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Weaving marine food webs from end to end under global change

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ABSTRACT

Marine food web dynamics are determined by interactions within and between species and between species and their environment. Global change directly affects abiotic conditions and living organisms, impinging on all trophic levels in food webs. Different groups of marine researchers traditionally study different aspects of these changes. However, over medium to long time scales perturbations affecting food webs need to be considered across the full range from nutrients to top predators. Studies of end-to-end marine food webs not only span organism sizes and trophic levels, but should also help align multidisciplinary research to common goals and perspectives. Topics are described that bridge disciplinary gaps and are needed to develop new understanding of the reciprocal impacts of global change on marine food webs and ocean biogeochemistry. These include (1) the effects of nutrients on biomass and production, (2) the effects of varying element ratios on food web structure and food quality, (3) bulk flows of energy and material in food webs and their efficiencies of transfer, (4) the ecological effects of species richness and the roles of microbial organisms, (5) the role of feeding behaviour in food web dynamics and trophic controls, (6) the spatial dynamics of communities and links between different food webs, (7) the combined effects of body size and behaviour in determining dynamics of food webs, and (8) the extent to which the ability of marine organisms (and communities) to adapt will influence food web dynamics. An overriding issue that influences all topics concerns the time and space scales of ecosystem variability. Threads link different nodes of information among various topics, emphasizing the importance of tackling food web studies with a variety of modelling approaches and through a combination of field and experimental studies with a strong comparative approach.

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1. Introduction

Food webs are theoretical constructs that simplify the many connections among living organisms. In his articulation of the concept, which he termed "food cycle", Elton (1927) emphasized that feeding was the main ecological process connecting organisms both directly and indirectly. Feeding processes are dynamic and the influence of biotic interactions can change, depending on the state of the community or the ecosystem. Changes in the physical and/or the chemical environment invoke responses, which can be transmitted through the food web, amplified (so they impact on a large area or over a long time or manifest throughout a community), or dampened (such that the effects are short-lived and remain localised). One of the challenges in marine ecology is to predict what changes might occur throughout a marine food web in response to global change, including the effects of climate change (changes in ocean temperature, ocean circulation and stratification), ocean acidification, pollution, nutrient availability, habitat destruction, coastal eutrophication, introduced species and intensive fishing.

There are at least three major disciplinary focus areas that study marine food webs: marine biogeochemistry, marine living resource management and marine conservation (Fig. 1). Each of these research communities typically has their own funding bodies, scientific journals and scientific meetings. They also view marine food web interactions from different perspectives linked to the delivery of specific ecosystem services: respectively, carbon sequestration, fisheries production, and maintenance of biodiversity (Fig. 1). Biotic and abiotic transformations of chemical elements determine global element cycles, with nutrients taken up and recycled in marine food webs. The bulk of material in the ocean moves through low trophic levels, primarily through the microbial communities (Fig. 1). Marine biogeochemical research focuses on the chemical elements, but the packaging of these into living organisms and their recycling via non-living material provides a natural interface between biogeochemical, microbial and planktonic studies.

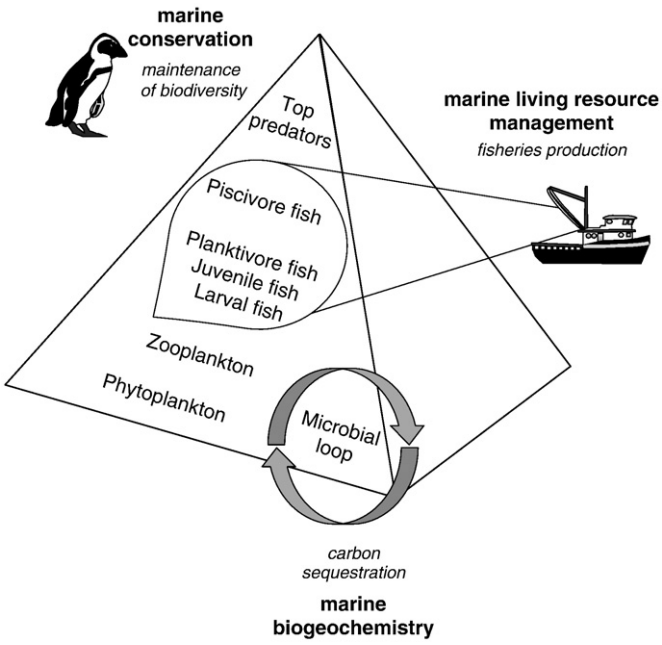


Fig. 1. Trophic pyramid illustrating the levels of interest for different disciplinary research focus areas to sustain delivery of essential ecosystem services.

For marine fisheries production, researchers aim to understand population dynamics of exploited species and the impacts of fishing at all levels, from species to ecosystems. Fish span the mid- to high-trophic levels in food webs (Fig. 1), but fish production depends on energy transfer from primary producers through many levels of the food web. Historically, the effects of fishing have been studied using population-level perspectives. Detailed fish stock assessment models use age or size structures to represent populations, tending to ignore spatial structure (e.g. Garrison and Link, 2000; Bakun and Weeks, 2006) and the genetic diversity of populations (Law, 2000; Kuparinen and Merilä, 2007). Closing the life cycle in these population models is done by empirical stock–recruitment relationships, largely ignoring environmental factors (Ottersen et al., 2006), maternal effects (Berkeley et al., 2004) and food web interactions (Bakun and Weeks, 2006). The recent shift to ecosystem-based fisheries management has extended the area of interest of fisheries scientists, also increasing the area of overlap with conservationists. Among the flagship species for conservation have been marine predators at high trophic levels, especially endotherms (Fig. 1). Similar to fisheries research, conservation research has expanded from a traditional single-species focus to issues of habitat modification, genetic changes and changes in community composition. With increasing concerns about biodiversity impacts of global change, there are also much stronger direct linkages to fisheries management.

The scope of marine food web research needs to be broadened to cut across traditional disciplinary clusters and to span all levels of the biotic system, from end to end. This paper describes different topics (or "threads") that underpin particular research approaches for studying marine food webs. Some of the current issues within these topics are highlighted, and these need to be addressed. However, no single approach can capture all aspects of a food web, no matter how detailed. The aim of this paper is to show why information exchange is needed between disciplines and why the threads of different food web models need to be woven together to improve our ability to predict dynamics of marine food webs under global change. Although multiple approaches are needed, their results have to be contextualised to inform other approaches. A research framework is presented that encapsulates these ideas and that can be used to guide future research activities.

2. Global change: the forcing hierarchy from individuals to communities

The functioning of marine food webs cannot be understood in isolation from the dynamics of the environment, including the effects of human activities. Global change provides multiple forcing factors acting simultaneously on marine ecosystems. Each factor impacts different levels of the food web differently, with some factors primarily having bottom–up effects and others top–down effects. The combined effect of all these factors makes it important to understand marine food webs from end to end, because it is not possible to isolate the effects of each factor.

The main forcing is climate forcing on the physical and chemical oceanography of the basins, which causes variations in the physical and chemical environment on a regional scale (e.g. coastal shelves, coastal upwelling) and subsequently impacts on the local scale of

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individual organisms. There is also localised physical and chemical forcing, such as habitat destruction and eutrophication, which can have both chronic and acute effects on marine food webs. Over the trophic spectrum, the influence of the environment varies, based on the organism's ability to control its position relative to the physical conditions it experiences, and its susceptibility to the chemical environment, including pollutants. Specific environmental variables, such as temperature, have a strong direct impact at all trophic levels, whereas others such as light and nutrients generally influence higher trophic levels only indirectly via bottom–up controls, such as the production of planktonic prey. Ocean acidification is a large-scale factor that potentially has direct impacts at a range of trophic levels.

At the level of the individual, physiology of marine organisms is influenced by temperature, salinity, turbulence, light and nutrients (Fig. 2, left side). More specifically, these variables influence the vital rates of organisms and hence the processes of production, mortality and motion of populations. The net results of environmentally-mediated changes in biological processes can cause top–down or bottom–up effects in food webs. The processes can be quantified through laboratory and field studies, and represented by growth models and individual-based models (e.g. Carlotti et al., 2000; Grimm et al., 2006). Similarly, the net results of physical processes like advection, spreading and vertical mixing occur at the level of the population, affecting distribution and abundance of marine organisms (Fig. 2, right side). Variations in these processes typically are quantified by applying hydrodynamic circulation models (deYoung et al., 2010). The interactions between observations and models at different levels of complexity are necessary to validate both field results and models, and to identify which processes dominate in different situations. The extent to which the individual and population-level processes impact the food web requires consideration of other issues, such as concomitant changes in community composition or food web structures. Typically, all the issues cannot be considered at the same time or using the same food web model. It is necessary to combine insights gained using different approaches and models to develop predictive capabilities.

3. Thematic areas: the threads linking end-to-end marine food web

Real food webs are complex and it is necessary to simplify them to try and understand them. Simplifications can occur in a variety of ways depending on the issues of interest. To address the broad range of issues and achieve an integrated understanding of food web dynamics under global change requires a merging of knowledge and approaches (Worm and Duffy, 2003; Pomeroy, 2004). This is encapsulated by the term “end-to-end food webs”, where the influences of ocean physics and chemistry are incorporated into the

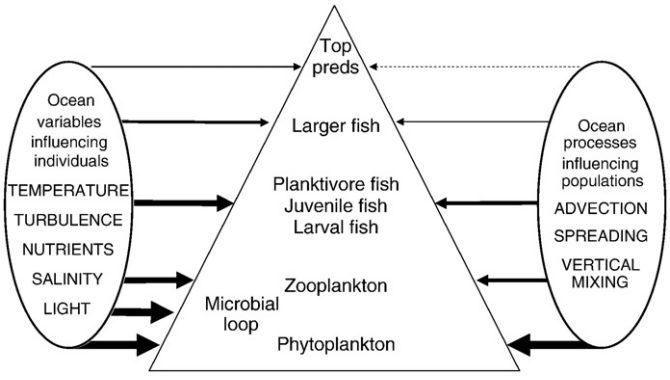


Fig. 2. The environmental forcing hierarchy in the oceans with relative impacts at different levels in the trophic pyramid.

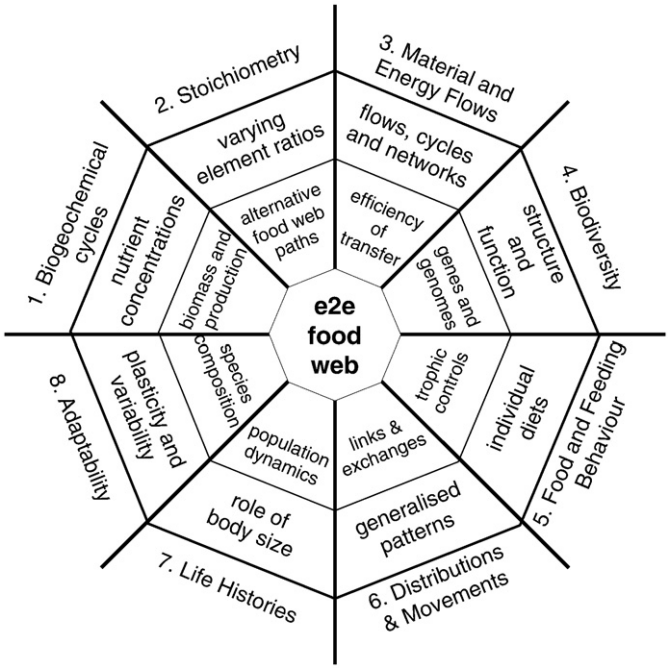


Fig. 3. A framework for end-to-end food web research. Eight major thematic areas are shown, with threads spanning small to large time and space scales and dealing with issues across different levels of organisation. Keywords illustrate processes, issues and approaches.

total feeding interactions, nutrient flows and feedbacks among primary producers, consumers and decomposers over a range of time and space scales. Food webs need to be both unravelled (to identify appropriate levels of detail) and rewoven (to capture the essential elements for simplification and generalisation) to make predictions of future change. The complexity implied by this process is represented in Fig. 3, which shows a framework for end-to-end food web research. Eight major themes are highlighted, each of which requires detailed study, with threads extending from the level of the nutrient or individual to the level of the food web, spanning small to large time and space scales. There are also threads that link thematic areas, and the different levels in the web can be rotated to line up within different themes. To accommodate the difficulty of integrating across so many levels and layers requires new information as well as new methods for dealing with existing knowledge and information. This section will discuss each of the themes in more detail, and suggest some cross-linkages that need to be made between themes.

3.1. Thread 1. Biogeochemical cycles

The cycling of elements within the earth system has important biological intermediaries. In the oceans, research on biogeochemical cycles and food webs tends to focus on processes at low trophic levels, where micro- and macronutrients are both taken up and remineralised. Microorganisms, especially bacteria, dominate these processes (DeLong, 2007). Until recently, marine bacteria had been considered mainly as decomposers of organic matter and they still retain that role in many food web models. In the mid 1970s a new paradigm of the microbial-based food web, or microbial loop, was developed (Fig. 4). In this conceptual model, microbes act not only as remineralisers but also as important consumers of the very large pool of dissolved organic matter that resides in the sea. Marine bacteria produce new biomass, providing pathways of carbon and energy flow that supplement the traditional phytoplankton–zooplankton–fish food chain (Fig. 4b; Azam et al., 1983). It is now known that most primary production in the ocean is carried out by small autotrophs such as

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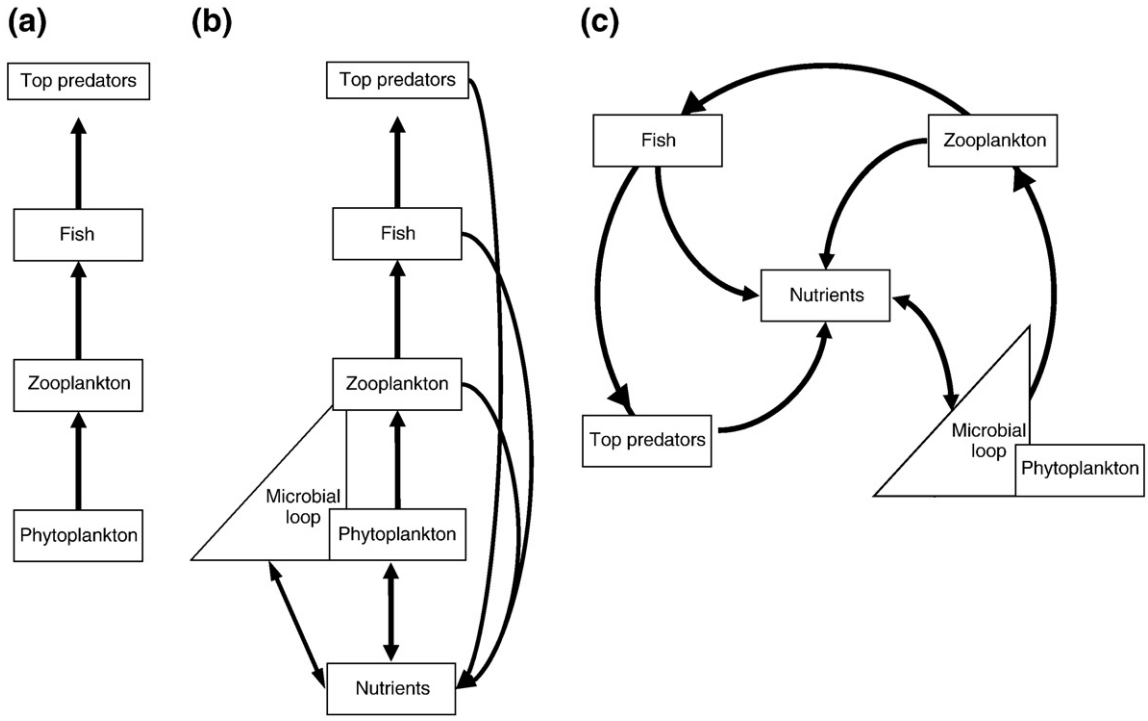


Fig. 4. Development of the marine food web concept. (a) The traditional linear food chain showing the one-way transfer of energy. (b) A nutrient-based food chain incorporating the microbial loop and showing feedbacks. (c) The nutrient-based food chain joined end-to-end and depicted as a continuous cycle.

cyanobacteria, which are consumed by tiny carnivores (usually small protozoa), which in turn are eaten by larger (but still small) microbes or metazoans. Depending upon the number of microbe-based trophic levels and the transfer efficiency at each step, some carbon and energy is passed up to larger organisms. However, because one consequence of being small is a high cost of living, a significant amount of the energy captured by detrital food webs is dissipated, and the efficiency of transfer is probably less than the 10–15% generally assumed for the traditional grazing food chain (del Giorgio and Cole, 2000). Thus the microbial food web supports mainly microorganisms and its primary role in ocean ecosystems is to remineralise inorganic nutrients (especially dissolved inorganic carbon, ammonium and phosphate) and, perhaps, produce growth factors (e.g., fatty acids, vitamins) (Nichols, 2003) that are essential for sustaining photosynthesis. Its important dynamic feature is the short time scale on which an element might move between steps and end to end, although microbial food webs can be switched on and off under unfavourable conditions (e.g. deep ocean, Gooday and Turley, 1990).

The microbial food web is a ubiquitous, persistent source of "pre-packaged" energy for metazoan organisms that are able to consume small prey. Changes in nutrients affect the pathways of energy flow and the structure of food webs in terms of total biomass and species composition. This in turn can feed back into biogeochemical cycles through changes in vertical and horizontal transport of material. For example, in the North Pacific subtropical gyre, environmental change (such as persisting ENSO conditions) has been shown to alter the phytoplankton community by favouring N-fixing diazotrophs for several years. This shifted the ecosystem from N-limitation to P-limitation, with elevated N:P ratios in suspended particles, exported particles and dissolved organic matter in the surface layer (Karl et al., 1997, 2001). Redfield et al. (1963) had shown that marine organisms tend to take up and release macronutrients in proportion to the relative composition of these elements C:N:P in their bodies, but in these recent studies N:P ratios were generally smaller than Redfield ratios in all forms below 500 m, suggesting either that waters below 500 m had yet to come to equilibrium with the elevated N:P ratios in surface waters, or there was preferential recycling of P relative to N above 500 m, a biological transformation that decouples the elements from theoretical Redfield ratios.

3.2. Thread 2. Stoichiometry and food quality

The Redfield ratios have become a paradigm in marine ecology, and are the key conversion factors by which ecologists connect the biological transformations of these elements in the ocean (e.g. Lancelot et al., 2000; Moore et al., 2002). The ratios, which have grown to include oxygen, silicon (for diatoms), sulphur (for dimethylsulphide producers), and the micronutrient iron, are generally considered to be constant, contrary to both the intention of the original authors and mounting evidence on many fronts. From the biogeochemical point of view, complete cycles of elements in the ocean (or the earth system) are linked, but there are critical points in these cycles, especially of nitrogen, where transformations in the form of the element decouple it from the other elements, and from the molar Redfield ratios (currently taken to be C:N:P = 106:16:1). Examples are atmospheric wet and dry deposition, nutrification through fixation of elemental N_2 by diazotrophs (Capone et al., 2005), denitrification in hypoxic or anoxic environments, formation of N_2O (e.g. Deutsch et al., 2001; Nevison et al., 2003), and other N-cycle processes (e.g. Zehr and Ward, 2002; Arrigo, 2005).

In the lower trophic groups of the marine food web, the main trophic coupling is between microzooplankton and small autotrophs such as cyanobacteria, both functional groups basically unknown at the time of Redfield. In cultures under a variety of nutrient regimes, both *Prochlorococcus* and *Synechococcus* were found to have C:P and N:P ratios much higher than Redfield ratios when grown on limiting phosphate (Bertilsson et al., 2003), indicating relatively low P cell quotas. This also indicates that POM derived from them will have elemental ratios different from Redfield ratios. Bacteria generally exhibit C:N and C:P ratios lower than Redfield ratios, with a 60-fold range in C:P for laboratory-grown cultures (e.g. Kirchman, 2000). In general, DOC:DON and DOC:DOP ratios both tend to be larger than Redfield ratios at all depths in the ocean (Benner, 2002), with DOC:

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DOP ranging between 300 and 600 in the deep ocean (Benner, 2002), suggesting remineralisation rates for dissolved matter increasing from C to N and especially to P. Change in the rate of reduction of Si relative to N during high production episodes in surface waters is often interpreted as change in the Si:N uptake of diatoms in response to changes in iron availability. However, during a diatom bloom diatoms become an increasing fraction of the phytoplankton community; the Si:N uptake ratio will increase because only diatoms take up silica (Sarthou et al., 2005; Denman et al., 2006).

What are ecologists to do? The Redfield ratios provide powerful constraints on multi-element models, yet there is ample evidence of marked and rapidly varying departures from these theoretical values. It is clear that ecologists should use different conversion ratios for inorganic and organic matter and that these ratios must be allowed to vary according to environmental and physiological cues. These ratios need to be factored into food web calculations and when determining food quality for different groups of consumers. In studies based on outputs of the Hawaii Ocean Time-series program, Christian (2005) found improved agreement with observations (both depth profiles and temporal change) when using a variable-ratio model than with a fixed-ratio model. The variable-ratio model had variable internal cell quotas for N and P based on the model of Geider et al. (1998). In both cases the inclusion of N_2 fixation was essential. To move towards mechanistic models of variable stoichiometry at the global scale, we need similar observations and analyses for other tropical regions, as well as temperate and subpolar regions. We also need to understand the implications for higher trophic levels of element ratios that change. Because the nutrient limiting primary production can and does change on short time scales, multi-element approaches are required not only in biogeochemical studies but also in fisheries food web models.

In the upper trophic groups of the marine food web, differences in element ratios occur among different taxa and between consumer groups and their food items. For macronutrients, these differences are most pronounced between plants and animals, but there can be effects throughout the food web if food quality changes over space or time, for example by an increase in the C:N ratio of lower trophic-level organisms. Selective grazing and differential recycling of nutrients can result in top–down control by herbivores on plant community structure, as has been postulated for lake ecosystems (Sterner, 1990). Ultimately, the structure, composition and dynamics of food webs will be constrained by the efficiencies with which macronutrients are used and transferred in each feeding interaction (Elser and Hessen, 2005), possibly causing switches between alternative feeding pathways (Shin et al., 2010). Stoichiometric constraints can determine food quality and the manner in which energy is transferred and nutrients are recycled in food webs (Mitra and Flynn, 2005; Elser and Hessen, 2005), leading to a diversity of possible outcomes in food web models (Mitra, 2006; Mitra and Flynn, 2007). Elser and Hessen (2005) suggest that dietary classifications (e.g. herbivore and piscivore) might need to be further refined to reflect different element ratio requirements. Many of these intriguing ideas have yet to be fully investigated in field studies in the ocean.

3.3. Thread 3. Material and energy flows

Food webs are constructed to visualise interactions among species or groups to understand how energy and material are transformed into living organisms, transferred among them and ultimately dissipated (energy) or recycled (matter). These interactions can be represented in simple trophic-level diagrams (Fig. 4), although these can distance top predators from the nutrient base (Fig. 4a and b). In end-to-end food webs the link to biogeochemistry can be emphasized by the central role given to nutrients (Fig. 4c) and by depicting the material flows in the food web as a continuous cycle. The roles of external forcing factors are omitted here (but see Fig. 2).

The biological and ecological processes responsible for dissipation and cycling within end-to-end food webs can be linked to functional groups (Fig. 5). The processes in this conceptual food web model are powered by external energy sources, mainly coming from solar power but also including chemotropy. Light energy enters the food web via photosynthesis and possibly other light harvesting mechanisms that are not well understood at present. For example, the unexpected discovery of a proteorhodopsin-based light-stimulated proton pump in marine bacteria is a mechanism for a novel type of phototrophy in the sea (Béjà et al., 2000). There is a remarkable diversity of proteorhodopsin genes in the marine environment (de la Torre et al., 2003; Venter et al., 2004) and the structure of the protein has been found to undergo a unique “spectral tuning” to match the wavelength of ambient light at various depths in the water column (DeLong et al., 2006). There is also evidence of horizontal transfer of the proteorhodopsin gene among unrelated microorganisms (Sabehi et al., 2007). The discovery of these new phototrophic processes and their roles in the ecological energetics of marine food webs warrant more detailed studies.

Material and energy in the food web are transferred from autotrophs to heterotrophs by ingestion and among the heterotrophs by ingestion and uptake (Fig. 5). In the microbial food web, transfer efficiencies are believed to be relatively low (del Giorgio and Cole, 2000). In traditional food webs, transfer efficiencies typically are based on constant (assumed correct) assimilation efficiencies and throughput times, although it has been shown that these vary according to circumstance (such as food type and food density) for both low- (plankton) and high trophic-level animals (top predators). Growth of an individual depends on the acquisition of energy based on feeding. However, energy only loosely equates with mass in absolute terms because of the matter making up the prey organism (e.g. energy density of cellulose vs fat, water composition of ctenophores vs tunas), the capacity of high trophic-level organisms to release energy (enzyme properties and chemical constitution of the prey e.g. chitinases vs silicates) and the cost (in time and energy) to do so. Variability in these factors has profound implications for our ability to understand energy flux in end-to-end food webs, especially when species compositions change.

In contrast to detailed, mechanistic approaches to understanding energy and material transfer, the metabolic theory of ecology (Brown et al., 2004; Allen et al., 2005) proposes that constraints imposed by body size and temperature can be sufficient to explain ecosystem-level flux, storage and turnover of carbon in low trophic levels (autotrophs, decomposers and labile soil carbon). These ideas were applied to oceanic ecosystems by López-Urrutia et al. (2006), who related the balance between community production and respiration to temperature and suggested that marine biota will provide negative feedback to CO_2 drawdown as a result of global warming, exacerbating anthropogenic effects. Although there is debate about the fundamental premise of the theory and there is controversy over its generality (e.g. van der Meer, 2006; O'Connor et al., 2007), these discussions highlight the need to identify and understand both general patterns in the ocean as well as specific instances of deviations from those patterns to predict the consequences of global change at the local and regional level.

Metabolism, exudation, cell lysis and mechanical breakdown close the loops in the food web from heterotrophs and detritus back to the energy fixers via nutrients (Fig. 5). Material in this food web cycles continuously between living and non-living components from end to end, fuelled by energy inputs. The challenge in understanding food web responses to global change is to advance beyond generic models (Figs. 4 and 5) to predict the range of dynamic behaviours that manifest as specific food webs with particular species compositions and unique responses to forcing factors. This capability cannot be achieved by simply building models that contain all the processes represented in Fig. 5. Many details (Fig. 3) are missing from such

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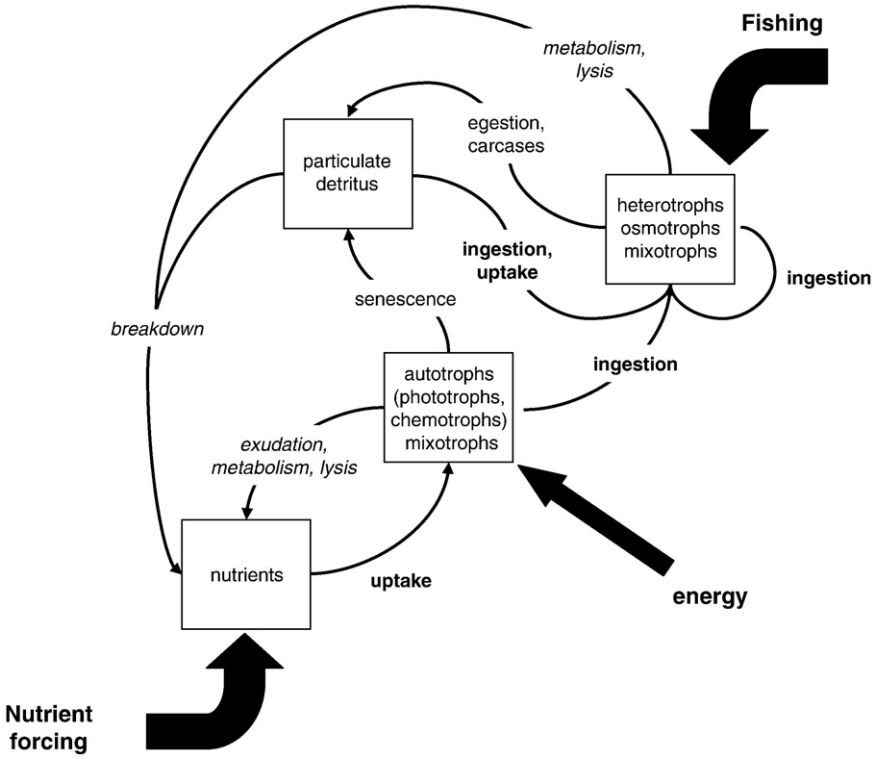


Fig. 5. An end-to-end marine food web (adapted from Cousins, 1980), showing the main links between nutrients (inorganic and organic), the energy-capturing microbial community (including phytoplankton), heterotrophs of all sizes from bacteria to whales, and particulate detritus. Viruses are included implicitly as agents causing cell lysis. Two forcing factors on the food web are represented by bottom–up nutrient (environmental) forcing, and top–down effects of fishing. Note that the web has no beginning or end, although energy input is needed (and is dissipated as heat by living components). The unresolved scientific issues are how perturbations are propagated throughout the entire web.

models and, although the details might not be important in understanding energy and material flows in most cases, they might be pivotal in altering food web structures and the dominance of different pathways.

3.4. Thread 4. Biodiversity

The species composition and species richness of an ecosystem are believed to affect and be affected by productivity and stability (Worm and Duffy, 2003). Most food web models are not resolved at the species level and this is not possible in many instances. Most marine bacteria are near the lower size threshold for detection using optical (brightfield) microscopes and they lack morphological differentiation. It is therefore difficult to assign any putative metabolic or ecological function to marine bacteria based strictly on microscopic examination. Alternative imaging techniques, such as laser-based flow cytometry, and molecular-based techniques have been used to identify individual species and functional groups. In 1988 a new group of photolithoautotrophic bacteria (picophytoplankton, <1 μm in size) was discovered in the North Atlantic Ocean using a shipboard flow cytometer (Chisholm et al., 1988). The characteristic chlorophyll-based fluorescence signal emitted from these tiny cells was too weak to be seen with a conventional fluorescence microscope, which explains how they were previously overlooked as photosynthetically active cells. Subsequent research identified them as the dominant phototrophs in temperate, subtropical and tropical marine ecosystems worldwide. Subsequent genomics-based techniques revealed that the *Prochlorococcus* group is actually comprised of many similar but genetically distinct 'ecotypes', each with a separate niche (Coleman and Chisholm, 2007; Martiny et al., 2008); this also appears to be true for other major groups of microorganisms (Pace, 1997). New ecological theory may be necessary to define interactions between and among these related microbes and their genomes and the consequences of these interactions for the wider food web (Karl, 2007). It is also clear that food web representations based on taxa rather than functional groups or size classes cannot be constructed adequately for microbial components in many oceanic ecosystems at present (DeLong et al., 2006).

Biodiversity monitoring typically falls within the realm of conservation research and usually has not been linked to models of food webs. However, historical disciplinary boundaries have softened over the last two decades with the increasing focus on ecosystem effects of various human activities. Marine biodiversity is believed to influence the delivery of ecosystem services such as fisheries production (Worm et al., 2006) and both species diversity (Stachowicz et al., 1999) and diversity of interactions (Bascompte, 2009) can determine the responses of food webs to perturbations. Analyses of patterns of species richness have also helped inform understanding of food web functioning. For example, wasp-waist ecosystems are defined as those with a reduced number of species at mid-trophic levels (Cury et al., 2000), leading to unique trophic controls in the food web with populations of (usually) one or two fish species exerting top down control on plankton groups and bottom–up control on predator groups.

Changes in species richness can act as indicators of change, as can dramatic changes in abundance of single species or guilds. In marine food webs the relationship between structure (in terms of species composition) and function (in terms of biomass and productivity) has been exemplified dramatically in cases where invasive species have become established in ecosystems. In the Black Sea, the invasive ctenophore *Mnemiopsis leidyi* had a large impact on the pelagic food web (Shiganova, 1998) lasting approximately two decades. The effects of this biological perturbation were exacerbated by eutrophication (Kideys, 2002) and overfishing (Purcell et al., 2001), highlighting the interplay among global change forcing factors. Subtle changes in food webs might be best detected by genomic studies of microbial

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communities. Rapid turnover in the microbial community suggests rapid adaptation to change, and changes in genomes might be used as an early warning signal of functional changes in food webs as a whole or as a tool for tracking change.

3.5. Thread 5. Food and feeding behaviour

Construction of food webs requires knowledge of what eats what. Predicting food web dynamics requires understanding of why and how diets change. Food web reconstructions are time consuming and expensive because they depend to a large extent on routine examination of stomach contents—lots of them (e.g. Daan, 1989). Estimates of diet also tend to be biased because of under-sampling and different retention times in stomachs. Digestive physiology of animals is finely tuned to lifestyle. For example, penguins transport food for their chicks in their stomachs, which also act as their digestion machines. Digestion (via gastric churning) varies during a foraging trip because of the need to replenish energy reserves of the adult while saving some food for the chicks (Peters, 1997). Field studies are needed to establish diet compositions and to monitor changes in these over time and space. Improved understanding is also needed of the factors causing diets to change, and the abilities of different groups of organisms to adapt; understanding the underlying processes should supplement empirical measurements. Variability in organism feeding behaviour and digestion is extreme. Future work must create appropriate 'field conditions' in the laboratory or examine animals feeding in the field to assess the full behavioural and physiological repertoire of feeding and digestion according to environmental circumstances.

In their search for prey, most simple organisms rely on physics (e.g. Brownian motion) for encountering potential food substances. The next level of complexity involves an increase in mobility, often assumed to be stochastic for modelling purposes, e.g. random walks. More complex animals process past and present information from their environment to make decisions. To understand the causal factors influencing feeding behaviour requires improved understanding of what animals really do in the wild (e.g. using GPS and dead-reckoning). To date, this has been best achieved through studies on top predators (Grémillet et al., 1999; Wilson et al., 2002; Williams et al., 2004). Applying current techniques to small- and medium-sized animals (e.g. chaetognaths) that cannot be fitted with high-technology equipment will be difficult, although very small animals can possibly be studied in the laboratory, as has been done for feeding studies on zooplankton (e.g. Paffenhöfer, 1988; Price, 1988; Kiørboe and Saiz, 1995). At the individual level, the process by which animals locate and secure food becomes more complex from the beginning to the end of the food web. Within animal groupings, this stems to a large extent from animal size and how allometry affects organism capacities. Large animals have complex neurological systems, enabling them to make complex probabilistic calculations regarding prey encounter. This is bolstered by enhanced sensory capacity (including ability to perceive and react to strategies adopted by conspecifics). Large animals also have low relative costs of transport and are able to move independently of the physical environment so that probabilistic solutions can be executed. Large animals have low mass-specific rates and can feed infrequently and thus exploit food resources that are temporally unpredictable. Therefore, it might be expected that large animals will be more adaptable than small animals in their ability to move away from unfavourable environments, although important exceptions are known to occur among land-based breeders such as seabirds (Fig. 6).

Individual feeding interactions aggregate to become trophic controls between populations or guilds. Top–down, bottom–up and mixed trophic controls have been postulated (Cury et al., 2000), but the thresholds for switching from one type of control to another are not well understood. When populations are reduced (e.g. by fishing) there can be compensatory effects within trophic levels (e.g. favouring a predator by removing its competitor) or cascading effects between trophic levels (e.g. relaxing predatory control of a prey species, which intensifies predation on its prey). Effects of fishing on the food supply of top predators, e.g. seabirds and marine mammals, have been the focus of scientific interest (Tasker et al., 2000), but top–down controls on lower trophic levels in the ocean have hardly been addressed, in contrast to freshwater systems (Pace et al., 1999). Evidence for top–down control in marine food webs exists from time series and other analyses of standing stocks at various trophic levels (Frank et al., 2005; Daskalov et al., 2007; Myers et al., 2007; Österblom et al., 2007). Studies on the feeding ecology of pelagic fish have revealed species-, size- and stage-specific predation on zooplankton, which has the potential to control prey populations, despite an overall limited consumption compared to standing stocks of prey (van der Lingen et al., 2006). However, an inverse physical forcing on predator and prey dynamics can mirror trophic control. Thus, detection of trophic controls requires detailed process understanding of predator–prey interactions and population dynamics.

3.6. Thread 6. Distributions and movements

Distributions and movements of organisms in the plankton (microbes, phytoplankton, zooplankton and larval fish) are, by definition, strongly influenced by physical processes (Fig. 2). Distributions of planktonic organisms can be closely linked to environmental variables, as has been shown in changing distribution patterns and species compositions in North Atlantic plankton (Beaugrand et al., 2002). In contrast, organisms in the nekton (adult fish, marine turtles and mammals, seabirds) can use individual motion to control their distributions and movements, although these are linked to plankton distributions by feeding requirements. Individual behaviour determines exposure to predators and prey (Fig. 6) and in changing environments there can be great fluidity in behavioural responses. There are potentially many permutations for space–time use by animals. These will be constrained by factors that depend on animal size but some commonalities have been noted in track patterns among diverse taxa (Viswanathan et al., 1999; Bartumeus et al., 2005). Since animals searching for prey or avoiding predators have similar constraints, commonalities are to be expected, and identification of these can facilitate comprehension of the scales of spatial changes.

Regular vertical migration is a striking feature of many marine organisms (Fig. 5; Hays, 2003), allowing animals to inhabit environments that are beneficial only part of the time with regard to predators and prey as well as increasing track length. Within major groups, different species exhibit different patterns of vertical migration. Physics indicates that vertical movement is affected by the direction and extent of vertical forces acting on the organisms and is related to the difference between overall body density of the animal and the surrounding water i.e. buoyancy. Although extreme selection pressure is to be expected for density conformers, animals that repeatedly migrate vertically can recover some energy lost moving against positive or negative buoyancy forces by moving vertically passively back to their start point (Williams et al., 2000). Animals that show the greatest vertical migration are likely to produce the greatest departure in body density from that of seawater, particularly if passive movement, or passive movement accentuated by active swimming, has a selective advantage. Density differences between organism and environment are also likely to produce the greatest rate of change of depth (in the absence of movement) in large animals, modulated by drag coefficients dependent on body shape. In order to fully understand vertical movement in the different trophic levels, the physical properties of vertical migrators need to be identified and translated into organism energy expenditure against the background of biological conditions that select for, and against, vertical movement. In a changing ocean, such estimates should be interpreted in the

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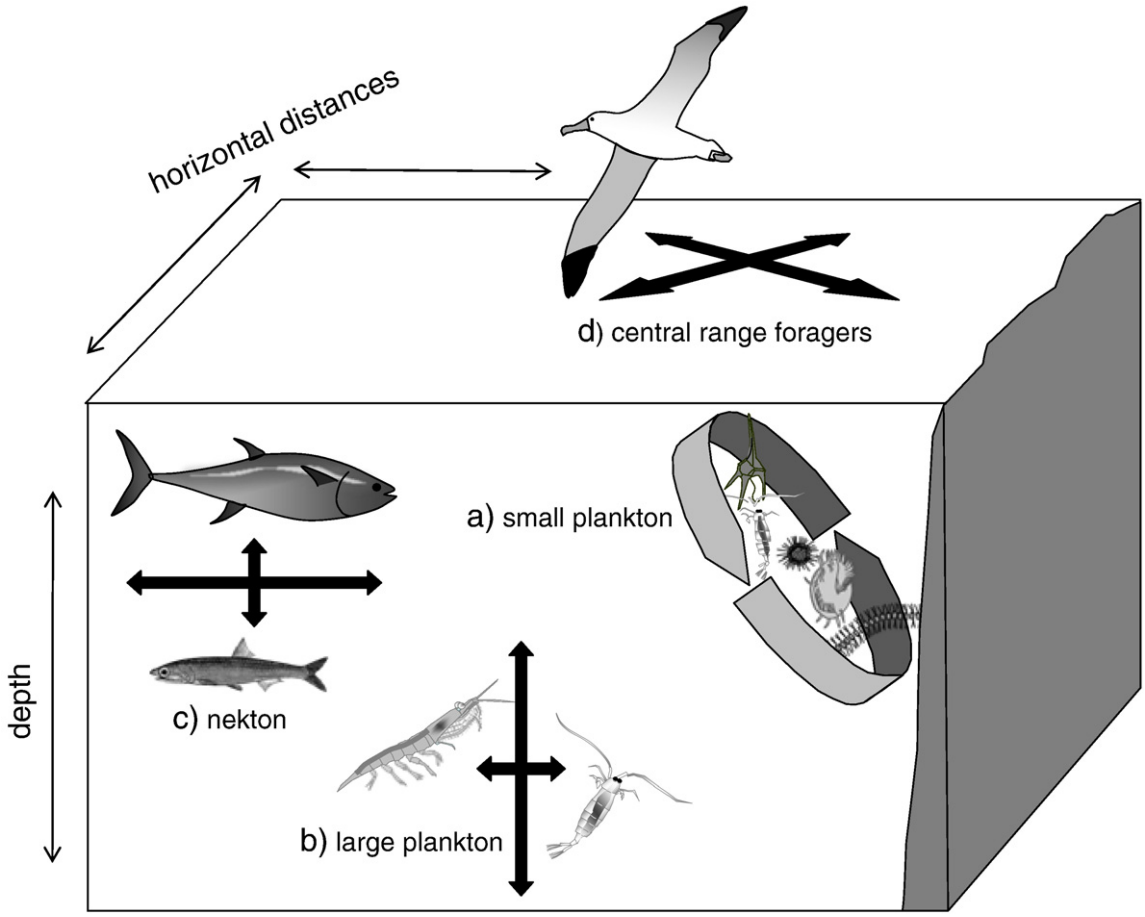


Fig. 6. Relative scales of horizontal and vertical movement of marine plants and animals. a) Small plankton tends to move vertically and horizontally with water masses. b) Large plankton use vertical movements rather than horizontal to control their positions. c) Nekton is able to cover large horizontal distances, and tend to use vertical movements for physiological control, feeding, or predator avoidance. d) Air-breathing predators can cover large horizontal distances but are tied to varying degrees to breeding locations.

context of vertical density and temperature structures in the water column in different regions and at different times.

Food web (and ecosystem) boundaries are artificial and arbitrary, and extensive vertical and horizontal movements will result in some animals moving regularly between "food webs". These animals can be links between disparate communities, with linkages strengthening or weakening as ecosystems change. Other processes like sedimentation, advection, upwelling and mixing also provide connections between food webs. The importance of these connections, which can provide food web "subsidies", and the extent to which they vary have not been elaborated in the ocean (see Polis et al., 2004). Linkages between food webs are particularly relevant for global studies and long time scales.

3.7. Thread 7. Life histories and population dynamics

Marine organisms span a range of sizes through their life span, typically changing diets as they grow so feeding linkages are determined by both the species and its life stage. Complicated interactions, such as ontogenetic reversals in the roles of predator and prey, are common. This feature is difficult to capture in taxon-based models, and it is necessary to adopt size-based or function-based approaches to capture the richness of interactions in marine food webs.

Many changes in feeding interactions derive from population and species level dynamics. For example, schooling in fish and swarming in zooplankton are not universal; only some species display this behaviour, which is often linked to body size. Intra-species collaboration to find food or minimise predation or find mates can collapse at population density thresholds, so that trophic interactions and other population processes (e.g. reproduction) are non-linear and discontinuous with population size. Similarly, the importance of stochastic processes at small population size (e.g. Allee effects) is recognised in the conservation biology literature, but seldom considered in marine food webs. At reduced population sizes, Bakun and Cury (1999) suggested that individuals of small pelagic species can become trapped in schools dominated by more abundant species (the "school trap hypothesis"), compromising their individual fitness and the ability of their populations to recover. The consequences of such behavioural factors on population dynamics are difficult to incorporate into deterministic food web models, but population-level issues can be key in affecting food web dynamics. Greater flexibility is required in models to accommodate these factors. One approach is to switch between food web structures and dynamics on the basis of the abundance of key species, as has been discussed for Benguela upwelling food webs (Smith and Jarre, submitted for publication) and described for Southern Ocean food webs (Murphy et al., 2007).

3.8. Thread 8. Adaptability

A key feature of living organisms is that all individuals are different. Species can display great plasticity in form in different environments (Via et al., 1995) and they are able to adapt and evolve in response to their environments and other selective forces. Selective breeding in aquaculture has caused genetic changes in populations (Law, 2000) and theory, models and data indicate that fisheries can cause phenotypic changes (Longhurst, 2006) as well as evolutionary changes in fish species, but the information to quantify these changes is still lacking (Kuparinen and Merilä, 2007). Selective pressures are also imposed by environmental change. How quickly are different

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taxa able to change their lifestyle as their environments change? On a general level, endotherms can accommodate temperature changes within limits, whereas ectotherms can't. In contrast, ectothermic fish can move away from unfavourable conditions because they live in a fluid environment, whereas endothermic seabirds and pinnipeds are tied to unmoving terrestrial breeding localities (Fig. 6).

Biological processes at the subcellular level and the level of the individual need to be incorporated into understanding of ecological change (Verity et al., 2002). Can genetic theory and data be used to predict which taxa are likely to adapt fastest to change? Globally, there are examples of taxa that appear to show a high propensity for adaptive change, e.g. cichlid fishes, island finches, host-specific insects (Bridle and Jiggins, 2000; Dieckmann et al., 2004). Marine microbes exhibit major differences in genome size and gene transfer potential among groups occurring in high and low nutrient environments (Polz et al., 2006). Changes in biodiversity can both cause and result from changes in productivity and stability of food webs (Worm and Duffy, 2003). Changes in the abundance of species, from primary producers to top consumers, have the potential to unbalance food webs (Bakun and Weeks, 2006), altering the character of the food web and ecosystem (Cury and Shannon, 2004; Österblom et al., 2007) and potentially feeding back to climate (Bakun and Weeks, 2004).

Food web interactions are complex and non-linear. In a changing ocean, ecological adjustments sometimes have unexpected and far-reaching consequences (Bakun and Weeks, 2006). It is this complexity that confounds our ability to understand and thus predict the full range of possible outcomes when ecosystems are perturbed. For example, there are a number of documented examples of introduced species having unpredictable impacts on marine species and food webs. On Gough Island in the South Atlantic Ocean introduced house mice *Mus musculus*, which have significantly larger body sizes on the island than elsewhere (Rowe-Rowe and Crafford, 1992), have been found to exert extensive predation mortality on seabirds, including chicks of Tristan albatrosses *Diomedea (exulans) dabbenena*. In South Africa, the introduced mussel *Mytilus galloprovincialis* was found to cause mass mortalities in populations of a mobile, burrowing, predatory crab *Ovalipes trimaculatus* through settlement by mussel larvae on the eyestalks and mouthparts of buried crabs, these being the only hard substrata protruding above the sandy bottoms in the surf zones where the crabs live (Branch and Steffani, 2004). Such unpredictable effects introduce a cautionary note to the limits of predictability in food webs and ecosystems. One way to accommodate these unpredictable biological effects is by including stochastic elements in food web models.

4. Meeting the challenges: tools for advancing end-to-end food web understanding

The essence of the end-to-end approach for predicting changes in marine food webs is synthesis. Detailed understanding is required of food webs in different ocean areas, and all the topics outlined in Fig. 3 have a role to play in addressing specific food web objectives. However, to understand the full consequences of change for food web dynamics requires that relevant threads be linked at appropriate times. Thus, for example, food web models that represent bulk flows of material and energy among trophic levels or functional groups cannot altogether neglect possible changes in species composition. Similarly, taxon-based models that aim to understand the roles of important species in the food web cannot ignore the size basis of many feeding interactions. Integrating across different food web approaches requires a combination of tools and disciplines using first principles understanding and empirical methods. Detailed process studies are required to understand causal mechanisms, especially those mechanisms that influence feeding behaviour. Field biologists and experimentalists study individual animals through the use of telemetry and other tools, and a rich array of behavioural responses has been identified. Both “lower” and “higher” organisms behave in complex ways in relation to their environment, and behavioural understanding should be extended from seabirds and mammals to zooplankton and fish. From the richness of modelled and observed behaviour of organisms, general relationships need to be identified and quantified. Current understanding of feeding behaviour within different groups of animals should be synthesized to derive general patterns of feeding responses, to identify exceptions to the norm and to understand why, when and where these exceptions occur.

Models are essential tools for understanding end-to-end food webs and there are a large number of existing and newly-developed food web models and modelling approaches that span a number of levels in the food web (Travers et al., 2007). To handle the complexity that this introduces for high trophic levels, deYoung et al. (2004) proposed a species-centric approach in which functional complexity is represented in greatest detail at the level of a key species, tapering off at trophic levels above and below. This rhomboidal modelling approach requires that information from the focus level be synthesized and condensed for adjacent levels. For two-way coupling of models the interfaces between the trophic levels become important, although links at the same trophic level cannot be neglected.

Integrating across scales and groups and linking food webs from end to end requires biogeochemical models and high trophic-level models. Functional groups tend to be used to represent low trophic levels whereas species are used for high trophic levels (Travers et al., 2007). These differences introduce complications of converting between energy, nutrients and mass, issues that are affected by food quality and ecological stoichiometry. Because no model can reproduce reality and no single model can capture all processes adequately, a multi-pronged approach is required to address questions about changes in biodiversity, nutrient cycling, productivity and energy flows in end-to-end marine food webs under global change (Fig. 3). These studies need to involve a range of marine environments and a correspondingly large number of food webs, from ocean gyres to coastal waters, from polar regions to the tropics, from the surface ocean to the deep sea, and for different seasons. The issues are larger than a single discipline or region, and a concerted international effort is required with continuous synthesis. The priorities for future study of end-to-end food webs will depend on the ecosystems, the questions being asked and the groups of people involved. This manuscript has provided a structure (Fig. 3) that captures different perspectives and broad issues, and that can be used to identify and prioritise issues into the future. Opinion concerning which of the issues are currently most important is contained in the text. However, the integrated study of end-to-end marine food webs is in its infancy and other directions for study are likely to develop in the future.

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