

Review

The dynamics of biogeographic ranges in the deep sea

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Anthropogenic disturbances such as fishing, mining, oil drilling, bioprospecting, warming, and acidification in the deep sea are increasing, yet generalities about deep-sea biogeography remain elusive. Owing to the lack of perceived environmental variability and geographical barriers, ranges of deep-sea species were traditionally assumed to be exceedingly large. In contrast, seamount and chemosynthetic habitats with reported high endemism challenge the broad applicability of a single biogeographic paradigm for the deep sea. New research benefiting from higher resolution sampling, molecular methods and public databases can now more rigorously examine dispersal distances and species ranges on the vast ocean floor. Here, we explore the major outstanding questions in deep-sea biogeography. Based on current evidence, many taxa appear broadly distributed across the deep sea, a pattern replicated in both the abyssal plains and specialized environments such as hydrothermal vents. Cold waters may slow larval metabolism and development augmenting the great intrinsic ability for dispersal among many deep-sea species. Currents, environmental shifts, and topography can prove to be dispersal barriers but are often semipermeable. Evidence of historical events such as points of faunal origin and climatic fluctuations are also evident in contemporary biogeographic ranges. Continued synthetic analysis, database construction, theoretical advancement and field sampling will be required to further refine hypotheses regarding deep-sea biogeography.

Keywords: biogeography; deep sea; dispersal; range; vicariance; establishment

1. INTRODUCTION

In the last 130 years, our view of the deep ocean floor that extends beyond the continental shelves (less than 200 m depth) radically changed (reviewed in Koslow (2007)). The deep sea was once considered a dark, homogeneous wasteland, unchanging through time and devoid of biodiversity. Exploration of this vast ecosystem continues to reveal a multitude of novel, high-productivity habitats, including chemosynthetic environments (Sibuet & Olu 1998; Van Dover 2000) and large organic food falls (reviewed in Smith & Baco-Taylor (2003)). Intricate canyons, expansive ridge systems and submerged mountains, as well as distinct suboxic environments provide habitat complexity (e.g. Wilson & Kaufmann 1987; Vetter & Dayton 1998; Van Dover 2000; Levin 2003; Cordes *et al.* 2009). Even the expansive mud bottom—the backdrop for this variation—experiences episodic storms and currents, patchy organic input and disturbance regimes linked to surface ocean processes (e.g. Tyler 1988; Gooday 2002).

Our perceptions of the deep sea as a ‘biological desert’ were transformed by findings of spectacularly high biodiversity (Sanders 1968; Grassle 1989) and remarkable *in situ* evolutionary radiations (Little & Vrijenhoek

2003). These findings stimulated much discussion regarding the maintenance of diversity in this food-poor habitat, leading to the idea that micro-habitat structure may create niche diversity and enhance species turnover on local scales (reviewed in Snelgrove & Smith (2002a)). High species turnover on the deep-sea floor, estimated at 45–80% over hundreds to thousands of kilometres (Grassle & Maciolek 1992; Glover *et al.* 2002; Brandt *et al.* 2005), is often cited as evidence of restricted species ranges. However, these turnover rates are similar to other systems (vascular plants Nekola & White (1999), e.g. intertidal invertebrates Nakaoka *et al.* (2006)). Moreover, high turnover does not necessarily preclude extensive geographical ranges if species are patchily distributed within those ranges.

These more recent claims of restricted ranges thus represent a radical departure from earlier studies, which suggested that the lack of perceived environmental variability and geographical barriers to dispersal would lead to exceedingly large ranges of deep-sea species. The biogeography of deep-sea organisms has historically been a black box characterized more by inference than data—unsurprising given the challenges of sampling this remote environment. However, modern research techniques, higher resolution sampling efforts and expansion of public databases now allow for a re-examination of existing hypotheses. In this review, we examine major outstanding questions concerning the biogeography of deep-sea invertebrates on the seafloor (figure 1). We ask: (i) do deep-sea

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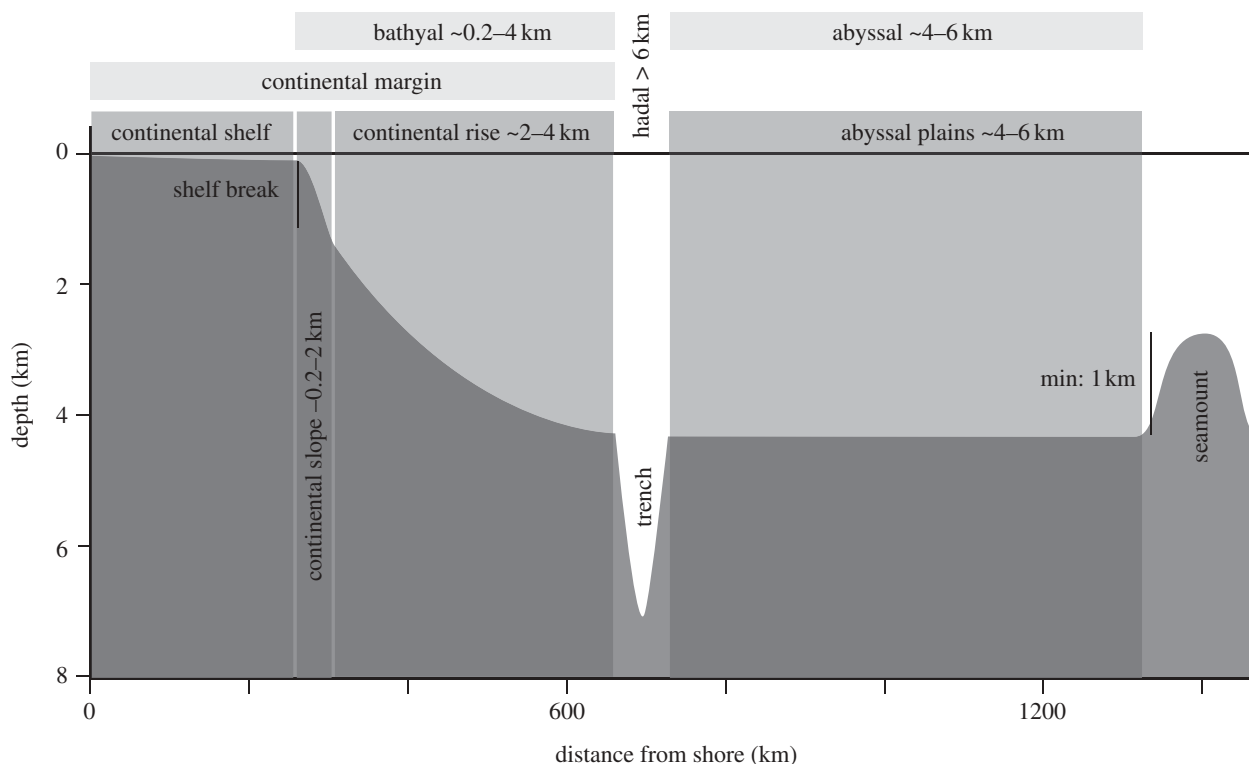


Figure 1. Profile of typical continental margin and deep-sea system. Major regions are labelled. Adapted from Gage & Tyler (Gage & Tyler 1991).

species exhibit broad geographical distributions? (ii) how has the history of the deep sea through the Phanerozoic shaped biogeography on the seafloor? (iii) what contemporary processes constrain ranges in the deep sea? In considering these questions, we strive to construct a new framework reflecting modern scientific developments, and identify future research needs.

(a) *Species distributions in the contemporary deep sea*

Severe undersampling of the deep sea, estimated to be much less than 1 per cent of the total seafloor McClain (2007), prevents full characterization of species ranges. For many species, we can only conservatively estimate the maximum linear range extent with any accuracy. However, the use of singular linear dimensions to characterize range is not without precedent as terrestrial and shallow-water biogeographers often employ these metrics to convey useful information, e.g. Rapoport's Rule (e.g. Fortes & Absalao (2004)). Based on such observations we can thus begin to describe some general patterns in species distributions.

Studies employing morphospecies as basic taxonomic units largely support earlier theories of cosmopolitanism in many groups inhabiting the soft-bottom seafloor, notably nematodes, foraminifera, mollusca and echinodermata (e.g. Madsen 1961; Sibuet 1979; Tyler 1980; Rex 2002; Gooday *et al.* 2004; Vanreusel *et al.* 2010). For example, approximately 25 per cent of known bivalve mollusc species occur in multiple ocean basins, most with ranges covering more than 20° latitude (Allen (2008), C. R. McClain & T. G. Gullett 2009, unpublished data). Many elaspod holothurians also appear widely distributed on the abyssal plains, with only a few bathyal taxa

confined to a single region (Hansen 1975; Young *et al.* 1997). Patterns in amphipod crustaceans are somewhat unclear, but several widely distributed abyssal species are known, and many others possess at least basin-wide distributions (Barnard 1961; Thurston 1990).

While chemosynthetic habitats such as hydrothermal vents, cold methane seeps and large food falls share many common taxa (reviewed in Smith *et al.* (2003)), regional and/or global distribution of this specialized fauna remains poorly resolved. At the generic level, several distinct groups appear broadly distributed, including *Osedax*, a group of bone-eating worms Glover *et al.* (2005), the wood-boring bivalve genus *Xylophaga* Voight (2009) and numerous vent and seep taxa (Van Dover 2000; Cordes *et al.* 2007). Even geographically isolated western Pacific vents share 50 per cent of genera with eastern sites (Hessler & Lonsdale 1991). However, at the species level, seep species may be restricted to individual or adjacent sites Sibuet & Olu (1998), whereas vent communities share 10–15% of species between regions or basins Desbruyeres *et al.* (2006), and are often broadly distributed within continuous ridge systems (e.g. Hessler & Lonsdale 1991; Tunnicliffe & Fowler 1996).

Like chemosynthetic systems, seamounts may represent island-like habitats potentially isolated by hydrography or sheer distance, leading to predictions of high endemism (McClain 2007; Brewin *et al.* 2009; Clark *et al.* 2010). Early studies reported that up to 36 per cent of taxa on seamounts were endemic, albeit with the caveat of severe undersampling of the deep sea (reviewed in Wilson & Kaufmann 1987; Rogers 1994; McClain 2007). Accumulating species-level data now indicate that seamount communities are comprised of non-endemic species drawn from a regional species pool, often with broad geographical distributions of

hundreds to thousands of kilometres (Brewin *et al.* 2009), reviewed in Samadi *et al.* 2006; O'Hara 2007; O'Hara *et al.* 2008; Thoma *et al.* 2009; Clark *et al.* 2010; Howell *et al.* 2010). For example, 79 per cent of the species on a well-studied California seamount possess ranges greater than 1000 km (McClain *et al.* 2009a). Thus, early hypotheses of large deep-sea species ranges appear to hold true for seamount fauna.

More recent biogeographic studies employing genetic tools are helping to unravel taxonomic problems that can complicate range-size determinations. These methods have identified cryptic species complexes misdiagnosed as single morphospecies, as well as distinctive morphotypes or life-history stages of a single species given synonymous species names (Raupach *et al.* 2007; Vrijenhoek 2008). Molecular studies also indicate cosmopolitanism in many groups, revealing surprising genetic homogeneity over large distances in vent (Won *et al.* 2003; Hurtado *et al.* 2004; Johnson *et al.* 2006), seamount (Bucklin *et al.* 1987; Smith *et al.* 2004; Jones *et al.* 2006; Samadi *et al.* 2006) and abyssal plain Bisol *et al.* (1984) populations separated by thousands of kilometres. Genetic analyses verified reportedly widespread distributions of a common polychaete worm throughout the abyssal Pacific, Atlantic and Southern Oceans Mincks *et al.* (2009), and in three abyssal foraminifera species found in the Arctic and Antarctic, separated by 17 000 km (Pawlowski *et al.* 2007).

In contrast to this evidence of extensive horizontal gene flow, multiple soft-bottom taxa show significant genetic differentiation along bathymetric gradients of only a few kilometres (France 1994; France & Kocher 1996; Howell *et al.* 2004; Zardus *et al.* 2006). Thus, biogeographic patterns are likely to vary considerably between the abyssal seafloor and the continental slopes, which experience considerable heterogeneity in carbon flux, topography, sediment type and current regime (Carney 2005; Zardus *et al.* 2006; Levin & Dayton 2009). Indeed, earlier studies suggested geographical ranges may increase (Allen & Sanders 1996; Wilson & Kaufmann 1987) with depth as environmental conditions become more homogeneous. More recent molecular work supports this idea, demonstrating genetic homogeneity among abyssal populations and restricted gene flow along depth gradients in Atlantic molluscs (Etter *et al.* 2005; Zardus *et al.* 2006).

A preponderance of evidence now suggests that deep-sea genera, and often species, are broadly distributed, regardless of habitat type. Interestingly, patchy habitats like seamounts and vents do not appear to differ from the surrounding abyssal plains in this respect. Seep species may prove an exception to the rule, but more comprehensive sampling will be required. In contrast, bathymetric gradients may pose significant constraints on species ranges relative to horizontal distances, indicating broad geographical distributions may be more frequent at greater depths.

(b) Processes governing species distributions in the deep sea

Variation in range size results from a complex interaction of physical, biological and historical factors (Brown *et al.* 1996; Holt 2003; Holt & Keitt 2005; Pineda *et al.* 2009).

Taxon-specific physiological adaptations and life-history strategies arise under historical selection pressures, and govern the intrinsic ability to move between habitat patches. Extrinsic factors in turn impact propagule survival during dispersal, provide physical barriers to movement and influence successful colonization of new patches. Overlain on these processes are species-specific niche requirements within the environmental landscape combined with biological interactions permitting populations to persist (Holt & Keitt 2005; Soberon 2007; Soberon & Nakamura 2009). Here, we examine the contribution of historical contingencies, intrinsic dispersal abilities and extrinsic factors that interact with both dispersal and the adult niche to determine geographical distributions of deep-sea species.

(c) History of the deep-sea environment and fauna

Extreme variability in temperature, oxygen and circulation characterize the deep-sea palaeoceanographic history (figure 2). Since the Eocene/Palaeocene boundary (approx. 55 Ma), deep water has cooled approximately 15°C, following minor warming in the Late Cretaceous Waelbroeck *et al.* (2001), and a similar cool period at the Eocene/Oligocene boundary (approx. 34 Ma). Deep-ocean circulation has alternated between two historical ocean types one driven by high-latitude deep-water formation (thermohaline, THC), resulting in cold, oxygenated deep water, and one driven by salinity-induced stratification at low latitudes (halothermal, HTC) resulting in warm, saline deep water and reduced global circulation (Jeppsson 1990; Horne 1999; Rogers 2000). THC conditions have prevailed since the Eocene/Oligocene transition, but a warmer, low-oxygen HTC phase dated back to the Triassic. During this period, deep-water anoxia was frequent and widespread (Jacobs & Lindberg 1998; Rogers 2000; Waelbroeck *et al.* 2001), with the most severe events associated with rapid THC–HTC transitions in the mid-Cretaceous, and at the Permian/Triassic and Ordovician/Silurian boundaries (Horne 1999).

Most current hypotheses for the origins of the deep-sea fauna centre on 'extinction and replacement'—a near-complete extinction of deep-sea fauna triggered by catastrophic anoxic events, with subsequent invasion and radiation of shallow-water species into the deep (Rogers (2000), reviewed in Horne 1999; Wilson 1999). Thus, the deep-sea fauna may be relatively young, dating back to the last major anoxic event at the Eocene/Oligocene boundary (reviewed in Wilson (1999)). However, many clades appear to have survived these anoxic periods (Clarke 1962; Wilson 1999; Raupach *et al.* 2009). The specialized fauna of contemporary oxygen minimum zones (reviewed in Levin (2003)) suggests the potential for evolutionary adaptation (Wilson 1999). Anoxic events may have eliminated vulnerable taxa producing a more resistant deep-sea fauna through time evidence by hypoxia tolerances among deep-sea fauna (Levin 2003). Anoxia may have also encouraged speciation rather than extinction, with low-oxygen waters posing barriers to gene flow, and promoting allopatric speciation in localized well-oxygenated refugia (e.g. along particular isobaths or in isolated basins) (Wilson 1999; Rogers 2000).

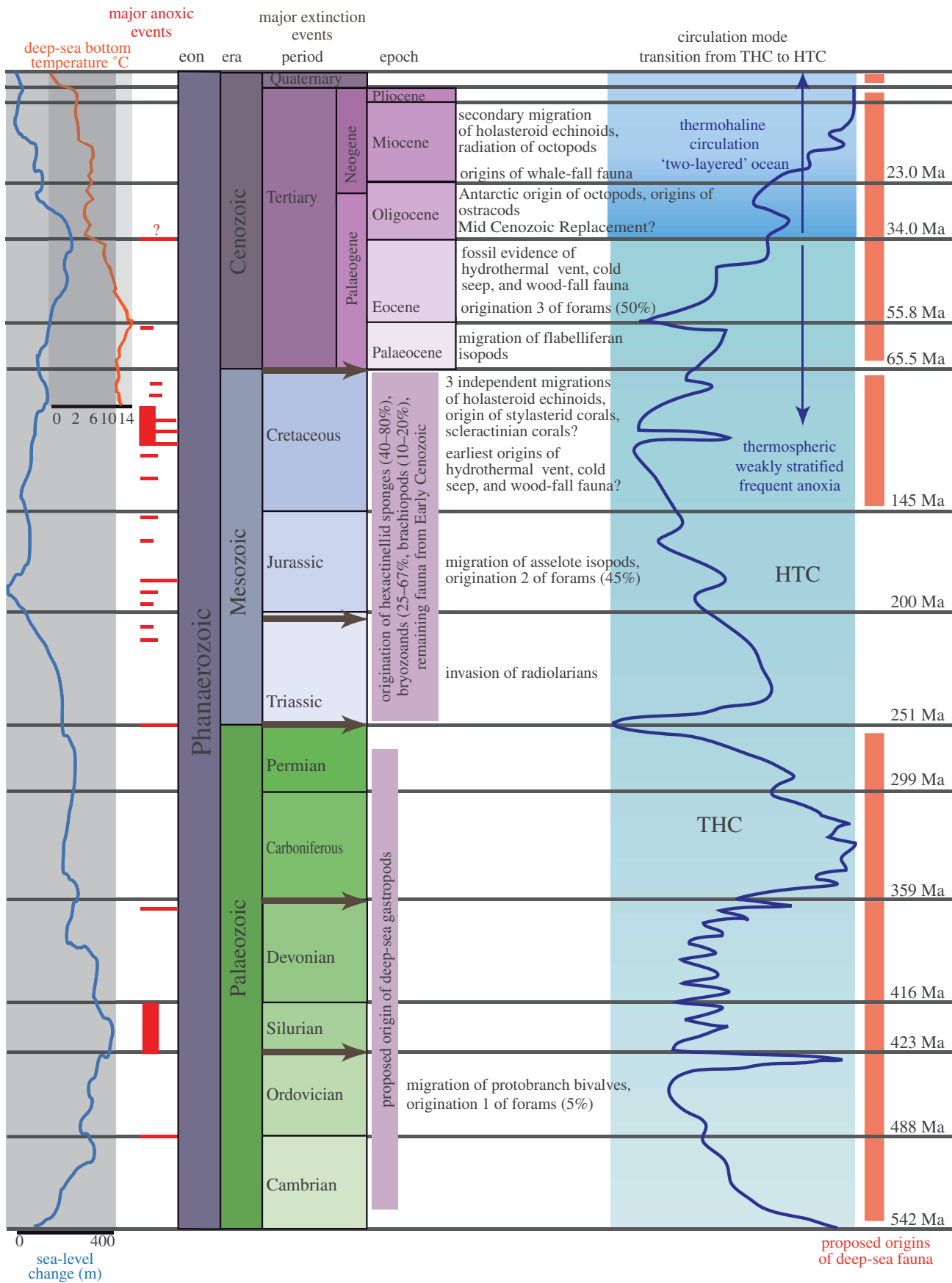


Figure 2. The geological, biological, chemical and physical history of the deep sea. Figure shows from left to right sea-level change in metres (light blue line); deep-sea bottom temperature in degrees celsius (orange line); major anoxic events (dark red blocks, width denotes regional vs. global); major extinction events (grey arrows within timescale), major migrations of fauna into the deep (text); circulation mode (dark blue line) and proposed origins of deep-sea fauna (light red blocks). Data for figure come from (Menzies & Imbrie 1958; Clarke 1962; Bensen 1975; Allen 1978; Lipps & Hickman 1982; Jeppsson 1990; Jacobs & Lindberg 1998; Horne 1999; Wilson 1999; Rogers 2000; Waelbroeck *et al.* 2001; Little & Vrijenhoek 2003; Smith & Stockley 2005; Kiel & Goedert 2006; Linder *et al.* 2008; Strugnell *et al.* 2008).

Adaptation, filtering and refugia may explain the apparent lack of common origin point for contemporary deep-sea fauna, which appear to be comprised of clades originating throughout the Phanerozoic, rather than a fauna of uniform age (demonstrated early by Menzies & Imbrie 1958; Wilson 1999; figure 2). For example, only approximately 5 per cent of the extant deep-sea foraminiferan genera date to the early Palaeozoic, while the rest are younger (Lipps & Hickman 1982). Asellote isopod crustaceans, abundant in the contemporary deep sea, date back to the Jurassic with evidence of impressive deep-sea radiations, whereas flabelliferan isopods have more recent Cenozoic origins (Wilson 1999; Raupach *et al.* 2004, 2007, 2009). Bivalve molluscs, early inhabitants of the deep sea, date to the late Ordovician but show evidence of more recent radiations (Allen 1978). In some groups, deep-sea invasions are reflected in onshore–offshore trends in fauna age, with older clades inhabiting bathyal depths and younger clades in the abyss (Menzies & Imbrie 1958; Jablonski *et al.* 1983; Jablonski & Bottjer 1991). Numerous contemporary taxa ranging from corals to echinoderms appear to have invaded the deep sea from shallower waters—some multiple times (Menzies & Imbrie 1958; Smith & Stockley 2005; Linder *et al.* 2008).

Molecular and fossil evidence places the origins of the hydrothermal vent fauna relatively recently (approx. 100 Ma; reviewed in Little & Vrijenhoek (2003)). The divergence of vesicomimid clams, found in all the chemosynthetic habitats, is coincident with those of large whales, leading some to posit whale-falls as evolutionary steps from shallow water to seeps and vents Baco *et al.* (1999), although more recent work suggests early Cenozoic whale-fall communities lacked vesicomimids and were compositionally more similar to wood-falls of the time (Kiel & Goedert 2006). Colonization of chemosynthetic habitats probably occurred in the order these habitats appeared: seeps to wood to whale (Shank *et al.* 1998; Kiel & Goedert 2006). These combined findings cast doubt on theories of a uniformly ‘young’ or ‘old’ deep-sea fauna of common origin.

With multiple points of origin and radiations, contemporary deep-sea clades bear unique biogeographic signatures. For example, the North Atlantic Ocean is dominated by asellote isopods originating in the Jurassic, whereas the South Atlantic contains more recent (Tertiary) flabelliferan isopods (Wilson 1999). Contemporary ranges reflect sites of invasion from the continental shelves, because physiological tolerance to conditions at these sites may dictate the routes by which invasions occurred, e.g. through an isothermal water column. Suggested invasion sites include the Antarctic continental shelf and the Mediterranean Ocean (reviewed in Gage & Tyler (1991)), but at times during the Phanerozoic more isothermal conditions may have permitted multiple invasions at multiple sites (Wilson 1999). In particular, molluscs are tied to multiple origin points Clarke (1962) while many crustaceans are linked to Antarctic origins Wilson (1999), which may explain the differences often observed in the biogeography of the two groups (Rex *et al.* 2005; Brandt *et al.* 2007). Contemporary deep-sea biogeography thus includes many taxon-specific patterns requiring historical context, highlighting the potential pitfalls of extrapolating single-taxon studies to the global deep-sea fauna.

(d) *Migration and larval dispersal*

Shallow-water marine environments, once considered open systems with free exchange of planktonic larvae, have transitioned to a view that local recruitment and small-scale population genetic structure commonly occur despite a lack of obvious physical barriers (Cowen & Sponaugle 2009). These notions have yet to be revisited in the deep sea, where many key physiologically limiting variables such as light, oxygen, temperature and pressure are relatively constant over great distances. As we have shown, cosmopolitan distributions are common, yet many taxa show significant population structure, suggesting extrinsic factors may limit dispersal potential.

Most marine invertebrates are relatively non-motile as adults, but migrations do occur in response to episodic food inputs (Jones *et al.* 1998; Billett *et al.* 2001), implying rapid movement over large spatial scales is possible. Shallow-water echinoids move at rates of about 1–4 cm min⁻¹ Domenici *et al.* (2003), indicating potential spatial scales for movement greater than 200 km (assuming life-spans of approx. 10 years; Ebert & Southon (2003)). Longer-lived deep-sea organisms may move even greater distances (Cailliet *et al.* 2001). However, significantly greater dispersal potential exists during the planktonic larval stage (Young *et al.* 1997).

The majority of marine invertebrates produce intermediate larval forms, although some diverse and particularly abundant deep-sea groups are direct-developing (e.g. nematodes, isopods). Larval forms vary widely in development time owing to nutritional mode (planktotrophic versus lecithotrophic), temperature and phylogenetic constraints. These variations in planktonic larval duration (PLD) are thought to translate into variations in dispersal distance (e.g. Kinlan & Gaines 2003; Bradbury *et al.* 2008; Shanks 2009). Larval type may thus provide some indication of a species’ dispersal potential, but the larval modes of most deep-sea invertebrates are unknown, and a ‘typical’ deep-sea strategy does not appear to exist (cf. Tyler & Young 1999; Young 2004). Lecithotrophic larvae are commonly observed in abyssal echinoderms and polychaetes, and in molluscs from a variety of habitats, but planktotrophic and brooding taxa also occur in significant numbers. Peracarid crustaceans, one of the most speciose groups in the deep, are entirely brooders.

In the absence of general patterns in reproductive strategy, we compiled direct measurements of PLD for various deep-sea taxa in order to estimate the potential dispersal distances given typical deep-sea current speeds and ideal conditions (figure 3). If currents are both linear and constant (we concede this is an unrealistic assumption), dispersal distances on the order of 10²–10⁵ km could occur, suggesting amazing intrinsic potential for dispersal among deep-sea invertebrates and the overwhelming effect of extrinsic factors that ultimately limit range size. Although dispersal potential is often assumed to influence range size (Thorson 1950; Jablonski & Lutz 1983; Scheltema 1986), quantitative tests provide little empirical support for this relationship, in both shallow and deep seas (Emler 1995; Young *et al.* 1997; Paulay & Meyer 2006; Lester *et al.* 2007).

In cold-water habitats like the deep sea and poles (e.g. Pearse & Lockhart (2004)), metabolic constraints may

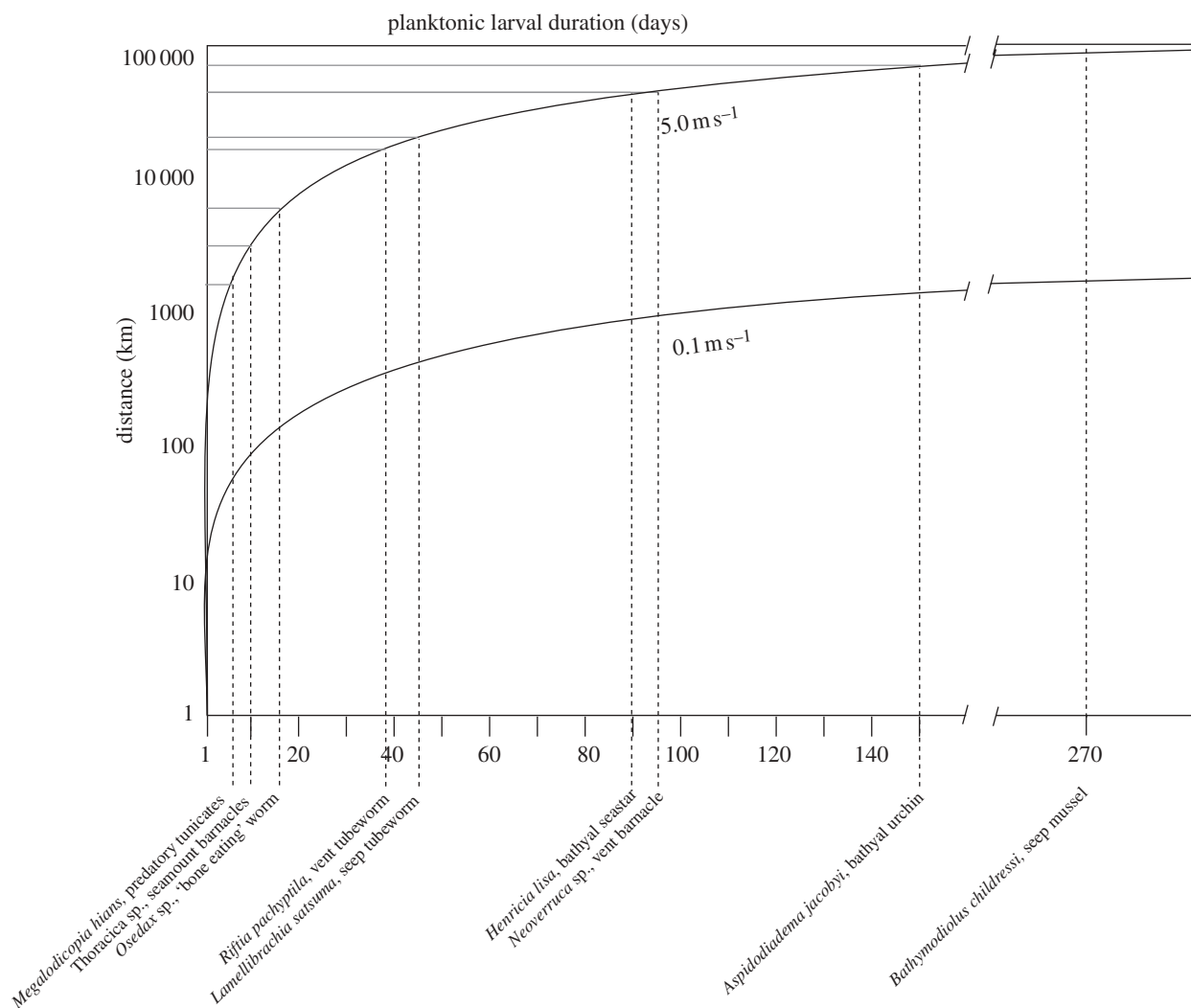


Figure 3. Potential larval dispersal distance of deep-sea fauna based on current speed, and published estimates of planktonic larval duration (Young & George 2000; Marsh *et al.* 2001; Watanabe *et al.* 2004; Havenhand *et al.* 2005; Buhl-Mortensen & Hoeg 2006; Miyake *et al.* 2006; Mercier & Hamel 2008; Arellano & Young 2009; Rouse *et al.* 2009). The two trajectories assume constant and unidirectional currents, and represent published estimates for lowest and highest velocity currents associated with surface waters or benthic storms (Havenhand *et al.* 2005). Note that currents demonstrating periodic changes in direction would greatly limit dispersal (Marsh *et al.* 2001).

significantly lengthen PLD (Brown *et al.* 2004; Bradbury *et al.* 2008). O'Connor *et al.* (2007) clearly demonstrated this temperature dependence in larval development across multiple vertebrate and invertebrate taxa. Thus, deep-sea taxa may exhibit greater dispersal distances than their shallow-water counterparts (cf. Bradbury *et al.* (2008)). Temperature effects may in part explain the discrepancy between dispersal distance and range size.

Pressure may also lengthen larval development times in the deep sea (Somero 1998). Some echinoderm larvae exhibit broader pressure tolerances than adults of the same species (Tyler *et al.* 2000; Villalobos *et al.* 2006; Pradillon & Gaill 2007), although hydrothermal vent tubeworms exhibit very narrow pressure and temperature tolerances. Adults of vent tubeworms live near vent fluids at 50°C at hundreds of atmospheres, while embryos develop best at approximately 5–10°C at ambient pressures. Thus, embryos are likely to leave the native vent site and develop in the water column (Pradillon & Gaill 2007).

(e) *Dispersal barriers*

Numerous shallow-water studies have shown evidence of restricted realized dispersal and local recruitment even in taxa with long PLD (e.g. Banks *et al.* 2007; Piggott *et al.* 2008; Zulliger *et al.* 2009), suggesting behavioural and/or environmental factors play an important role in limiting dispersal. For example, currents connect suitable habitat patches in order for propagules to colonize new areas and minimizing dilution of larval cohorts along their dispersal trajectory (e.g. Van Dover *et al.* 2001; Tokuda *et al.* 2006; Young *et al.* 2008). Hydrographic features may trap planktonic larvae over seamounts or other topography (McClain 2007; Brewin *et al.* 2009), or pose wall-like barriers to dispersal between basins (e.g. Antarctic polar front, (Rogers *et al.* 2006; Hunter & Halanych 2008), Pacific equatorial currents Won *et al.* (2003)). Currents transiting the equatorial Pacific hamper dispersal between southern and northern vents along the East Pacific Rise (EPR) (Won *et al.* 2003). Oxygen minimum zones may represent a similar barrier, isolating communities above and below inhospitable

waters (Rogers 2000). Currents also influence directionality of dispersal, potentially linking isolated habitat patches separated by thousands of kilometres, and minimizing dilution of larval cohorts along their dispersal trajectory (e.g. Van Dover *et al.* 2001; Tokuda *et al.* 2006; Young *et al.* 2008).

Topography also impedes exchange between deep-sea populations and figures prominently in attempts to classify deep-sea biogeographic provinces (electronic supplementary material, appendix S1). The Gibraltar sill segregates the Atlantic and Mediterranean deep-water masses and prevents Atlantic fauna from colonizing the relatively species-poor Mediterranean (reviewed in Sardà *et al.* (2004)). Disruption of currents by seamounts or fracture zones, particularly along oceanic ridge axes, may limit dispersal and generate genetic diversity among hydrothermal vent systems (Van Dover *et al.* 2002; Tyler & Young 2003). These discontinuities interrupt the 'ridge highway' between vent sites, producing species with smaller ranges (e.g. Won *et al.* 2003; Johnson *et al.* 2006; Young *et al.* 2008), although exceptions do occur (Hurtado *et al.* 2004). Mid-oceanic ridges may also prevent dispersal on the abyssal plains. Half of the known species of deep-sea bivalves are restricted to either the eastern or western Atlantic McClain *et al.* (2009b), suggesting a role of the Mid-Atlantic Ridge. Similarly, the Walvis Ridge may isolate peracarid crustaceans in the Angola Basin (Brandt *et al.* 2005). Landmasses also provide obvious physical barriers, but approximately 15–20% of species are shared between the Pacific and Atlantic (Vinogradova 1997). Recent studies provide evidence of genetic homogeneity between major ocean basins Zardus *et al.* (2006) and shared fauna between ocean basins. Inconsistencies in the role of topographic features as barriers to dispersal lends support for the filtering concept presented by Monnoit & Monnoit (1978), who noted these features were less barriers and more zones of faunal mixing.

The sheer distance between suitable habitat patches can form an insurmountable barrier (i.e. 'isolation by distance'; Wright (1943)), as demonstrated in shallow-water systems where genetic clines exist in some taxa with high dispersal potential (Sotka & Palumbi 2006). Indeed, distance-decay relationships, in which similarity decreases with distance, are common features of ecological systems (Nekola & White 1999; Soininen *et al.* 2007). Thus, even in relatively homogeneous habitats like the abyssal plains, distance effects on dispersal may lead to population differentiation and faunal turnover on regional scales. Few studies explicitly examine deep-sea species turnover or gene flow over large spatial scales between seamounts McClain (2007) or between oceanic basins Allen (2008), but the role of distance has been invoked frequently for chemosynthetic environments (Vrijenhoek 1997; Won *et al.* 2003; Shank & Halanych 2007; Audzijonyte & Vrijenhoek 2010). In the 'stepping stone' model, gene flow occurs only among neighbouring vent populations and decreases with increasing distance. Tests of this model yield mixed results possibly owing to differences in distance between vent sites at fast and slow spreading centres Van Dover (1995) or sampling issues (Audzijonyte & Vrijenhoek 2010). Dispersal distances that exceed between-site distances at fast spreading centres may generate homogeneous

populations over larger distances, whereas greater spacing of vent sites at slow spreading centres could prevent dispersal between sites (Desbruyères *et al.* 2001).

(f) Niche requirements

The role of niche-specificity, including habitat requirements and species-level interactions (e.g. competition, predation), in governing deep-sea biogeographic ranges is very poorly studied. Nonetheless, specific niche requirements will of course govern species' abilities to establish a population at a given location even if dispersal to that location is possible. Phenotypic and faunal patterning in deep-sea habitats provide some evidence of niche effects. For example, oxygen concentration appears to drive intra- and interspecific clines in invertebrate phenotypes McClain & Rex (2001), with oxygen minimum zones contain distinct suites of tolerant species (Levin 2003). Similarly, calcium carbonate dissolution is known to restrict depth distributions in taxa with exoskeletons (e.g. McClain *et al.* (2004)). Trophic requirements will also play an important role, not only for chemosynthetic fauna restricted to specialized and patchily distributed habitats, but for heterotrophic fauna as well.

A sizeable literature explores the unique adaptations of deep-sea deposit-feeders that enable them to subsist in the food-poor soft-sediment environment (e.g. Jumars *et al.* (1990)). Diversity of deposit-feeding strategies corresponds to a high degree of niche diversity that actually allows surprisingly large numbers of species to coexist in an extremely food-limited environment (Snelgrove & Smith 2002b). Organic carbon flux also influences biodiversity and standing stock over large spatial scales (Rex *et al.* 2006; Smith *et al.* 2008; McClain *et al.* 2009b), and generates bathymetric and latitudinal gradients in alpha diversity (Rex *et al.* 1993; Levin *et al.* 2001). However, effects of flux on biogeography are only explored in the context of bathymetric zonation (Carney 2005). The relationship between species ranges and the considerable horizontal variation in vertical flux (Lampitt & Anita 1997; Lutz *et al.* 2007) requires additional attention. For example, an abyssal source-sink system may exist in which extremely oligotrophic areas cannot sustain viable population sizes without input from eutrophic areas (Rex *et al.* 2005). Under such a scenario, little faunal turnover would be expected along horizontal gradients in flux extending into oligotrophic abyssal regions.

A promising approach to uncovering relationships between environmental factors and species ranges in the deep sea has recently been demonstrated using ecological niche models (ENMs), which linked specific niche requirements of stony corals with spatial gradients in abiotic factors (Tittensor *et al.* 2009). Applied in terrestrial settings for a decade (reviewed in Hirzel *et al.* 2002), ENMs and similar models have only recently been employed in the deep sea (Metaxas & Bryan 2007). Tittensor *et al.* (2009) are the first to examine deep-sea communities at a global scale using ENMs to disentangle important environmental variables influencing coral distributions on seamounts and predict locations of suitable habitat.

2. CONCLUSIONS

The sheer size of the deep sea continues to confound attempts to ascertain broad-scale patterns. However, a

clear articulation of biogeographic patterns and processes is vital to advancing conservation efforts and mitigating increasing anthropogenic threats (Glover & Smith 2003; Orr *et al.* 2005; Robison 2009). Although, generalizations remain tentative owing to gross undersampling and incomplete taxonomic information, many taxa appear broadly distributed across the deep-sea floor. Surprisingly, this trend is apparent not only among soft-bottom taxa inhabiting the vast abyssal plain, but also in highly patchy environments such as hydrothermal vents and seamounts. However, though maximum linear extent of abyssal seafloor and vent species ranges are similar, areal extent is likely to be smaller in vent species confined to long but narrow ridges. Methane seep and large food-fall assemblages may have more restricted ranges, but the extent to which this pattern reflects undersampling, as opposed to limited gene flow in spatially and temporally patchy habitats, remains unclear. At the generic level, overwhelming evidence indicates high levels of cosmopolitanism across all habitats.

Many taxa probably possess an amazing intrinsic ability for larval dispersal, which may be further augmented by extended larval development in cold deep waters. Dispersal potential is thus expected to increase with depth and exceed that of shallow marine taxa. However, barriers to dispersal such as currents, landmasses and topographic features can of course curtail this potential. These barriers clearly define general patterns of biogeography in the deep (electronic supplementary material, appendix 1), although many dispersal barriers appear semipermeable across habitat types, affecting taxa differently. Deep-sea biogeographic patterns also clearly bear the signature of historical events, as evidenced by multiple points of evolutionary origin, and the apparent role of variable deep-water oxygen concentrations. All current evidence points to a deep-sea fauna composed of taxa, neither entirely old nor young, filtered through many climatic fluctuations (figure 2).

Sampling remote deep-sea systems is fraught with difficulty. Acquiring faunal samples requires considerably financial and technological input and years of forward planning. Rough seas, either owing to inclement weather or increased winds frequent at higher latitudes, or equipment and technological issues amplified by the isolation of being at sea often limit ship-based sampling even further. Far less than 1 per cent of the deep sea Stuart *et al.* (2009) has been sampled and our conclusions hinge on this fact. The small area and uneven distribution of deep-sea floor sampling, concentrated in the Northern Hemisphere in proximity to American and European oceanographic institutions, impedes more comprehensive biogeographic synthesis (Stuart *et al.* 2009). Recent modelling work Tittensor *et al.* (2010) suggests that in some instances up to an order of magnitude more sampling may be required to detect true endemism in the deep sea. Rare species Rabinowitz (1981), especially those narrowly distributed and locally rare, may be exceptionally difficult to sample in the deep sea, leading to overestimation of the contribution of broadly distributed species to deep-sea biodiversity. However, work on gastropods suggests that local rarity may not equate to small geographical range (Rex 2002).

The way forward for deep-sea biogeography includes maximizing the yields on data already collected,

continued and dedicated financial support by funding agencies with understanding of the risk, development of technologies that decrease risk and expenditure, and continued sampling. Areas of particular need include:

- *Detailed phylogenies in a geographical context*, which will clarify timing and points of origin for deep-sea invasions, and identify possible triggers for such events (e.g. Linder *et al.* 2008; Raupach *et al.* 2009).
- *Population genetics and phylogeography for all deep-sea habitats and especially for the abyssal plains*. Genetic data—severely lacking in habitats other than seamounts and hydrothermal vents—would elucidate scales of connectivity and identify environmental gradients that may be generating biogeographic breaks in a system traditionally perceived as relatively homogeneous. Across all deep-sea habitats, a clearer understanding is needed of the relationship between population and species genetic differentiation, i.e. ‘concordance of intraspecific and interspecific’ phylo-biogeographic patterning Palumbi (1996), with a recognition of the continuum that represents gene flow and structure (Palumbi 1994; Bohonak 1999; Taylor *et al.* 2000).
- *An integrated biogeographic framework of hard-substrate areas of the deep sea*. The current paradigm views individual seamounts or hydrothermal vent areas in isolation and should be broadened in scope to consider other hard-substrate habitats like deep-water reefs, ridge lines, slopes and canyons. Recent work indicates many shared species between these various habitats (Carney 1994; Van Dover 2000; O’Hara *et al.* 2008; McClain *et al.* 2009a), and such an approach would thus yield more realistic estimates of endemism/cosmopolitanism.
- *Assessment of the effects of productivity patterns on biogeography*, in the contemporary ocean as well as over geological timescales. Carbon flux shapes patterns in biodiversity and the evolution of deep-sea faunas (Gooday 2002; Smith *et al.* 2008; McClain *et al.* 2009b) and will probably prove important in deep-sea biogeography.
- *Reproductive patterns and estimates of larval dispersal ability in deep-sea fauna*, which are largely lacking for groups other than echinoderms and vent species (e.g. Young *et al.* 1997; Tyler & Young 2003). Realistic scales of dispersal must be quantified if we are to understand the processes that generate contemporary biogeographic patterns and, more importantly, to develop effective conservation strategies for deep-sea habitats.
- *Improved biogeographic schemes and habitat suitability models* using state of the art analyses to guide conservation (e.g. Bachraty *et al.* 2009; Tittensor *et al.* 2009). The unprecedented amount of environmental data publicly available (e.g. National Oceanographic Database, NODC, <http://www.nodc.noaa.gov/>), efforts to compile and synthesize data from deep-sea habitats in online databases (e.g. Ocean Biogeographic Information System, OBIS, <http://www.iobis.org/>; Census of Marine Life, CoML, <http://www.coml.org/>) and methodological advances (see Elith *et al.* 2006; Nogues-Bravo 2009) will facilitate additional such efforts. Environmental conditions may successfully characterize a species distribution,

but understanding the role of biological interactions in defining the biogeographic range or interact with environmental parameters will be key to understanding deep-sea biodiversity (Soberon 2007; Soberon & Nakamura 2009).

- *Explicit analyses of faunal turnover (beta-diversity) and biogeographic ranges* in relation to both dispersal limits, environmental heterogeneity (e.g. distance decay Nekola & White (1999)), and each other. Large-scale environmental and biological datasets are becoming sufficiently comprehensive to provide the necessary tools for such analyses.
- *Examination of whether deep-sea biota follow macroecological and biogeographic 'rules'*. Conformity or deviation will provide valuable insights into structuring forces in the deep sea as well as in other environments (McClain *et al.* 2009b).
- *Explicitly linking knowledge of deep-sea biogeography to future climate change scenarios*. Species will either move (range shifts), acclimatize (phenotypic plasticity), adapt (evolution) or die (extinction) (e.g. Hofmann & Todgham (2010)). What scope do deep-sea taxa possess for acclimatization and adaptation? How will ranges be affected? Answers will require continued initiatives to forge collaborations among disparate disciplines (e.g. Evolution and Climate Change in the Oceans programme).
- *As ever, more sampling, more sampling and even more sampling*. . . combined with the continued development of databases (e.g. OBIS, Seamounds Online (<http://seamounds.sdsu.edu/>), and Dryad (www.dryad.org/)) and the continued promotion of data sharing, synthesis and collaboration (e.g. CoML, National Evolutionary Synthesis Center, and the National Center for Ecological Analysis and Synthesis; see also Sidlauskas *et al.* (2009)).

If we have learned anything over the last few decades of deep-sea exploration, it is that we still have much to learn. Historically, two different positions are taken with regard to biogeographic research. The first focuses on individual clades and seeks to identify 'diverse ways that biotas have developed, both spatially and temporally though global history' McDowall (2004) (e.g. Ebach *et al.* (2003)). The second emphasizes identifying 'overarching biotic relationships' (McDowall 2004). We advocate proceeding with both as new data and exploration on both fronts will consistently force us to re-evaluate existing paradigms. We must be equally open to the idea that generalities and departures from them may exist, but exceptions to 'rules' present valuable opportunities for new insight.

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