Spatial and Temporal Scales of Disturbance to the Seafloor: A Generalized Framework for Active Habitat Management

SIMON F. THRUSH,1 CAROLYN J. LUNDQUIST, AND JUDI E. HEWITT
National Institute of Water and Atmospheric Research, Post Office Box 11-115, Hamilton, New Zealand

Abstract. The direct effects of marine habitat disturbance by commercial fishing have been well documented. However, the potential ramifications to the ecological function of seafloor communities and ecosystems have yet to be considered. Ecological research has demonstrated that natural disturbance processes play an important functional role in seafloor ecosystems by affecting spatial heterogeneity. When the space and time scales of human disturbance are greater than those the natural ecosystems are adapted to, changes in community structure and function are inevitable. Changes restricting the size, density, and distribution of organisms can lead to functional extinction and threaten resilience at all levels of biological diversity. This is particularly true in soft-sediment ecosystems, where the organisms create much of the heterogeneity within the habitat and also play crucial roles in many processes. Thus, there is a need to develop a scientific framework for the management of seafloor habitats, focusing on sustaining fisheries and maintaining biodiversity. Simple heuristic models can indicate disturbance regimes that, through their frequency, extent, or intensity, could result in catastrophic changes across the seafloor landscape. Our model implies that when disturbance is infrequent relative to recovery time and only a small proportion of the landscape is affected, the system is stable, but when the disturbance frequency is shorter than the recovery time and/or a large proportion of the system is disturbed, the system may flip into an altered state. Once features have been lost, it may not be a simple matter of reducing the disturbance regime to ensure their recovery. Even such a simple model emphasizes the need to understand the scales of mobility and the processes affecting recovery. We need to carefully and explicitly consider the implications of alterations of these ecosystems; they may not only reflect loss of conservation and natural heritage values but also loss of opportunity and the ecosystem services provided by diverse and heterogeneous seafloor ecologies.

Introduction

Over the last 20 years, fishing industries have begun to be subjected to the same degree of environmental scrutiny as many other industries. Studies of the direct effects of disturbance to seafloor habitats and communities have indicated the potential for profound effects (see reviews by Dayton et al. 1995; Jennings and Kaiser 1998; Walling and Norsøe 1998; Auster and Langton 1999; Hall 1999; Kaiser and de Groot 2000). Despite the often significant challenges in conducting these impact studies, some consistent responses to habitat disturbance have emerged across broad spatial scales (Thrush et al. 1998; Kaiser et al. 2000; McConnaughey et al. 2000; Cryer et al. 2002). Common changes in seafloor communities that occur across a variety of habitat types include reduced habitat structure, lower diversity, and the loss of large and long-lived sedentary species. This knowledge has clearly informed the debate over fisheries management and marine conservation and also raises the profile for both scientists and resource managers to understand interactions between broad-scale habitat disturbance and the functioning of benthic ecosystems.

In this paper, we develop a simple framework, based on basic ecological principles, that can help identify conditions that may lead to qualitatively different seafloor landscapes and thus help communication among scientists, managers, and stakeholders (see Done and Reichelt 1998). We use a modified version of a simple ratio-based model that was initially developed by Turner et al. (1993) to investigate the impact of disturbance at differing spatial and temporal scales on
forest habitats: the model simplifies many of the complexities of disturbance–recovery dynamics and the potential for recovery processes to change over space or time scales in a nonlinear fashion. Nevertheless, consideration of disturbance within a space and time ratio framework provides an indication of disturbance regimes that, through their frequency, extent, or intensity, could result in catastrophic changes across the seafloor landscape.

**The Value of Seafloor Habitats and Communities**

Any decisions that involve opening new areas for exploitation or changing industry practice inevitably involve balancing values. There are usually important social, ethical and economic considerations, but it is also important to consider the possible threats to ecological function. By definition these functions sustain marine ecosystems and facilitate the provision of ecosystem goods and services. If these natural functions fail, many of the social and economic considerations become academic.

Soft-sediment seafloor habitats account for about 70% of the surface of the planet; they are diverse and heterogeneous across many scales of sampling. Even deep-sea basins that were once considered constant and uniform exhibit high levels of both local biogenic complexity (e.g., Jumars and Eckman 1983; Levin and Goody 1992) and regional diversity (Levin et al. 2001). Throughout the marine environment, organisms that inhabit sediments often create much of the habitat structure, ranging from the micro-scale changes around individual animal burrows to the formation of extensive biogenic reefs. This biologically created heterogeneity and three-dimensional structure both above and below the sediment–water interface influences a number of important ecological processes.

These ecological processes include purely biological functions, such as providing refugia and juvenile habitat for many exploited populations, providing settlement sites for larvae and juveniles, and serving as a source of food for fish and other predators (e.g., Sainsbury 1988; Tupper and Boutilier 1995; Lindholm et al. 1999). Other important ecological processes occur as a result of interactions between hydrodynamics and seafloor organisms. These interactions influence sediment stability and the transport of food, larvae, sediments, and chemicals (e.g., Eckman and Nowell 1984; Frechet et al. 1989; Wildish and Khristmanson 1997). Typically, animals increase the particle exchange between water and sediment by a factor of 2–10 (Graf 1999). The density and spatial arrangement of organisms are important in determining the magnitude of the effect (e.g., Green et al. 1998; Nikora et al. 2002).

Below the surface of the sediment, animals continue to play important ecological roles by influencing biogeochemical processes such as the transformation and exchange process of organic matter and nutrients (Herman et al. 1999). For example, about one-third to half of the nutrients that fuel primary production in the sea above continental shelf environments may be derived from the sediment (Pilskaln et al. 1998). Continental shelf sediments, while occupying only 7% of the marine environment, are responsible for 52% of the global organic matter mineralization (Middleburg et al. 1997). Similar to organism–hydrodynamics interactions, larger organisms appear to be particularly important in influencing these biogeochemical processes (Thayer 1983; Sandnes et al. 2000).

These results highlight the fundamental ecological value of seafloor communities in terms of biodiversity and ecosystem process. The current threat to benthic communities from habitat disturbance by fishing is that a decrease not only in the density of individual organisms but also in the size of individuals and their spatial extent may mean we risk losing important ecological processes; that is, fishing disturbance may result in organisms becoming functionally extinct (Dayton et al. 1998).

**The Disturbance Ecology of Seafloor Communities**

Basic ecological research on marine benthic communities can provide some useful insights into disturbance. Many types of processes disturb seafloor ecosystems, ranging in size from the small bite marks in the sediment created by feeding fish to processes that impact larger areas, such as storms or volcanic eruptions. Spatial heterogeneity in community structure is related to the spatial extent and/or the frequency of disturbance events; in order for disturbance to create patchiness, it must be small relative to the colonization potential of the benthic community but not so small as to enable the adjacent assemblage to quickly infill the disturbed patch. The key to predicting the effect lies in the scale of disturbance in space and time and the scales of ecological response to that disturbance (recovery or succession). Empirical studies of small-scale disturbance processes cannot simply be directly scaled up to indicate the effects of broader-scale disturbances because the relationship between heterogeneity and disturbance is nonlinear (Kolasa and Rollo 1991).

Over much of the continental shelf, where most fishing is conducted, natural disturbance events covering a large area are rare. The types of large natural disturbance phenomena that potentially impact a particular area of the continental shelf are highly dependent on location. Storms rarely stir the seabed below...
about 60 m, although there are exceptions. Green et al. (1995), for example, reported on the impact at 25-m depth in the North Sea of a force 9 gale associated with long-period waves generated by hurricane-force winds in the Norwegian Sea. The storm resulted in a significant wave height exceeding 3 m for more than 40 h, with a maximum recorded wave height of 11.82 m. Despite the severity of the storm, the authors calculated that maximally only the top 1 cm of sediment was eroded. The distribution of iceberg scour is limited to the polar continental shelves, and hyperpycnal sediment flows across the continental shelf are also restricted to areas of extreme terrigenous sediment loading (Foster and Carter 1997; Wheatcroft 2000). Toxic algal blooms and anoxic/hypoxic events are other broad-scale disturbance phenomena that are also restricted to specific locations. The frequency of disturbance events is also important; typically in nature, the larger the event, the less frequently it will occur (Bak 1994). When the space and time scales of human disturbance are greater than those that the natural ecosystems are adapted to, then changes in community structure and function are inevitable.

Despite the problems with direct extrapolation, it is insightful to consider what we have learned from disturbance–recovery experiments in a variety of benthic habitats. Understanding recovery processes allows us to consider the potential for long-term chronic degradative changes as the cumulative effects of individual disturbance events spread across the seafloor landscape. Rates of recovery may be expected to be dependent on the spatial scale of disturbance because of the increased distance colonists need to travel to reach the disturbed area (this is particularly important for species with limited mobility) or because of interactions between the spatial scale of disturbance and habitat stability (Connell and Keough 1985; Hall et al. 1994; Thrush et al. 1996; Zajac et al. 1998). Species composition is also important, with communities dominated by large, slow-growing organisms with poor dispersal ability exhibiting slow recovery (e.g., Beukema et al. 1999; Thrush and Whitlatch 2001). Recovery may also be habitat dependent due to differences in the available pool of colonists, productivity, depth, or temperature (e.g., Pearson and Rosenberg 1978; Sousa 2001). The ecological intensity of response will also be determined by the resident species; even low-intensity disturbance can have significant effects on sensitive species (Jenkins et al. 2001).

While we have some understanding of the factors influencing recovery rates, it is important to note that there is still an appreciable amount of variability in the relative importance of the various factors that influence the recovery processes (Thrush and Whitlatch 2001; Whitlatch et al. 2001). Fishing is a large-scale disturbance and has both immediate and chronic effects. Disturbances that lead to biotic impoverishment tend to be chronic, while those that lead to enhanced diversity tend to be transient and localized (Caswell and Cohen 1991). The important point is that we should be able to gain some understanding of the effects of any disturbance to the seafloor by understanding the space and time scales over which the event occurs and how they interact with the rate of recovery of the seafloor community. This emphasizes the value of quantifying the extent, spatial distribution, and frequency with which different types of fishing gear are dropped on to or dragged over the seabed.

### Scales of Fishing Disturbance

Unfortunately, data on the frequency and area of the seafloor swept by fishing gear are usually limited. The data available are often based on broad-scale fisheries management units not necessarily related to the spatial variation in seafloor habitats or biodiversity (National Academy of Sciences 2002). The spatial distribution of fishing effort on the seafloor is patchy, reflecting the relative availability of the target species. This patchiness in the distribution of fishing disturbance is a typical characteristic of ecological data, and the interpretation of such data is dependent on the scale of observation. Patchiness inevitably requires an increased sampling effort, either to generate precise estimates of the mean (by averaging over the variability) or to sample at fine resolution and characterize the spatial structure. High-resolution characterization of fishing disturbance tends to reveal fine-scale patchiness in habitat disturbance; this patchiness changes the spatial extent, frequency, and magnitude of disturbance (e.g., Rijnsdorp et al. 1998; Pitcher et al. 2000a). Different fisheries have different fishing methods and may use different types of gear that also influence the potential for and nature of disturbance to the seafloor.

Obviously, even defining the level of disturbance is a complex issue; nevertheless, it is useful to consider a few different examples to gauge the magnitude of possible effects. National Academy of Sciences (2002) reported that, on average, 56% of the New England region was swept by trawl gear more than once a year, and scallop dredges also covered a smaller but not insubstantial area. These data were based on recorded landings from 0.5° latitude × 0.5° longitude statistical blocks. Friedlander et al. (1999) recorded trawl tracks in side-scan sonar images of the seafloor to show that a typical fishery in Northern California trawled across the same section of seafloor an average of 1.5 times per year, with selected areas trawled as often as three times per year. For a fishery for scampi *Metanephrops*
challengeri on the continental slope off New Zealand (200–600-m water depth), Cryer et al. (2002) used data derived from the GPS coordinates for the start and end of each trawl to calculate that an average 2,100 km² was swept each year by trawlers. These statistics suggested that within the study area, trawlers swept about 20% of the upper continental slope each year, although about 80% of all scampi trawls were made in an area of about 1,200 km². In some areas, the extent and frequency of disturbance can be even more extreme. Pitcher et al. (2000b) identifies one harbor in Hong Kong where every square meter of the seafloor is trawled three times a day. In general, it is apparent that the extent, patchiness, and frequency with which fishing gear is dragged across the seafloor are variable. To understand the ecological consequences of this disturbance, we need to consider the space and time scales of disturbance relative to the time scales of recovery of the affected benthic communities.

**Managing Habitat Disturbance: The Model**

Without a doubt, we need to manage habitat disturbance to the seafloor. Zoning the oceans is seen as an important tool to allow fisheries to occur embedded in functioning ecosystems (e.g., Pauly et al. 2002). Understanding the implications of different disturbance regimes on the seafloor should provide insight into how these regimes may be balanced in terms of spatial extent or frequency to maintain ecologically valuable seafloor communities. Simple heuristic models can indicate disturbance regimes that, through their frequency, extent, or intensity, could result in catastrophic changes across the seafloor landscape.

We created a simple patch model as a conceptual framework for examining the effects of fishing disturbance on benthic communities. This model is a simplistic representation of benthic community successional dynamics from a pioneering community to a mature community, created to demonstrate the effect of varying size and frequency of trawling disturbance on the proportion of mature structured habitat remaining within a landscape.

The model simplistically plays out the effects of repeated disturbance events on a seafloor habitat that is structured by certain archetypal communities. These archetypes are defined by structural attributes; they are cartoon communities defined by their slowest-growing representatives that will, finally, dominate community structure. The temporal dimension is considered by the frequency of disturbance, while the spatial dimension is considered by the ratio of size of the disturbed area to size of the habitat. The spatial dimension of the model is scale invariant, allowing for comparisons among spatial scales, while the temporal dimension is presented as a frequency (events per year) for ease of interpretation. The temporal dimension can be considered at various time scales either by changing the duration of the time step in the model or by calculating the scale-invariant ratio of the frequency of disturbance to recovery time.

The assumptions on which the model is based have important implications for the interpretation of its results. The model presents a simple representation of how the space and time scales of disturbance interact with recovery of seafloor communities. The aim is not to predict the consequences of a specific disturbance regime on a specific habitat but to provide a simple heuristic tool to facilitate greater consideration of disturbance regimes and seafloor communities in fisheries management. Models of this type make very broad generalizations about how ecosystems work. They highlight this generality and often help to identify gaps in our understanding. Key assumptions of the model include: (1) disturbance homogenizes habitat within the entire model cell and resets the cell to the pioneer stage; (2) equal colonization potential by all successional stages of all cells within the landscape; (3) equal likelihood of disturbance of all cells in the landscape regardless of disturbance history; and (4) fishing disturbance is the only disturbance operating at the scale of the model. These assumptions can be relaxed in order to give a more realistic interpretation of community dynamics; however, the simplest version is a conservative approach for assessing habitat and community response to fishing disturbance.

The model consists of a 100 x 100 cell grid, with each of 10,000 cells containing a habitat of successional stages. Successional stages last for discrete periods of time (represented in years) that reflect the average times of succession from a pioneer community immediately following a disturbance through intermediate stages to a mature final successional stage. The model commences with all cells containing a habitat of the final successional stage of a particular archetypal community; different model versions simulate different archetypal communities. Disturbances are created during each time step, after which affected cells are converted into successional stage 1, representing a pioneer community of immediate post-disturbance state. The successional stage of each non-disturbed cell is increased by 1 after each time step in the model. Disturbances are created at random locations within the model landscape to represent fishing disturbance. The spatial dimension of disturbance is calculated as the number of disturbed cells relative to the number of cells in the entire landscape. The temporal dimension of disturbance is defined as the frequency of disturbance events per time step (year).
The model simulates three different community archetypes: a fast recovering community (dominated by short-living species that characterize an infaunal community not dominated by large, deep-burrowing fauna), an intermediate community (reflecting an infaunal community dominated by larger infauna or disperse epifauna; we also use it to reflect a bivalve-dominated community that would provide hard substrate for colonization to create a biogenic reef community), and a relatively slow recovering community (such as a fully developed biogenic reef dominated by bryozoans) (Table 1). The three archetype communities thus have different numbers of successional stages reflecting increased habitat complexity. These archetype communities have recovery times of 2, 6, and 15 years, respectively. It is important to note that these archetype communities are largely based on our knowledge of shallow water coastal communities.

The model simulates a range of space and time scales of disturbance (frequency = 0–12.5 disturbances/year; spatial extent = 0–100% of the landscape disturbed). In each simulation, a total of 1,100 combinations of different space and time scales of disturbance are run for 100 time steps (years). Mean and variance of the number of model cells in each successional stage are calculated at each time step.

Model Results

Contour plots illustrate how disturbance over different space and times scales affect the persistence of the three archetypal communities (Figure 1). Contours of each community represent the maintenance of either 50% (Figure 1a) or 90% (Figure 1b) of the mature community. These plots illustrate that there is only a small proportion of the domain where disturbance can be both spatially extensive and frequent and a reasonable proportion of the mature community can be retained. Over most of the domain, high-intensity disturbance can only occur over a small spatial extent, or conversely, extensive disturbance can only occur infrequently. These constraints become more severe for the slow-to-mature archetypal communities. Note the model simply portrays the proportion of the landscape in the mature successional stage, it does not indicate that large, infrequent disturbances or small, frequent disturbances can be considered to be the same.

Another way to consider the model results is to consider the relative proportions of the landscape occupied by the different successional stages of the three archetypal communities under specific spatial and temporal disturbance regimes (Figure 2). We present average proportions of different successional stages for combinations of disturbance frequency (0.25/year, 1/year, and 4/year) and extent (4%, 25%, and 81% of the landscape) for the three archetypal communities. Figure 2 shows the ever increasing dominance of early successional stages with increasing spatial extent and frequency of disturbance. Mature stage assemblages are only eliminated at both the highest extent and frequency of disturbance (81% and 4/year) for the archetypal short-lived community that takes 2 years to reach maturity. For the intermediate community archetype that takes 6 years to reach maturity, less than 25% of the

Table 1. Community dynamics of three archetype benthic communities.

<table>
<thead>
<tr>
<th>Community Type</th>
<th>Successional stage</th>
<th>Age of cell</th>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short-lived infauna</td>
<td>Pioneer</td>
<td>1</td>
<td>Small polychaetes and amphipods</td>
</tr>
<tr>
<td></td>
<td>Mature infaunal</td>
<td>2+</td>
<td>Small mollusks, ophiuroids, and large polychaetes</td>
</tr>
<tr>
<td>Intermediate community</td>
<td>Pioneer</td>
<td>1</td>
<td>Small polychaetes and amphipods</td>
</tr>
<tr>
<td></td>
<td>Colonization by mature stage dominants</td>
<td>2–5</td>
<td>Large suspension feeding bivalves, juvenile burrowing crustaceans, juvenile sponges, and large crustaceans</td>
</tr>
<tr>
<td></td>
<td>Mature stage</td>
<td>6+</td>
<td>Adult bivalves and encrusting fauna (sponges, hydroids, tunicates), adult large burrowing species and other species affiliated with large burrows</td>
</tr>
<tr>
<td>Biogenic reef</td>
<td>Pioneer</td>
<td>1</td>
<td>Small polychaetes and amphipods</td>
</tr>
<tr>
<td></td>
<td>Hard substrate coloni-</td>
<td>2–5</td>
<td>Large suspension feeding bivalves, juvenile burrowing crustaceans, juvenile sponges, large crustaceans</td>
</tr>
<tr>
<td></td>
<td>zation</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Colonization by mature stage dominants</td>
<td>6–14</td>
<td>Erect bryozoans and sponges colonizing hard substrate</td>
</tr>
<tr>
<td></td>
<td>Mature biogenic reef</td>
<td>15+</td>
<td>Mature individuals forming complex biogenic reef</td>
</tr>
</tbody>
</table>

*Deep bioturbators or organisms creating habitat structure.
landscape is occupied by the mature successional stage when 25% of the habitat is disturbed one time or more a year or when 81% of the landscape is disturbed at least once each 4 years. For the slowest recovering community where mature successional stages occur after 15 years, mature stages would be eliminated under these disturbance regimes.

Discussion

The model provides a very general assessment of how seafloor landscapes dominated by different community types will change as a result of changes in the disturbance regime. Here, we argue that these changes are largely wrought by habitat disturbance associated with fishing, but it would be possible to add other types of seafloor disturbance to the model. That is, we could subject the model landscape to either multiple anthropogenic disturbances or include natural disturbance phenomena with space and time scales comparable to fishing.

The model illustrates how increases in the disturbance regime result in loss of late-successional-stage species, especially those that take on the order of 10–15 years to recover. The community archetypes represented in the model reflect species that can add significant structural complexity to the seafloor and influence ecosystem processes. The model provides no support for a recent meta-analysis of fishing impact studies that concluded that intertidal cockle communities are the most heavily impacted (Collie et al. 2000), as we might expect comparatively high rates of recovery in these intertidal communities (e.g., Hall and Harding 1997). Output from the model indicated that as the age to maturity of the late successional stage increases, the extent and frequency of disturbance increasingly restricts the spatial extent of the mature stage. This highlights the extreme sensitivity to disturbance of deep-water and polar habitats with very slow rates of recovery (e.g., communities dominated by coldwater corals). The biology of these species is largely unknown, but they appear to have exceptionally slow growth and low reproductive rates, with individual colonies being hundreds to thousands of years old (e.g., Druffel et al. 1995). Large reefs about 40 m tall have been reported; they are marine equivalents of the oldest terrestrial forests (Squires 1965; Roberts 1997). Even where deep-sea communities are dominated by small, burrowing infauna, recovery from large-scale disturbance may be of the order of hundreds to thousands of years (Young et al. 2001).

The model illustrates how changes in communities may not only be related to the spatial extent and frequency of fishing but also to temporal history, supporting the conclusions of Collie et al. (1997) and Bradshaw et al. (2002). Where communities are dominated by species that live for 10 or more years and require about 10 years to re-establish following disturbance, the long-term physical effect of bottom fishing is to homogenize the substratum, restrict species diversity, and create communities dominated by disturbance-tolerant species (Veale et al. 2000). Site history is an important problem when interpreting studies of the impacts of fishing gear. Some European waters have a long history of fishing by bottom trawling (de Groot 1984; Frid et al. 2000; Kaiser and de Groot 2000; Pranovi et al. 2000). There is also a long history of transformation of marine coastal ecosystems in the western Atlantic (Steele and Schumacher 2000; Jackson 2001) and eastern Pacific (Dayton and Tegner 1984;
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Dayton et al. 1998). Thus, in some areas, the identification of effects is hampered by the potential historical loss of late-stage, large, and long-lived species. Information generated from comparatively pristine systems is important to understanding effects in potentially degraded ones. Assessments of environmental effects centered only on the study of disturbed areas have been described by Loehle (1991) as analogous to early psychologists defining human behavior largely from studies of the mentally ill.

Encapsulating generalities about disturbance and recovery processes in the model inevitably highlights the need for more sophisticated approaches and better empirical data. The model increases some aspects of our understanding of disturbance recovery processes and provides a picture of independent disturbance events at the landscape scale. It does not take into account any scale dependency in recovery or the potential to increase the variability in response with increasing scale. The model also assumes a constant source of colonists that are capable of settlement and growth within all model cells; there are no intrinsic processes such as facilitation or inhibition (e.g., inhibition of colonization due to disturbance-related changes in sediment stability, particle size, or settlement sites or the facilitation of colonization through provision of settlement sites). In reality, disturbance effects are also likely to be influenced by the landscape attributes of the disturbance and the spatial structure of populations and communities. These complex ecological processes are likely to make our model conservative, in other words, the model represents a minimal ecological response to different disturbance regimes. For communities that take longer to achieve maturity, these effects are likely to be

![Figure 2](image-url) Proportion of model landscape occupied by different successional stages of the three archetypal communities under different frequencies and extents of disturbance.
exacerbated. Except in the most heavily fished areas, fishing will not directly disturb all of the seafloor. We need to gain an understanding of the implications of this habitat fragmentation, the scope of such refugia to provide colonists, and how potential recovery is limited by the frequency of disturbance.

It is generally acknowledged that our understanding of the ecology of seafloor populations, communities, and ecosystems is limited. But even the simple model described here emphasizes the need to understand the scales of disturbance and the processes affecting recovery. It is critically important for ecologists to define and describe key species in seafloor communities, including the roles that such species play in ecological, hydrodynamic, and biogeochemical processes, and, in particular, the role of organism size, density, and spatial arrangement. Even more fundamental, however, is basic natural history information encompassing life history and the physiological ecology of the species that may form the basis for archetypal communities, especially the species that are slow to colonize and grow that define mature successional stages. Better information on the disturbance regime associated with fisheries as well as other natural and anthropogenic factors would also lead to better predictions about the consequences of habitat disturbance.

The model takes individual disturbance events and translates these to changes in the seafloor landscape via community recovery rates. It aims to inform decisions and encourage fruitful debate, and it is particularly relevant to managing habitats within a risk-assessment framework. It is not necessarily restricted to one community type or region. By altering the data that define the disturbance regime and the nature of seafloor habitats and communities, the model could be easily applied across or within different regions. Deciding how much of the mature successional stage to maintain in the landscape may be influenced by knowledge of the role of the community in affecting biodiversity or ecosystem processes and the potential risk imposed by loss of communities with slow recovery rates. Lack of knowledge or concern about conservative simplifications in the model should result in precautionary management decisions such as maintaining a higher proportion of the landscape in mature community. In particular, the model indicates that to maintain any proportion of the mature stage where greater than 1–2 years is needed to reach maturity, compromises will need to be reached over the spatial extent and/or temporal frequency of disturbance. This may seem an obvious statement, but models provide for a more informed discussion on the relative consequences of different disturbance regimes.

There is some evidence that a loss of resilience in ecological systems increases the potential for the system to shift to an alternative state (Scheffer et al. 2001). Our ratio model implies that when disturbance is infrequent relative to recovery time and only a small proportion of the landscape is affected, the system is stable and exhibits low variance over time. When the frequency of disturbance is similar to the recovery time and a large proportion of the habitat is affected, the system can still be stable but exhibits higher variance (Turner et al. 1993). However, when the disturbance frequency is shorter than the recovery time and a large proportion of the system is disturbed, the system may flip into an altered state. For example, frequent disturbance may extirpate functionally important species that provide nursery habitats for exploited populations, resulting in the loss of these valuable ecosystem services. Once these features have been lost, it may not be a simple matter of reducing the disturbance regime to ensure their recovery. We need to carefully and explicitly consider the implications of alterations of these ecosystems; they may not only reflect loss of conservation and natural heritage values but also loss of opportunity and ecosystem services provided by diverse and heterogeneous seafloor ecologies.

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