

Ecological theory and continental margins: where shallow meets deep

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Continental margins, where land becomes ocean and plunges to the deep sea, provide valuable food and energy resources, and perform essential functions such as carbon burial and nutrient cycling. They exhibit remarkably high species and habitat diversity, but this is threatened by our increasing reliance on the resources that margins provide, and by warming, expanding hypoxia and acidification associated with climate change. Continental margin ecosystems, with environments, constituents and processes that differ from those in shallow water, demand a new focus, in which ecological theory and experimental methods are brought to bear on management and conservation practices. Concepts of disturbance, diversity–function relationships, top-down versus bottom-up control, facilitation and meta-dynamics offer a framework for studying fundamental processes and understanding future change.

An introduction to continental margins

Located adjacent to the heavily exploited and trafficked coastal zone, the continental margins (100–4000 m depth) comprise ~15% of the seabed. They are dynamic, heterogeneous settings shaped by tectonic, terrestrial and oceanographic influences [1]. Water masses with distinct hydrographic characteristics overlie the bottom, creating strong gradients in pressure, temperature, oxygen, food supply and substrate stability that rival in intensity any on the planet [2,3]. Canyons, gulleys, mounds and banks interact with currents to create flow conditions suitable for reefs of corals [4], sponges [5], cnidarians, and giant, agglutinated protozoans [6], while plate subduction squeezes methane-rich fluids from the crust, supporting large beds of siboglinid worms, clams, and mussels [7]. These structure-forming species in turn create crucial habitat for numerous protozoan and invertebrate species [4–7]. Given this significant abiotic and biotic heterogeneity, it is not surprising that the continental margins host unexpectedly high rates of population differentiation [8] and some of the planet's highest species diversity [9].

The margins also provide essential ecosystem functions and services [10]; they are where 90% of the ocean's carbon burial occurs [11], yielding realized and potential energy resources in the form of oil, gas and methane hydrates, as well as forming a major sink for anthropogenically generated carbon dioxide. Thus, climate remediation schemes to sequester CO₂ [12,13] could eventually target or indirectly influence the margins. As shallow-water fishery resources are depleted, fisherman exploit increasingly deeper popu-

lations, often generating disturbance that has devastating long-term consequences for sustainability and margin habitats [14,15].

Despite increasing human dependence on the margins and accelerating levels of human-generated disturbance (Box 1), the scientific knowledge required for sound management remains limited. Although this is partly the result of poor access and the great expense of research at sea, the conduct of margin research in relative isolation from other ecological endeavors has also slowed conceptual advances. Here, we identify the features of the continental margin that might benefit from tests of emerging theories about ecosystem biodiversity, structure and function, and provide a modern ecological framework for the management of human impacts in crucial margin habitats.

Deep-sea diversity: a historical perspective

Unexpectedly high diversity in the deep sea was first recognized during the 1960s [16]. Sampling of macrofauna yielded up to 56 species per 100 individuals or 100 species per 0.25 m² [17]. Initially, the Sanders 'time-stability' hypothesis [18] invoked equilibrium conditions and competitive niche diversification to explain this high marine diversity. The focus soon shifted to disequilibrium theories [19,20] emphasizing life-history adaptation, predation pressure, environmental grain and small-scale physical and biological disturbances. These debates more or less paralleled in time the diversity–stability debate among terrestrial ecologists [21]. Limited experimental testing of these ideas in the deep sea (and on land) yielded equivocal, often conflicting results [17].

Disturbance has long been embraced as a strong force that acts to generate diversity on many scales in the deep sea. Manifestations of disturbance range from small-scale tubes, tracks, pits and fecal mounds, to intermediate-scale phytodetritus falls, benthic storms, methane eruptions and mud slides, to debris flows and turbidity currents that can extend for hundreds of km [3]. Contemporaneous disequilibrium, in which the deep sea consists of successional patches subject to varied forms of biotic forcing, can explain how small-scale, periodic or episodic events that generate heterogeneity in space and time might enhance diversity [22].

Sampling of the North Atlantic margins revealed bathymetric diversity gradients, with mid-slope diversity maxima for multiple taxa [23]. Geometric constraints have been explored and rejected as sole explanations for observed mid-slope diversity maxima [24]. Although it is generally recognized that depth itself is probably not a primary driver of diversity, it is often the best predictor,

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Glossary

Agglutinated protozoa: single-celled organisms such as Foraminifera or gronids that can glue sediments or other particles together to form elaborate, sometimes large dwelling structures (called tests).

Alpha diversity: biodiversity within a single area, habitat, community or ecosystem.

Bathyal: referring to depths of 200–3000 m, also considered the continental slope.

Bathymetric diversity gradient: changes in diversity with water depth. Here, we refer to diversity in the benthos (sea floor).

Beta diversity: rate of turnover of species across habitats, ecosystems or an environmental gradient.

Bottom-up control: regulation of community structure by food supply, usually primary producers.

Chemosynthesis: the process of carbon fixation by microbes via chemical energy, in this case via sulfide oxidation or methane oxidation.

Contemporaneous disequilibrium: community dynamics characterized by patches subject to differential predation, food inputs and physical disturbance. These maintain the seafloor as a successional mosaic, which has high diversity when viewed as a whole.

Demersal fishes: fish that live on or near the sea floor.

Deposition centers: Regions with high organic matter flux to the seabed. This is the result of high surface production or advective input, often through a confluence of currents and topography that causes enhanced particle deposition.

Dispersal kernels: a probability function that describes the distribution of larvae as a function of distance from the source of those larvae.

Diversity–stability debate: an ecological debate active during the 1950s–1970s that argued more diverse assemblages or communities should be more stable (in abundance and composition and their interactions over time).

Ecosystem engineers: organisms or structures produced by organisms that alter substrate, flow regime, geochemical setting, food supply, or predation pressure for associated organisms

Episymbiosis: symbioses in which organisms (here microbes or animals) live on the surfaces of other organisms.

Foundation species: species that have a key role in structuring communities through the provision of habitat or via food chain interactions. In some cases this role may be larger than implied by species abundance or biomass.

Geometric constraints: the presence of physical boundaries to species distributions (e.g., upper depth of 0 and lower depth of 4000 m for the margin), which leads to maximal diversity in the middle.

Hypoxic: low oxygen conditions (in the deep sea, oxygen concentrations of $\leq 22 \mu\text{M}$, 0.5 ml L^{-1} or 10% saturation).

Insurance hypothesis: one explanation for a possible positive relationship between species diversity and ecosystem function. This hypothesis states that different species perform optimally under different conditions, at different times. As most environments fluctuate in time, those with more species are likely to exhibit superior function (i.e. production, remineralization, etc.) integrated over time.

Mass effect model: a metacommunity model in which the distribution of large, abundant, source populations influences the structure and dynamics of communities occupying smaller or disturbed patches.

Oligotrophic: low-nutrient conditions

Oxygen minimum zone (OMZ): midwater ocean layers with oxygen concentrations $\leq 0.5 \text{ ml L}^{-1}$; typically affects the continental margin at depths of 100–1000 m. OMZs result from a confluence of upwelling, high primary productivity and oxygen demand, stratification that reduces mixing, and ‘old’ seawater.

Patch dynamics model: a metacommunity model in which habitats that are patchy in time and space exhibit colonization dynamics that interact with species’ competitive interactions to structure assemblages.

Sanders time-stability paradigm: a theory that explains high faunal diversity in the deep sea; based on the belief that extreme physical, chemical and biotic stability in the deep sea allows extreme specialization of organisms over time, generating the observed coexistence of many species.

Seep ecosystem: seafloor assemblages fueled by chemosynthesis based on reduced compounds (methane, sulfide) in fluids seeping from the sea floor.

Species sorting model: a metacommunity model in which strong environmental gradients govern niche specialization, and thereby regulate community structure.

Subduction: movement of the earth’s crust in which one plate is dragged beneath another; referred to here as the downward movement of oceanic crust beneath the continents.

Top-down control: regulation of community structure by consumers.

continental margins (e.g. northern to southern hemispheres or oligotrophic to eutrophic settings) or from stable (passive) to tectonically active margins are needed to promote understanding of (i) whether diversity is always maximal at mid-slope depths; (ii) if so, why? and (iii) whether there are fragile mid-slope features whose persistence is required to sustain diversity.

Most key ideas about deep-sea diversity generation and maintenance were developed during the 1970s and have yet to be revisited in a truly modern context in which margin systems are recognized as exceptionally heterogeneous on a scale of hundreds of meters. Trawling, drilling, mining and waste-dumping activities represent common sources of anthropogenic disturbance that contrast in scale and intensity with natural agents. Often these disturbances homogenize the seabed surface, removing diversity-generating biotic structures [25], but they can also have analogs in natural disturbance events [26], including benthic storms, turbidity flows, mass wasting and mud volcano eruptions or from upwelling-induced hypoxia, which eliminates structure-forming biota. We suggest that biotic responses to both anthropogenic and natural disturbance be documented with an eye to ecological theory involving functional groups or guilds, and successional processes including facilitation and inhibition. The spatial scale of these disturbances, their frequency and intensity can dictate the population responses, sources of colonizers and speed of recovery [27].

Diversity and ecosystem function

Ecologists have begun to explore the relationship between species (or functional) diversity and ecological functions and services [28]. Although they first appeared with a terrestrial focus, biodiversity–ecosystem function (BEF) hypotheses have now been adopted by marine scientists working in shallow water [29] but are just starting to be addressed in the context of deep-water functions [30]. The current paradigm integrates two disparate approaches: the ecosystem approach, which identifies element, energy or biomass cycling and production as functions of interest, and the population–community approach, which examines species-level, and functional-group or biological trait dynamics. While they represented for many years a clear dichotomy in deep-sea science, these approaches are now converging to target diversity–function relationships. Most shallow marine studies on BEF involve small-scale experiments conducted at low levels of species richness [29]. Experimentalists have yet to consider BEF relationships in deep-sea ecosystems where many species coexist at low densities. The use of multiple biological traits as a proxy for function enables inclusion of many species and the detection of human-induced changes [31]; application of such methods to changing diversity–function relationships resulting from disturbance on margins could prove valuable.

The unexpectedly high variation in biotic diversities observed on margins [3,9,17] can provide opportunities for exploring mechanisms linking diversity and function, redundancy and function, and temporal variation in these relationships. Order-of-magnitude changes in metazoan and protozoan species diversity (i.e. β diversity) occur over

and no consensus exists regarding the relative importance of other contributing factors, such as sediment grain size, productivity or water flow [3]. Comparisons of bathymetric trends in diversity and standing stock across different

Box 1. Humans as agents of change on continental margins

The continental margins are an emerging frontier for commercial interests, with increasingly attractive natural mineral, fuel and food resources [86,87]. As with most new frontiers, there are few regulations and economics rules behaviors. Here, we highlight the realized and potential forms of the human footprint on continental margins.

- Upper continental slope fisheries are now common on seamounts and along Pacific and Atlantic continental margins [14,15,88]. As most deep-sea fishes are long-lived, slow-growing and mature late, these fisheries are unlikely to be sustainable [88]. Most deep fisheries involve destruction of the benthic habitat, especially biotic structures such as deep corals, which form over centuries if not millennia [25,58,59].
- As terrestrial and shelf oil and gas resources are depleted, exploration and drilling activities move deeper. Drilling is now common at depths of 500–1000 m and occurs as deep as 3000 m on margins [87].
- Large-scale mining of manganese, phosphorite, carbonates, metals and other minerals from seamounts, the slope, hydrothermal vents and the abyssal plain might soon become commercially feasible, and possibly common practice [86,87,89]. Concerns include effects of disturbance on ecosystem functions, connectivity and persistence of endemic species.
- Humans have generated sites of localized, deep-water organic enrichment or toxic inputs through waste disposal. Examples include sewage dump sites off New Jersey, USA and long-lived radioactive wastes buried in the North Atlantic [26,86].
- Large-scale areas of eutrophication occur offshore through persistent urban, industrial and agricultural runoff. Eutrophication contributes to toxic algal blooms or creates hypoxic ‘dead zones’ in coastal regions, which affect the deeper margin both directly and through organism and nutrient transfer.
- Changing CO₂ concentrations and corresponding alteration of temperature, ice cover, freshwater inflows, oxygenation, stratification and circulation are modifying the continental slopes [40,41,90,91]. These induce variations in surface production, pH and water mass distributions that can result in indirect but potentially strong effects on biodiversity and ecosystem function (e.g. [30,32]).
- Removal of large amounts of hydrocarbons from the seafloor can destabilize the margins, causing mass wasting and disturbance. Even slight warming could destabilize frozen gas hydrates (methane ice), leading to release of massive quantities of methane and further warming (the clathrate gun hypothesis) [92].
- Proposals for climate-change remediation include iron additions to the open ocean (to stimulate productivity and subsequent sinking of sequestered carbon) and direct injection of CO₂ into the deep sea. Side effects of iron fertilization can include oxygen depletion [12,93]. Liquid CO₂ is toxic to most marine organisms and would act to create ‘patches of death’ on the sea floor, with unknown larger-scale consequences [13].

short distances and depth gradients beneath upwelling regions where oxygen minima impinge on the continental slope [32]. Benthic macrofaunal (α) diversity at mid-slope depths (1500–2500 m) rivals that of the terrestrial tropics, with up to 40–50 macrofaunal species per 100 individuals [23], whereas shallower, hypoxic slope sediments within an oxygen minimum zone (OMZ) might support only one–ten species [32]. Cyclical climate features, such as ENSO, seasonal monsoons, reversing winds or basin flushing events, alter the diversity and composition of margin benthos through changes in temperature, oxygenation and productivity [30,33]. These gradients and cycles generate significant shifts in the relative importance of prokaryotes versus eukaryotes, and protozoans versus metazoans. For example, giant filamentous sulfide-oxidizing bacteria dominate benthic biomass and form huge mats

on the Chile margin during normal summer conditions but these disappear and are replaced by annelids in winter and during El Niño events [34]. Foraminifera (protozoans) take over carbon processing from macrofaunal invertebrates on the Pakistan margin after monsoon-driven production pulses drive oxygen depletion, or where permanent severe hypoxia persists [35].

Thus, margins offer a unique opportunity for richness–function studies that explore the consequences (e.g. carbon remineralization, carbon burial and productivity) of shifts favoring different organizational life forms. There has yet to be a systematic effort to apply the diversity gradients that occur on the deep-sea margins to the BEF debate, but it is clear that these ecosystems can offer novel contributions to ecological theory.

BEF mechanisms and management

Many of the mechanistic hypotheses offered to explain positive diversity–function relationships [28,29] could readily be tested on continental margins. Complementarity (niche differentiation and facilitation), sampling effects (e.g. local dominance of highly productive or functional species), and species rotation in response to temporal change (insurance hypothesis) are likely to be important owing to the heterogeneous and dynamic nature of margin habitats, and will contribute to aggregate ecosystem functional attributes. An additional facet of margin diversity is the large number of rare species, often encountered as species with restricted ranges or low abundance (e.g. singletons) in samples [36]. Current research in terrestrial and shallow water systems suggests that rare species are tied to habitat diversity [37]; they have crucial functional roles and could be particularly vulnerable to habitat loss and extinction [38], emphasizing the importance of considering rare species in habitat-based approaches to conservation [36,37].

Margin systems can foster an understanding of diversity consequences that could be crucial for managing changing habitats and resources. Humans are increasingly modifying species diversity on margins. Removal of benthic margin species occurs locally through fishing, bycatch and even eutrophication, which creates hypoxia and sulfide stress. Addition of species can occur through structural modifications such as placement of sunken ships and platforms in deep water and through introductions [39]. Global climate change is likely to alter large-scale biodiversity gradients on the continental margins through expansion of OMZs and hypoxia [40,41], ocean acidification, which could selectively impair calcifying taxa [42], and warming effects, which interact with both hypoxia and acidification [43]. Whether we can bring to bear the accumulated knowledge of BEF in terrestrial, aquatic and shallow marine systems to predict effects of changing diversity on trophic, nutrient cycling and food production functions in deep water, remains to be determined.

Bottom-up versus top-down control

The combining of ecosystem and population approaches in ecology, alongside strong gradients in diversity and production on continental margins, offers an unusual opportunity to study community control agents. Deep-sea

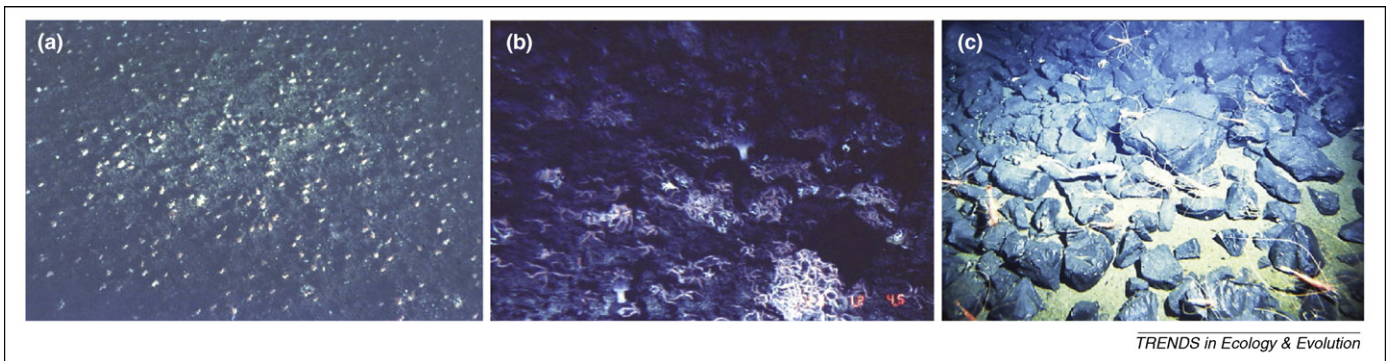


Figure 1. Predator aggregations. Dense aggregations of predators occur where food supply is abundant. At the lower boundaries of Oxygen minimum zones (OMZs), megafauna converge to feed on a wealth of smaller invertebrates. They experience an overabundant food supply and physiological release from hypoxia. (a) The crab *Encephaloides armstrongi* can reach densities of 50–100 ind m^{-2} on the Oman margin at 1000 m [100]. High densities of (b) ophiuroids and (c) shrimp and rattail fishes (*Nezumia liolepus*) aggregate at the lower OMZ boundary on Volcano 7 off Acapulco, Mexico, at 800–850 m [101]. Reproduced with permission from Brian Bett (a).

ecosystems are traditionally viewed as food limited, largely because the biomass of sea-floor benthos mirrors the particulate organic matter (POC) flux from surface waters to the seabed [44] and tracks POC flux in time [45,46]. Where surface production and POC flux to the sea bed are highest (e.g. nearshore and beneath upwelling areas), so too is benthic biomass; i.e. bottom-up control). Natural spatial and temporal variability in food supply to the continental margins occurs through upwelling and phyto-detritus falls [47], interannual (e.g. El Niño-driven) production changes [33,34], episodic falls of large carcasses [48], tectonic triggering of organic debris flows, and ephemeral supply of fluids containing methane and sulfide at seeps and vents [49]. In all cases, including those where organic matter is manipulated experimentally, strong bottom-up responses by benthic protozoans and metazoans are evident, manifested as changes in composition, dominance, species richness and functional attributes [17,47]. Topographic enhancement of particle fluxes, low-oxygen regimes, and seasonal surface production all contribute to sharp continental margin gradients in food supply from surface waters that can be exploited to address productivity–diversity relationships. To date, margins with differing productivity levels have yielded productivity–diversity relationships that vary from positive in oligotrophic (low production) areas, to unimodal, to negative in upwelling regions [3].

Some margin food webs differ from those in photosynthesis-based terrestrial or shallow marine systems in being supported by chemosynthetic processes [7]. A diverse assortment of aerobic and anaerobic microbial carbon fixation mechanisms, including methane and sulfide oxidation, provides energy for higher trophic levels at settings such as pockmarks, brine seeps, mud volcanoes, gas hydrate outcrops and hydrocarbon seeps [49]. In such systems, the primary producers can be symbiotic or free-living bacteria that support high animal biomass. It remains to be determined whether classic food web models predicting structure from number of trophic groups and interaction strengths [50], and cascading responses to disturbance and change, will apply equally well to margin systems that are reliant on chemosynthetic production and symbiosis.

The long-standing focus on bottom-up forcing has, however, distracted attention from the fact that both bottom-

up and top-down processes usually occur simultaneously on continental margins [51]. Dense aggregations of higher-order consumers, including demersal fishes, rays, squid, shrimp, ophiuroids and whelks, persist beneath upwelling areas (e.g. at OMZ boundaries), on topographic high points where particle flux is enhanced, or at organic matter depocenters where the confluence of currents and topography create organic flux hotspots (Figure 1). Removal of these organisms, either by targeted fisheries, as bycatch, or through their intolerance to expanding hypoxia or acidification, could provide human-induced ‘experiments’ that reveal the ecological roles of predators on margins [52]. Loss of top pelagic predators such as sharks, sailfish or marlin, and resulting trophic cascades are known to alter benthic biomass and patterns of diversity in the coastal and open ocean [53,54]. Practical application of top-down theory requires examination of response variables (i.e. benthic infaunal composition, food-web structure, or prey size structure) before predator removal, when predator densities are low, and potentially after removal or loss ceases. Study of open and closed fishing grounds, use of size-specific fishing gear, and reintroduction or seeding of species could provide alternative experimental designs.

Humans can also introduce predators to margins. During the 1960s, the highly predatory red king crab *Paralithodes camtschaticus* was introduced from the Bering Sea to the Barents Sea to establish a Russian fishery. By 2004, the Norwegian margin supported a large, reproductive population at depths to 300 m that threatened scallop and other bivalve populations [44]. Another bivalve predator, the opisthobranch *Philine auriformis*, was accidentally introduced from New Zealand to San Francisco Bay in 1993, making its way into shelf and upper slope waters (300 m) off southern California, where it grew to large body sizes. Its success in deep water was attributed to efficient feeding on bivalve resources [55]. Thus, both intentional and unintentional introductions have decimated bivalve prey populations at upper slope and outer shelf depths. Species range expansions, induced by warming or spreading hypoxia, can also bring new predators to margins. The predatory Humboldt squid (*Dosidicus gigas*) has traveled north from Mexico in deep hypoxic waters (200–700 m) and might now compete with valuable market squid (*Doryteuthis* (formerly *Loligo*) *opalescens*) off the coasts of California and Oregon [56]. As with

shallow-water invasions, there is much to be learned about the structural stability of deep-water communities when invasive species appear. Our challenge is to integrate both top-down and bottom-up ecological approaches in a realistic way, to maximize sustainability of resources and to maintain the integrity of ecosystem structure and functions.

Ecosystem engineering and facilitation

Fishing effects and anthropogenic disturbances on margins extend beyond the cascading effects of top predator loss. Removal or damage to biological structures by trawling, dumping, mining or other forms of disturbance might cause loss of fundamental ecosystem-structuring agents [57]. For example, deep-water coral reefs (non-zooxanthellate), sponge beds, fields of giant agglutinated protozoans, and seep-associated clam, mussel, tubeworm and pogonophoran beds, are taxa that provide specialized habitats for unique assemblages of species, creating seafloor biodiversity hotspots (Box 2). These biogenic habitats are fragile and patchy, and their study requires deep submergence vehicle technology. Structurally similar biotic reefs, beds and fields are known to provide refugia and alter water flow, food supply, larval supply, geochemical conditions, and substrate in shallow water [57] but such effects are only beginning to be explored on margins and seamounts. Trawling, in particular, induces loss, fragmentation or reconfiguration of three-dimensional structures, and truncates the activities of the structure-forming organisms [58,59]. Such disturbances offer unwelcome change, but should be studied to document the role of structural 'foundation' species such as *Lophelia pertusa* [60] in maintenance of diversity and productivity on margins [58,59]. On bathyal margins, biogenic reefs [4] and methane seep assemblages [49,61] host a wealth of smaller species including foraminifera, nematodes, annelids, mollusks and echinoderms. Unfortunately, these habitats and their species are subject to damage by trawling often before they are ever discovered, characterized and catalogued [5].

Identification of foundation species and their diversity-promoting attributes will provide the underpinnings of effective conservation, regulation and remediation of margin resources and habitats.

Many of the effects of biotic structures described above are facilitative, and fall within a broader class of 'positive' interactions. Facilitation is widespread but often overlooked in the deep sea. On open continental margins, we predict facilitation will be significant in the 'harshes' benthic environments: within OMZs (at bottom-water O_2 concentrations of 0–0.5 ml L^{-1}) [32], in sulfidic sediments at methane seeps [49], and where benthic storms scour the bottom [62]. Facilitation is predicted to take the form of pumping and burrowing by subsurface fauna; these activities enlarge the habitable portion of the sediment column by introducing oxygen, providing refuge and stimulating microbial activity, which provides food for deposit feeders. At methane seeps these activities also enhance remineralization, through sulfate transport and stimulation of sulfate reduction. Reducing margin habitats at OMZs, methane seeps and whale falls reveal an increasing range of novel animal-microbe interactions [63,64].

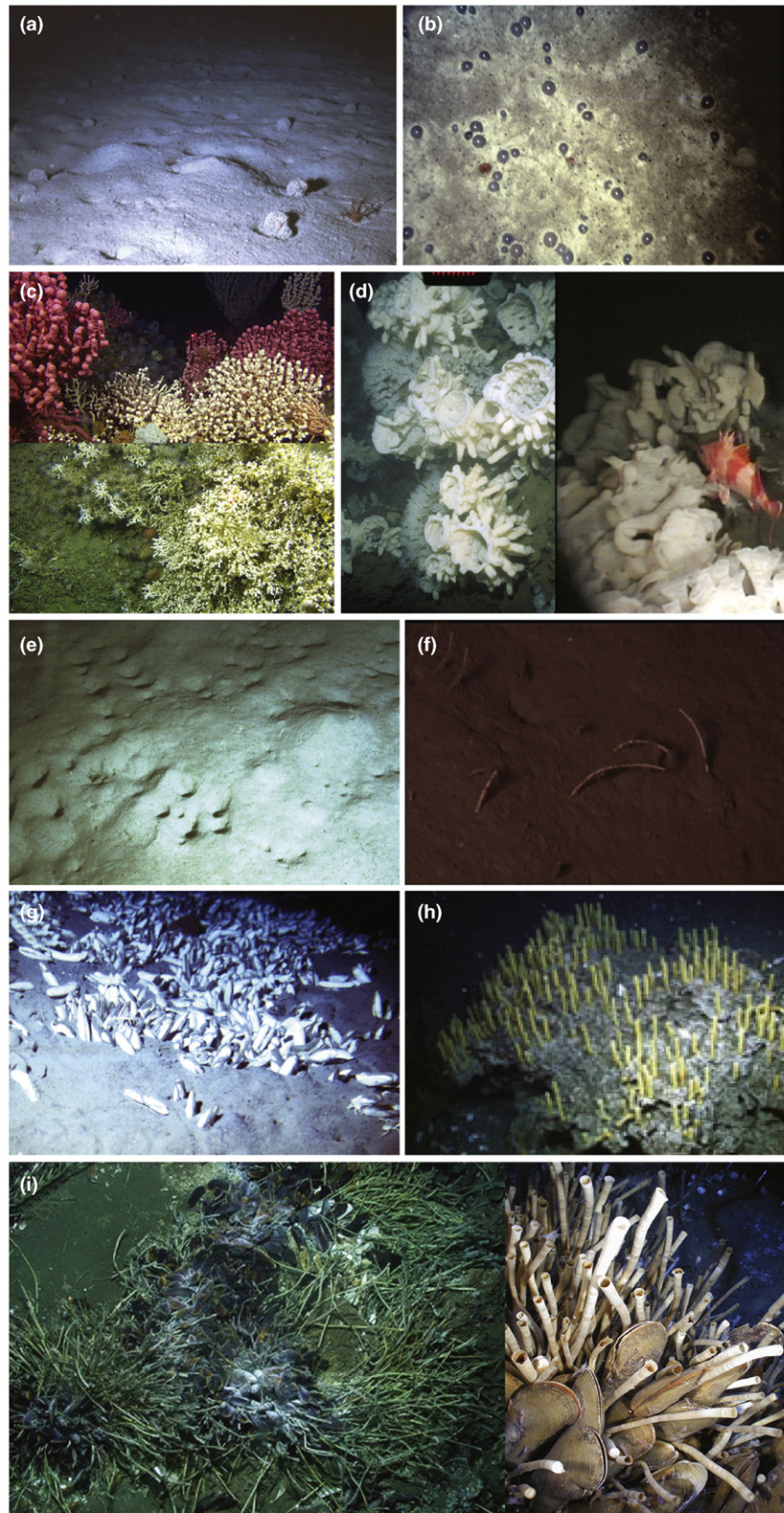
Another class of facilitation, associational defenses against predators [65], has not been studied in deep water, but it is likely that margins might include seep sites where high sulfide contents of structural species such as tubeworms, clams or mussels, deter predators [66], reducing predation pressure on associates dwelling on the tube, shell or byssus threads. Physiological facilitation is likely to be widespread where sulfur toxicity is a problem. Sulfur detoxification by dense mats of free-living sulfur bacteria (*Beggiatoa* and *Thioploca* spp.) in basins of the southern California borderland, and on the Peru, Chilean and Namibian margins might facilitate persistence of invertebrates in otherwise sulfidic sediments [67,68]. Massive episymbiosis of sulfide-oxidizing bacteria on nematodes, annelids, mollusks, and crustaceans could provide similar direct benefits to animals at methane seeps and in low oxygen settings [68,69]. Host detoxification of sulfide might also

Box 2. Examples of ecosystem engineers in the deep sea

- Dense aggregations of xenophyophores [giant single-celled Foraminifera (Figure 1a)] are found on the slopes of continental margins and seamounts. These multinucleate protozoans form large, agglutinated tests, which entrain organic particles that provide food for numerous invertebrate and protozoan species dwelling within [6].
- Large gromid protozoans, forming spheres the size of a golf ball, populate the seafloor on the Oman margin, 1175 m [94] (Figure 1b). A similar species is also present in the Bahamas at 750 m.
- Deep-water corals provide attachment substrate, food, access to stronger flows and refuge from predators, enhancing the biodiversity of associated invertebrates [95] (Figure 1c).
- Dense stands of glass sponges form vast reefs, aboveground forests and belowground spicule mats that modify the seascape and provide habitat for numerous associated invertebrates (Figure 1d). Sponge reefs, located on the outer shelf and upper slope, can be 19 m high and cover 700 km² of seabed off Canada. They are fueled by methane and strong tidal currents, and provide key nursery habitat for juvenile rockfish [5].
- Belowground tunnels and caverns, made by large burrowers such as thalassinid shrimp, sipunculans and echiurans, form a vast subsurface network (Figure 1e). Many of these taxa form mounds of

pseudofeces (excavated sediments). The increased vertical relief and passive flushing of burrows modify the flow and geochemistry above and below the seabed, with consequences for associated animals and remineralization and organic matter burial processes [96].

- Fields of tube-building protozoans (Figure 1f) populate the high particle flux margins off Cape Hatteras, North Carolina and Kaikoura Canyon, New Zealand. First thought to be polychaetes, these are now recognized as the foraminiferan, *Bathysiphon filiformis*. The tubes support recurrent assemblages of associated invertebrates and protozoans [97].
- Clam beds at methane seeps (Figure 1g) support higher infaunal diversity than do surrounding non-seep sediments or heavily sulfidic, bacterial mat-covered seep sediments [98].
- A forest of whelks and their egg towers (Figure 1h) is the result of breeding aggregations of *Neptunia amianta*, common at mid-slope depths on the California and Oregon margins.
- Vestimentiferan tubeworms and mussels (Figure 1i) form a patchwork of bushes at methane seeps. They house diverse microbial symbionts internally, and support many associated invertebrate taxa among the tubes. The associated assemblages experience succession as the bushes mature and senesce [61].



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Figure 1. Structure-forming taxa on continental margins. (a) Xenophyophore fields. (b) Gromid lair (*Gromia sphaerica*) on the NW Atlantic margin, 2200 m, Oman margin seafloor, 1640 m. (c) Deep-water coral reefs, 250 m, Norwegian margin. (d) Deep-water sponge reef and red banded rockfish, 180 m, Hecate Strait. (e) Burrow and mound field (underground caverns). (f) Tube-building protozoans (*Bathysiphon filiformis*), 850 m, North Carolina margin. (g) Clam beds, 4445 m, Kodiak margin, AK, USA. (h) Whelk towers, 800 m, Hydrate Ridge, OR, USA. (i) Vestimentiferan worms and mussels, Gulf of Mexico. Reproduced with permission from Brian Bett (b); MAREANO Project, Institute of Marine Research, Norway (c); Natural Resources Canada (d); and E. Cordes and the Expedition to the Deep Slope 2007 Project (i).

Review

Table 1. A conceptual framework for applying ecological theory to exploration, research, monitoring and management of continental margins

Theory and/or concepts	Exploration	Research	Monitoring	Human threats	Vulnerable habitats	Management ^a
Connectivity						
Metapopulation theory	Substrate	Larval biology	Fragmentation	Targeted fishing/bycatch	Vents, seeps, canyons, seamounts, deep coral reefs	MPAs Fishing practices Waste disposal site EIS requirements
Meta community theory	Habitat types	Recruit sources/sinks	Recruitment	Trawling, sea floor mining, eutrophication, dumping, oil and gas extraction	Vents, seeps, canyons, seamounts, deep coral reefs	
	Patch structure	Dispersal kernel Experiments testing models: dispersal, community assembly	Recovery following trawl/mining disturbance			
Trophic structure						
Bottom-up forcing	Feeding types		OM inputs/fluxes (natural/artificial)	Eutrophication, ocean (Fe) fertilization	Open slope, all habitats	Climate change/ remediation
	Food sources	Microbial roles and metabolism	Temporal patterns and climate change effects	Altered river flows	Canyons, shelf, upper slope	Geoengineering effects
	Regional, bathymetric variation in food inputs	OM transfer across habitats		Climate change (CO ₂ , pH, warming and methane release)	Open slope, methane seeps	Dumping protocols
	Temporal variation in food inputs			Waste disposal	Open slope, canyons	
Top-down forcing	Predator distributions, abundances	Predator roles, resilience	Predator, prey abundances	Fishing, trophic cascades	Open slope	Fishing practices
	Assemblage size structure	Stock structure	Species abundance	Climate change (CO ₂ , pH, warming)	Open slope	Bycatch regulation
		Trophic cascades	Composition shifts			Cultural preferences
Food web structure	Biomass/size structure/trophic levels	Interaction strengths/energy transfer	Trophic level/biomass structure	Fishing, shellfish harvest, introduced species	Seamounts, canyons, open slope, seeps and vents	Fishing practices
		Comparisons of open/closed fishing grounds	Tracking changes during/after stock removal	Climate change (all)		Protected stocks
Biodiversity	Species richness/ dominant taxa	Endemism	Species richness, extinctions			Habitat/ ecosystem-based MPAs
Contemporaneous and/or disturbances	Bathymetric and regional diversity patterns	Symbioses	Effects of anthropogenic structures	Energy extraction rigs, ships, platforms		
	Organization: protozoans	Genetic diversity	Proxies for diversity (e.g. habitat structure)	Trawling and mining, energy extraction	Open slope, seamounts, vents, possibly seeps	Fishing practices
		Roles of habitat heterogeneity	Natural and human-induced patch structure	Benthic storms, slides, mass wasting and slope destabilization	Open slope, canyons	EIS requirements
		Context-dependent diversity	Changing hydrography Climate cycle influence	Hypoxia, acidification	Open slope	Remediation (mining etc.)

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Table 1 (Continued)

Theory and/or concepts	Exploration	Research	Monitoring	Human threats	Vulnerable habitats	Management ^a
Ecosystem engineering	Map substrates	Evaluate substrate–organism relationships	Evaluate climate change impacts on calcifying reef organisms	Ocean acidification	Coral reefs	Bottom fishing practices
	Map biotic reefs	Experimental study of belowground foundation species		Hypoxia	Eastern Boundaries, upper slope	Designation of fragile/endangered habitats
	Map fragmentation by disturbance	Experiments to reveal mechanisms underlying biotic associations	Recovery following loss of biotic structure/habitat	Trawling	Reefs, seamounts, canyons, seeps	MPA design
	Sediment geochemistry in relation to biota	Animal–microbe–sediment interactions	Fluid flux, population and community structure	Trawling, warming, hypoxia, slope destabilization	Chemosynthetic ecosystems, oxygen minimum zones	Remediation requirements EIS components
Biodiversity–function relationships	Functional measures (production, remineralization, structure)	Mechanisms underlying BEF relationships	Long-term changes in diversity and function (e.g. fish species and production)	Climate change (acidification, hypoxia, warming)	All	Climate change/remediation
		Using human disturbance affecting species richness as experiments		Trawling, mining	Canyons, seamounts, open slope, vents	Protection goals
		Roles of protozoa versus metazoa Context dependence of relationships		Platform introduction CO ₂ injection	Open slope Continental rise and abyssal systems	MPAs
Invasion biology	Identify invasives, vectors	Dispersal kernels, population lags	Population dynamics	Intentional introductions	Open slope	Harvest, removal, vector control
	Species distributions, habitats	Competition, predation		Climate change-related range extensions	Open slope	Biosecurity - biodiversity maintenance
		Altered ecosystem functions Trophic consequences Habitat alteration				

^aAbbreviations: EIS, Environmental impact statement; MPA, marine protected area.

explain widespread evolution of commensal endosymbiotic annelid species dwelling within bivalves and tube worms at hydrothermal vents and methane seeps. Up to six endosymbiotic microbial forms have been found in the oligochaete *Olavius crassitunicatus* within the nearly anoxic, organic-rich sediments of the Peruvian upper slope (0.02 ml O₂ L⁻¹) [70], and within the mussel *Idas* sp. from the Nile Delta seeps in the Mediterranean Sea [71]. The symbionts include sulfate reducers, sulfide oxidizers and spirochaetes; complex symbiont interactions must facilitate the persistence of metazoan life in these remarkably hostile environments but the nature of these interactions are mostly unknown.

Nutritional facilitation occurs when larger animals bury labile organic matter reaching the seabed, making it available to subsurface feeders. Such activities have been reported on the continental margin for sipunculans [72], echiurans [73] and maldanid polychaetes [74]. The baffle-like structures of xenophyophore (protozoan) tests in the genera *Syringammina*, *Galathea* and *Psammmina* trap food particles and provide shelter for meiofauna

and macrofauna in high-flux settings such as seamounts and steep continental slopes [6]. Fishing, mining or energy extraction activities have the potential to disrupt facilitative interactions through sediment disturbance or species removal. Alternatively, when stress is increased (as through waste disposal or expanding hypoxia) the effect might be to increase the importance of facilitation through the interactions described above. Facilitative interactions have joined competition, predation and disturbance in receiving recognition as primary ecological agents structuring shallow-water communities [75]. Given the wealth of symbiotic interactions present in extreme margin environments, we speculate that they have even more significant roles in the deep sea, and suggest that preservation of facilitative interactions and foundation species functions be incorporated in the development of regulations for resource use.

Metadynamics

Until now, we have focused on ecological processes that involve mainly adult phases on margins, rather than on

early life stages and their movements. Many margin habitats occur as isolated patches separated from similar settings and substrates by tens to hundreds of kilometers. This is especially true of methane seeps, deep-water coral and sponge reefs, large organic falls (e.g. whale carcasses), canyons, ridges and seamounts. This patch structure raises questions about the extent to which constituent populations function as metapopulations and their assemblages as metacommunities. In an environment where <1% of the habitat has been seen by humans, and most of the small species are likely to be undescribed [17], it is difficult to contemplate tests of models of population connectivity [76] or metacommunity dynamics [77]. However, such models do abound, and for fragile (sponge and coral reefs) or exploited continental margin systems (fisheries on banks, seamounts and in canyons), their systematic incorporation into a research framework might be the only means of providing the knowledge required for sustainable management of these resources.

Population connectivity questions on land and in the coastal zone have been addressed through models of genetic exchange and selection (e.g. closed populations, source-sink, island/panmixis and local adaptation), landscape structure (e.g. patch size and quality), biophysical forcing (e.g. spatially explicit, time integration causing retention and advection), and recruitment limitation (e.g. larval supply and density dependence) [78]. The roles of larval supply, behavior, mortality, advection, diffusion, and their interactions in shaping dispersal kernels remain at the frontiers of shallow-water connectivity research [79], with new genetic, geochemical and numerical modeling approaches now being used [80]. Only rarely does the connectivity literature address deep-sea populations. This usually involves genetic structure in relation to depth [8], geography [81] or larval transport [82] at hydrothermal vents. Limited results show varied dispersal strategies among species [83] but suggest that ephemeral habitats impose metadynamics [84].

Metacommunity models offer a conceptual approach for understanding assemblage composition and reassembly following disturbance [77]. Perhaps most applicable to the margin settings is the species-sorting model, in which species exhibit niche specialization, and environmental or habitat gradients structure assemblages. Variations in geochemical parameters, sediment stability, substrate, flow and food availability all create distinct margin 'niches'. The patch dynamics model contains elements of contemporaneous disequilibrium in which tradeoffs between colonization potential and competition govern assemblage structure within patches. Most applicable to settings where patches are homogeneous, this model provides a framework for understanding community recovery following trawling, mass sediment disturbance or seasonal hypoxia. The mass effect model applies source-sink dynamics at the community level, suggesting that assemblages in large habitat patches influence smaller ones in close proximity. Such understanding is important in the creation of deep-water conservation areas designed to sustain biodiversity and fisheries resources. Rex *et al.* [85] have suggested that abyssal bivalve diversity in the Atlantic Ocean is supported largely by recruits from con-

Box 3. New ecological perspectives from margin research

The margin ecosystem has largely remained outside the mainstream ecological literature but includes many features that can contribute novel understanding of general ecological and evolutionary processes controlling biodiversity and community structure. Here, we provide instances where continental margin research could contribute to ecological theory and practice.

Latitudinal trends

One of the best known terrestrial biogeographic patterns is that of increasing diversity with decreasing latitude. This pattern has spawned a glut of explanatory hypotheses, involving food supply, temperature, area and mid-domain null hypotheses [99]. The intensity and form of latitudinal gradients in temperature, area and primary productivity differ between the ocean and land, offering unusual opportunities to test hypotheses concerning the role of these parameters in diversity generation. For example, the ocean has a relatively greater proportion of area at low latitudes, more uniform primary productivity across latitudes and a different temperature variability regime.

Roles for protozoa

Increasing water depth and decreasing oxygenation both result in the greater importance of eukaryotic protozoans relative to metazoans with respect to ecosystem structure and functioning. Few terrestrial, aquatic or shallow marine models address the consequences of different organizational life forms. The margins offer settings where protozoan and metazoan abundance and dominance shift rapidly in space and time, with probable consequences for key global services (e.g. carbon remineralization, carbon burial and productivity) [35].

Competition and predation

Where high-density aggregations of animals occur, competition and predation are likely, but spinoffs of these phenomena, including territoriality, allelopathy, mimicry, refugia or propagule banks, have yet to appear in the margin benthos literature. We predict that, as these phenomena are investigated, the margin biota will reveal the involvement of microbial symbionts in many of these processes, offering a new perspective on ecological interactions.

Chemosynthesis-based food webs

An unusual assortment of microbial carbon fixation mechanisms, including methane and sulfide oxidation, provide energy for higher trophic levels at a variety of margin settings, including pockmarks, mud volcanoes and hydrocarbon seeps [7,49,61]. In such systems, the primary producers can be symbiotic or free-living bacteria and archaea, while the consumers are largely invertebrates. The relative nutritional contributions of different aerobic and anaerobic microbial processes to these food webs, and the extent to which archaea enter metazoan food webs at all, are currently unknown.

tinental margin populations. If this is generally true, the margins might have a key role in sustaining abyssal diversity.

Conservation opportunities on margins

The integration of relevant ecological theories into conservation and management practices will require both forward thinking and a new research agenda to test rigorously the theories described above. Such tests will require repeated access to continental margin settings with visually guided instruments, selective sampling ability and measurements for testing physical models. The pressures of existing and impending exploitation of fisheries and energy resources offer unprecedented opportunities to conduct experiments and test ecological hypotheses across gradients and thresholds in environmental conditions and community types. It is time to integrate key ecological understanding

and concepts into the science and regulatory agency mandates, by embracing these concepts in exploration, research, monitoring and management phases (Table 1). The ocean margins are experiencing massive shifts in environment in response to carbon dioxide buildup; ocean warming, increasing nutrient inputs, expanding hypoxia and acidification are just some of the manifestations. Here too, the prediction of biotic responses and search for solutions under conditions of the 'new normal' will require an understanding of ecological concepts at the programmatic and management level*.

The application of ecological theory to the study and management of continental margins should yield benefits for the field of ecology itself. The unusual assemblages, dominant ecological roles for protozoans and symbionts, alternative food sources and high levels of physico-chemical heterogeneity add novel interactions and ecosystem-forcing mechanisms to our understanding of global ecology (Box 3). In more remote areas of the globe, continental margins offer true unperturbed baseline settings, providing an opportunity for more rigorous tests of ecological theory in real ecosystems. Comparisons of pristine margins with those modified by humans should also yield new insight into systems with long-lived organisms and limited disturbance and possibly enable detection of climate-induced change. By merging basic ecological understanding with lessons from decades of anthropogenic influence on the coastal zones, we should learn what general principles govern species and ecosystem responses to perturbations, and could discover some completely different controls of resilience and diversity on continental margins.

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* European programs embracing ecological concepts to study continental margins include: the HERMES (Hotspot Ecosystem Research on the Margins of European Seas; <http://www.eu-hermes.net/>) and MarBEF (Marine Biodiversity and Ecosystem Functioning; <http://www.marbef.org/index.php>) projects, both funded by the European Commission's 6th Framework Programme, under the priority Sustainable Development, Global Change and Ecosystems; and the BIOFUN (Biodiversity and Ecosystem Functioning) project, which is part of the EUROCORES EuroDEEP (Ecosystem Functioning and Biodiversity in the Deep Sea) programme. (<http://www.esf.org/activities/eurocores/programmes/eurodeep.html>).

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