REVIEW ARTICLE

On some hypotheses of diversity of animal life at great depths on the sea floor

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Abstract

Multiple hypotheses have emerged to explain the apparent paradox of high diversity of the deep-sea benthos when the environmental conditions are often predicted to inhibit rather than promote diversity. Many fundamental facets of these paradigms remain incompletely understood despite being central to understanding how deep-sea ecosystems, and more generally all ecosystems, function. Here, we examine nine major paradigms of deep-sea diversity that deserve, in our opinion, a fresh research impetus. We purposely challenge many of these ideas to generate dialogue and encourage further research. Some of the axiomatic predictions of these paradigms are: (i) the deep sea is highly diverse; (ii) stable environments reduce competition; (iii) species have finely partitioned niches; (iv) biological cropping promotes diversity; (v) disturbance controls diversity; (vi) patch mosaics structure assemblages; (vii) productivity controls diversity; (viii) recovery from disturbance is slow; and (ix) the deep sea is notoriously under-sampled. We critically examine the evidence for each of these predictions and highlight areas where knowledge gaps exist and linkages to general ecological theory should occur. We conclude each section with ideas about questions and hypotheses that may fruitfully be tackled in future projects.

Introduction

Why life abounds in countless forms in the deep oceans is one of the most exciting, yet equally challenging, questions in biology. Although it had been known for well over a century that animals inhabit the deep ocean (Sars 1872; Mosely 1880), the explicit statement of 'remarkable' diversity of the deep-sea benthos (Hessler & Sanders 1967; Sanders 1968) has been highly influential in shaping our views of the deep sea. Several influential paradigms followed, aiming to explain the apparent paradox of high diversity in an environment that was seemingly homogenous and stable, and where food was scarce (Snelgrove & Smith 2002). These paradigms remain at the forefront of ecological thinking and research in the deep oceans, but — surprisingly — many fundamental facets remain incompletely understood today.

Here we examine nine major paradigms of deep-sea diversity that deserve, in our opinion, a fresh research impetus. A central tenet of our arguments is that a more complete understanding of the processes creating and regulating diversity in the deep ocean can benefit from a re-examination of existing paradigms from both theoretical and empirical points of view. Our primary intent is to encourage debate. We therefore introduce each paradigm with an explicit statement (at times purposefully provocative, but purely with the intent to stimulate further discourse) to initiate dialogue and to set the stage for each paradigm's principal message and subsequent evaluation. We posit that many of the 'big ideas' in deep-sea research

dealing with diversity remain just as intellectually stimulating today as they were at the time of their original publication, offering exciting opportunities for further examination; often such examinations will, or should, involve explicit tests of the theories' original predictions.

The deep-sea benthos is not more bio-diverse than the sea floor in shallow water

'Diversity in the deep sea is exceptionally high' — many a deep-sea paper begins with this mantra (or variations thereof). The notion can be traced to Hessler & Sanders (1967, p. 71): 'From this comparison to soft bottom, shallow marine biocoenoses, we conclude that the diversity of benthic invertebrates in the deep-sea well exceeds that of temperate, shallow water, benthic communities and is actually comparable to that found in shallow water, tropical communities. These data clearly refute the classically held notion of a depauperate deep-sea fauna'. Sanders (1968), by introducing the technique of rarefaction, provided a more rigorous test of this idea, demonstrating that diversity in the deep-sea off New England was more than twice that of boreal shallow water sea bed, tropical estuary, and disturbed tropical shallow water locations. Indeed, the diversity values of Sanders's deep-sea samples (300–2500 m) were only slightly lower than that of a tropical, shallow-water system. Grassle (1989, p. 15) later asserted that, 'Because of the large surface area and the many undescribed species, the animal diversity in the deep sea may rival that found in tropical rain forests'.

However, as noted by Snelgrove & Smith (2002) and Gray et al. (1997), the notion of exceptionally high diversity of the deep sea is based on very few specific comparisons of species diversity between 'shallow' and 'deep' data sets; more than a decade later, this statement still holds true. Thus, making unambiguous and robust assessments on whether species diversity on the deep-sea floor is higher or lower than elsewhere in the ocean is very difficult at present. The primary literature indicates that species diversity of the deep benthos varies by ocean basin and taxon. In the Northwest Atlantic, the rarified number of expected species of macrofauna is greater in the deep sea (250–2180 m) than shallower samples (38–167 m) (Etter & Mullineaux 2001; Maciolek & Smith 2009). Also for the Northwest Atlantic, Rex (1981) found a complex set of diversity patterns with depth: some groups (gastropods and cumaceans) were always more diverse at greater depth, whereas others (e.g. polychaetes, megafauna) did not show consistent depth-related patterns in diversity.

Beyond the continental margins of the Western Atlantic, answers to the question of higher diversity in the deep sea become more varied still. The late John Gray forcefully challenged the concept of high deep-sea diversity, asserting that species richness per unit area is not consistently higher in the deep sea (Gray 1994; Gray et al. 1997). Comparing samples from the Norwegian Shelf from 70–305 m to Grassle & Maciolek's (1992) samples from 1500–2150 m collected off the eastern coast of the USA, Gray (1994, p. 206) found that 'for 40,000 individuals only approximately 550 species were found in the deep-sea, considerably less than the Norwegian shelf's 620 species'. Gray et al. (1997, p. 97) reached the conclusion that 'species richness per unit area is as high, if not higher in shallow sedimentary habitats as was reported for the deep-sea' based on a heterogeneous set of published data sets in terms of sampling, location, and taxa. Similarly, off the Central Californian coast, Oliver et al. (2011) documented that species diversity of macrofauna species richness per unit area declines with depth, and that the rarified expected number of species is similar for shallow and deep-water samples (30–2000 m). In the Arctic, polychaete diversity below 200 m is neither consistently higher nor lower than in shallower samples (Bodil et al. 2011; Piepenburg et al. 2011). In the meiofauna, mixed bathymetric patterns emerge for taxon richness and species diversity in nematodes from the Northeast Atlantic and Mediterranean, ranging from declines below 2000 m to a lack of distinct depth–diversity relationships (Danovaro et al. 2009).

Empirical data clearly show that hundreds of invertebrate species can be obtained by sampling only a few square meters of the deep sea floor. However, broadly similar species counts are also possible from comparable samples taken on the shelf and near-shore sea floor. Fundamentally, it remains of great interest to know whether levels of diversity in the deep ocean match, or exceed, those found in shallower seas. However, the question of whether species diversity is higher in the deep sea than in shelf or coastal systems cannot be answered with confidence at present: a comprehensive and robust comparative analysis of marine diversity is needed that draws upon the considerable amount of benthic sampling that has occurred since the seminal paper of Sanders (1968).

We do not doubt that many areas of the deep sea contain large numbers of species, many of which are unique, and hence are characterized by animal diversity that rivals levels found in some shallow water and tropical regions. Thus, we do not assert that the deep sea is NOT highly diverse, but caution against the uncritical and near-universal adoption of this notion as a blanket statement before a more complete analysis has been carried out. It also seems sensible and fruitful to ask more specific questions, focusing on processes that create, maintain, limit, and regulate species diversity rather than seeking a blanket statement of species numbers in a particular habitat type for the oceans at large.

The stability of the deep sea reduces competitive interactions

The first theory published to explain the co-existence of many species in deep-sea sediment samples came in one of the first papers to describe the potential existence of high species diversity in these habitats (Hessler & Sanders 1967). Fundamentally, the thesis was that deep-sea species exhibited minimal niche overlap, ultimately minimizing competitive exclusion and allowing the existence of many species in the same area. The fundamental premise of the theory is that the environmental stability of the deep sea enables evolutionary processes that produce intense niche partitioning to fine levels; modern co-existence of species thus reflects competitive interactions of the past. Hessler & Sanders (1967, p. 75) state, '…the theory of climatic stability seems best to explain high diversity in the deep-sea. The most characteristic aspect of physical parameters in this environment is their temporal uniformity. Temperature, salinity, oxygen, light, rate of sedimentation, food supply, and so on, all vary within quite narrow ranges, particularly at greater depths. This stability results in ideal conditions for the evolution of the complex web of the biologically diverse community'. Sanders (1968, p. 253–254) formally conceptualized the idea as the 'stability–time hypothesis': 'Where physiological stresses have been historically low, biologically accommodated communities have evolved'.

The salient argument in the Sanders (1968) formulation of the stability–time hypothesis is the explicit recognition of evolution as the key mechanism. A logical consequence of the premise of long-term stability – promoting niche diversification – is weak or infrequent disturbance. Grassle & Sanders (1973, p. 651–652; also see Sanders 1979) clearly distinguished between ecological and evolutionary disturbance processes to explain high species diversity in the deep sea. They identified two complementary 'types' of diversity: (i) '*Long-term, equilibrium, or evolutionary high diversity*. Increase in diversity is a product of past biological interactions in physically stable, benign, and predictable environments. The time scale is geologic – at least thousands of years – and the resultant product is a biologically-accommodated community. These assemblages are broadly distributed rather than localized. Diversity increment is slow, the result of speciation and/or a low rate of immigration into the environment'. (ii) '*Short-term, non-equilibrium, or transient high diversity*-induced by unpredictable physical or biological perturbations or stress resulting in biological "undersaturation" of the environment. Because there is at least a partial biological vacuum, more species can temporarily occupy the habitat until population sizes build up to densities where the species must interact. The effects are local

and the time scale is always short – days, weeks, months, or years – and this type of diversity is manifested primarily in predominantly physically-controlled habitats. The increase in diversity is rapid and is brought about by immigration of other species from the surrounding areas'.

Intense niche diversification and specialization is at the core of the stability–time hypothesis. However, Dayton & Hessler (1972) argued that specialization was difficult to envision among deposit-feeding species. They suggested that deep-sea species were likely to harvest a variety of available food particles, requiring generalist traits and behavior to survive in the food-poor deep sea. The evidence for this comes from two studies demonstrating that the gut contents of megafauna contained a suite of species and phyla, suggesting little selection for prey type, a finding largely supported by more modern work (Hudson *et al.* 2004). More broadly, there appears to be little consensus about whether temporal stability inhibits, promotes, or does not strongly influence diversity (Fjeldsa & Lovett 1997a,b; Carnaval *et al.* 2009; Marske *et al.* 2013). Recent research (Botero *et al.* 2013) showed that, for mammals and birds, environmental harshness (lower productivity, decreased rainfall, and more variable and unpredictable temperatures) leads to greater intra-specific divergence, a finding contrary to the stability–time hypothesis. Yet stability predicts genetic diversity in Brazilian forests (Carnaval *et al.* 2009). Likewise, in lake zooplankton, large fluctuations in pH, phosphorus and dissolved organic carbon concentration reduced species richness (Shurin *et al.* 2010). However, variation in temperature promoted lake zooplankton richness (Shurin *et al.* 2010).

Responses to the stability–time hypothesis have largely focused on documenting disturbances across a variety of scales, challenging the idea of a stable deep sea, or comparing diversity among assemblages under different disturbance regimes (both are discussed later). However, these tests focus primarily on short-term ecological responses, but do not examine predictions of the evolutionary formulation as envisioned by Grassle & Sanders (1973). We envision four major areas of inquiry with regard to the stability–time hypothesis. (i) While it is clear that deep-sea systems do experience disturbance across a variety of scales (both temporal and spatial), it is less clear whether the frequency, magnitude, and predictability of these disturbance events are different between deep-sea and shallow-water systems on evolutionary time scales. (ii) Because modern phylogenetic comparative methods were unavailable at the time when the stability–time hypothesis was put forward, explicit tests of this evolutionary hypothesis were also impossible. Technical advances have changed this situation, and it should now be possible to compare rates of diversification between

deep-sea and other systems: this is an exciting prospect. (iii) In addition, the stability–time hypothesis predicts that niche width is minimal, and that generalist strategies are rare (*i.e.* close niche partitioning is predicted to promote the existence of narrow specializations). We also find exciting the potential of quantitative studies that examine niches, comparing shallow and deep species. (iv) Intense diversification, predicted by the stability–time hypothesis, leads to the expectation that phylogenetic diversity should decrease with depth within a clade. This results from specialization, as a consequence of stability, leading to diversification leading to more finely splitting species with genera and decreasing average genetic and taxonomic distance. Rex & Waren (1981) examined this idea, comparing species to genus ratios for gastropods, finding more species per genus down the slope; in the abyss, arguably the most stable of deep-sea habitats, ratios were lower, not supporting the predictions of the stability–time hypothesis.

Competition does not structure deep-sea communities

Competition and predation have long been recognized as key mechanisms in determining species diversity and assemblage structure (Cody & Diamond 1975). Ecologists have focused for decades on the question of how species diversity is maintained in natural communities (Hutchinson 1959), generally emphasizing the dual and asymmetric roles of competition and predation for the maintenance of species diversity (Chase *et al.* 2002). Classic theory predicts that co-existence of competing species requires that species differ ecologically; this implies that niche differences between species − and, by implication, strong niche partitioning over evolutionary times − are key to maintaining diversity (Volterra 1926). Whereas classic models built around competition, acting as a primary driver for niche partitioning, have been challenged by the neutral theory of biodiversity (Hubbell 2001), the importance of niche differentiation in the maintenance of species diversity remains firmly recognized (Levine & HilleRisLambers 2009). Evaluating the role of competition in shaping species fitness and assemblage structure is further complicated by models that predict a greater importance of competitive effects under productive environmental conditions (Gaucherand *et al.* 2006), the existence of asymmetric competition (Lawton & Hassell 1981), and the fact that competition and predation can either strengthen or weaken diversity maintenance (Chesson & Kuang 2008).

In the context of diversity maintenance for deep-sea benthic assemblages, the key contention of the stability–time hypothesis is that competition in the past has favored strong niche differentiation, thereby leading to current communities where competitive interactions are minimized. In the deep sea, competition is most likely related to food (Smith *et al.* 2008). Even in more food-rich sedimentary environments in shallow water competition is likely for food (Peterson 1979). However, in soft sediments competitive exclusion is rare (Wilson 1990; Grant 2000). Others have argued that low-productivity environments (Huston 1979) lead to weak or non-existent competitive interactions as population growth rates and densities of competing consumers are relatively slow (McClain *et al.* 2012a,b,c). As Grant (2000, p. 103) stated for invertebrates in sedimentary environments, 'Population densities are low, and it is difficult to envisage mechanisms whereby one individual could completely prevent other individuals from obtaining access to resources such as detritus'.

We know of no studies that have tested, or conclusively shown, that competition is important in maintaining species diversity of deep-sea communities. As Grant (2000) noted, most examples of competition in soft sediments involve a species making the environment unsuitable for another (*e.g.* large burrowing animals). McClain & Barry (2010) suggested that inter-guild competition among large mobile deposit feeders reduced the densities of macrofauna largely due to sediment disturbance in Monterey Canyon. They further suggested that this mechanism may also account for the decrease of species in shallow water (*i.e.* high megafaunal densities on the shelf and upper slope may suppress macrofaunal diversity due to disturbance from bioturbation). By contrast, multiple examples also exist of facilitation, where a megafaunal and macrofaunal species promotes the diversity of a set of other species usually by providing habitat structure. McClain (2005) noted that slope communities of deep-sea gastropods show evidence of character displacement in terms of shell morphology, indicating prior competitive interactions. Rex & Waren (1981) examined species-per-genus ratios. Low species to genus ratios are believed to indicate a greater degree of competitive displacement because competition is thought to be greatest among congenerics due to similar ecologies. Slope communities were found to exhibit the highest species-per-genus ratios, indicating that competitive displacement was lower, a finding in contrast to that of McClain (2005), who found morphological/anatomical divergence in support of greater competition on the slope.

Demonstrating competition in any environment, especially the deep sea, is challenging. The key requirement of any test is that it should be able to show a reduction of fitness under competitive interactions: one must be able to show that at least one aspect of a species' fitness is reduced when interacting with another species (*e.g.* Claar

et al. 2011). An experimental design testing for fitness effects would require repeated sampling and manipulation, either through the removal or addition of competitors. However, these types of experimental manipulations can be challenging (Inouye 2001). More insightful, but logistically more difficult, are response surface experiments that alter the densities of two competing species (Inouye 2001). No matter what the design, the potential pitfalls of competition experiments are well documented (Snaydon 1994). Even given these potential pitfalls and logistical issues, we issue a call to the field to overcome these barriers. We find the prospect of a research program, experimental or not, specifically examining the roles of competition in the deep sea to be of fundamental importance and excitement.

Predation effects do not increase diversity in deep-sea assemblages

In direct response, and as an alternate explanation, to the stability–time hypothesis, Dayton & Hessler (1972, p. 202) proposed the 'biological cropping hypothesis': 'We suggest the hypothesis that by preying on the populations of other, smaller deposit feeders, croppers such as holothurians, echinoids, ophiuroids, asteroids, cephalopods, and some polychaetes, decapods, and fish are largely responsible for the maintenance of the high species diversity of small deposit feeders observed by Hessler & Sanders (1967) by reducing the probability of competitive exclusion'. The classic view is that predation differentially targets numerically dominant species, i.e. superior competitors: this top-down control disrupts competitive hierarchies and prevents competitive exclusion from occurring. Grassle & Sanders (1973, p. 644) responded that 'the available life history data indicate that a predation hypothesis to explain the high diversities is unlikely, and the Dayton-Hessler hypothesis cannot work with the assumptions of non-selective predation and uniform distributions...'. As a rebuttal to the 'biological cropping hypothesis', Grassle & Sanders (1973) argued that the populations of prey species were not composed mostly of young stages, did not possess high reproductive outputs to withstand high mortality, and did not exhibit early maturation.

There are very few experimental tests of the role of predation in structuring deep-sea benthic assemblages and maintaining diversity. However, Gallucci et al. (2008) conducted experiments on the deep-sea floor in the Arctic, working at the experimental site 'Hausgarten'. Six experimental cages, designed to exclude large mobile megafauna, were deployed at 2500 m and sampled after 4 years. At the end of the experiment, chlorophyll a and paeopigments were high inside the cages and sediment

grain sizes were more homogenous inside the cages. Total density of nematodes was higher in predator-free treatments, mainly as a consequence of increases in species that were previously rare. However, no change in species diversity was observed within or outside the cages. The authors suggested that it is biogenic disturbance (i.e. bioturbation), or differences in food that lead to abundance changes and ultimately concluded that the 'lack of any changes in species richness inside the cages after 4 years suggests that (mobile megafauna) cannot fully account for the maintenance of the remarkable high levels of species coexistence in the deep sea'. In the same year Thistle et al. (2008) reported on megafaunal exclusion experiments with five cages at 730 m depth off the southwestern coast of the USA. After 143 days, they sampled the caged plots and five paired control plots. Abundance, but not diversity, was reported: abundances of harpacticoid copepods, nematodes, kinorhynchs and polychaetes were significantly lower inside cages than in controls.

The paucity of explicit tests about the role of predation in deep-sea sedimentary environments makes it impossible to draw firm conclusions whether predation can act, and under which circumstances, to maintain and/or promote high diversity in the deep-sea benthos as posited by Dayton & Hessler (1972). At best, the 'biological cropping hypothesis' should be viewed as 'unresolved' at this stage. Prior experiments have yielded mixed macrofaunal and meiofaunal responses to megafaunal exclusion. We are excited about the potential for future caging experiments or employing natural experiments that encompass known gradients in megafaunal density (e.g. McClain & Barry 2010). We emphasize that it is important that future work will need to separate the effects of megafauna as predators (e.g. Dayton & Hessler 1972; Thistle 1979a,b), bioturbators (e.g. Smith et al. 1986; McClain & Barry 2010), facilitators and engineers (e.g. Thistle 1979b, 1983a,b; Thistle & Eckman 1990; Thistle et al. 2008), and competitors (e.g. McClain & Barry 2010), as each invokes a different process to account for high diversity.

Deep-sea alpha- and beta-diversity is not controlled by disturbance

Events thought to disrupt steady-state conditions by changing fundamental attributes of individuals, populations, communities, or systems are, by convention, viewed as disturbance – a putative driver of community assembly and diversity that continues to be popular in the literature (Connell 1978; Dornelas 2010; Fox 2013). Definitions of 'disturbance' are varied, but most encompass one or several of the following elements: (i) disturbance constitutes time-bounded, discrete events; (ii) the

proximate effects of many events are killing, displacement, or damage of individuals and/or removal of biomass; and (iii) disturbances causes temporary and localized shifts in demographic rates (Sousa 1984; Peetraitis *et al.* 1989; Hughes *et al.* 2007; Dornelas 2010). In a broader ecological context, beyond the immediate impacts on individuals, disturbance could have positive effects on some species by unlocking resources that positively influences carrying capacity and demographic rates (*e.g.* supply of animal carcasses to scavengers; Schlacher *et al.* 2013a,b) and enhance habitat heterogeneity on a seascape level (Levin & Sibuet 2012).

The ecological effects of disturbance depend primarily upon the intensity of the disturbance force itself and the susceptibility of organisms. Most authors characterize disturbance regimes in terms of five attributes: (i) extent (size of the disturbed area); (ii) frequency (number of disturbance events per unit of time, return interval); (iii) intensity (strength of the disturbing force); (iv) predictability (variance of time intervals between events); and (v) turnover rate (mean time for the area to recover) (Sousa 1984).

That disturbance influences diversity is a long-standing thesis in ecology. Indeed, the most frequently-cited model linking disturbance with diversity is Connell's (1978) intermediate disturbance hypothesis (IDH): it predicts that diversity peaks at intermediate levels of disturbance, flanked by lower levels of diversity both under stable conditions due to competitive exclusion and under intense disturbance due to conditions exceeding thresholds of species' tolerances. Support for the IDH is, however, equivocal both on empirical and theoretical grounds (Fox 1981; Hughes *et al.* 2007). Importantly, the dynamic equilibrium model of Huston (1979) shows that disturbance and productivity interact in shaping diversity (Kondoh 2001). This model is of fundamental importance for deep-sea systems: because low productivity is postulated to favor competitors with low growth rates, relatively low levels of disturbance are needed to prevent competitive exclusion. This expectation concurs with the conventional wisdom of food-poor deep environments, and implies that – all else being equal – disturbance events in the deep sea produce strong effects, or that low levels of disturbance will suffice to prevent competitive exclusion.

The main types of physical disturbances in the deep sea concern geologic events and large-scale mobilizations of sediments (*e.g.* earthquakes, benthic storms, slumps, turbidity flows), whilst changes to ocean chemistry (*e.g.* oxygen levels, pH) constitute chemical disturbance forces (Falkowski *et al.* 2011; Kawagucci *et al.* 2012; Harris 2014). In addition, organisms can also have profound consequences on both habitats and the assemblages that

they interact with, and these interactions (*e.g.* scavenger feeding, bioturbation) have consequently been treated as biological 'disturbance' events (Grassle & Sanders 1973; Smith 1994).

In sedimentary environments, physical disturbance caused by currents and waves declines with increasing particle size (Sousa 1979). As many areas of the deep sea floor are composed of very fine, unconsolidated sediments that are readily displaced, the expectation is that the deep-sea benthos lies, hypothetically, at the upper end of disturbance effects caused by hydrodynamic forces. A major physical disturbance occurs in the form of 'benthic storms' than can mobilize and displace deep-sea sediments. These events affect the global ocean (*i.e.* current regimes that exceed $0.2 \ m·s^{-1}$ at some time over a 2-year period are estimated to cover about 8% of abyssal sea floor), typically last from 2–22 days, and commonly have a return frequency of eight to 10 storms per year (Harris 2014). Proximate effects of benthic storms encompass the erosion of habitat, increased sediment instability, and the sweeping of surficial organic matter, microorganisms, larvae, and juveniles from the storm-affected area (Aller 1989). High-kinetic conditions during storms can have dual and opposing effects on the benthos: they may enhance the flux of food particles to consumers, promoting higher densities of benthos, whilst lowering habitat stability and persistence of organisms *via* erosion, transport, and re-deposition of sediment and individuals (Thistle *et al.* 1991). These generalized faunal response can, however, strongly differ between taxa (Thistle *et al.* 1991), and erosive processes that modify habitat stability can locally either enhance or reduce sediment fauna diversity (Thistle 1983a,b, 1998; Lambshead *et al.* 2001).

Catastrophic slope failures can mobilize massive amounts of sediment, resulting in submarine slides, sediment slumps, debris flows, and turbidity flows (Urlab *et al.* 2013). Very large submarine landslides have a frequency of around one to two per thousand years (Urlab *et al.* 2013). Mass wasting occurs on both the shallow-sloping continental margins as well as on more steep-sided geologic features (*e.g.* flanks of seamounts, walls of ocean trenches, ocean ridges), with submarine fans estimated to cover 2.3% of the ocean floor globally (Harris 2014)). As dislodgement and burial of fauna are the direct impacts on the fauna, expectations are that these – sometimes massive disturbance events – result in large ecological effects. For example, deposition of turbidite material up to 14 cm thick at 5000 m depth in the Venezuela Plain resulted in a temporary cessation of bioturbation about 2000 years ago – community recovery is possibly still incomplete (Young & Richardson 1998).

However, it must be borne in mind that substantial parts of modern sedimentary habitats on abyssal plains

have been formed over geologic time by massive, episodic turbidity flows (Weaver *et al.* 1987; Young & Richardson 1998). Potentially positive ecological effects of mass-wasting events were suggested by Angel & Rice (1996): they theorized that while mass-wasting events (*e.g.* sediment slumps, turbidity flows) cause localized mass kills, they also create very large mosaics in time and space that may promote diversity of deep-sea species in the global ocean (Angel & Rice 1996).

Chemical disturbance largely comes in the form of low-oxygen water masses that impinge on the sea floor, mostly along continental margins, creating oxygen minimum zones (OMZs) that cover over 1,000,000 km^2 of permanently hypoxic shelf and bathyal sea floor (Helly & Levin 2004). Such sea-floor OMZs are regions of low diversity, and – more generally — deep-sea diversity commonly decreases with falling oxygen level (Levin & Gage 1998). The oxygen content of the global ocean is declining in several areas ('ocean de-oxygenation'), possibly expanding oxygen-depleted waters in bathyal and abyssal regions (Falkowski *et al.* 2011). This global change – if continuing – is expected to have profound biological consequences, including impacts on deep-sea diversity and functioning. Paleoclimatic records show that past oceanic anoxic events represent extreme changes in the climatic and paleoceanographic state of the planet, resulting in a biotic diversity crisis on a global scale, including the deep sea; these gigantic disturbance events occur at temporal scales of 10s to 100s of millennia (Jenkyns 2010).

Biological processes that substantially modify the quality, extent or nature of deep-sea habitats, or that interfere directly with organisms and organismal interactions, have conceptually been treated as 'biological disturbances' in the literature. Consequently, they include a broad range of mechanisms, such as the feeding activities of scavengers and predators, bioturbation and defecation bouts, plowing by urchins, episodic phytodetritus inputs, sunken animal carcasses, and many others (Billett *et al.* 1983; Gage & Tyler 1991). For example, Smith (1994) put forward a conceptual framework of pulsed events (*i.e.* biogenic mounds, pulses of phytodetritus, whale falls) thought to disrupt the hypothesized equilibrium dynamics of deep-sea communities. Biological disturbance can enhance habitat heterogeneity (Aller & Aller 1986) and can result in localized increases in species diversity during community recovery (Kukert & Smith 1992). Intriguingly, they can add new habitat (albeit an ephemeral one) in the form of carcasses (*i.e.* whale falls and other large vertebrates) that create localized hotspots of abundance and diversity for metabolically and taxonomically distinct assemblages of organisms (Smith *et al.* 1989). While nekton falls create habitat, negative disturbance effects (*sensu stricto*) are postulated to consist of mechanical disruption

of the infaunal community by the feeding activities of scavengers, changes to sediment chemistry and burial (Smith 1986). Undoubtedly, falls of animal carcasses to the deep-sea floor constitute important inputs to food webs and locally enhance the abundance and diversity of scavengers feeding on sunken carrion (Kemp *et al.* 2006). Notwithstanding the trophic role — and some localized disturbance impacts on the resident benthos (*e.g.* displacement, burial, changed sediment chemistry, sediment winnowing during feeding by scavengers) — the spatial footprint on key benthic attributes (*e.g.* microbial biomass, organic content, invertebrate abundance and diversity) can be very limited, not exceeding a few meters beyond the carcass (Smith 1986; Smith *et al.* 1998).

Grassle & Sanders (1973) posited that: '….disturbances in the deep sea are much less frequent, less severe, and of smaller spatial extent than in physically controlled communities'. Much evidence of disturbance in the deep sea has been accumulated since 1973, providing an opportunity for a formal comparative analysis of disturbance regimes to test this bold contention. Sunken animal carcasses (*e.g.* whales and smaller vertebrates; Smith *et al.* 1989) provide pulses of trophic subsidy to deep-sea consumers. Besides their role in food webs, these 'carrion events' may also create spatial heterogeneity (*sensu* Smith 1986), hypothetically enhancing diversity at broader spatial scales. Most disturbance research in the deep sea deals with either sessile animals on hard substrates (Harris 2014) or meio- and macrofauna- of limited mobility in sedimentary environments (Kukert & Smith 1992). By contrast, how mobile megafauna are influenced by disturbance events is largely unknown. By analogy to other systems, expectations are that the population dynamics and distributions of mobile consumers are altered by disturbance-related changes to benthic habitats and assemblages (Williams *et al.* 2010) or changes to food supply (Schlacher *et al.* 2013a,b). Hughes *et al.* (2007) showed that feedbacks between diversity and disturbance could influence patterns of diversity in nature; these feedbacks are intriguing, yet largely untested empirically. While the focus of much deep-sea work has been on documenting the effects of disturbance on diversity, the reciprocal process (*i.e.* the influence of diversity on the outcomes of disturbance, such as magnitude of biological shifts, resistance, and resilience) remains unexamined.

Deep-sea ecology has traditionally addressed disturbance-associated ecological effects from a number of perspectives, providing a solid platform to further examine the role of episodic events, incorporating theories from the broader ecological literature, and evaluating established models. Several avenues appear potentially fruitful to us: (i) are disturbances themselves of lower intensity but of greater biological impact in the deep ocean?;

(ii) do carcass falls create significant habitat heterogeneity or complexity (postulated to be a form of biological disturbance)?; (iii) are known disturbance effects transferable from meiofuana and macrofauna to mobile megafauna?; (iv) do reciprocal feedbacks between diversity and disturbance operate in deep-sea assemblages?

Diversity of the deep-sea communities is best predicted through patch-mosaic dynamics

Arguably one of the most influential ideas about deep-sea diversity, the patch-mosaic hypothesis, was presented by Grassle & Sanders (1973, p. 654–656): 'In species with highly specialized microhabitat preferences, patchiness may develop on a much smaller scale than would be expected in shallow water. Disturbances that occur in the deep sea may also result in small-scale temporal mosaics. If a fish stirs up the bottom or mud slumps occur, a slow and highly localized succession will take place...However, competitive exclusion proceeds so slowly in the deep sea that a temporal mosaic results. In other words, a spatial mosaic emerges from local successional sequences that are out of phase. (This has been called the "contemporaneous disequilibrium hypothesis")'. The 'patch-mosaic model' has been invoked multiple times in discussions of deep-sea diversity (*i.e.* a Google Scholar search yields nearly 500 papers that mention patch mosaic).

The patch-mosaic model has five components.

1 A heterogeneous set of microhabitats with long temporal duration exists on the deep-sea floor. 'Deep-sea microhabitats tend to persist longer, be smaller in spatial extent, and be separated by longer distances between patches in comparison with the most closely studied shallow-water marine communities'. (Grassle & Maciolek 1992, p. 313).

2 Species have finely partitioned niches that match these microhabitats.

3 Disturbance occurs at small spatial scales (less than 1 m and likely a few centimeters), creating numerous patches that differ in successional states: this collection of patches forms a mosaic of different assemblages across the seascape.

4 Local co-existence is achieved across patches because species are differentially adapted to different successional stages.

5 Slow rates of colonization and community assembly in the deep sea enable the simultaneous existence of patches at different successional stages.

The model assumes that disturbance is frequent and widespread enough to create localized disturbances to the sea floor that form the postulated mosaic of patches; conversely, disturbance must not be too frequent or intense, because patches must have a half-life that enables succession and colonization to occur and hence create a set of assemblages in different successional stages.

Physical disturbance is not necessarily the only process that could create a landscape of distinct (micro)habitats. Complementary mechanisms could include spatially localized or temporally pulsed imports of food, the creation of biogenic structures or bioturbation – processes that alter carbon availability, carbon quality, or chemical characteristic of the sediment (Etter & Mullineaux 2001). This alternative form of the patch-mosaic model was recognized and given great importance later by Grassle (1989, p. 12). 'The mosaic of food resources and, to a lesser extent, physical disruption of the bottom, maintain the high diversity in deep-sea communities'. The two forms of the theory differ in whether disturbance and succession dynamics or simply habitat heterogeneity at fine scales drives high diversity. In both theories, species have high niche specificity matched to either specific successional states or microhabitats.

In prior sections we have outlined the evidence and unanswered questions about the role of disturbance and predation for deep-sea benthic communities. Research looking at testing the patch-mosaic hypothesis has focused on the spatial dispersion of species, identifying specific microhabitats on the sea floor or creating experimental habitats. Often the recurring finding that species accumulation curves rarely reach an asymptote is given as evidence of high species turnover at small scales (Etter & Mullineaux 2001; Snelgrove & Smith 2002). Several papers (Jumars 1975, 1976, 1978; Thistle 1978; Jumars & Eckman 1983; Lamont *et al.* 1995) have suggested that the spatial distribution of many species may not be significantly different from random. Although random spatial arrangement of organisms is purported to be at odds with the patch-mosaic model, if similar patches are as distant as proposed, it may be extremely difficult to analytically distinguish a patch mosaic from random expectations. In addition, the variance-to-mean ratio used by many of these studies may be ineffective in detecting different spatial patterns (McClain *et al.* 2011). More recent work using different measures of spatial dispersion (Morista's I, Mantel tests, distance–decay) found that intra-specific species aggregation was common, consistent with the patch-mosaic model (McClain *et al.* 2011).

Microhabitats may result from biogenic activities. The work of Thistle (Thistle 1979a,b; Thistle & Eckman 1988, 1990) has shown that copepods are significantly impacted by the activities of polychaetes. One species of copepod was found in higher densities near mud balls of a cirratulid polychaete (Thistle & Eckman 1988). Harpacticoid copepods also tended to avoid polychaetes that are sessile surface-deposit feeders, providing support for a disturbance (patch-mosaic) or predation (biological cropping)

model for deep-sea diversity. Small sponges also increased species and functional diversity in nearby sediments, possibly by offering a wider variety of sediment microhabitats (Hassemann & Soltwedel 2011). Alternatively, or in conjunction with a disturbance, a mosaic may occur from variability in sedimentary carbon. Experimental work enriching nutrients in colonization trays has found high abundances of species in treatments that are rare or absent in the background environment (Levin & Smith 1984; Snelgrove *et al.* 1992, 1994, 1996; Bernardino *et al.* 2010). On-board microcosm experiments with deep-sea nematodes also yielded different community compositions among control, enriched, and disturbed sediments (Gallucci *et al.* 2008). Sediment diversity is also known to impact alpha-diversity (Etter & Grassle 1992) and, to the extent that sediment structure varies at centimeters scales, may generate patterns in beta-diversity, supporting the patch-mosaic model.

Testing of species compositional shifts at small scales, and specifically tying such shifts to microhabitat factors, appears rare outside of experimental work. McClain *et al.* (2011) found a high degree of species turnover in cores (7-cm diameter) separated by distances ranging from a few centimeters to hundreds of meters. This turnover appeared to be partly due to differences in sediment carbon concentrations. Geographic distance *per se* (*i.e.* how far samples are separated in space) was only a weak predictor of differences in species compositions. This could indicate that spatial heterogeneity exists at multiple scales, including centimeter scales. Alternatively, patches may be far larger than sampled in this study. Of course, the relevant scale of patch-separation distance also depends on the dispersal capabilities of the species that exploits the patches. This highlights that the spatial scaling of 'patchiness' is something where more research is required. More work of this nature and how this small-scale turnover varies geographically and by depth is greatly needed. It has been suggested that patches in shallow water are homogenized quickly (lasting days to weeks) due to more frequent bioturbation and currents, while patches in deep-sea sediments can persist for years (reviewed in Etter & Mullineaux 2001). More quantitative work explicitly comparing patch longevity, scale and size between deep and shallow benthic environments would elucidate the role that patch mosaics play in driving the potential high diversity of deep-sea systems. New work should also identify the nature of patches, *i.e.* the chemical, physical or biological traits that are most important in defining the 'nature or type' of a patch. We advocate a more complete treatment of patch characteristics, in terms of size, edge characteristics, configuration, connectivity, sediment properties, food resources, chemical conditions, longevity, and other attributes.

Deep-sea alpha- and beta-diversity is controlled by productivity

Given the well-known food limitation of the deep ocean, it is only logical that there has been much research devoted to understanding if and how productivity explains patterns in deep-sea diversity. Technically, productivity is not *in situ* for the soft-bottom benthos in the deep sea. Instead, consumers of the deep-sea benthos rely on sinking organic matter (*e.g.* marine snow, animal carcasses) from production occurring near the ocean surface. However, in the terrestrial literature, where the theory of diversity and food supply was developed, the term productivity is more apt as productivity is mostly *in situ*. Consequently, the body of research dealing with the relationship between energy supply and biological diversity is commonly referred to as 'productivity–diversity relationships' (PDRs). It should be noted that whilst in the deep-sea sedimentary benthos one deals with external food supplies rather than *in situ* productivity, and thus examines food-supply–diversity relationships rather than PDRs *sensu stricto*, we here retain the widely used productivity terminology to be consistent with the broader ecological literature on the topic.

As stated by Gooday *et al.* (1990, p. 112) 'The presence and persistence of life itself on the ocean-floor can be viewed as a response to organic inputs'. 'Here we show that many aspects of ecosystem structure and function in the abyss are strongly modulated by the rate and nature of food flux to the seafloor' (Smith *et al.* 2008, p. 518). As such, the abundance and biomass of benthic organisms is related directly to the amount of food reaching the sediment surface (Gooday 2002; Smith *et al.* 2008; McClain *et al.* 2012a,b). Much of the published work on how productivity influences diversity in the deep sea has been driven by questions about the shape of the relationship between productivity and diversity, and by the extent to which productivity can explain observed depth and latitudinal patterns. In contrast to these approaches based primarily on examining *patterns*, few papers have examined specific hypotheses or mechanisms. This is not unique to deep-sea biology, as ecology more widely is challenged by developing a better understanding of the processes the underlie PDRs (Waide *et al.* 1999).

The PDR is well explored, both empirically and theoretically (*e.g.* Rosenzweig & Abramsky 1993; Chase & Ryberg 2004; Cardinale *et al.* 2009; Chase 2010), but arguably poorly tested. At regional and global scales, unimodal, concave-down, and positive PRDs are all observed (Waide *et al.* 1999). The unimodal relationship also appears to be more common in studies that compare diversity among community types as opposed to holding community types constant (Mittelbach *et al.* 2001). PDRs are also thought

to switch from being unimodal at scales where assemblages of species compete, to positive at larger scales where species disperse across different types of habitats (Chase & Ryberg 2004). A variety of hypotheses has been proposed to explain PDRs and it is important to recognize that these individual hypotheses predict the positive, negative (or at least the negative part of the unimodal PDR), and unimodal PDRs (reviewed in Rosenzweig & Abramsky 1993; Waide *et al.* 1999). Theories that predict positive PDRs include the species-energy theory, aka more-individuals hypothesis, and theories invoking various forms of inter-specific competition. Negative PDRs are predicted by theories focusing on habitat homogenization, dynamic instabilities, Allee effects, and predator–prey ratios. Theories predicting the full unimodal relationship are rarer, but include changes in environmental heterogeneity with productivity, trade-offs in competitive abilities, and links between disturbance and productivity. Below we review four of the major theories currently critically considered in the ecological literature, and discuss deep-sea research addressing them. We note that Rex & Etter (2010) comprehensively summarized diversity gradients in relation to latitude and depth, both variables serving as proxies for productivity. By comparison, here our goal is to synthesize the main ideas and predictions of topical theories from the broader ecological literature as they apply to deep-sea diversity and productivity.

Species energy theory [more-individuals hypothesis (Srivastava & Lawton 1998)]

Originally proposed by Wright (1983), this theory suggests that a positive PDR results because productivity influences population size. As productivity decreases, the abundance of individual species also decreases. Rare species at low productivities are at increased risks of stochastic extinction, *i.e.* Allee effects. With increased productivity, Allee effects are diminished as populations sizes are larger and the likelihood of co-existence increases (Wright *et al.* 1993). This theory predicts only a monotonically increasing PDR and assumes no direct causal relationship between productivity and species diversity (Cardinale *et al.* 2009). Species energy theory is pragmatically very similar to the dynamic equilibrium models (Huston 1979; as applied to the deep sea by Rex 1983). In the latter, more productivity results in faster population growth rates and faster recovery after disturbance. Populations with low abundances and low growth rates, linked to low productivities, will be more likely to become extinct. The key difference between the two is that the dynamic equilibrium model predicts a downtrend in diversity with increasing productivity as abundant species begin to competitively exclude others.

It is commonly observed that many taxa are more abundant (larger population sizes) in regions of greater overlying ocean productivity or increased carbon flux to the deep benthos (McClain *et al.* 2012a,b). Less clear is whether the more-individuals hypothesis accounts for changes in species diversity. Clearly the unimodal diversity relationship seen in some groups with depth (reviewed in Rex & Etter 2010) and productivity (Tittensor *et al.* 2011; McClain *et al.* 2012a,b) argues against this. In some regions like the Norwegian Sea and Mediterranean, the relationship between diversity and depth is negative (Rex & Etter 2010), suggesting a positive PDR and support for the more-individuals hypothesis in some scenarios. Allee effects have been invoked to explain low abyssal diversity in deep-sea gastropods and bivalves in the Northwest Atlantic. This idea serves as the backbone to the source-sink hypothesis as presented by Rex *et al.* (2005). 'For many species, bathyal and abyssal populations may form a source-sink system in which abyssal populations are regulated by a balance between chronic extinction arising from vulnerabilities to Allee effects and immigration from bathyal sources. An increased significance of source-sink dynamics with depth may be driven by the exponential decrease in organic carbon flux to the benthos with increasing depth and distance from productive coastal systems. The abyss, which is the largest marine benthic environment, may afford more limited ecological and evolutionary opportunity than the bathyal zone' (Rex *et al.* 2005, p. 163).

Resource ratio theory

Originally proposed by Tilman (1982), this theory predicts a concave down unimodal PDR. The theory rests on the ideas that a high level of one resource (*e.g.* productivity) will cause another resource to be limiting and that no single species can be competitively dominant at all resource ratios. Thus, at the low end of the productivity gradient productivity is limiting. At high productivities, another resource becomes limiting. If species have trade-offs in the capture or utilization efficiency for different recourses then at both ends of the gradient different species will have the competitive advantage. When resources are balanced then these different species can co-exist because neither group is competitively superior. The easiest test of this would be to examine whether intermediate productivity assemblages represent merely composites of high and low productivity assemblages. Brault *et al.* (2013) examined nestedness of assemblages over increasing depth in bivalve assemblages. In the Northwest Atlantic, where productivity is moderate at intermediate depths, species diversity was high but the nestedness exhibited no corresponding peak. A peak in

nestedness was seen at intermediate depths in the Northeast Atlantic but there was no corresponding peak in diversity. These data suggest that the resource ratio theory may not be a strong explanatory model to account for the relationship between productivity and diversity in the deep sea.

More specialization theory

This theory (Schoener 1976; DeAngelis 1994) predicts a positive PDR. A minimum amount of resource is needed to support specialist species. Thus, at low productivity some resources are too rare to support these species. At high productivity, this theory predicts that greater specialization is possible and prevents competitive exclusion. Interestingly, this predicts the exact opposite pattern of specialization with depth as proposed by Sanders (1968). The more specialization theory predicts greater specialization at shallower depths where productivity is highest. By contrast, Sanders's (1968) stability–time hypothesis predicts that as depth increases, and environmental stability increases, greater specialization will occur. Work from the Northwest Atlantic suggests that the proportion of singletons increases with increasing species richness, potentially suggesting that rare species become abundant with increased productivity (Etter & Mullineaux 2001). However, this pattern is also somewhat consistent with the more-individuals hypothesis.

One more trophic level

Increased productivity allows for greater food chain length and complexity (Post 2002), predicting a positive PDR. More trophic levels are thought to promote overall diversity by promoting the existence of species of high trophic position whilst preventing competitive exclusion at the lower trophic levels. (Abrams 1993; Moen & Collins 1996). Rex (1973) argued that one of the factors that may cause the observed decline in diversity at depth was that the low energy availability of the abyssal plain led to decreased consumer density and did not permit for predator species. Likewise, the energetic limits of the deep oceans may exclude or greatly constrain some species with high metabolic demands, such as nudibranchs (McCain et al. 2014) and sharks (Priede et al. 2006). The differences in metabolic demands among taxa (McClain et al. 2012a,b,c) may also account for differing PDRs among different groups. For example, for most groups including isopods, gastropods, bivalves, forams, cumaceans (Rex et al. 1993, 1997; Culver & Buzas 2000; Rex et al. 2000; Gage et al. 2004), diversity decreases with increasing latitude in the North Atlantic. Yet, the peak in deep-sea nematode diversity occurs at boreal latitudes (Mokievsky & Azovsky 2002). Is this reflective of different energetic demands of nematodes?

Competitive exclusion

A negative PDR is expected if increasing productivity leads to abundant species competitively excluding each other (Rosenzweig & Abramsky 1993). This is essentially the second half of the dynamic equilibrium model (Huston 1979) and is in some aspects very similar to the resource ratio hypothesis in that it invokes competition under high productivities (Tilman 1982). McClain & Barry (2010) proposed a variation related to this hypothesis based on a guild competition model. Based on studies in Monterey Canyon, they proposed that increased productivity leads to greater megafaunal densities and more bioturbation of deep-sea sediments. This bioturbation creates a disturbance regime and suppresses macrofaunal diversity. It is worth noting that this is in contrast to the patch-mosaic model, which invokes disturbance as a mechanism for increased diversity.

Rex (1976) invoked a variant of this idea to explain that pulsed nutrient inputs could accelerate competitive exclusion and thus lead to decreased diversity under conditions of overall greater productivity caused by pulsed carbon inputs (Huston 1979). Indeed, a specific test of seasonality in productivity versus diversity by Sun et al. (2006) demonstrated that both foram species richness and evenness decline with greater seasonality in overhead production in the North Atlantic. Levin & Gage (1998) used sedimentary organic-matter content as a proxy of food availability to examine diversity–productivity relationships within existing data sets from the deep Indo-Pacific. Their study included a broad range of sedimentary organic carbon content (<0.5% to >6%), and, presumably, food availability. They found negative correlations between sedimentary organic-carbon concentrations and the local diversity of total macrofauna and polychaetes. Dominance in particular, was positively correlated with sediment POC concentrations, suggesting that competitive interactions may shift along POC gradients.

Other key aspects of how productivity controls diversity remain largely unexplored. Prior research has focused on the relationship of productivity and alpha-diversity but much less work has focused on beta and gamma-diversity. Heterogeneity in resource level is often invoked in the context of patch mosaics to explain local-scale patterns in beta-diversity. However, the role of heterogeneity in environmental conditions and habitat properties is surprisingly poorly resolved in the marine benthos (Meager et al. 2011; Meager & Schlacher 2013), including the deep sea (McClain et al. 2011). Patterns of beta-diversity and

the role of productivity at regional and larger spatial scales have also only recently been explored (*e.g.* Wei *et al.* 2010a,b; McClain *et al.* 2012a,b; Gambi *et al.* 2014). These suggest that suites of species are adapted for specific productivity regimes, lending support to the resource allocation hypothesis of Tilman (1982). However, these studies indicate that as opposed to high and low productivity assemblages that co-exist at intermediate levels of productivity, a host of unique assemblages occur over productivity gradients.

Whilst models and theories abound that link productivity to diversity in the deep sea and elsewhere, many theoretical and empirical facets remain to be addressed. (i) Quantifying diversity with non-taxonomic metrics (*e.g.* functional or phylogenetic) may elucidate further the processes between these different patterns. (ii) Incorporating differences in metabolic demands may also yield insights into why diversity patterns over productivity gradients differ. (iii) Modern genetic approaches may shed more light on Allele effects and how likely these are in accounting for extinction risk in small/sparse populations under conditions of low productivity. (iv) Studying the rates and extent of species and assemblage turnover along gradients of energy and productivity will provide better insights into the degree to which species are adapted to specific productivity/food levels or are 'productivity generalists': the degree of specialization is expected to have consequences for diversity under specific conditions of resource availability. (v) Distinguishing the roles of food availability in structuring diversity in spatially heterogeneous seascapes from those of physical or geologic habitat diversity will be valuable, especially when multiple scales are included.

Slow recovery of deep-sea systems is common but not ubiquitous

Disturbance is omnipresent: all seascapes carry signatures of disruption and hence their ecological features display the legacy of these historical perturbations. Life at multiple levels of ecological organization invariably reacts to such disruptions, creating a 'temporal mosaic' of life, poignantly expressed by Paine *et al.* (1998): 'we argue that cycles of disruption and recovery are the usual state of affairs'.

Recovery studies use a set of complementary ecological attributes and metrics to document rates of changes following disturbance: (i) the speed of the initial colonization process and the presence of early colonists (*e.g.* species present in de-faunated habitats or new substrate added such as wood-fall experiments); (ii) the return of bulk measurements of assemblage attributes, most commonly in the form of abundance, biomass or diversity (*e.g.* number of species, various diversity indices); (iii)

the re-establishment of assemblages with compositions resembling that present before the disturbance event or at control sites; and (iv) the restoration of functions (*e.g.* respiration, remineralization). It is important to distinguish short-term invasion of newly created or disturbed habitats by early colonizing species ('colonization') from the re-establishment of assemblage structure and function to levels that resemble states before the disturbance or those of background assemblages not impacted. Often rapid initial colonization of disturbed or cleared habitats or experimental units is observed, followed by a slower increase in biomass, abundance and species numbers, either *via* growth of individuals that had initially colonized the patches or *via* continual arrival of species from the regional species pool (Collie *et al.* 2009).

Conventional wisdom holds that rates of colonization and recovery are sluggish in the deep sea (Grassle 1977). We can identify three main arguments that are likely to have been influential in the formulation of this paradigm: (i) slow biological rates in deep-sea organisms; (ii) life-history traits that may delay recovery; and (iii) habitat properties seen as unfavorable to quick recovery.

i Slow biological rates in deep-sea organisms

It has been argued (or at least it is often implied) that ecological processes, including recovery, of deep-sea populations and assemblages are slow because biological rates of deep-sea organisms are also slow (Smith 1994). It is true that organisms living in colder, deeper waters have slower times of turnover than organisms in warmer waters (vents/shallow). It should be noted, however, that this is primarily a temperature effect: if body size and temperature are accounted for, deep-sea benthic species do not have inherently different metabolic rates (Childress 1995; McClain *et al.* 2012b). Species of the deep-sea benthos also have comparatively longer lifespans (perhaps a consequence of low-temperature environments or lower food availability) and tend to grow slower as a consequence of living in food-poor and cold environments (McClain *et al.* 2012b). Overall, slower biological rates are likely to translate into slower ecological processes (on average) because of temperate and energy limitation in the deep-sea.

ii Low fecundity/larval output/long generation time

Slow recovery in the deep sea has also been linked to life-history characteristics of the fauna at bathyal and abyssal depths. For example, Grassle (1977) stated that: 'small brood size and the high proportion of adults in a number of deep-sea benthic taxa suggest relatively low rates of recruitment, growth and mortality in the deep sea'. Undoubtedly, a critical parameter in recovery dynamics is the number and fitness of colonizers capable of reaching

a patch, specifically the density of potential recruits and their ability to disperse. It follows that life-history traits that influence the size of the potential colonizer pool and its dispersal capability will be important in the recovery of deep-sea populations and assemblages. In addition, recruitment of deep-sea species to new habitat patches can be limited because of low larval supply and high post-settlement mortality (Lacharité & Metaxas 2013).

There are multiple selective pressures in the evolution of life-history traits in deep-sea organisms (*e.g.* environmental stability, nutrient availability, low population densities, low temperature, and limited food) shaping several traits (*e.g.* age at first maturity, brood size, egg size, developmental mode), but three broad hypotheses are particularly germane in the context of discussing recovery: (i) k-strategists are predicted to be dominant in deep-sea assemblages (*i.e.* species are thought to allocate more energy to growth, efficiency, persistence, and competitive ability than to producing offspring in energy-limited environments); (ii) reproductive output is predicted to decrease with depth, because of food limitation in deep water; and (iii) brooding is the predominant development mode in deep-sea animals, whilst larval development is less common under conditions of more stable and more continuous habitats in the deep sea. Taken together, this combination of traits suggests that fewer potential colonizers, having more limited dispersal capabilities, are available to repopulate de-faunated habitat patches and re-establish assemblages in the deep sea. However, support for these predictions is ambiguous. Young (1983) comprehensively reviewed life-history data for deep-sea species, finding that whilst certain k-selected traits become more common in certain taxa, opportunistic r-strategists are well represented. In addition, evidence for bathymetric trends in fecundity is mixed and, if present, highly taxon-specific, and larval dispersal is viable and common in deep-sea animals (Young 1983; Lacharité & Metaxas 2013).

iii Relatively stable, muddy sediments recover more slowly
Habitat properties of the benthos, substrate type in particular, may constrain faster recovery in the deep sea. Experimental data from shallow-water benthic systems indicate that assemblages in fine-grained, relatively stable ('muddy') habitats recover more slowly than those in coarser sands (Collie *et al.* 2000; Dernie *et al.* 2003). Large expanses of the deep ocean consist of muddy sea floor, suggesting that recovery may be slower than in shallower regions where coarser substratum is more prevalent. Mechanistically and intellectually related is the contention that greater stability of deep-sea habitats confers greater predictability, favoring less opportunistic life histories (Grassle 1977).

Ideally, answers to the question of whether recovery in the deep sea is as slow as often suggested would draw on actual recovery rates. However, empirical data on measured recovery times following disturbance in the deep sea encompass a remarkable wide range; here we sketch some examples to illustrate the range of recovery values found in the literature. Khripounoff *et al.* (2006) reported data for sediments in the Clipperton-Clarion Fracture that had been experimentally disturbed 26 years before, showing that physical and chemical properties of the sea bed had not changed in the main impact zone since the end of the experiment, indicating a lack of habitat recovery within two to three decades. Similarly, Miljutin *et al.* (2011) showed only limited recovery of meiofauna for the same site: a 26-year period was insufficient for the nematode assemblage to re-establish its former density, diversity, or structure. Significantly, this limited recovery was in response to a small disturbance at a scale much smaller than envisaged under industrial mining operations (*i.e.* a dredge skimmed the upper layer of sediments to a depth of *c.* 4.5 cm in a track that was 1.5 m wide). Using sediment trays to observe colonization rates in the deep sea and then extrapolating measured colonization rates to background fauna levels, Smith & Hessler (1987) estimated that that community recovery of macrofauna may take more than 2–5 years. In experimental disturbance tracks, mimicking mining activities at a potential manganese nodule site on the abyssal plain off Peru at *c.* 4000 m depth, recovery times depended strongly upon the mobility of the fauna, body size and the metrics considered (Bluhm 2001): in the megafauana there was no clear sign of recovery in terms of diversity, abundance, or assemblage structure 7 years after the experimental disturbance, but some signs of re-colonization by a few mobile taxa after 3 years (Bluhm 2001). Smaller macrobenthos (peracarids, mollusks, polychaetes) may be somewhat faster to re-establish populations in disturbed patches, but detectable signs of mining disturbance remained after 7 years, indicating incomplete recovery (Borowski & Thiel 1998; Borowski 2001). Williams *et al.* (2010) found no consistent and clear signal of recovery in the megabenthos on Australian and New Zealand seamounts 5–10 years after fishing had ceased. In the Norwegian Sea at 380 m depth, deleterious effects of sea-bed drilling on the megabenthos (mainly sponges and cnidarians) remained after 3 years, albeit confined to a relatively narrow (*c.* 60 m) area from the oil well (Gates & Jones 2012).

Notwithstanding this considerable variability in deep-sea recovery rates, it should also be noted that not all shallow-water systems recover quickly. For example, hypoxia and anoxia are widespread disturbance events that can largely or completely decimate the resident fauna. In terms of

recovery rates, a broad generalization from hypoxia-stressed systems in coastal and shelf settings is that recovery can be extended, being in many cases in the range of several years (often >3 years). Although some shallow systems can recover more quickly from periodic stress events, many others show slow or no recovery. Thus, hypoxia in shallow-water settings illustrates that slow recovery of the benthos is not a unique feature of the deep sea (Diaz & Rosenberg 1995). Slow recovery of the benthos from fishing impacts at Georges Bank at 50–90 m depth also supports this argument: the biomass of the larger macrobenthos on the gravelly sea bed took about 5–10 years to recover following fishing closure (Collie et al. 2009). In the most 'shallow' of habitats forming the land–ocean boundary, the fauna of beach habitats modified by sediment deposition ('nourishment') showed minimal recovery within a year (Schlacher et al. 2012).

Conversely, not all colonization of 'empty' or 'fresh' habitat in the deep sea is slow. Artificial sediment cones, resembling fecal mounds, show relatively fast rates of fauna establishment, with background levels being reached within weeks to months (Smith et al. 1986; Smith & Hessler 1987). Pusceddu et al. (2013) observed that meiofauna assemblages at 1000–2000 m depth in the Lacaze-Duthiers and Cap de Creus canyons recovered within 6 months from the disturbance effects caused by a dense shelf water cascading event. In the Campos Basin at 900 m depth, Santos et al. (2009) reported that fairly localized (c. 500 m) impacts from drilling activities on macrobenthos diminished at most sites within a year, suggesting considerable recovery. For hydrocarbon drilling sites in the Faroe–Shetland Channel (c. 600 m depth) Jones et al. (2012) showed that partial recovery of the deep-sea megabenthos can occur between 2 and 10 years following spatially isolated and relatively small (100–200 m) physical disturbances to the sea bed. Finally, in the deep (4000 m) Peru Basin, smaller macrobenthos (sampled with box cores) may approach reference conditions within 3 years following experimental sea-bed disturbance (Borowski 2001).

Although some ideas about the most likely drivers that shape the trajectories and speed of recovery have emerged in the literature, actual recovery trajectories are far from uniform, difficult to predict, and subject to chance to some degree. As ecological systems are inherently complex and stochastic processes are omnipresent, small changes in the succession process (e.g. local environmental conditions, chance events in the arrival sequence of colonizing species, substrate heterogeneity) will create different recovery trajectories that may be very difficult to predict (O'Neill 1999). It is thus an interesting scientific challenge to better conceptualize recovery trajectories in the deep sea, develop testable predictive hypotheses, and experimentally test them.

It has been postulated that refugia may be important in recovery (Power 1999); parts of the habitat in larger disturbed areas are thought to better resist impacts (e.g. corals in rocky clefts and crevices escaping the physical impacts of bottom trawls on rugged seamounts; Althaus et al. 2009). The role of refugia is an aspect of recovery that is seldom explicitly measured (but see Tittensor et al. 2010), but of potential importance. Recent discussions about likely mining impacts and how to mitigate such impacts mention the putative role of refugia (e.g. areas or seamounts purposefully excluded from mining or other human activities; Schlacher et al. 2014), but we believe that the idea deserves broader examination in deep-sea systems.

Re-establishment (and possibly active restoration) of habitat properties, biogenic structures and ecological features (biomass) all essentially relate to the recovery of structure (sensu lato). What may, however, be equally (arguably more) relevant in a management context is to examine the question of whether, and at which rate, ecological functions return to ambient levels and whether 'recovered' areas can continue to supply economically important ecosystem services (e.g. benthic secondary production available as a fisheries resources or supporting fisheries, carbon processing, nutrient remineralization, sediment stability, bioturbation).

In instances where economically important resources form over geologic time scales [e.g. growth rates of ferromanganese nodules are in the order of 1–100 mm per 10^6 years, suggesting millennial recovery intervals following mining (Piper & Williamson 1977; Reyss et al. 1982)], restoration of the resource is unrealistic in the context of human experiences and the lifespan of economies; recovery of some deep systems from some forms of human disturbance may well be out of our reach.

Too few good ideas impede progress in deep-sea diversity research

Whilst the heading for this section may seem utterly preposterous, some introspection of where the field is heading is probably a constructive exercise. This paper initially set out by encouraging debate, and we hoped that this could be achieved by engaging with the 'big ideas' — many of them classic ones — of deep-sea diversity research. Somewhat surprisingly, our examination of the contentions and predictions made decades ago shows that every old hypothesis is also a new one (Table 1). We still have many meters to dive into the bathyal and beyond before most of these are answered. They remain fresh and scientifically exciting, and the discipline can draw on a cornucopia of good ideas.

Looking critically at the paradigms that collectively define a discipline is, of course, not unique to diversity

Table 1. Major paradigms explaining deep-sea diversity.

The challenge	The thesis	The assessment	Future work ideas and/or questions
'The deep-sea benthos is not more bio-diverse than shallow water.'	'From this comparison to soft bottom, shallow marine biocoenoses, we conclude that the diversity of benthic invertebrates in the deep-sea well exceeds that of temperate, shallow water, benthic communities and is actually comparable to that found in shallow water, tropical communities.' Hessler & Sanders (1967, p. 71). Also see Sanders (1968) and Grassle (1989, p. 15).	Although many areas of the deep sea do support large numbers of species, and deep-sea biodiversity may rival or exceed levels found in shallow water, a blanket statement of 'exceptional biodiversity' in the deep sea is unwarranted, chiefly because a true global comparative analysis of marine biodiversity is unavailable. See retorts of the idea by Snelgrove & Smith (2002), Gray (1994) and Gray *et al.* (1997).	Large-scale and comprehensive analysis of marine biodiversity across multiple depths latitudes, habitats and productivity regimes. Targeted questions about processes predicted to create, maintain, limit and regulate species diversity. Role(s) of environmental heterogeneity at multiple depths for biodiversity.
'The stability of the deep sea reduces competitive interactions.'	'Stability-time hypothesis' of Sanders (1968, p. 253–254): 'Where physiological stresses have been historically low, biologically accommodated communities have evolved.' Fundamental premise is that environmental stability favors evolutionary processes that create intense niche partitioning to fine levels: modern co-existence of deep-sea species reflects past competitive interactions. See Grassle & Sanders (1973, p. 651–652) and Sanders (1979).	Predicted fine-scale niche diversification is difficult to demonstrate and general ecological theory is ambiguous as to whether stability promotes or reduces diversity.	Is the frequency, magnitude and predictability of disturbance events (converse of stability) different between deep-sea and shallow-water systems on evolutionary time scales? Are rates of evolutionary diversification between deep-sea and other systems different? Does niche width vary systematically with depth and stability? Does phylogenetic diversity decline with depth within a clade?
'Competition does not structure deep-sea communities'	A key contention of the stability-time hypothesis is that competition in the past has favored strong niche differentiation among deep-sea species, diminishing competitive interactions in modern communities (Sanders 1968). Two major opinion pieces advocate that competition in the soft-sediment benthos, and particularly in the deep, are not important in structuring communities (Wilson 1990; Grant 2000).	Role and importance essentially unknown: no published study has tested whether competition is important in maintaining species diversity in deep-sea assemblages.	Is fitness of deep-sea species reduced under competitive interactions? Response surface experiments that alter the densities of two competing species.
'Predation effects do not increase diversity in deep-sea assemblages'	The classic view is that predation maintains population sizes at densities small enough to prevent competitive exclusion and hence maintains species diversity, *i.e.* the biological cropping hypothesis of Dayton & Hessler (1972, p. 202).	Paucity of explicit tests about the role of predation in deep-sea sedimentary environments making it impossible to draw conclusions about whether predation can act, and under which circumstances, to maintain and/or promote diversity in the deep-sea. Moreover, life history traits of deep-sea organisms do not reflect strategies adapted to heavy predation Grassle & Sanders (1973, p. 644). Two recent caging experiments suggest that predation may actually promote diversity and overall abundance (Gallucci *et al.* 2008; Thistle *et al.* 2008).	Future predator exclusion or addition (*e.g.* caging) experiments to identify the role of top-down effects on diversity in deep-sea assemblages. Mensurative ('natural') experiments that encompass known gradients in predator and/or megafaunal identity and density. Future research needs to separate the effects of megafauna as predators, bioturbators, facilitators and engineers, and competitors.

Table 1. Continued

The challenge	The thesis	The assessment	Future work ideas and/or questions
'Deep-sea alpha- and beta-diversity is controlled by disturbance.'	Classic expectation is that disturbances in the deep sea are less frequent, less severe, and of smaller spatial extent than in more physically-dynamic environments (Grassle & Sanders 1973). Also see Connell (1978).	Accumulated evidence that disturbance is not uncommon in the deep sea and acts at multiple scales and through multiple processes. However, the exact consequences of the diverse types of disturbance on deep-sea diversity are difficult to predict at present.	Are disturbances themselves of lower intensity and/or frequency, but of greater biological impact in the deep ocean? Do carcass falls create significant habitat heterogeneity or complexity? (postulated to be a form of biological disturbance). Can measured disturbance effects be up-scaled from small invertebrates to larger mobile animals? Do reciprocal feedbacks between diversity and disturbance operate in deep-sea assemblages?
'Diversity of the deep-sea communities is best predicted through patch-mosaic dynamics'	'Patch-mosaic model': the deep-sea floor is a patchwork habitat created by disturbance, maintaining diversity through the simultaneous existence of multiple distinct assemblages in different phases of succession. 'A spatial mosaic emerges from local successional sequences that are out of phase' (Grassle & Sanders 1973, p. 654–656)	Spatial heterogeneity in habitat and biological properties is not uncommon in sedimentary properties in the deep sea and is created by multiple processes. However, what the underlying cause of this heterogeneity (e.g. disturbance, food resource patchiness) is and how it maps out on diversity is much less clear.	What is the spatial scaling of 'patchiness'? How does turnover in habitat attributes and biological characteristics vary geographically and with depth? Is patch longevity and size predictably different between deep and shallow benthic environments? What traits of patches (*i.e.* chemical, physical, or biological) are most important in defining the nature or type of a patch in the deep sea?
'Deep-sea alpha- and beta-diversity is controlled by productivity.'	Because the low rates and poor quality and quantity of food fluxes, food is thought to be the primary limiting resource in the deep sea and thus the primary driver of ecological traits, including diversity (Gooday *et al.* 1990; Smith *et al.* 2008, McClain *et al.* 2012a,b).	Productivity–diversity relationships (PDRs) are often inferred from proxy variables such as depth and latitude. Exact studies of PDRs for deep-sea taxa are rare. Rarer yet is an understanding of mechanistic processes by which PDRs actually arise in the deep sea. The variability in reported patterns suggests that productivity influences on alpha diversity are likely to involve more than one mechanism, are modulated by habitat conditions, and can be taxon specific.	What is the role of productivity in determining beta- and gamma-diversity? At which scale does heterogeneity in environmental conditions, including localized variation in productivity, drive diversity? How important is productivity in shaping diversity, particularly beta-diversity, at larger spatial scales? How do differences in metabolic demands modulate PDRs? How common (or important) are Allee effects in low-productivity settings in the deep sea? Is spatial variation in productivity or energy availability simply a special case of environmental heterogeneity?

Table 1. Continued

The challenge	The thesis	The assessment	Future work ideas and/or questions
'Slow recovery of deep-sea systems is common but not ubiquitous.'	Conventional wisdom holds that rates of colonization and recovery are sluggish in the deep sea because of a combination of slow biological rates, life-history traits that may delay recovery, and habitat characteristics unfavorable to quick recovery.	A good number of case studies document prolonged recovery of deep systems. Conversely, there is opposing evidence of relatively rapid colonization of fresh habitats in the deep sea. Slow recovery can also occur in shallow-water environments. Evidence for life-history traits thought to impede recovery is mixed for deep-sea species.	To which degree are recovery trajectories of deep-sea species and assemblages stochastic? How important are refugia in recovery? Do functional properties and ecological processes follow similar recovery trajectories as structural components of assemblages? Is full recovery a realistic expectation for impacts that are large and sustained, and which remove extremely slow-growing organisms and/or habitats (*e.g.* mining of deep seamounts)?

research on sedimentary sea floors in the deep sea. A careful stock-take of generalization, propositions, notions, assertion and theories is at times necessary. For example, a recent surge of theoretical and empirical work on seamount diversity has made tremendous gains in weeding out dated generalizations whilst generating new insights (Samadi *et al.* 2006; Hall-Spencer *et al.* 2007; McClain 2007; O'Hara 2007; O'Hara *et al.* 2008; Brewin *et al.* 2009; McClain *et al.* 2009; Thoma *et al.* 2009; Tittensor *et al.* 2009; Clark *et al.* 2010; Howell *et al.* 2010; McClain *et al.* 2010; Rowden *et al.* 2010a,b; Shank 2010; Tittensor *et al.* 2010). We feel that this example provides a model for soft-sediment deep-sea benthos.

A pessimistic worldview may focus on seeking reasons for why deep-sea ecology has not engaged closer and more forcefully with the 'classic ideas' or the models put forward to explain diversity in the soft-sediment deep benthos. Indeed some may argue, incorrectly, that we lack data, samples and a basic understanding of the deep-sea soft benthos to proceed forward − we disagree. The mantras of 'less than 5% of the deep ocean floor is explored' and 'we know more about Mars than the deep sea' are repeated too often unquestionably. These statements ignore generations of sampling, analyses, and sweat that have provided the huge intellectual gains of the last centuries in deep-sea biology. The current amount and scale of sampling that have occurred in the deep oceans (Rex *et al.* 2006; Stuart *et al.* 2009) are impressive, and large-scale analyses have been conducted (Rex *et al.* 2006; Wei *et al.* 2010a,b; McClain *et al.* 2012a,b; Jones *et al.* 2014) that have made good use of these collections.

However, utilizing old data sets will also have limitations, but fewer than frequently claimed. To answer new

and old questions in deep-sea ecology new cruises, using new gear in new areas of the global ocean, will certainly be needed. Deep-sea ecology will and must proceed by generating new information whenever necessary, effective and practicable. However, we also argue that a lack of data is not invariably the prime impediment in all cases: concerted efforts to link existing independent data streams together to examine long-standing questions of deep-sea diversity will be equally fruitful. Notwithstanding the source of evidence (new or old data), it is the ideas, questions, hypotheses, and theses that build on the 'classic paradigms' that shall emerge fresh in the limelight.

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