral reefs, there are consumer–producer relationships at small spatial scales, for example, between sheltering damselfish and coral (Holbrook *et al.*, 2008, 2011). Damselfish feed on zooplankton in the water column, but shelter around coral heads from predators, which serves to translocate nutrients to coral from the water column. These nutrients presumably enhance productivity of zooxanthellae, thereby benefiting coral. Holbrook *et al.* (2008) found that outplanted nubins of *Pocillopora eydouxi* coral grew on average 50% faster on host colonies that had resident fish relative to those that lacked fish.

Nutrients also are translocated across the seascape to coral reefs, essentially creating a daily pulse dynamic. Many species of carnivorous fishes forage in seagrass beds, sand flats, and mangrove habitats at night, but shelter on coral heads during the day (Ogden & Ehrlich, 1977). Through this behavior, fish translocate nutrients from adjacent ecosystems to coral (Meyer & Schultz, 1985b). Sites that consistently shelter fishes can create CND hot spots with up to tenfold higher rates of N and P delivery (Meyer *et al.*, 1983; Shantz *et al.*, 2015)

and up to 70% faster coral growth relative to patches with low densities of fish (Meyer *et al.*, 1983; Meyer & Schultz, 1985a; Holbrook *et al.*, 2008; Shantz, *et al.*, 2015). Herbivorous fishes (parrotfishes, surgeonfishes) tend to feed at higher rates in these CND hot spots, targeting nutrient-enriched algae that compete with corals for space, acting as another positive feedback on coral growth (Shantz *et al.*, 2015).

The ecological relevance of CND in eutrophic conditions is likely more context dependent than in oligotrophic systems. Kelp forests proliferate along temperate coasts in many oceans and are considered one of the most productive systems in the world – largely attributed to the high rates of nutrient supply, especially of nitrate, from oceanic upwelling along nearby coastal shelves. Yet, along the southern coast of California, USA, upwelling events are often seasonal, whereby in the summer months, weakened upwelling reduces nitrate inputs to levels below those required to satiate nitrogen demand for growth of giant kelp (*Macrocystis pyrifera*; Dayton & Tegner, 1984; Brzezinski *et al.*, 2013). Despite the low supply of nitrogen during these summer months, data suggest that kelp growth rates are just as high in summer (Brzezinski *et al.*, 2013). One possible source of this 'missing nitrogen' is from consumer-derived nutrients. Both fishes (Bray *et al.*, 1986) and epifaunal invertebrates (Hepburn *et al.*, 2012) are potential sources of nitrogen around kelps. For example, epifaunal bryozoans can supply up to 122% of the nitrogen needed for kelps to maintain positive growth (Hepburn & Hurd, 2005). This highlights the importance in understanding spatial and temporal coupling between producers and consumers to assess the importance of CND.

The degradation of habitat and alteration of the recipient community via human-driven environmental change may also fundamentally alter the relative impact of CND for ecosystem function (Vanni *et al.*, 2006; Wilson & Xenopoulos, 2011; Spooner *et al.*, 2013). For example, on reefs in the Florida Keys, USA, where coral cover is at historical lows due to coral disease and bleaching, Burkepile *et al.* (2013) showed that there were positive relationships among fish biomass, fish-derived nutrients, and macroalgal abundance. These data suggest that the fish-derived nutrients that previously may benefit coral may now fuel macroalgal production. Further, a negative relationship was found between macroalgal abundance (as facilitated by fish-derived nutrients) and the abundance of juvenile corals. As macroalgae can directly impair coral recruitment, growth, and survivorship (Roff and Mumby, 2007; Vega Thurber *et al.* 2012), these data suggest that on reefs where coral abundance is now low, fish-derived nutrients may act as a negative feedback preventing

coral recovery. This suggests that fish excretion may be important in maintaining steady-state ecosystem dynamics (here coral vs. macroalgal states on reefs), but that other drivers of environmental change may ultimately determine the context in which these interactions occur.

Emerging theory and future directions

Ecological stoichiometry and metabolic theory

A fundamental challenge with respect to CND research is the need for extensive data. Central to our ability to predict the ecological ramifications of altered CND, in particular due to anthropogenic change, is our ability to quantify them at the scale of the individual, population, and community. While we are increasing the precision in estimating past, current, and future ecological attributes of populations and communities (e.g., biomass, trophic interactions), the lack of empirical stoichiometry data on consumers and their diets limits our ability to apply these data toward predictions of nutrient dynamics. For example, bioenergetics models have been widely used to predict trophic interactions and population dynamics of fish and invertebrates (Hansen *et al.*, 1993; Ney, 1993). This modeling technique allows estimation of all major physiological processes using a mass-balance approach, thus providing the ideal framework through which to additionally estimate nutrient dynamics, for example, excretion, egestion, and accumulation of nutrients in biomass (Hansen *et al.*, 1993). Among the most important parameters for these nutrient-explicit bioenergetics models is the relative demand for nutrients by the consumer, which is largely mediated by body nutrient content. Yet, obtaining these data empirically requires processing whole organisms, a daunting task when considering large and/or rare, but ecologically important species.

Because CND are driven by a combination of basic animal physiology (e.g., they are well described by mass-balance models) and environmental conditions, they provide an ideal framework through which to test some of the most basic tenets in ecology. For example, a fundamental dilemma is to reconcile the degree to which ecological processes are generalizable among taxa and ecosystems or are determined primarily by taxonomic identity. Two primary bodies of theory provide a foundation for making such predictions: the metabolic theory of ecology (MTE) and ecological stoichiometry theory (EST). These two theories are concerned with different fundamental currencies, energy (MTE) and materials/elements (EST), and thus may differ in their predictive capacity. A recent analysis explored which was more useful in predicting patterns of CND using an extensive dataset of excretion rates from invertebrates and vertebrates (102 species). They found that individual recycling rates are highly predictable across species – highlighting the utility of MTE and thus body size – to explain most of the variation in excretion rates across species (Allgeier *et al.*, 2015a). Surprisingly, body nutrient composition was a poor predictor of excretion rates, and thus, CND were not in alignment with tenets of EST (though, notably, this work did not test the importance of food resources, an integral component of EST). Nonetheless, a key finding was that explanatory models were substantially improved when including taxonomy (family, more than species identity), again reaffirming the importance of taxa-specific attributes (Vanni *et al.*, 2002; Allgeier *et al.*, 2015a).

Ecological stoichiometry theory also predicts that animals' body nutrient stoichiometry should be relatively constrained within certain levels of taxonomic resolution (Sterner & Elser, 2002). However, work in both freshwater (Cross *et al.*, 2003; Small & Pringle, 2009; El-Sabaawi *et al.*, 2012) and terrestrial ecosystems (Hawlena & Schmitz, 2009) has shown that animals shift their body nutrient content to better align with the stoichiometry of their food resource. For example, recent work on Trinidadian guppies has shown that reduced predation and altered resources can alter the stoichiometry of these fishes, with implications for nutrient cycling, primary production, and food web structure (Bassar *et al.*, 2010). Other evidence for within-species variation in body stoichiometry has been found in freshwater ecosystems (Cross *et al.*, 2003; Small & Pringle, 2009; El-Sabaawi *et al.*, 2012), yet few studies have been conducted toward this end in marine ecosystems. This is especially important in the context of human-driven eutrophication of coastal ecosystems (Cloern, 2001), which may fundamentally shift nutrient baselines leading to altered stoichiometric relationships.

Establishing predictable relationships between body nutrient content and other more easily measured variables (e.g., body size) represents one of the greatest challenges to quantifying CND. Yet, body nutrient content has proven to be poorly predicted by any individual-based (e.g., body size) or ecological (e.g., diet) covariates (Fagan *et al.*, 2002; Hendrixson *et al.*, 2007; Lemoine *et al.*, 2014). A central issue is that while to some extent, the amount of nutrients (C, N, or P) stored in an entire animal is driven by that animal's biomass, the degree to which these properties vary with taxonomy (often at the species level) is substantial (Fagan *et al.*, 2002; Hendrixson *et al.*, 2007; Lemoine *et al.*, 2014). One promising avenue is that the content per body mass of different nutrients are often correlated, for example, C and N (Czamanski

et al., 2011), suggesting that with limited information of taxa-specific nutrient demands, we may be able to extend findings to other nutrients.

Biodiversity–ecosystem function research

There is consistent evidence that CND are highly contingent on the identity of species (Allgeier *et al.*, 2015a, Vanni & McIntyre, 2016, Vanni *et al.*, 2002). This provides an ideal framework through which to test basic questions about the importance of biodiversity (i.e., species richness species and their evenness) for ecosystem function (herein, BEF), but also applied questions about how altering species abundance and diversity may impact CND. The BEF subdiscipline has long focused on the importance of nutrient retention and supply by consumers (Loreau *et al.*, 2001), but a remaining challenge is to better understand how community assembly influences these processes, particularly in light of anthropogenic change. BEF research has a long history in marine ecosystems, particularly within rocky intertidal ecosystems (Paine, 1966). Much of this classic work focused on the importance of diversity for stability and species interactions. More recent research has sought to understand how attributes of species richness and evenness in the consumer community affect the functioning of these ecosystems, for example, seaweed uptake and retention of nutrients (Hillebrand *et al.*, 2009).

Rocky intertidal ecosystems provide a model system to test the relative importance of consumer recycling for primary production within the context of strong abiotic bottom-up drivers (Menge *et al.*, 2003). For example, Bracken *et al.* (2008) showed that changes in species richness and evenness of the seaweed assemblage in a rocky intertidal system altered the performance of the producer community to take up and retain nutrients. Subsequent research in these same systems revealed that CND by mussels played an important role for enhancing primary production, even in areas where bottom-up abiotic forces from coastal upwelling were assumed to dominate (Aquilino *et al.*, 2009). A next step toward a more integrated understanding of CND in the context of BEF theory is to manipulate densities and species composition of both the producer and consumer communities and test biodiversity-mediated ecological feedbacks.

Recent research in tropical coastal ecosystems has also extended the BEF literature to include species-specific processes of nutrient recycling and storage of nutrients in highly diverse ecosystems (Allgeier *et al.*, 2014; Allgeier *et al.* 2015b). One important finding was that the number of species within the community was the best predictor of the amount of nutrients recycled and stored by these communities (Allgeier *et al.*, 2014; Allgeier *et al.* 2015b). Other analyses have shown that human fishing pressure is reducing fish-mediated nutrient processes of storage and supply by nearly half on Caribbean reefs, via selective harvest of certain trophic groups and size classes, despite very little change in the richness of coral reef fish communities (Allgeier *et al.*, 2016). Thus, both the identity of species and their composition within the community are important for mediating CND in reef systems (Allgeier *et al.*, 2016). These findings from some of the most highly diverse species assemblages suggest that the BEF framework is not comprehensive in understanding human impacts on CND (McIntyre *et al.*, 2007; Allgeier *et al.*, 2016).

CND and meta-ecosystems

Meta-ecosystems theory is a recent attempt to provide a theoretical tool to understand the emergent properties that arise from spatial coupling of local ecosystems (Loreau *et al.*, 2003). Rooted in meta-community theory (Leibold *et al.*, 2004; Holyoak *et al.*, 2005), the meta-ecosystem concept incorporates a landscape–ecosystem ecology perspective. In doing so, this perspective unifies these two subdisciplines, community and landscape ecology, in a spatially explicit framework. This allows for incorporation of the flow of materials (e.g., energy and nutrients) with trophic interactions, as they pertain to biogeochemical interactions, that is, supply and uptake of nutrients, between producers and consumers (Gravel *et al.*, 2010; Massol *et al.*, 2011). In this way, meta-ecosystem theory additionally assesses feedback dynamics between consumers and their habitats, thus allowing for a more dynamic model of the relationships between organisms and the environment.

For example, consider the rocky intertidal systems discussed above. These systems are highly influenced by dispersal (Connell, 1985), top-down pressures from predators (Paine, 2002), physical perturbations (Menge & Lubchenco, 1981), bottom-up nutrient inputs from upwelling (Menge *et al.*, 2003), as well as nutrient supply from consumers (Hillebrand *et al.*, 2009). While community interactions are strong drivers in these ecosystems (Paine, 2002), biogeochemical processes play additionally important roles in how they are structured and function (Bracken & Nielsen, 2004; Hillebrand *et al.*, 2008; Aquilino *et al.*, 2009). Possibly the most data-replete application of meta-ecosystems theory to date applied extensive data on community dynamics of species interactions and primary production in rocky intertidal ecosystems to test the importance of abiotic (oceanographic) and biotic (the biological community) forcings at multiple spatial

scales over several years (Menge *et al.*, 2015). Their findings supported previous work showing that at larger scales, oceanographic bottom-up factors are critical determinants of patterns associated with community structure and assembly; however, at smaller scales, species interactions, dispersal, and local currents become more relevant (Menge *et al.*, 2015). While this study represented a powerful test of these two overarching processes for the structure and function on local communities, it failed to additionally incorporate CND, which has been shown to be critical in the feedback dynamics between consumers and primary producers (Bracken & Nielsen, 2004; Hillebrand *et al.*, 2008; Aquilino *et al.*, 2009). Such feedback dynamics represent an explicit component of meta-ecosystems theory, and this example demonstrates that CND still tends to be overlooked in even the most well-studied ecosystems. Integrating CND into the meta-ecosystems framework represents a next step toward building models that more appropriately encompass the complexity needed to capture real-world ecological interactions.

CND and global change

Human activities rarely, if ever, act independently on ecosystems, particularly in marine environments (Breitburg & Reidel, 2005). In particular, two of the most ubiquitous stressors to the marine environment are fishing pressure and nutrient pollution, both of which typically occur in concert, and both of which can alter the relative importance of consumer supply for a given ecosystem. For example, on coral reefs, overfishing has reduced fish-derived nutrients (Allgeier *et al.*, 2016) which deliver N in the form of ammonium (NH_4^+), a species of N that is highly beneficial to coral (Shantz & Burkepile, 2014). However, fish-derived nutrients are being replaced by anthropogenic nutrient inputs from fertilizer and sewage, which is delivered largely as nitrate (NO_3^-), a species of N that has been found to hinder coral growth (Shantz & Burkepile, 2014). Further, Allgeier *et al.* (2014) provided evidence that there may be a critical link between the ratio of nutrient supply by coral reef fish communities and coral health. Specifically, they showed that fish communities across 122 coral reefs in the Caribbean supply nutrients to the local ecosystem at a remarkably consistent ratio of ~15 : 1 to 22 : 1 N : P. The potential ecological relevance of this finding is that under experimental conditions, coral growth rate enhanced when subjected to N:P supply ratios that mirrored the range found across the Caribbean fish communities (e.g., Atkinson *et al.*, 1995). In contrast, coral growth declined, often resulting in death, when nutrient ratios deviated above or below this range (e.g., Ferrier-Pages *et al.*, 2000) – ratios that

are symptomatic of either overfishing or anthropogenic nutrient loading (or both). These findings highlight the complexities associated with shifting baselines of marine nutrient regimes from consumer to anthropogenically dominated, whereby simply changing the species or ratio at which N is supplied, even with little change in the rate of delivery, could have consequences for ecosystem function (Allgeier *et al.*, 2014).

There are additional consequences for the interaction of nutrient pollution and overexploitation of consumers at a global scale (Galloway & Cowling, 2002; Galloway *et al.*, 2008; Maranger *et al.*, 2008; Doughty *et al.*, 2015). Consider marine systems from a simplistic mass-balance approach. The fate of all the nutrients entering the ocean (from rivers and the atmosphere) is as follows: (1) to accumulate in microbial, primary producer, or animal biomass; (2) to be buried in the deep ocean; or (3) in the case of N to enter the atmosphere via denitrification (Table 1 and Fig. 2). Human activities are directly altering two of these processes: the amount of nutrients stored in biomass (reduction via harvesting) and the amount of nutrients entering the system via riverine inputs (increase via runoff, deposition, etc.; Maranger *et al.*, 2008; Table 1 and Fig. 2). Yet considered from a mass-balance perspective, human activity is not only reducing the capacity by which marine ecosystems can store and recycle nutrients, but it is also adding additional pathways through which these nutrients are now being processed. Specifically, marine-derived nutrients are processed via pathways of human consumption and livestock feed (Table 1), and either reenter the marine environment through riverine, sewage, or industrial conduits (some of these nutrients are processed via freshwater and terrestrial primary producers and microbes), or become lost nearly entirely from the system via landfills. In these ways, human activities are drastically altering nutrient pathways with myriad unintended, and often unidentified, ecological consequences (Vitousek *et al.*, 1997).

Beyond conspicuous human-induced alteration of consumer populations via exploitation and habitat degradation, changes in the temperature and chemistry of future oceans may have important implications for CND. Given that CND are directly linked to metabolism and that most marine organisms are ectothermic, rising ocean temperatures and higher metabolic rates will likely mean higher rates of excretion of metabolic waste products. However, ocean acidification has been shown to reduce the aerobic scope of some fishes and reducing their activity (Munday *et al.*, 2009), thus highlighting a potential interaction that may result in unexpected outcomes of climate change for CND. The potential impact of climate change on CND has received virtually no attention to date.

Conclusion

Consumer-mediated nutrient dynamics represents an important avenue of research in ecology. Among the most important roles of CND in the field is that it challenges traditional perspectives of direct, top-down, dynamics, providing an alternative framework through which to approach long-standing discussions in ecology (e.g., consumer vs. resource control of primary production). Importantly, this framework can also be applied toward conservation and management, and emerging ecological theory. We show that CND in marine ecosystems are inarguably important and that a surprisingly extensive body of research currently exists within this marine subdiscipline. Nonetheless, further efforts are needed to fully incorporate CND into models of marine ecosystem function to better approximate the complex dynamics of the real world in the context of global change.

Acknowledgements

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