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Interactions in the Marine Benthos: Global Patterns and Processes

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Chapter 19.   Interactions In The Deep Sea
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Introduction
The deep–ocean floor extends over two thirds of the world's surface, and is thus the largest benthic habitat on the planet. The myth of depauperate deep–sea communities was debunked in the 1960s by the pioneering work of Hessler and Sanders (Hessler and Sanders, 1967; Sanders and Hessler, 1969) with their newly developed epibenthic sled. They showed deep–sea diversity to be equivalent to that found in shallow tropical marine habitats, and greater than in boreal tropical and temperate estuaries and boreal shallow marine habitats. They also identified depth as the most important correlate of faunal abundance and as a factor driving community composition. Technological developments over the last 50 years have continued to drive advances in our knowledge of this diverse and heterogeneous biome. Efforts to enumerate and catalogue the diversity have led to claims of high levels of endemism (E.g., Wolff, 1970; Belyaev, 1989; Stocks and Hart, 2007; Ebbe et al., 2010) but poor knowledge of the global species pool and uneven regional sampling probably artifactually inflate these estimates (e.g., Rowden et al., 2010; Clark et al., 2012).

The term "deep sea" encompasses many different habitats, shaped by their physical characteristics – geographic location, slope, depth – which determine their biodiversity and dominant fauna, and their connectivity. Here, we first explore biogeography and phylogeography of these habitats, and consider some of the molecular work which is testing various biogeographic schemes. We then look briefly at some of the abiotic parameters that characterise various deep-sea habitats. Interactions in the deep sea are many, but they are often not well investigated. Few studies on competition and predation match the detail of those conducted in shallow waters. In constrast, symbioses have been better researched, being the basis of much productivity at hydrothermal vents and cold seeps, and highly prevalent in filter-feeder dominated habitats on the steep slopes of submarine canyons and seamounts. Finally we explore where sufficient bodies of work exist to allow us to infer processes from patterns, and conclude that very much more work on ecological interactions in the deep-sea is needed.

Biogeography and phylogeography
The sparseness of biological samples on a global scale has made delineation of biogeographic boundaries based on faunal differences extremely challenging, although depth certainly plays an important role. Carney (2005) discussed the potential impacts of high pressure on biochemical reactions and the need for

specialized membranes and proteins to counteract this. Reviewing studies of zonation on the continental slope, Carney (2005) recognized several transition zones at bathyal depths but found faunal boundaries in the bathyal zone to be "fuzzy" and taxon–specific, although sharp local boundaries could be associated with local hydrographic regimes.

Attempting a global biogeography of the deep–ocean floor, Watling et al. (2013) treated the lower bathyal (800 – 3 500 m) as a single depth zone, excluding the shallower upper bathyal (300 – 800 m), which mostly falls within national EEZs, from their classification. They defined 14 biogeographic provinces within the lower bathyal (Arctic, Subantarctic, Antarctic, Indian Ocean, seven Pacific Ocean provinces, and three Atlantic provinces), and a further 14 in abyssal (3 500 – 6 000 m) depths (Arctic, east and west Antarctic provinces, Indian Ocean, six Pacific provinces, and four Atlantic provinces). The areas within lower bathyal regions are discontinuous, since they are formed by seamounts, mid–ocean ridges, and the lower slopes of continental margins and oceanic islands. In contrast, the abyssal provinces tend to extend across ocean basins, where they may be incised by mid–ocean ridges (for example the abyssal Indian Ocean province, the abyssal North Atlantic province). Ten hadal provinces (deeper than 6 500 m) were also described, and follow the scheme of Belyaev (1989), originally published in the Russian literature. The ten hadal provinces comprise either individual trenches (e.g., the Java hadal province for the Java trench; the Peru–Chile hadal province for the Atacama trench), or collections of two or more geographically close trenches (e.g., the Mariana hadal province for the Volcano, Mariana, Yap and Palau trenches). Despite an increase in hadal research in recent years (e.g., Fujii et al., 2013, Blazewicz–Paszkowycz et al., 2015; Lacey et al., 2016; Linley et al., 2016, 2017) there remain insufficient data to test whether the hypothesized hadal provinces reflect community diversity.

Both the bathyal and abyssal provinces of Watling et al. (2013) were proposed mostly based on hydrographic data (temperature and salinity) and fluxes of particulate organic carbon, and are strongly influenced by water masses; for example, the North Atlantic abyssal province is the area north of the equator influenced by North Atlantic Deep water, and the South Atlantic bathyal province encompasses the area south of the equator to the Antarctic Convergence where Antarctic Intermediate Water dominates. Although faunal data are limited, there is at least some support for these divisions. For example, Watling et al. (2013) report that the composition of cumaceans (Watling, 2009) and protobranch bivalves (Allen and Sanders, 1996) in the North Atlantic appears to reflect the proposed abyssal biogeographic provinces, although not all taxa show such differences.

There appear to be fewer extensive bathyal data sets with which to test the bathyal provinces (Watling et al., 2013), but hydrothermal vent studies provide a subset of relevant data. Vent habitats occur at mid–oceanic ridges, convergent plate boundaries, and subduction zones. They are well known for clear differences in dominant fauna among locations, with, for example, caridean shrimps, such as *Rimicaris excoculata*, and bathymodiolid mussels dominating

Atlantic sites, *Riftia* tubeworms dominating sites on the East Pacific Rise, and the smaller *Ridgea* tubeworms dominating in the NE Pacific (Ramirez–Llodra et al., 2007). An analysis of the community composition at 63 vent fields (Bachraty et al., 2009) yielded a biogeographic model with six provinces, which mapped reasonably well (Table 19.1) to the bathyal provinces of Watling et al. (2013). A previous analysis of vent provinces also yielded a six–province solution but with different boundaries (Van Dover et al., 2002). Tyler and Young (2003) proposed a nine–province solution that included less–well explored areas at higher latitudes. As vent studies progress and extend (e.g., to the Rekjanes Ridge in the Northern Atlantic Boreal province), correlations between proposed models can be better tested.

Cold seeps have been grouped into five geographic provinces (Gulf of Mexico, Atlantic, Mediterranean, East Pacific and West Pacific; Tyler et al., 2003) and these map less well to the provinces of Watling et al. (2013). However, numerous seep sites have been discovered since biogeographic provinces based on seep communities were originally proposed, including new sites in the Black Sea (Klaucke et al., 2006) and Antarctica (Domack et al., 2005). Furthermore, in–depth analyses across the Atlantic Equatorial Belt suggest seep faunal communities are influenced far more by depth than by geographic location (Olu et al., 2010).

Genetic data can be used to test whether barriers to gene flow are congruent with biogeographic hypotheses. For example, even where species transcend biogeographic boundaries, genetic subdivisions may be found that correspond to those boundaries. Populations of several hydrothermal vent species on the Northern East Pacific Rise (Cocos plate province) are genetically different from those on the Southern East Pacific Rise (Southeast Pacific Ridges province), including those of the extremophile *Alvinella pompejana* (Jang et al., 2016)*,* and the giant tube worms *Tevnia jerichonana* (Zhang et al., 2015) and *Riftia pachyptila* (Coykendall et al., 2011). Further genetic subdivision is seen in the southern region of the Southern East Pacific Rise at the Easter microplate in *A. pompejana* and *T. jerichonana*. Furthermore, two species of bythograeid crabs meet at the Easter microplate (Mateos et al., 2012), as do two species of *Bathymodiolus*, the latter hybridizing in this region (Johnson, Won et al., 2013). Although areas south of the Easter microplate are distinguished as the northern Pacific Antarctic Ridge, they are still part of the Southern East Pacific Rise biogeographic province (sensu Bachraty et al., 2009). The ephemeral nature of vents, and therefore the historical local extinction of and decolonization by specialized vent fauna, may not render these animals best suited to test biogeographic provinces, because their biogeographic history is affected by forces to which other animals are not subjected. For example, populations of *Riftia pachyptila* that were less than half a kilometre apart on the Northern East Pacific Rise were genetically distinguishable using AFLPs, and hydrodynamic forces, which entrain larvae in hydrothermal plumes, might lead to dispersal and delivery of larvae at the cohort level (Shank and Halanych, 2007).

Genetic studies of deep–water corals, often the dominant fauna in other bathyal habitats, are in their infancy, but are increasingly being used to delimit species

and better define the distribution of species that often have variable morphologies. For example, in the cosmopolitan genus of bamboo coral *Acanella*, recent DNA sequencing has confirmed the distinctiveness of several Pacific and Atlantic species, and led the authors to resurrect a Mediterranean species, synonymize two widely used names (*A. eburnea* junior to *A. arbuscula*), describe new species, and provide expanded range limits for species (Saucier et al., 2017). Similar reviews of genera such as *Anthothela* and *Primnoisis* (Moore et al., 2016, 2017), *Narella* (Baco and Cairnes, 2012), the Pacific genera *Pacifigorgia*, *Leptogorgia* and *Eugorgia* (Soler–Hurtado et al., 2017) are helping to clarify the taxonomic landscape and provide new information on species ranges and the distances over which populations can interact. Such basic information is crucial to understanding biogeography. Few studies on deep-water coral population genetics have been conducted to date, however the scleractinian *Stephanocyathus spiniger* and the antipatharian *Stichopathes filiformis* seem to maintain panmixia across ocean expanses (Miller et al., 2010), while other species such as the scleractinians *Lophelia pertusa* (Morrison et al., 2011; Dahl et al., 2012) and *Desmophyllum dianthus* (Miller et al., 2011), the octocorals *Corallium rubrum* (Constantini et al., 2011), *Paragorgia arborea* (Herrera et al., 2012), *Callogorgia delta* (Quattrini et al., 2015) and species of *Narella* (Baco and Cairnes, 2012), and the antipatharians *Antipathes robillardi* and *Stichopathes variabilis* (Miller et al., 2010) show distinct genetic structuring over varying spatial and/or bathymetric scales.

Genetic differentiation by depth, hypothesized to occur due to physiological gradients (see Rex and Etter, 2010) has been identified in other benthic deep-sea invertebrates apart from corals, including molluscs (Jennings et al., 2013, Strugnell et al., 2017), polychaetes (Schüller, 2011, Brasier et al., 2017) among others (reviewed in Morrison et al., 2017 and Taylor and Roterman, 2017). Noting the relatively wide depth band of their lower bathyal, Watling et al. (2013) acknowledged a potential need for further subdivision by depth in some oceans and this appears to be supported by available molecular data.

Abiotic Interactions
With the exception of chemosynthetic habitats, deep–sea communities are highly dependent on the amount of particulate organic carbon (POC) reaching the seafloor. A predictive model of POC flux based on sediment trap data, net primary production data from remote sensing, sea–surface temperature and global bathymetry data (Lutz et al., 2007), shows wide discrepancies in POC supply to deep benthic communities. POC flux to the sea floor is strongly affected by depth and is consequently substantially higher around continental margins, ridges and seamount chains. Other processes also act to enhance POC supply in these regions. For example, modifications to local currents caused by submarine canyon topography can cause local upwelling, enhancing net primary production, while downwelling may develop over the canyons themselves, trapping POC within the canyon system (Fernandez–Arcaya et al., 2017). Nepheloid layers of suspended particulate material often form in canyons due to local hydrodynamics (e.g., Wilson et al., 2015), as can internal waves, and these facilitate the development of high biomass benthic communities in these areas (E.g., Johnson, White et al., 2013). Particle modelling has demonstrated increased

supply at the seafloor near shelf breaks (Thiem et al., 2006), a suggested factor in the prevalence of corals and other filter feeders in these locations (e.g., Quattrini et al., 2015).

Local hydrodynamics also strongly affect food availability to benthic filter feeders at seamounts (Clarke et al., 2010), although the exact mechanism is disputed. There is little observational evidence for the classical 'Taylor's cone' theory, whereby flow across the top of the seamount creates anticyclonic flow around it and associated upward movement of nutrient rich waters (Genin and Dower, 2007), but tidally forced circulation may facilitate retention of POC (White et al., 2007). Additionally trapping of vertically migrating zooplankton around seamounts likely plays a role in enhanced food availability (Genin and Dower, 2007). Seasonal effects on reproductive development of macrofauna (e.g., Sumida et al., 2000) illustrate the importance of benthopelagic coupling in bathyal regions. At abyssal sites in geographic areas with marked climate seasonality, e.g., the Porcupine Abyssal Plain, an annual pulse of phytodetritus still reaches the benthos despite the extreme depth, and is an important food resource (Iken et al., 2001).

Ecological Interactions In The Deep Sea
The difficulties of gathering data in the deep sea limit evaluations of ecological interactions. There are few observations of phenomena like detailed time series of overgrowth of sessile species (Elliott et al., 2016) or responses of predator populations to prey outbreaks (Witman et al., 2003). The full range of ecological interactions undoubtedly occurs. Time series studies have identified dynamic benthic assemblages, with variation in feeding group dominance (Taylor et al., 2017), but the importance of ecological interactions generally remains to be characterized.

Competition And Predation
The arrival of a new resource like a whale carcass or a baited camera provides examples of interactions between predatory/scavenging species. For example, Yeh and Drazen (2009) saw events they interpreted as *Histiobranchus* sp. preying on aristeid shrimp around baited cameras. Abundances of other species were negatively associated, which could be interpreted as a competitive interaction (Yeh and Drazen, 2009), although negative associations are only suggestive of an interaction given other potentially confounding processes. A further example of a potential predatory interaction is seen in the avoidance behaviour of squat lobsters, *Munidopsis crassa*, leaving a porpoise carcass when *Benthoctopus* sp. was present (Kemp et al., 2006). A whale fall, which provides a sudden pulse of energy to the deep–sea floor, becomes the platform for a unique ecosystem (see Smith et al., 2015) and is the site of numerous ecological interactions. Nematode abundance around an artificially placed whale carcass was shown to decrease close to the carcass, presumably due to either predation by, or competition with, other organisms attracted to the carcass (Debenham et al., 2004). Conversely nematode abundance 30 m from the carcass increased over a year and a half, potentially due to organic enrichment of the surrounding sediment as the carcass decomposed. Enhanced prey availability at whale falls must lead to enhanced predator interactions, although these are not well

documented. Observations of pycnogonids at whale carcasses, sunken wood, and cold seeps provide evidence that these enriched habitats do attract predators (Braby et al., 2009). In Monterey Bay, at depths of 3 000 m, two species of pycnogonids were found to be in higher than normal abundance at these habitats, where they were seen feeding on the anemones *Anthosactis pearseae*, which attaches directly to whale bone, and *Liponema brevicornis*, which favours soft sediment. The anemones were presumed to accumulate in these habitats due to local enrichment, but also due to the topography that disrupted currents in a manner favourable to filter feeders.

Vent communities can be highly structured with zonation of species distributions thought to reflect environmental gradients (Cuvelier et al., 2011; Kim and Hammerstrom, 2012; Marsh et al., 2012). There is potential for species to compete for space on environmentally optimal surfaces. For example, Lenihan et al. (2008) found fewer invertebrate recruits on blocks with high densities of *Bathymodiolus*, even when transplanted to locations with otherwise high recruitment. Relatively low recruitment was interpreted to reflect potential interactions like predation (either by filter feeding on larvae by mussels or by organisms associated with mussels) and/or competition involving space pre–emption mediated by larvae choosing not to settle in mussel beds or by other means.

A rare caging experiment indicated the role of predatory fish at vents (Micheli et al., 2002). The dominant zoarcid fish (*Thermarces cerberus*) feeds on gastropods and amphipods. When predatory fish were excluded with cages, gastropods and amphipods increased in number and sessile invertebrates became less common (Micheli et al., 2002). This effect on the community was stronger at treatments placed nearest to hydrothermal vents.

Symbioses, Facilitation and Parasitism
The roles of chemoautotrophic microbial symbionts in sustaining deep–sea food chains are well known. Vestimentiferan worms, bathymodiolid mussels, vesicomyid clams, *Rimicaris* shrimps, among others, harbour chemoautotrophic symbiotic bacteria. Several squat lobster species of the genera *Kiwa* and *Shinkaia* even garden chemoautotrophic bacteria on dense specialized setae which they consume potentially as their primary food source (Baeza, 2011).

More broadly, commensal invertebrates seem fairly common (Figure 19.1), with species like scale worms recognized from mussel hosts (e.g., Pettibone, 1986). Where organisms like sea pens, corals, sponges and xenophyophores provide structure or attachment points, a diverse assemblage of facultative and potentially obligate symbionts can be found (Beaulieu, 2001; Buhl–Mortensen et al., 2010; Fig 19.1A, D-F). Some species associations may occur as hard substrate is not otherwise available or they may reflect fitness improvements from better feeding opportunities or avoidance of predation (Barry et al., 2017). The importance of structural supports to biodiversity may increase with depth, reflecting associated declines in habitat complexity and productivity (Buhl–Mortensen et al., 2010).

Among corals, which are well–known for enhancing habitat substrate, eleven families of deep–water Alcyonacea are regularly found with symbionts (see review by Watling et al., 2011 which includes a complete list of octocoral hosts and their symbionts). Common octocoral symbionts include scale worms (family Polynoidae), copepods, ascothoracids (parasitic crustaceans previously considered to be cirripedes), brittle stars, and various amphipods. Some families seem to have evolved more numerous symbioses than others. Watling et al. (2011) list *Anthomastus grandiflorus* as the only deep–water species of Alcyoniidae (true soft corals) to host a symbiont (the commensal polynoid *Harmothoe acanellae*), and *Victogorgia josephinae* as the only anthothelid to host associates. In contrast, they report *Paragorgia arborea* (family Paragorgiidae) to host a commensal amphipod (pleustid), sphaerodorid worm, and an anemone, as well as a parasitic zoanthid and copepod, while other *Paragorgia* species are also reported to host associates. Among the Primnoidae, Watling et al. (2011) reported 17 symbionts from 11 species. Many of these relationships are unique to the species involved. For instance, each of five species of *Chrysogorgia* (Octocorallia, Chrysogorgiidae) hosts a different species of *Thalassomembracis* (Crustacea, Ascothoracidae). Conversely, there are symbiont species reported from more than one host and these hosts may be quite different: for example *Gorngoniapolynoe muzikae* has been reported from species of both *Candidella* (family Primnoidae) and *Acanthogorgia* (family Acanthogorgiidae). Few of these relationships have been studied in detail, although the brittle star *Ophiocreas oedipus* is thought to colonize its *Metallogorgia* host when both are young, with the single symbiont growing with the coral until the latter dies (Mosher and Watling, 2009). In contrast, multiple *Gorgoniapolynoe caeciliae* must colonize the primnoid *Candidella imbricata* because the longevity of the symbiont species is much less than that of the coral, leading to considerable turnover of symbionts during the coral's life (Watling et al., 2011). Interestingly, the presence of the worm affects the morphology of the coral providing a refuge for the symbiont species (Eckelbarger et al., 2005). Similar host manipulation is seen in the symbiosis between species of eunicid worms and deep–water hermatypic scleractinians (Oppelt et al., 2017), and in the relationship between eunicids and black corals, where the hosts' skeletal spines are modified (Molodtsova and Budaeva, 2007).

The benefit for the symbiont is often obvious, even when the coral is not induced to produce a specialist refugium. The increased height above the substrate is beneficial to filter feeders, and it has further been suggested that octocorals, with their presumed secondary–metabolite laden tissues (to protect themselves from predation) also offer protection from predation to the symbiont. Most of the known relationships between octocorals and their symbionts, if not clearly parasitic, have been classed as commensal, i.e., with no obvious benefit to the host. Parasites include the zoanthid *Isozoanthis primnoidus* associated with the cold water coral *Callogorgia verticillata*, which appears to progressively harm its host, overgrowing the coral coenchyma and polyps, and incorporating coral sclerites into its own tissue for protection (Carreiro-Silva et al., 2011). A similarly parasitic relationship has also been found for a species of *Epizoanthus* overgrowing *Paragorgia arborea* (Buhl-Mortensen and Buhl-Mortensen, 2004). In this intensive study, 47 species were found associated with *P. arborea* and 97

with *Primnoa resedaeformis*. While some of these species were feeding on the host corals, a large number were identified as using the corals as substrate or for refuge, indicating the enormous role octocoral gardens can play in biodiversity through commensal relationships.

A recent study, however, has suggested that there may be tangible host benefits. Girard et al. (2016) studied the relationship between the ophiuroid symbiont *Asteroschema clavigerum* on the plexaurid octocoral *Paramuricea biscaya*. They monitored damage and recovery of *Paramuricea* following the Deepwater Horizon oil spill in the Gulf of Mexico. They found that recovery of the colony was negatively correlated with how far away that part of the colony was from a symbiotic ophiuroid, and suggested that ophiuroids both removed material that was deposited on polyps and inhibited settlement of hydroids on the colony. Although these effects were associated with a catastrophic impact event, the authors suggested that some benefit from sedimentation in natural conditions might be conferred on the coral host.

The presence of potential hosting benefits might explain the prevalence of host: symbiont associations in black corals. Black corals (Hexacorallia, Antipatharia), unlike other corals, are not able to retract their polyps and are thus particularly vulnerable to sedimentation events. In a comprehensive review of black coral ecology, Wagner et al. (2012) listed known symbionts. Among deep–water black corals, chirostylids are particularly prevalent, and have been recorded on species of *Bathypathes, Leiopathes, Parantipathes* and *Antipathes* (Wienberg et al., 2008; Le Guilloux et al., 2010). Chirostylids appear to feed on particles trapped in the mucus secreted by the black corals, and hence obtain their food while potentially cleaning the host (Le Guilloux et al., 2010). In shallow–water associations between decapods and antipatharians, it has further been suggested that the decapod might deter other predators (e.g. Glynn, 1980), although some decapods have also been shown to feed on antipatharian tissue (Wirtz and d'Udekem–d'Acoz, 2001).

Aside from emergent structures, burrowers and other agents of disturbance may facilitate other species by creating small–scale heterogeneity. Fish associate with sponge and coral reefs, potentially giving the habitats value in sustaining both fish populations and fisheries. Unfortunately testing these sorts of hypotheses is difficult: statistical models of fish–habitat associations are subject to issues of scale, temporal variability and potential confounding variables (Kutti et al., 2014; Pham et al., 2015).

Just over a decade ago, de Buron and Morand (2004) asked the question why there were not more deep–sea vent parasites. They identified over 15 vent examples and 126 non–vent parasite species. In answer to the question 'why not more?' their answer was that the level of collection and identification was limiting the apparent prevalence of parasitic relationships.

Inference Of Process From Pattern
It has been tempting to make broad statements about the importance of trophic interactions in shaping deep–sea ecology and evolution. Examples include Sanders' (1968) stability–time hypothesis and Rex's explanations for bathyal

diversity peaks (Rex, 1981). The stability–time hypothesis addresses a similar issue to the paradox of the plankton (Hutchinson, 1961): richness in a habitat expected for other reasons to species poor. In Sanders' hypothesis the richness is a result of a long evolutionary niche diversification in a stable environment. Rex (1981) suggested that interactions between competition, predation and productivity shape the change in species richness with depth, with a humped diversity–productivity relationship occurring along the depth gradient. Such broad statements about the causes of patterns in species diversity are not widely accepted as sufficient explanations. Stability–time ideas have been contradicted by observations of disturbance and population turnover even at abyssal depths (Levin et al., 2001, although see McClain and Schlacher, 2015, contrasting the relevant time scales of disturbance). A general explanation invoking species interactions for the peaking of diversity in the mid–bathyal zone needs consistent explanations for competitive exclusion mechanisms, and a framework for explaining why the pattern does not seem to be universal (Stuart and Rex, 2009; Rex and Etter, 2010). Terrestrial ecology has grappled with whether a humped diversity–productivity relationship is common (Adler et al., 2011), what models of competition actually predicted under high productivity (Abrams, 1995) as well as the low predictive value of single variables (Grace et al., 2016). Deep–sea ecology will need a similar approach, an understanding of proxy variables, and inclusion of additional variables (Etter and Grassle, 1992), particularly as the r^2 is often low in diversity depth regressions (Rex and Etter, 2010). With respect to the absence of a single accepted theory that successfully integrates an understanding of species interactions into an explanation of pattern, deep–sea ecology is no different from many other areas of ecology. Brown (1981) describes a widespread belief during the 1960s and 1970s that interspecific competition was the main factor limiting diversity. This belief was followed by disappointment as many of the models for competition were often shown to rely on unrealistic assumptions and to produce ambiguous predictions that were not clearly testable.

The difficulties in inferring process have contributed to a situation where 'every old hypothesis is also a new one' (McClain and Schlacher, 2015). Older hypotheses have not been refuted or built on as the demonstration of processes like competition or niche partitioning is difficult and some of the predictions cannot be distinguished from the predictions of alternative hypotheses. Wider applications of tools like stable isotopes and sequence analysis are likely to identify more detailed examples of trophic specialization (e.g., Levesque et al., 2003; Govenar et al., 2015).

Concluding remarks
We are, however, still some distance from an evaluation of the effects of ecological interactions in shaping deep–sea communities (McClain and Rex, 2015). Levin et al. (2001) offer a synthesis of the roles of ecological interactions and other processes in a series of conceptual models spanning gradients of food input, flow strength, oxygenation, sediment heterogeneity and disturbance. While an important step, such syntheses do not generate testable predictions that would allow ecological interactions to be evaluated. Levin and Dayton (2009) identified links between ecological theory and management of

continental margins. This is potentially the area where the clearest picture of the role of ecological interactions will be developed in the near future: not in the description of general patterns, but in the management of environmental change and human impacts.

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Figure 19.1 Animal-animal associations in the deep sea. A. Chirostylid on black coral *Bathypathes.* B. The zoanthid *Epizoanthus paguriphilus* providing a shell for the hermit crab *Parapagurus pilosimanus.* C. The carrier crab *Paramola cuvieri* carrying a black coral, probably *Parantipathes*. D. Yellow zoanthid on the sponge *Aphrocallistes beatrix*. E. Yellow zoanthid and brittle star *Asteroschema* on the bubblegum coral *Paragorgia*. F. Brittle star *Asteroschema* on the plexaurid coral *Paramuricea.* All photos taken by NUI Galway during cruise CE14009 aboard RV Celtic Explorer using ROV Holland I, copyright Marine Institute.

Table 19.1 Comparison of proposed biogeography schemes. Note that numbering and abbreviations are those used in the original studies.

Bathyal provinces (Watling et al., 2013)	Vent provinces (Bachraty et al., 2009)	Cold Seep provinces (Tyler et al., 2003)
BY1. Arctic		Atlantic
BY2. Northern Atlantic Boreal		Atlantic
BY3. Northern Pacific Boreal	Northwest Pacific (NW) and Northeast Pacfic (NE)	[some deep 'West Pacific' seeps are in the North Pacific **abyssal** province]
BY4. North Atlantic	Northern Mid–Atlantic Ridge (MAR)	Gulf of Mexico, Mediterranean, Atlantic
BY5. Southeast Pacific Ridges	Southern East Pacific Rise (SEPR)	
BY6. New Zealand–Kermadec	Southwest Pacific (SW)	
BY7. Cocos plate	Northern East Pacific Rise (NEPR)	East Pacific
BY8. Nazca plate		East Pacific
BY9. Antarctic		
BY10. Subantarctic		
BY11. Indian	Southwest Pacific (SW)	
BY12. West Pacific	Southwest Pacific (SW) and slight overlap with North West Pacific (NW)	West Pacific
BY13. South Atlantic		Atlantic
BY14. North Pacific		