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Review article

Shelf and deep-sea sedimentary environments and physical benthic disturbance regimes: A review and synthesis

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ABSTRACT

Physical disturbances of the seafloor play a key role in ecosystem function and are postulated to exert control over spatial patterns of biodiversity. This review investigates the role of natural physical sedimentological processes that occur in shelf, slope and abyssal environments that also act as disturbances to benthic ecosystems and which, under certain circumstances, give rise to benthic disturbance regimes. Physical sedimentological processes can cause both press (process that causes a disturbance by acting over a timespan that is intolerable to benthos) and pulse (process that causes a disturbance by exceeding a threshold above which benthos are unable to remain attached to the seabed or are buried under rapidly deposited sediment) types of disturbance. On the continental shelf, pulse-type disturbances are due to temperate and tropical storm events, and press-type of disturbances identified here are due to the migration of bedforms and other sand bodies, and sustained periods of elevated turbidity caused by seasonally reversing wind patterns. On the continental slope and at abyssal depths, pulse-type disturbances are due to slumps, turbidity currents; benthic storms may cause either press or pulse type disturbances. A possible press-type of disturbance identified here is inter-annual changes in abyssal bottom current speed and/or direction. It is concluded that: 1) physical sedimentary disturbance regimes may characterize as much as 10% of the global ocean floor; 2) multidisciplinary research programs that integrate oceanography, sedimentology and benthic ecology to collect time series observational data sets are needed to study disturbance regimes; and 3) predictive habitat suitability modeling must include disturbance regime concepts, along with other biophysical variables that define the fundamental niches of marine species, in order to advance.

1. Introduction

Research work conducted in shelf and deep-sea environments over the last decade has highlighted the importance of physical disturbances in understanding benthic ecosystem function and biodiversity. Kostylev (2012) notes that the “interaction of sediment and flow as a most common agent of natural disturbance, together with the effects of benthic organisms on this interaction, are at the core of benthos-sediment coupling”. Natural disturbances capable of removing, burying or killing the existing benthos create patches of clear space available for colonizing organisms. After such events, an ecological succession ensues with the early colonizers eventually replaced by a climax community consisting of more abundant and larger animals with higher bioturbation rates and deeper mixing depths than those which existed prior to the depositional event. The assemblage present at any one time is therefore governed by the rate of ecological succession and the spatial and temporal attributes of physical seafloor disturbances (e.g. Thistle, 1981, 2003).

Disturbances of the seafloor are, of course, also caused by human activities and much research has been carried out to quantify the impact and the rates of recovery of marine life from anthropogenic disturbances. Examples include bottom trawling for fish (Collie et al., 2000; Thrush et al., 2005; Puig et al., 2012), aggregate and mineral seabed mining (Jewett et al., 1999; Hobbs, 2002), port construction and shipping channel maintenance, laying of pipelines, oil spills and oil and gas exploration and production (Gates and Jones, 2012). In the deep sea, the potential for future manganese nodule mining precipitated research into the possible impacts on, and responses of, the benthos (Jankowski et al., 1996; Morgan et al., 1999; Sharma, 2001). In general, these studies are based upon an artificial, deliberate disturbance of an area of seabed (or installing artificial surfaces representing the seafloor) and measuring the rates of colonization and regrowth of the original community. There are, however, differences between studies based on artificially manipulated environments versus the study of natural disturbances, and results from manipulated studies should be used with caution to infer natural rates and processes (Tyler, 2003).

Examples of natural physical sedimentary processes that disturb benthic ecosystems include continental shelf sediment mobilization during extreme storm events (Williams, 1988; Preen et al., 1995;

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Halford et al., 2004), submarine canyons and fans subject to pulses of sediment influx from slope sediment failures (Young et al., 2001; Hess et al., 2005) and benthic storms that mobilize sediments at abyssal depths. However, there have been few studies published regarding recovery rates of the benthos from natural disturbances at shelf depths and even fewer published studies on the continental slope and at abyssal depths (Kostylev, 2012). The study of such dynamic sedimentary environments (and ecosystems) requires a multidisciplinary approach involving the collection of co-located marine geological and benthic ecology time-series data.

Despite the clear linkages that exist between dynamic shelf and deep-sea sedimentary environments and the benthic ecosystems that they support, there is surprisingly little known about their interdependencies or interactions. In order to be able to model and predict biological recovery of benthic habitats severely disturbed by human activity (such as fishing, waste disposal, seabed mining and anthropogenic global climate change), we must first understand and be able to quantify the natural disturbance processes with which the benthos are inextricably linked.

1.1. Scope and aims

In this review, disturbance regime theory of dynamic sedimentary environments is considered in the context of benthic ecology. Examples of faunal succession rates documented for sedimentary continental shelf environments are compared with examples of shelf disturbance regimes driven by storms and other sediment suspension and transport processes. An overview of deep-sea disturbance regimes highlights the significance of benthic storms and the episodic, down-slope gravity flows characterizing submarine canyons and fan complexes. Finally the applications of disturbance regime theory to predictive habitat mapping (habitat suitability models) are considered.

Only physical disturbance of the benthos related to dynamic sedimentary processes is addressed in this review; biotic (e.g. predation, nutrient availability), chemical (e.g. dissolved oxygen, salinity, pH), glacial or iceberg-related disturbances or any anthropogenic agents, among many others, are not included. It is acknowledged that, although we focus here on one set of physical sedimentological disturbance processes, many natural disturbance processes are contemporaneous and may interact with one another resulting in complex ecological responses (e.g. Levin and Dayton, 2009). The aim of this review is to highlight aspects of marine geoscience where further research could help to improve our understanding of marine sedimentary ecosystems in shelf, slope and abyssal environments.

2. Definition of “disturbance regimes”

2.1. Disturbances clear patches of habitat for recolonization

A fundamental tenet of landscape ecology is that ecosystems and species evolve in response to a particular regime where environmental disturbance can play a significant role in controlling such things as life cycles, food and nutrient supply and habitat availability (Thistle, 1981). A definition of disturbance was provided by Pickett and White (1985) as “any discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment” (i.e. alters niche opportunities for the species capable of living in a given setting). For the purposes of this discussion, emphasis is placed on substrate availability and a “disturbance” will be considered to create a patch of open space that is available for opportunistic species to colonize (see Sousa, 2001, for further discussion on the concept of “disturbance”).

For landscape ecologists, storms causing a large tree to fall in the forest, fire destroying an area of forest or scrubland and a tree succumbing to drought are examples of important disturbances that create patches of open space. An ecological succession ensues, with different species arriving over time and competing for space, until the disturbed patch finally reverts to a mature, fully recovered, state (Connell, 1978; Huston, 1979). Hence, landscapes that are subject to disturbances exhibit a degree of patchiness that relates to past disturbances, their colonization by opportunists and gradual recovery. Hierarchies of patches coexist at multiple scales, created by a range of physical and biological processes (Wu and Loucks, 1995). Patchy landscapes, taken as a whole, contain a greater number of species (greater biodiversity) per unit area than either the disturbed or undisturbed habitat alone.

Examples of physical disturbances involving seabed sediments include muddy seabeds of the continental shelf mobilized during extreme storm events (Swift et al., 1981; Morton, 1988); macrotidal estuarine sediment regimes subject to severe storm events (e.g. Yeo and Risk, 1979; Harris and Collins, 1988); the migration of large sedimentary bedforms burying benthos (e.g. Daniell et al., 2008); seasonal sediment pulses entering the heads of shelf-incising submarine canyons (Okey, 1997; Ogston et al., 2000; Mullenbach et al., 2004); and submarine fans subject to sediment influx from slope sediment failures (e.g. Posey et al., 1996). Such processes can exert a physical stress on organisms, tearing plants from their place of attachment (Thomsen et al., 2004), mobilizing sediment, burying plants and animals (Aller and Todorov, 1997), damaging organisms by abrasion (Cheroske et al., 2000), or by limiting light availability (Carruthers et al., 2002; see also reviews by Hall (1994), and Sousa (2001)). In each of these examples, a natural sedimentary process gives rise to a disturbance that disrupts the ecosystem, community or population structure and changes the availability of habitat or resources.

Natural physical disturbance is the dominant effect structuring benthic communities (Hall, 1994; Sousa, 2001). However, there are also bioturbation effects of benthos on sediments. These include sediment stabilization, sediment mixing, biodeposition, compaction, and hydrodynamic effects (e.g. Murray et al., 2002). For example, Botto and Iribarne (2000) describe how the effects of different species of burrowing crabs may cause the same sediment type to be either more easily eroded or more difficult to erode; one species stabilizes the sediment by placing fine and cohesive sediment on the surface, while another disrupts the sediment by pelletizing it and making it more easily eroded. Although in this review we focus on physical disturbance of sedimentary environments, it is acknowledged that the sedimentary environments are, in turn, effected by the benthos.

2.2. The intermediate disturbance hypothesis

The effects of disturbances on biodiversity have been conceptualized by the “intermediate disturbance hypothesis” (IDH; Connell, 1978; Huston, 1979). Where disturbances are too frequent, diversity is low because few species can thrive under such stressful conditions. Where disturbances are rare or infrequent, competitive exclusion takes its toll as weaker, less-well adapted species are eliminated. The IDH predicts that it is the intermediate zone of quasi-stable environments that allow for the greatest diversity of species to exist, as shown in coral reef studies by Connell (1978) and in a number of other studies of marine benthic communities (Sousa, 2001; see review by Hughes, 2012).

If the IDH applies to complex communities such as coral reefs (Connell, 1978), then it seems reasonable that it should apply more broadly to other marine environments, as has been suggested by Field (2005). From his analysis of natural and anthropogenic shelf processes, Field (2005) concluded that “every habitat represents a time-averaged response to the dominant physical processes, which is as important in defining the habitat as geologic setting and community structure.” Kostylev and Hannah (2007) proposed that habitats are best understood within a “disturbance” – “scope for growth” stability diagram, which, according to ecological theory, defines traits of species and emergent properties of ecological communities such as species competition and biodiversity. Kostylev (2012) noted that, from a physical sedimentological perspective, the quadrants of the “disturbance” – “scope for growth” stability diagram can be plotted on a Hjulstrom (1935) diagram