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The Gray Zone: Relationships between habitat loss and marine diversity and their applications in conservation

Laura Airoidi^{a,*}, David Balata^a, Michael W. Beck^b

^a Dipartimento di Biologia Evoluzionistica Sperimentale and Centro Interdipartimentale di Ricerca per le Scienze Ambientali, Università di Bologna, Via S. Alberto 163, I-48100 Ravenna, Italy

^b The Nature Conservancy and Institute of Marine Sciences, 100 Shaffer Road-LML, University of California, Santa Cruz, California 95060, USA

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ABSTRACT

Structurally complex habitats are becoming rarer across temperate marine environments; indeed the coastal and marine world is getting flatter. In some cases marine habitats are lost entirely (e.g., wetlands are filled), but in many cases the loss is a gradual transition from a more complex to a less complex habitat (i.e., a change from canopy-forming to turf forming algae). We explore the multiple ways habitat loss affects marine species diversity, and propose a conceptual model that identifies the main interactions and feedbacks between these processes. The loss of habitat structure generally leads to lower abundances (biomasses) and often to declines in species richness. There is often also a suite of colonizing species that prosper from these transitions. These sets of expanding species can amplify the changes to the system, cause variable effects on species richness and other components of diversity, feed back to affect the various components of habitat loss (e.g. maintain new environmental conditions) and prevent the recovery of the system. Less well studied are the effects on between-habitat (β) diversity and functional diversity. We argue that we need to understand these latter changes to better manage and conserve the structure and function of ecosystems and the diverse services that humans continue to expect from them. Calling for more of the approaches and thinking that John Gray championed we discuss how this work can focus efforts in research, conservation, restoration and management.

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1. Introduction

John Gray made a career of understanding the complex interplay of interactions and impacts to marine biodiversity and worked successfully in the gray zone between science and management to bring observational and experimental approaches to this interface. He was a champion of conservation, but in a sensible way that recognized there were other management objectives and needs in the marine environment and that we should strive to avert those grave impacts and worry less when impacts were relatively trivial. John was very much aware that the major threat to marine biodiversity is in the limited perception humans assert over the oceans, their marine life and their threats, and was committed to ensuring that the scientific knowledge about marine processes and human impacts was transferred in unbiased manner to the society and the decision making process. We need more scientists capable of working in this gray zone. This paper is mainly about habitat loss and marine diversity, but it is also a call to bring more of the approaches and thinking that John championed to what should be a much greater interface between science and marine management.

Structurally complex habitats are clearly becoming rarer across temperate marine environments at local, regional and global scales (e.g. Suchanek, 1994; Duarte, 2002; Thrush and Dayton, 2002; Reise, 2005; Lotze et al., 2006). In Europe, it is estimated that for each day between 1960 and 1995, a kilometre of coastline was developed, causing losses of coastal wetlands and seagrasses exceeding 50% of original area with peaks above 80% for many regions (Airoidi and Beck, 2007). Conspicuous declines, sometimes to virtual local extinction of kelps and other complex macroalgae have been observed in several countries around the world likely as a consequence of decreased water quality and/or overfishing (Benedetti-Cecchi et al., 2001; Steneck et al., 2002; Guidetti et al., 2003; Graham, 2004; Connell et al., 2008). Biogenic temperate reefs are probably among the most threatened habitats globally (Barbera et al., 2003; Roberts and Hirshfield, 2004; Airoidi and Beck, 2007), and much of the continental shelf and some deeper ocean seafloors have been homogenized by bottom trawling and dredging (Thrush and Dayton, 2002; Gray et al., 2006). Indeed the coastal and marine bottoms are getting flatter, and that is recognized in common treatment in policy, conservation, and management.

In spite of this recognition, habitat loss has not been as much a focus of marine science and conservation as in terrestrial environments. This is certainly in part related to the limited knowledge and perception of the extent - spatial and temporal - and importance of these losses, particularly for temperate coastal systems (Airoidi and

* Corresponding author. Tel.: +39 0544 937314; fax: +39 0544 937303.
E-mail address: laura.airoidi@unibo.it (L. Airoidi).

Beck, 2007). Here we argue that the limited focus on marine habitat loss is also related to the fact that the consequences of these losses are not fully explored. Habitat loss has been indicated as one of the major threats to marine biodiversity (Beatley, 1991; Gray, 1997). However, the prevailing focus tends to be on species richness (Wolff, 2000; Dulvy et al., 2003), while other consequences on between-habitat or functional diversity do not seem to have received so far as much attention.

We will explore the multiple ways habitat loss affects marine diversity based on available information from the scientific literature, and propose a conceptual model that identifies the main interactions and feedbacks between these processes. We also discuss how this work can focus efforts in research, conservation and management. The paper focuses on temperate systems where the consequences of the loss of native habitats are less explored compared to other marine systems (e.g. Suchanek, 1994; Airolidi and Beck, 2007), but most of the points raised herein are broadly applicable.

2. Definitions

Habitat and diversity loss are terms that are increasingly commonly associated to describe a modern crisis of marine systems (Gray, 1997). At the same time, these terms are often defined in inconsistent ways (e.g. Gray, 2000; Beck et al., 2001). Here 'habitat' indicates a focus on the predominant features that create structural complexity in the environment, such as plants (e.g., seagrass meadows, kelp forests), or animals (e.g. oyster reefs, burrowing fauna in sandflats), and 'loss' indicates a focus on a measurable reduction in habitat abundance and distribution (Airolidi and Beck, 2007). Loss clearly occurs when e.g. natural habitats such as salt marshes are filled with sediments and blocked from the sea to form agricultural fields. Frequently, however, the loss initiates a transition from a more complex to a less complex habitat, e.g., shellfish reefs or seagrasses are dredged and mud or sandflats are created, or perennial

canopies of kelps, fucoids and other complex, erect macroalgae are lost leaving space to turf-forming, filamentous or other ephemeral seaweeds (Fig. 1). Areas are rarely converted from less complex to more complex natural habitats unless there is active habitat restoration.

The most common usage of species 'diversity' typically refers to the number of species in a given area of habitat (species richness) and on their relative abundances. Indeed a major focus in conservation biology is the prediction of the decrease in species number and abundance in response to a reduction in the area of the habitat (Hanski, 2005). Additionally, there are other fundamental but often overlooked components of diversity (Gray, 1997), related to species identity (i.e. species are not equivalent from a conservation point of view), between-habitat diversity (also commonly indicated as β diversity, where the focus is on the variation in species richness and identity between habitats) and functional diversity (where the focus is on the range of functional attributes of species, e.g. size, feeding or mobility modes). Habitat loss also poses serious threats to genetic variation in individuals and populations. A review of such effects is beyond the scope of this paper and we redirect the reader to other work (e.g. Olden et al., 2004; Keyghobadi, 2007).

3. Studies on habitat loss and species diversity

Over the past 50 years, there has been significant research effort devoted to the study of species assemblages and ecology of complex temperate marine habitats such as seagrass beds, shellfish reefs or kelp forests (e.g. Wells, 1961; Schiel and Foster, 1986; Jones et al., 1994; Bruno and Bertness, 2001; Duffy, 2006). A review of ISI literature (using a variety of terms and synonyms related to "habitat", "loss", "diversity" and "marine") however, surprisingly revealed how few of these studies have focused on attempting to document directly how diversity changes following the loss of these complex habitats, and the functional consequences of these changes. Indeed, it is only recently

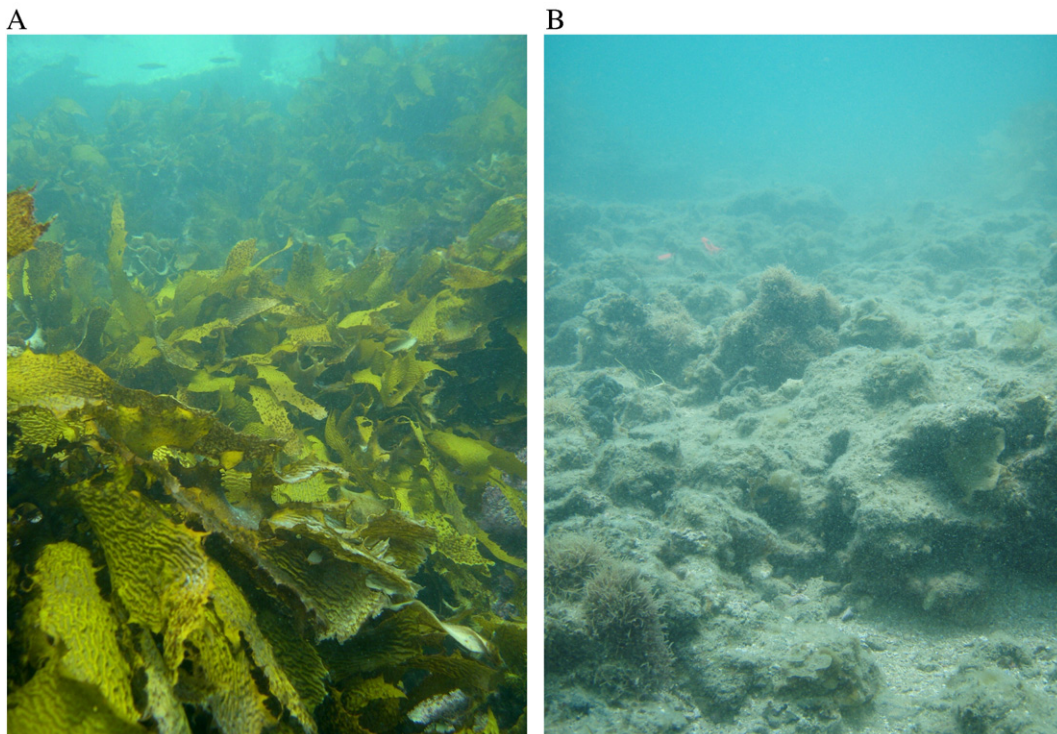


Fig. 1. Typical appearance of (A) kelp habitats in Southern Australia and (B) macroalgal turf habitats replacing lost kelps close to urban areas (Connell et al., 2008, photo courtesy Andrew Irving A and Sean Connell B).

that the evidence of the dramatic loss of complex marine habitats has been brought to attention (Short and Wyllie-Echeverria, 1996; Jackson et al., 2001; Coleman and Williams, 2002; Thrush and Dayton, 2002; Lotze et al., 2006; Airoidi and Beck, 2007). Despite growing concern, at present there do not seem to be many direct empirical analyses of the effects of habitat loss on diversity changes in the marine realm, and the lack of historical baselines makes it difficult to analyse these relationships conclusively (Dayton et al., 1998; Jackson et al., 2001). Most evidence is drawn indirectly from comparisons between areas dominated by a type of habitat and adjacent areas lacking that habitat or from small scale experiments that can hardly reproduce the large scales, spatial and temporal, typical of human-induced habitat loss (Table 1). Most of these comparisons focus on only few habitats (i.e. seagrasses and canopy-forming algae) and taxa (e.g., fishes, macroinvertebrates and macroalgae). More rarely, evidence of local change in diversity is available from long-term monitoring studies (e.g. Graham, 2004).

Some studies indicate that in the transition from complex to simpler habitats there is often a set of colonizing species that do particularly well. The habitats lost and their residents can indeed be replaced largely or entirely by new habitats (see examples in Table 1), albeit often dominated by fewer species that tend to thrive in these human disturbed environments (Airoidi, 1998; Thrush et al., 2006). Despite growing scientific concern (e.g. Mckinney and

Lockwood, 1999; Jackson et al., 2001; Sax and Gaines, 2003), limited attention is generally given to the additional consequences related to the expansion of these sets of colonizing species. However, colonizing species can amplify the changes to the system, sometimes adding further alterations to basic natural processes that may feed back to affect the various components of habitat loss and prevent the recovery of the system or even further accelerate the process of loss.

Few studies have analyzed the consequences of habitat loss on between-habitat diversity. It is now clear that habitat loss causes a major reduction of spatial diversity in species distribution (Bulleri et al., 2002; Thrush et al., 2006; Balata et al., 2007a), a process also described as “biotic homogenization” (Mckinney and Lockwood, 1999). Explicit considerations of the dynamic processes associated with scenarios of habitat change across seafloor landscapes and their implications for both local and regional biodiversity are, however, rare (Thrush et al., 2006). The ecosystem functional consequences of habitat loss have also been little explored, due primarily to the logistic, economic, and environmental costs of testing experimentally these effects at sufficiently large scales. Recent historical reconstructions, however, highlight the profound ecosystem changes that can follow the local to regional loss of biogenic habitats (for example in the Chesapeake Bay, Jackson et al., 2001, and in the Wadden Sea, Lotze et al., 2005).

Table 1
Studies showing the effects of the loss of a variety of marine habitats on species diversity within target taxa

| Habitat lost | Transition to | Effects/Target taxa/Nature of study | Reference |
|--|--|--|--|
| Seagrass <i>Zostera marina</i> | Bare mud or macroalgae | Decreased fish abundance, biomass, species richness, dominance, and life history diversity. All but two common fish species declined in abundance and biomass with the complete loss of eelgrass (D) | Hughes et al., 2002 |
| | Macroalgae | Decreased fish and decapod abundance and biomass, and decreased fish species richness (E) | Deegan et al., 2002 |
| | Sediments | 90% habitat loss caused significant decrease of epifaunal species richness and total epifaunal density and changes in species composition with respect to 0, 10 or 50% habitat loss in 16 m ² plots, while no effects observed in 4 m ² plots (E) | Reed and Hovel, 2006 |
| | Seagrass <i>Halodule wrightii</i> | Decreased abundances and diversity of epifaunal and infaunal invertebrates and fishes, changes in species composition (E) | Micheli et al., 2008 |
| Seagrass <i>Posidonia</i> spp. | Sand | Changes in fish species composition presumably related to decrease in drifting vegetation (D) | Vanderklift and Jacoby, 2003 |
| Oyster beds | | Decreased number of species and abundance of amphipods, mussels, scale worms, crabs (R) | Wells, 1961; Ruesink et al., 2005 |
| Kelp <i>Macrocystis pyrifera</i> | Sea urchin barrens | 36% reduction in species richness, reduced abundance for >90% of species, and major alteration of food web interactions (D, M) | Graham, 2004 |
| Canopy <i>Cystoseira</i> spp. | Algal turfs | Decreased cover up to disappearance of several species of understory macroalgae and invertebrates, changes in species composition. Homogenisation with neighbours habitats (E) | Benedetti-Cecchi et al., 2001; Bulleri et al., 2002; Mangialajo et al., 2008 |
| Canopy <i>Hormosira banksii</i> | Bare rock, encrusting or turfing algae | Loss of almost all epifaunal species, loss of furoid and coralline algae, blooms of ephemeral algae, limited effects on sessile invertebrates and mobile gastropods. After two yrs diversity (Shannon index) decreased by 36 to 44% and overall species cover decreased by 71 to 83% (E) | Lilley and Schiel, 2006 |
| Canopy <i>Fucus vesiculosus</i> | | Increased biomass production but decreased diversity (Shannon-Wiener index) of understory ephemeral macroalgae. Loss of buffering control of the negative effects of nutrient enrichment on species richness (E) | Eriksson et al., 2006 |
| | Filamentous macroalgae (<i>Cladophora glomerata</i>) | Increased macrofauna abundance and biomass but lower species richness (Margalef's index). No changes in Shannon-Wiener diversity (D) | Kraufvelin and Salovius, 2004 |
| Macroalgal biogenic formations ('coralligenous' reefs) | Turf-forming macroalgae | Decreased species richness and abundance of erect and encrusting macroalgae. Homogenisation between habitats | Balata et al., 2007a,b |
| Coral biogenic formations on seamounts | Bare rock or coral rubble and sand | Decreased abundance and species richness of benthic fauna (D) | Koslow et al., 2001 |
| Maerl | Sediments | Decreased species richness, abundance and biomass of fish, crustaceans, and other large epibenthic species; changes in species composition, shifts from long-lived to opportunistic species (D) | Bordeclore et al., 2003; Hall-Spencer et al., 2003 |
| Complex soft-bottom habitat categories | Simpler soft-bottom habitat categories | Loss of macrofauna species, particularly large and habitat-specific species, drop in the proportion of species with different functional attributes, decreased spatial variability and between-habitat diversity (M) | Thrush et al., 2006 |

D=quantitative descriptive, E=experimental, M=modelling, R=review.

4. Relationships between habitat loss and species diversity

To our knowledge no study has simultaneously considered the effects of habitat loss and replacement on the components of species diversity described above at a community level. It is likely that if such studies were conducted they would reveal multiple layers of indirect effects, feedbacks and emergent properties, where the resulting effects on patterns of diversity might vary in magnitude and direction depending on how losses and gains are distributed among taxonomical and ecological groups. Based on available

information from the literature, we propose here an hypothetical model that synthesizes these complex interactions (Fig. 2). In this model we identify (1) the major components of habitat loss (see below), (2) the consequences of these losses on species diversity, where we recognize that these changes are amplified by synergies and feedbacks related to the expansion of colonizing species during the transition from complex to simpler habitats, and (3) the resulting large-scale homogenization of marine systems. We will also identify how some of these relationships are relatively well studied, while others are not.

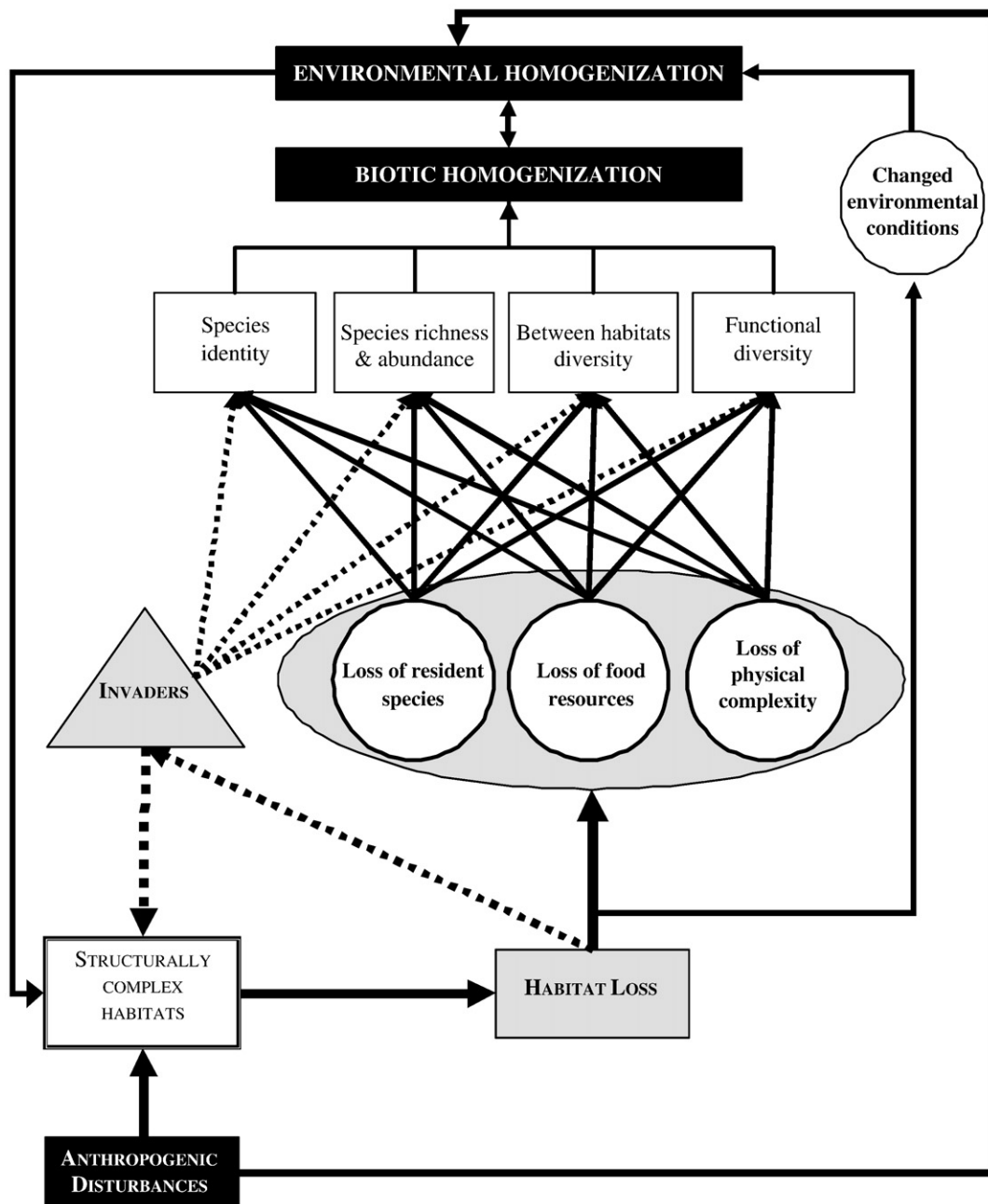


Fig. 2. Diagram of links between habitat loss and patterns of diversity, the possible feedbacks between these different processes, and the overall resulting biotic and environmental homogenization. Coastal development, destructive harvesting and fishery practices, and decreased water quality are among the main causes of habitat loss. Habitat loss operates at three levels: loss of native resident species, loss of food resources, and loss of environmental complexity and related environmental function. These different components of habitat loss act differently on species identity, species richness and abundance, between-habitat (β) diversity and functional diversity (the links are hypothesised based on available information from the literature. Strength of the link is not suggested). Habitat loss also opens the way to new sets of species gaining broader distribution and abundance (here named “invaders”, which includes previously less abundant species, species expanding from nearby areas and habitats, and alien species), that can have synergic effects on diversity and negative feedbacks on habitat loss (indicated by the dashed lines). For further explanations see text.

4.1. Components of habitat loss

Studies generally identify three major components of habitat loss:

1. **the loss of resident species.** Communities consist of species that differ greatly in their ecology and how they respond to habitat loss. The major threats are reported for species that have narrow distributions up to being exclusive to certain habitats (Thrush et al., 2006). Indeed, many biogenic formations support unique assemblages: examples include macroalgae and invertebrates associated with kelp forests (Graham, 2004), epiphytic or epibenthic species associated with seagrass meadows (Green and Short, 2003 and references therein, Micheli et al., 2008), faunal assemblages on polychaete reefs (*Sabellaria alveolata*) (Dubois et al., 2006) and the hundreds of unique species that colonize deep sea seamounts (Roberts and Hirshfield, 2004). The risk of extinction for these species can be estimated with the use of species-area relationships (Ugland et al., 2003; Thrush et al., 2006) or using population or metapopulation models (Hanski, 2005). The overall community level predictions, however, would likely be multiplicative rather than a sum of the effects on individual species, because of the interactions between species leading to chains of impacts;
2. **the loss of food resources.** Seagrass meadows, saltmarshes, kelp forests and other vegetated habitats and their resident organisms are known to be highly productive compared to structurally simpler habitats such as sandy habitats (Ferrell and Bell, 1991; Duffy, 2006; Hosack et al., 2006). They export vast quantities of carbon, nitrogen and phosphorus to coastal food webs either through direct transfer of animal biomass (i.e. predation, movements of individuals) or outwelling of dissolved and particulate organic matter (Edgar, 1990; Bustamante and Branch, 1996; Graham 2004). There is indirect evidence that the loss of these food resources can affect negatively the productivity of individual species or groups of species, with effects that are likely to propagate along food chains (Worthington et al., 1992; Edgar and Shaw, 1995a,b; Jackson et al., 2001; Dobson et al., 2006). In southern California, for example, the loss of giant kelps has led to the loss of numerous species with close trophic associations with the giant kelp itself and to a profound simplification of the trophic food web (Graham, 2004). Limited knowledge and tools make it difficult at present to make clear predictions of the changes to the trophic structure and productivity of systems that likely accompany the loss of most biogenic marine habitats, but an increasing body of evidence suggests that food chain length is a function of habitat size (Dobson et al., 2006 and references therein);
3. **the loss of ecosystem functions and properties related to the influence of the habitat on the environment.** Structurally complex habitats strongly shape the physical environment, e.g. by modifying light conditions, hydrodynamism, sedimentation, providing shelter and refuges, and buffering the effects of disturbances (Jones et al., 1994). When these habitats are lost, many of these functions are also lost (Dobson et al., 2006). For example, it has been shown that the replacement of macroalgal canopies by turfs affects sediment dynamics on rocky coasts, where whiplash by fronds prevents accumulation of sediments while turfs tend to bind and stabilize sediments even on exposed coasts (Airoldi, 2003 and references therein). Similarly, experiments have shown that canopies of *Fucus vesiculosus* can control the net primary production of understory algal species buffering the negative effects of nutrient enrichment (Eriksson et al., 2006). Although the potential loss of these functions is widely recognised as one of the major threats following habitat loss, direct research to quantify these effects and the underlying mechanisms is surprisingly scarce.

4.2. Effects of habitat loss to species diversity

The main reported effects of marine habitat loss are reductions in overall abundance and biomass often associated with declines in

species richness although these latter effects are much less studied (Table 1). Studies on seagrasses, which are amongst the marine habitats where most work on habitat loss focussed, generally indicate greater richness and densities of fishes in vegetated than unvegetated areas, and substantial differences in the composition of fish assemblages (Hughes et al., 2002; Heck et al., 2003; Vanderklift and Jacoby, 2003). Significant reductions in species richness and abundance have been reported in studies focusing on the effects of the direct removal of biogenic habitats on soft bottoms from e.g. direct harvesting, trawling, or dredging, where entire sets of species that find unique conditions for their anchorage are removed with their habitats (Koslow et al., 2001; Thrush and Dayton, 2002; Hall-Spencer et al., 2003). In the Wadden sea, the destruction of biogenic habitats has caused the regional extinction of at least 26 species during the past 2000 years (Wolff, 2000).

Frequently, the biological and environmental changes determined by the loss of native habitats promotes the colonization or expansion of sets of species (here named “invaders”, which includes previously less abundant species, or species expanding from nearby areas and habitats) that seem to do well in the new disturbed conditions (Table 1). Similar to observations in terrestrial systems (see McKinney and Lockwood, 1999) the changes in marine species are not randomly distributed across ecological and functional categories. There is indeed a clear trend towards the expansion of smaller (down to microscopic) species with generalistic, opportunistic and/or invading traits (Airoldi, 1998; Jackson et al., 2001; Kraufvelin and Salovius, 2004; Thrush et al., 2006). These sets of expanding species can amplify the changes to the system, cause variable effects on species richness and other components of diversity, feed back to affect the various components of habitat loss (e.g. maintain new environmental conditions) and prevent the recovery of the system (Fig. 2). One particularly well studied example is the expansion of turf-forming, filamentous or other ephemeral seaweeds following the regression of algal canopies (Fig. 1). This habitat shift seems to be favoured under conditions of decreased water quality and/or enhanced sediment loads (Airoldi, 1998; Airoldi, 2003; Benedetti-Cecchi et al., 2001; Irving and Connell, 2002; Gorgula and Connell, 2004; Balata et al., 2007b). Once established, turfs and sediments seem to provide positive feedbacks for each other that inhibit the recovery of canopy habitats and prevent the system from regenerating (Airoldi and Virgilio, 1998; Connell, 2005). Similarly, the extensive loss of oyster reefs in some temperate estuaries has caused a shift from systems dominated by benthic primary production to systems dominated by planktonic primary production, which can drive the further loss of habitats (e.g. seagrasses) through altered environmental conditions (e.g. turbidity) (Jackson et al 2001 and references therein).

Sets of invaders can also include aliens (Galil, 2007). Experiments show that alien species tend to invade disturbed habitats more easily than undisturbed ones (Ceccherelli et al., 2000; Valentine and Johnson, 2003; Scheibling and Gagnon, 2006; Britton-Simmons, 2006). Also, in some cases, alien species are deliberately introduced to replace lost habitats of significant commercial value (e.g. oyster reefs, Ruesink et al., 2005). Whether aliens once established might feedback negatively on native habitats further accelerating their loss is much debated (see the “driver” or “passenger” models in Macdougall and Turkington, 2005). One example of potential negative feedbacks on native habitats is in the outbreaks of diseases and parasites carried by alien species (e.g. native *Ostrea edulis* reefs in Europe were decimated by the competition with and diseases brought by *Crassostrea gigas* introduced to replace lost reefs, Airoldi and Beck, 2007). Whether drivers or passengers, alien species are known to exert significant effects on the richness and other components of diversity of native assemblages (McKinney and Lockwood, 1999; Bax et al., 2003; Buschbaum et al., 2006; Piazzini and Balata, in press).

There is evidence that these transitions from one type of habitat to another can significantly affect not only species identity, abundance and richness (e.g. Micheli et al., 2008), but can also lead to significant

reductions of spatial diversity in species distribution (between-habitat diversity, e.g. Bulleri et al., 2002; Balata et al., 2007a) and functional diversity (Dobson et al., 2006; Thrush et al., 2006). Modelling and empirical work clearly shows that habitat loss can cause significant between habitat homogenization and loss of a variety of functional attributes, significantly reducing functional diversity (Dobson et al., 2006; Thrush et al., 2006). The functional consequences of the transitions from complex to simplified habitats are, however, still largely unexplored.

4.3. Habitat loss and biotic homogenization

The effects of habitat loss can extend well into other habitats and scale up to affecting whole coastal regions and processes. In fact many biogenic marine habitats can influence the environmental conditions at large spatial scales by e.g. buffering the sediment load, eutrophication, hydrodynamism and erosion of whole coastlines. Oyster and other shellfish reefs, for example, can control water turbidity of whole bays, with positive impacts on submerged aquatic vegetation due to greater light penetration and higher rates of photosynthesis (Meyer and Townsend, 2000). Oyster reefs can also control large-scale eutrophication by mediating water column phytoplankton dynamics and denitrification (Dame and Allen, 1996; Newell, 2004; Newell and Koch, 2004). In the Chesapeake Bay, hypoxia and other symptoms of eutrophication became manifested in the 1930s following the overexploitation of oyster reefs (Jackson et al., 2001 and references therein). Similarly the influence of seagrasses goes well beyond their local distributional area; they support complex trophic food web through export of detritus, provide nursery areas for many organisms, are a net sink of carbon and other elements and can attenuate the wave action over large scales (Short and Wyllie-Echeverria, 1996). It has been estimated that the removal of 1 m³ of mat can cause 20 m of coastal regression (Orth et al., 2006; Green and Short, 2003), but with few exceptions the large-scale consequences of habitat loss are poorly known.

At large spatial scales the loss of habitat can be rendered as a biotic homogenization. Biotic homogenization occurs as a reduction in overall structural complexity, native biota, functional traits and the expansion of few widespread and less complex broadly tolerant biota (Mckinney and Lockwood, 1999). The biotic homogenization amplifies and at the same time is amplified by the homogenization of environmental conditions which is occurring globally via direct and indirect anthropogenic effects, such as replacing wetlands with aquaculture ponds or largescale increases of turbidity and nutrients. Lotze et al. (2006) illustrate the consequences of the feedbacks among anthropogenic activities and biotic-environmental homogenization in a dozen estuaries globally.

5. Implications for conservation, management and research

The loss of structurally complex marine habitats leads to significant changes in species identity, richness and abundance. While these effects are being increasingly recognised and studied, the declines in between-habitat and functional diversity are largely overlooked, together with the possible synergic problems caused by the parallel expansion of small, generalistic, opportunistic and/or invading species. The ultimate effects and feedbacks of the overall simplification and homogenization of marine seafloors on ecosystems functions are largely unexplored in marine systems. These ecosystem functions are critical and closely tied to the delivery of ecosystem services to humans.

The conservation of coastal and marine habitats has been driven in part by the effects of habitat loss on declines in species richness, which has been one of the major focus of recent research (Wolff, 2000; Dulvy et al., 2003). However, looking at the effects of habitat loss just on species richness is not sufficient. For example, estuaries are characterized by relatively low species richness but are extremely productive and unique systems and they provide some of the most substantial

services to human through their ecosystem functions (e.g., Gray, 1997; Costanza et al., 1997). Recently developed models also suggest that the loss of ecological functions that occurs as habitats are lost can be disproportionately greater than what would be predicted from a decline in species richness (Dobson et al., 2006; Thrush et al., 2006). This is because the species that are most lost are not randomly distributed among ecological and functional categories, but include large, specialist species that often affect disproportionately the biological and physical environment.

To comprehensively inform management actions, we must also understand how habitat loss affects all components of species diversity and the ecosystem functions and services that diversity provides across all four major classes of (i) regulating services such as shoreline buffering from storms, (ii) provisioning services such as fish production, (iii) cultural services such as tourism and (iv) supporting services such as primary production (Millennium Ecosystem Assessment, 2005). For example, large structurally complex plants like mangroves provide buffers from waves and storms (e.g., Danielsen et al., 2005). Likewise structurally complex habitats such as seagrasses and marshes have greater abundances of fish than less structurally complex habitats such as sand flats (Heck et al., 2003; Minello et al., 2003). Kelp forests and biogenic formations attract divers and other tourists because of their complexity and the abundance and diversity of macrofauna. Larger plants will often provide substantial primary production; although for many marine systems even single celled algae can provide significant primary production because of high turnover.

Well planned monitoring of the changes to coastal habitats could be particularly insightful and robust if underpinned by solid experimental information on the relationships between the functional attributes of habitats and the distribution and abundance of target taxa. Nevertheless, so far, few effective long-term, large-scale monitoring programs have been instigated for temperate marine habitats. These programs would be pivotal to quantify trends of changes in habitat and species distributions and unequivocally attribute the causes to human activities. This monitoring should be coupled with studies designed to treat management actions that result in habitat loss as large-scale experiments (Carpenter et al., 1995). Such an approach would require long-term financial, institutional, logistical and intellectual commitment, and urges improved communication between managers and researchers, but the benefits for managing habitat loss on global scale are clear.

While the general appreciation of ecosystem functions and services can help bolster the impetus for action, we need better science on effects of habitat loss on species diversity and functions to inform decisions. With this understanding we can begin to better prioritize and manage coastal habitats based on the functions and services they provide. This understanding is the type of knowledge that John Gray championed for connecting science to conservation and management action.

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