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Ghoti papers

Ghoti aims to serve as a forum for stimulating and pertinent ideas. Ghoti publishes succinct commentary and opinion that addresses important areas in fish and fisheries science. Ghoti contributions will be innovative and have a perspective that may lead to fresh and productive insight of concepts, issues and research agendas. All Ghoti contributions will be selected by the editors and peer reviewed.



Etymology of Ghoti

George Bernard Shaw (1856–1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

The unintended consequences of simplifying the sea: making the case for complexity

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Abstract

Many over-exploited marine ecosystems worldwide have lost their natural populations of large predatory finfish and have become dominated by crustaceans and other invertebrates. Controversially, some of these simplified ecosystems have gone on to support highly successful invertebrate fisheries capable of generating more economic value than the fisheries they replaced. Such systems have been compared with those created by modern agriculture on land, in that existing ecosystems have been converted into those that maximize the production of target species. Here, we draw on a number of concepts and case-studies to argue that this is highly risky. In many cases, the loss of large finfish has triggered dramatic ecosystem shifts to states that are both ecologically and economically undesirable, and difficult and expensive to reverse. In addition, we find that those stocks left remaining are unusually prone to collapse from disease, invasion, eutrophication and climate change. We therefore conclude that the transition from multispecies fisheries to simplified invertebrate fisheries is causing a global decline in biodiversity and is threatening global food security, rather than promoting it.

Keywords Ecosystem change, fisheries, invertebrates, phase shift, resilience, simplification

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Introduction

The biodiversity of the world's oceans is changing. Human impacts are causing an accelerating loss of populations and species in virtually every marine ecosystem on the Earth (Worm *et al.* 2006; Valdes *et al.* 2009). As a result, we are seeing marine ecosystems, and the fisheries they support change on a global scale (Steneck 1998; Jackson *et al.* 2001; Sala and Knowlton 2006; Daskalov *et al.* 2007).

Fisheries that target large predatory finfish are rapidly declining (Myers and Worm 2003, 2005). To keep up with demand, fishers are increasingly targeting smaller, pelagic species and bottom-dwelling invertebrates (Pauly *et al.* 1998, 2002; Steneck *et al.* 2002; Essington *et al.* 2006; Estes *et al.* 2011). Behind these all too familiar 'fishing down' or 'through the food web' and 'boom-and-bust' cycles lies a complex interplay of ecological, economic, social and historical factors. In general, however, they share a common pattern. New fishing technologies and rising demand cause the intensity and effects of fishing to escalate over time. As a result, stocks of large-bodied fish become depleted, and in their place, new species are targeted (Worm and Myers 2003; Hughes *et al.* 2007). Despite offsetting fishing demand to previously little or unexploited species, the ecological functions that larger fish performed within the ecosystem (such as grazing macroalgae or feeding on benthic invertebrates) are diminished or lost (Holmlund and Hammer 1999; Worm and Duffy 2003). As a result, ecosystems become dominated by a handful of species such as prawns, lobster, macroalgae and jellyfish that used to form the diet of, or were outcompeted by, larger fish (Myers and Worm 2003) (Fig. 1). This cycle of diminishing fish stocks and offsetting fishing demand to new species may occur several times, and with this rise and fall of various species, the ecosystem may experience several different states each supporting distinct ecological communities (Steneck *et al.* 2004).

Paradoxically, species that come to dominate overfished, simplified ecosystems can reach high enough densities that they form a resource many times more economically valuable than those targeted before (Thurstan and Roberts 2010; Steneck *et al.* 2011). This may explain why calls from scientists for an ecosystem-based approach to help restore depleted fish stocks are often met with little enthusiasm, or even resistance, from fishers,

managers and politicians (Steneck *et al.* 2011). In the short-term arena, where these players generally make their decisions, there appear to be strong economic incentives to maintain 'business as usual'. It has even been suggested that intensive fishing is a necessary process required to keep up with rising demand (Pauly *et al.* 2002; Hilborn 2007a; Harman 2011; Atrill and Halls 2012). That, through overfishing, we are effectively manipulating nature in order to create simplified assemblages dominated by targeted populations, comparable to monocultures in agricultural systems. These have the advantage in that they are easier to manage, more abundant in the environment and economically more efficient than pre-existing fisheries. After all, advances in human civilization have largely been built on this approach in terrestrial environments (Foley *et al.* 2011).

In response to these arguments, we examine the consequences of simplified, less diverse marine ecosystems and the fisheries they support by drawing on economic and ecological perspectives, illustrated through several case-studies, and address the question of whether simplifying the seas is a sensible management strategy. Based on our findings, we then make the case that restoring the diversity of ocean ecosystems is necessary to ensure fisheries sustainability and resilience into the future.

The ecology underlying change

The number and types of species present within an ecosystem (i.e. its biodiversity) determine ecosystem function through processes such as predation, herbivory, habitat provision and mediating the cycling of energy and nutrients, which maintain ecosystems as the recognizable entities they are (Chapin *et al.* 2000; Loreau *et al.* 2001; Deutsch 2003; Worm and Duffy 2003). However, fishing can reduce the biodiversity of ecosystems by damaging habitats and lowering the abundance of target and non-target species (Auster *et al.* 1996; Collie *et al.* 1997; Pauly *et al.* 2002; Airolidi *et al.* 2008). When fishing pressure persists at too high level for too long, certain species can be driven to local extinction or at least to such low levels that any influence they have on ecosystem structure and function is essentially lost (McClanahan 1995; Sala *et al.* 1998). If these species played a key functional role within the ecosystem and the



Figure 1 The ecological effects of intensive fishing. Fishing effort increases over time (left to right). As a result, large finfish become depleted, fishers are forced to target new species, and biogenic habitat structures are damaged or lost. However, the ecological functions that larger finfish and habitat-forming organisms performed within the ecosystem become diminished or lost. Consequently, biodiversity of the system declines, and the ecosystem shifts to a new state dominated by species that were once preyed on by larger fish or are resilient to habitat-modifying fishing methods. These species can, however, go on to support large and lucrative fisheries.

traits they conferred are replaced by other species, it can alter ecosystem function and result in the emergence of a new, unfamiliar ecological state (Pauly and Christensen 1995; Naeem and America 1999). It appears then that a system's biodiversity does play a key role in maintaining its stability. However, recent studies suggest the reality may be more complicated.

Marine ecosystems are complex and dynamic and are increasingly thought to be able to exist in, and shift between, several possible alternate states (Scheffer *et al.* 2001; Beisner *et al.* 2003; Deutsch 2003; Daskalov *et al.* 2007). A phase shift, that is, a slide from one alternate state to another, occurs when external (e.g. climate change or overfishing) and/or internal perturbations (e.g. predator–prey cycles and density-dependent mortality) to the system pass a critical threshold. This causes the nature of the system to change, triggering a reorganization of its structure, altering its dynamics and bringing about a series of feedbacks that can further reinforce the change (Scheffer and Carpenter 2003) (Fig. 2). In some cases, crossing the threshold requires only a relatively small perturbation to bring about a sudden and dramatic change (Gammaitoni *et al.* 1998). For example, it has been reported in several lake systems that a change in phosphorus

input can trigger a sudden shift from clear to turbid water, two different states capable of supporting different communities of animals and plants (Jeppesen *et al.* 1999; Van Nes *et al.* 2002; Ibelings *et al.* 2007). In other cases, such as the change from a grassy to a shrub-dominated rangeland (Ludwig *et al.* 2000), the response is more gradual. Nevertheless, once the threshold has been passed, the feedbacks are altered and the dynamics of the system shift from one state to another (Folke *et al.* 2004).

The problem with simplified ecosystems

The extent to which an ecosystem can absorb natural and human disturbances without degrading or unexpectedly shifting to an alternate state is often referred to as its 'resilience' (Holling 1973; May 1977; Steneck *et al.* 2011). Highly resilient ecosystems can absorb perturbations and return to their previous state, whereas low-resilience systems may shift under even a relatively small disturbance. But what makes some ecosystems more resilient than others?

In theory, if species with similar functional roles are able to replace or compensate for one another, then ecosystems encompassing high species diversity will be more resilient because the

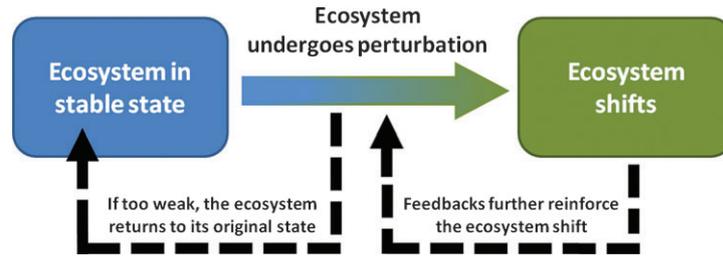


Figure 2 Theory underlying ecosystem change. An ecosystem begins as a stable, recognizable entity. However, perturbations to the system trigger an ecological reorganization. If the perturbation is weak, the system absorbs the disturbance and reverts back to its previous state. If the perturbation is strong, the system shifts to an alternative state and can trigger a number of feedbacks that further reinforce the shift and promote its stability.

likelihood of the ecosystem losing all species capable of performing a particular ecological function is low (Chapin *et al.* 1996; Lavorel and Garnier 2002; Hooper *et al.* 2005). Ecologists have therefore frequently proposed that an increase in species diversity will confer an increase in resilience by ensuring the system against loss of function (Elton 1958; Mcnaughton 1977; Tilman 1996; Yachi and Loreau 1999; Loreau *et al.* 2001). Despite being an area of intense debate (Chapin *et al.* 2000; Worm and Duffy 2003), there is growing evidence that species diversity plays a significant role in ecosystem function and resilience in several systems including kelp forests (Johnson and Mann 1988; Ste-neck *et al.* 2002, 2004; Hughes *et al.* 2005; Worm *et al.* 2006), microbial microcosms (McGrady-Steed *et al.* 1997; Naeem and Li 1997), grasslands (Tilman 1996; Walker *et al.* 1999; MacDougall *et al.* 2013), mycorrhizal fungi (van der Heijden *et al.* 1988) and marine invertebrate communities (Stachowicz *et al.* 2002; Levine *et al.* 2004). The relevance of all these to fishing is that as many heavily exploited marine ecosystems are inadvertently being transformed into simpler, managed systems, which typically contain only a few dominant species, they too are expected to have low resilience and be more susceptible to other human impacts, such as climate change, eutrophication and species invasions, and therefore more susceptible to phase shifts.

The Black Sea gelatinous invasion

The overfishing of large predatory species can often open up suitable niches for other species to occupy (Worm *et al.* 2006; Daskalov *et al.* 2007; Oguz *et al.* 2008). Overfishing in the Black Sea,

for example, has made the system more susceptible to changes in climate, hydrography, nutrient loading and invasions by both native and non-native species (Llope *et al.* 2011). As a result, many shallow areas have become oxygen depleted (whereas the deep Black Sea has long been anoxic), and the system has shifted from a fish-dominated community to one dominated by jellyfish and ctenophores: the most dramatic, large-scale gelatinous plankton invasion event to date (Oguz *et al.* 2008).

The turning point for these changes occurred in the 1960s when fishing first reached industrial levels, and stocks of pelagic predators such as bluefish (*Pomatomus saltator*, Pomatomidae) and dolphinfish (*Coryphaena hippurus*, Coryphaenidae) became severely depleted (Daskalov 2002; Sala and Knowlton 2006). As a result, predation pressure was reduced and populations of planktivorous fish expanded. This led to greater grazing pressure on zooplankton and, coupled with eutrophication, allowed the biomass of phytoplankton to increase abruptly during the early 1970s (Daskalov *et al.* 2007). This had further knock-on effects; phytoplankton blooms at the surface meant greater quantities of dead phytoplankton were sinking to the depths and being decomposed through bacterial action, a process that consumes oxygen. As a result, shelf waters became hypoxic, causing mass mortalities of mussels and other benthic filter feeders (Daskalov 2002; Llope *et al.* 2011). In turn, this led to an increase in unutilized detritus and nutrients within the system and, consequently, further oxygen depletion. In this altered ecosystem, a gelatinous invader – the comb jelly (*Mnemiopsis leidyi*, Boinopsidae) – proved highly successful, reaching biomasses of more than 2 kg m^{-2} in some cases (Shushkina

and Musaeva 1983; Zaitsev and Mamaev 1997). However, cooler temperatures between 1991 and 1993 countered the invasion and allowed planktivorous fish to recover, meaning small pelagics are again controlling the food web as the main top predator of the system. Curiously, the Black Sea has shown further signs of recovery since then and appears to be linked to the collapse of the Soviet Union and the loss of state subsidies, which previously supported intensive farming practices and the application of fertilizers (Mee *et al.* 2005).

Hypoxia in the Baltic

The Baltic Sea is unusual in that it is essentially a large brackish lake that receives infrequent inflows of seawater from the North Sea that rapidly sink into deeper basins as they are forced underneath a less-dense layer of freshwater at the surface (Schinke and Matthäus 1998). When the period between inflows is long (known as 'stagnant periods'), continued bacterial decomposition in the depths causes natural depletion of oxygen (Hille *et al.* 2005). However, in recent years, overfishing, climate change and eutrophication have intensified this process, resulting in severe anoxia and ecosystem shifts at several different trophic levels and time periods.

During the early 20th century, the hunting of marine mammals resulted in the near elimination of top predators and, coupled with increasing pollution and climate change, caused the Baltic to shift from an oligotrophic to a eutrophic state (Österblom *et al.* 2007). In response, the system became dominated by cod (*Gadus morhua*, Gadidae), whilst deeper waters became severely hypoxic, wiping out important food chains across 100 000 km² of the seabed (Elmgren 1989; Folke *et al.* 2004). Intensive fishing then contributed to a 10-fold decline in cod biomass between 1980 and 1992 (MacKenzie *et al.* 1996) causing the system to shift again, but towards a community dominated by planktivorous sprat (*Sprattus sprattus*, Clupeidae) and herring (*Clupea harengus*, Clupeidae), thereby imposing major changes on zooplankton community composition (Möllmann *et al.* 2008). These changes are likely being reinforced as cod eggs are not adapted for hypoxic waters, and the large populations of sprat and herring may be feeding on cod eggs and larvae and also competing with their juveniles (Koster and

Möllmann 2000; Hinrichsen *et al.* 2002). The collapse of cod and other large predators has also led to an increase in smaller organisms, which prey upon the grazers of macroalgae (Roberts 2012). As a result, herbivory rates have declined and macroalgae have spread, further driving down oxygen levels through their decay.

Denmark and other nations bordering the Baltic have made several efforts to reduce nitrogen runoff to the Baltic Sea. As a result, nitrogen inputs have halved since the early 1980s (Conley *et al.* 2007), yet the ecosystem remains in a low-oxygen state (Roberts 2012). It has been proposed that severe hypoxia has eliminated the functional influence of large, deep-burrowing organisms within the sediment, hindering the recovery of the system. Normally, these organisms ingest particles of food from the water column and deposit their faeces deep into the sediment, reducing the nutrient content of the water column (Bianchi *et al.* 2000; Middelburg and Levin 2009; Karlson *et al.* 2010). However, their absence has allowed sediments to become dominated by smaller opportunistic taxa that live close to the sediment surface and release their faeces back into the open water, thereby stimulating further plankton blooms at the surface and further oxygen depletion (Hille *et al.* 2005; Woulds *et al.* 2007). Hypoxic sediments are also less able to retain phosphorous, which has triggered a large-scale relocation of phosphorous from within the sediment to the water column, again boosting plankton growth and oxygen depletion (Hille *et al.* 2005).

Sulphur eruptions of the Benguela upwelling system

In some ecosystems, the diversity of lower trophic levels is equally as important as top predators. A curious case-study is provided by the recent changes observed in the Benguelan upwelling system off Namibia. Here, trade winds drive intense upwelling and force cold, nutrient-rich water to the surface, stimulating large blooms of phytoplankton (Bakun 1990; Ohde *et al.* 2007). Like other upwelling areas (Brüchert *et al.* 2006), high productivity at the surface has resulted in severe hypoxia at depth and enabled high concentrations of hydrogen sulphide and methane (the waste products of microbial metabolism) to build up within the sediment (Brüchert *et al.* 2009). Such conditions are estimated to cover more than 50%

of the Benguelan shelf (Brüchert *et al.* 2006) and further contribute to oxygen depletion as hydrogen sulphide reacts with oxygen as it rises to the surface, thereby stripping it from the water (Bakun and Weeks 2004; Ohde *et al.* 2007). Occasionally, this process is so intense that the rising gasses rush upwards in a sudden 'eruption' of sulphide and methane, turning the sea a bright turquoise (Fig. 3). Such effects can persist for more than 2 months and cover an area of 20 000 km² (Weeks *et al.* 2002).

This phenomenon is not new. Sulphur eruptions have been reported since the 19th century (Weeks *et al.* 2004; Utne-Palm *et al.* 2010), but observations suggest they are increasing in both frequency and intensity (Weeks *et al.* 2004). It has been hypothesized that the increasing eruptions are linked to overfishing of pelagic fish (Bakun and Weeks 2004). Up to a few decades ago, sardines (*Sardinops sagax*, Clupeidae) and anchovy (*Engraulis encrasicolus*, Engraulidae) shoaled off Namibia in great numbers to feed on vast quantities of phytoplankton. These large shoals provided prey for tuna (Scombridae), swordfish (Xiphiidae) and large colonies of seabirds, sustaining one of the world's most spectacular concentrations of marine life (Roberts 2012). In response, a large industrial sardine fishery was developed during the early 1960s, but through a combination of overfishing and environmental fluctuations, the

fishery collapsed just a decade later (Cury and Shannon 2004). The large sardine stock was once estimated to exceed 10 million tons but for the past 30 years has not exceeded 1 million tons, and in some years, fluctuations have been so severe that the population has nearly vanished (Boyer 1996; Bakun and Weeks 2004). The Benguela upwelling ecosystem has therefore lost a key component that previously limited the extent of phytoplankton blooms and resulting sulphur eruptions.

Increased sulphur eruptions are a cause for concern. Hydrogen sulphide is a respiratory poison (Bagarinao 1992), and its diffusion from the sediment to the water column has been implicated in several massive kill events of fish and invertebrates. These trigger mass feedings by seabirds and large 'walkouts' by lobster and other edible crustaceans, which people readily collect from the shore as they try to exit the water (Weeks *et al.* 2002; Bakun and Weeks 2004). One event in particular killed off 80% of the hake population, leaving few individuals to sustain future catches (Bakun and Weeks 2004). Corrosive fogs of hydrogen sulphide are also released, which irritate the eyes and throats of coastal inhabitants, and are offensive in smell (Weeks *et al.* 2002, 2004). Climate change is predicted to further increase the frequency of sulphur eruptions (Bakun 1990), making the waters even more anoxic and less suitable to

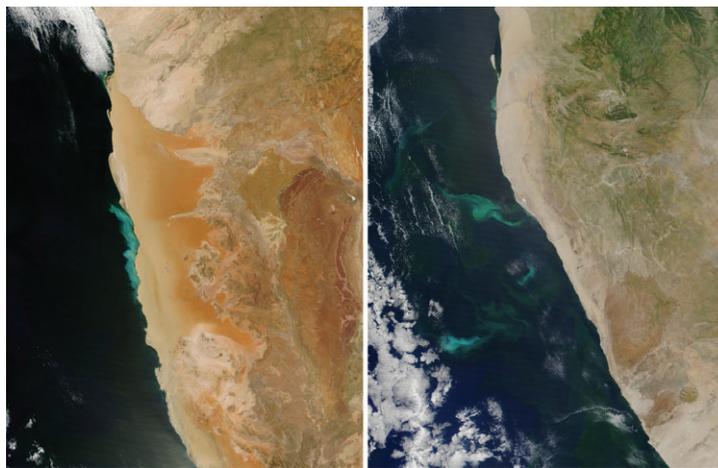


Figure 3 Sulphur eruptions observed off the coast of Namibia. Evidence suggests that this natural phenomenon may be increasing in frequency and intensity and may be linked to the overfishing of planktivorous fish. Satellite images courtesy of Jacques Desclotres and the MODIS Rapid Response Team.

support fisheries (Bakun and Weeks 2004; Monteiro *et al.* 2008).

Other changes linked to the decline in pelagic stocks have been observed in the Benguelan upwelling ecosystem. The loss of sardine has forced many animals of higher trophic level to switch to feeding almost exclusively on a single species of bearded goby (*Taenioides jacksoni*), making it the new predominant prey species (Utne-Palm *et al.* 2010). Despite the increase in predation pressure and the decline in water quality, gobies appear to be thriving as they possess an unusually high tolerance to hydrogen sulphide and low concentrations of oxygen (Boyer and Hampton 2001). In addition, prior to the period of intensive fishing, large jellyfish (e.g. Scyphozoa and Hydrozoa) were not a prominent feature of the Benguelan ecosystem, yet the abundance of jellyfish now exceeds that of fish, reaching biomasses of more than 12 million tonnes (Lynam *et al.* 2006). The jellyfish prove a nuisance as they disrupt fishing, spoil catches and block power station coolant intakes (Boyer and Hampton 2001). They will also likely hinder any measures to recover fish stocks as jellyfish prey upon fish eggs and larvae and are strong competitors for resources (Pauly *et al.* 2009).

Impacting ecosystem services

Some reports suggest that the major shifts observed in the Black Sea, Baltic and Benguela upwelling system occurred during a similar time frame (i.e. between the 1980s–1990s) and therefore likely involved a common large-scale atmospheric driver (Young 2011). However, all these systems underwent dramatic change after intensive fishing simplified their food webs and affected the ecological roles performed by various functional groups. Indeed, simplified systems are often predicted to be less capable of providing the ecological processes that maintain their stability and allow for the long-term exploitation of their resources (Peterson *et al.* 1998; Chapin *et al.* 2000). In 2006, an extensive meta-analysis conducted by Worm *et al.* found many cases in which loss of biodiversity impaired the filtering and detoxification functions performed by filter feeders, submerged vegetation and coastal wetlands and that these impairments were likely linked to a

global increase in harmful algal blooms, fish kills, shellfish fishery and beach closures and oxygen depletion. Their study also revealed that increasing occurrences of species invasions have coincided with the loss of native biodiversity and that in the majority of cases, the invaders could not compensate functionally for the loss of native biodiversity because they comprised of other species, mostly microbes, gelatinous plankton and small invertebrate taxa. They also found that fisheries in species-poor ecosystems were more prone to collapse and less likely to recover from over-exploitation. Their study therefore supports the notion that complex, more intact marine ecosystems provide a range of ecological services, which maintain ecosystem function and support the long-term exploitation of marine resources. But when we simplify ecosystems to just a few dominant species, we trigger ecological changes that impact upon these services thereby affecting resource extraction and human welfare (Brand 2009).

From finfish to invertebrates

We have established that shifting to lower-diversity regimes can cause ecosystems to change, with knock-on effects for ecosystem services. But what are the socioeconomic drivers that cause such adverse effects to occur? As we will now explore, the over-exploitation of finfish stocks has, in some ecosystems, resulted in unusually high densities of commercially valuable invertebrates, which can go on to support highly lucrative and successful fisheries (Caddy and Rodhouse 1998; Steneck *et al.* 2011). In these cases, the serial over-exploitation of fish stocks has created simplified systems – akin to agricultural monocultures – of targeted resources that are easier to manage, more abundant in the environment and economically more valuable than the finfish fisheries they replaced (Hilborn 2007a).

Prawns in the Clyde

The Firth of Clyde, a large inlet of the sea that extends over 100 km into Scotland's west coast, gained considerable media attention after it was identified as one of the most degraded marine environments in the United Kingdom (BBC Springwatch 2007; BBC Panorama 2010; Clover and

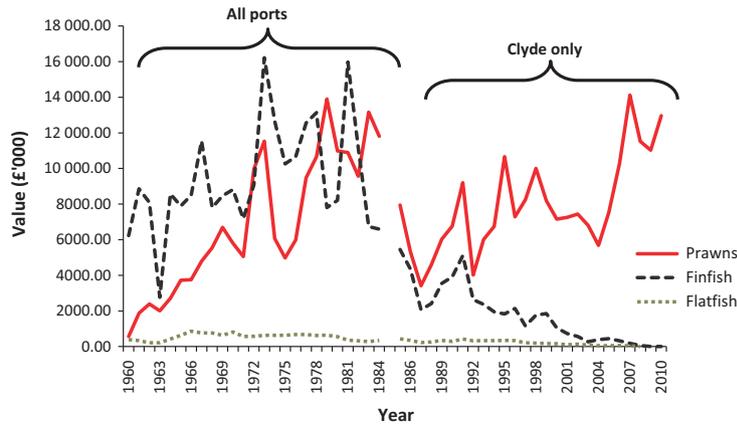


Figure 4 *Nephrops* prawns now dominate Firth of Clyde landings by value (values corrected for inflation using www.thisismoney.co.uk/historic-inflation-calculator). Data from the Scottish Government. Data pre-1985 represent all fish landed in the local ports Ayr and Campbeltown, whilst data post-1985 represent only those fish caught and landed within the Firth of Clyde.

Smith 2010; Smith 2010), primarily due to over a century of intensive fisheries exploitation (Thurstan and Roberts 2010). Fishing in the Clyde has origins dating back to medieval times (Tivy 1986) and, over the centuries, has supported many important fisheries targeting a wide range of species including herring, cod, mackerel, whiting (*Merlangius merlangus*, Gadidae), haddock (*Melanogrammus aeglefinus*, Gadidae), turbot (*Psetta maxima*, Scophthalmidae), skate (*Dipturus batis*, Rajidae) and even basking sharks (*Cetorhinus maximus*, Cetorhinidae) (Thurstan 2007; Thurstan and Roberts 2010). Today these fisheries no longer exist.

The Clyde follows the typical 'boom-and-bust' pattern exhibited by many of the world's over-exploited fisheries. During the 19th century and before, landings were spread between many different species and targeted by an artisanal fleet using sailing vessels, traps, lines and nets (Thurstan and Roberts 2010). Fishing effort steadily increased as a greater proportion of the fleet began to take advantage of technological advancements such as beam trawls, otter trawls, Newhaven scallop dredges and steam- and diesel-powered engines. Despite, and likely because of, increasing fishing effort and two spatial closures to trawling being revoked in the late 20th century (Heath and Speirs 2011), large catches of fish were not sustained, and landings of demersal species, such as haddock and cod, declined by more than 90% (Thurstan

and Roberts 2010). As a result, a remarkable shift has been observed over the last two decades in the groups of species landed from the Clyde. In 1985, finfish made up more than 60% of the landings by weight and 37% by value, but by 2008, this had fallen to just 2% by weight and 0.5% by value (Fig. 4). Now *Nephrops* prawns (*Nephrops norvegicus*, Nephropidae) are the most valuable fishery in the Clyde, making up 84% of landings by weight and 87% by value. These are targeted by around 120 vessels, of which the majority (90%) of landings are made by trawlers resident to the Clyde (Thurstan and Roberts 2010; Murray and Cowie 2011). The remaining percentages are composed solely of other invertebrates such as scallops (*Pecten maximus*, Pectinidae), crabs (*Cancer pagurus*, Cancridae) and lobster (*Homarus gammarus*, Nephropidae) (Howell et al. 2006; Keltz and Bailey 2010). Since 2003, the only landings of fish in the Clyde have been as by-catch from the *Nephrops* fishery (Heath and Speirs 2011).

The physical and ecological effects of overfishing in the Clyde have resulted in an altered, simplified ecosystem in which *Nephrops*, crabs, scallops and other invertebrates now thrive (Thurstan and Roberts 2010) (for contrasting views see Combes 2007). Reversing this shift will likely prove difficult as there are several ecological and social feedbacks preventing the return of the Clyde to the diverse, highly productive ecosystem it once was (Box 1).

Box 1. Barriers to recovery within the Firth of Clyde

1. *The decline in nursery habitat:* Mobile fishing gears, like trawls and scallop dredges, alter the physical structure of the seafloor by ploughing sediments and destroying structural biological features such as maerl, seagrass and macroalgal beds (Eleftheriou and Robertson 1992; Hall-Spencer and Moore 1998; Jennings and Kaiser 1998; Kaiser *et al.* 2000). Such habitats often support high levels of juvenile fish density, growth and survival, and contribute disproportionately to the production of adult recruits and biodiversity in general (Beck *et al.* 2001; Kamenos *et al.* 2004a,b; Howarth *et al.* 2011). The decline of these 'nursery habitats' within the Clyde has undoubtedly altered marine ecosystem function and will likely hinder any future recovery of fish stocks (Bradshaw *et al.* 2001). In addition, many commercially exploited fish species have been shown to spend significant parts of their juvenile life stage in inshore nursery habitats, migrating progressively offshore as they age and develop (Zeller and Pauly 2001; Espeland *et al.* 2007; Gibb *et al.* 2007; Knutsen *et al.* 2007). Interfering with this transition will therefore also contribute to the decline of finfish fisheries further out at sea.
2. *High levels of by-catch:* In addition to the habitat-altering properties of trawls and dredges, the high levels of juvenile by-catch associated with their use (especially given the fine-mesh of prawn trawls) will also likely prevent the recovery of bottom fish populations. Discard ratios are very high in the Clyde *Nephrops* fishery, with 9 kg of by-catch produced for every 1 kg of *Nephrops* caught (Bergmann *et al.* 2002), and it is likely that the majority of these organisms die when returned to the sea (Bergmann and Moore 2001).
3. *Nephrops are highly valuable:* *Nephrops* alone generate almost as much income as all finfish combined did in the past (even when inflation is taken into account, Fig. 4). There is therefore likely to be little desire to return to a diverse mixed fishery (Steneck *et al.* 2011), especially given the current level of investment in the *Nephrops* fishery. Profit margins in this fishery may not be as high as they once were (Thurstan and Roberts 2010), but this single species remains the mainstay of the fishing industry in the Firth of Clyde.
4. *The abundance of euphausiids and copepods:* These planktonic organisms constitute important prey for juvenile cod and haddock, yet their abundance is 10–100 times lower in the Firth of Clyde than in the 1950s. This finding is consistent with studies conducted in the Gulf of Maine, where the virtual eradication of cod and haddock has led to a reduction in zooplankton abundance, thought to be a result of enhanced predation by small pelagic fish and the planktonic stages of crabs and shrimps (Frank *et al.* 2005). However, its causes in the Clyde remain unknown, as are its consequences on the recovery of groundfish (Bailey *et al.* 2011).

Although a prawn-dominated state appears beneficial in a fisheries sense, there is a possibility that the *Nephrops* stock may be unusually prone to collapse. It is known that populations within low-diversity ecosystems are inherently unstable, being more prone to sudden fluctuations in stock size, invasion and disease (Worm *et al.* 2006). In fact, there are already signs of high rates of parasitism of Clyde *Nephrops* by a microscopic dinoflagellate belonging to the genus *Haematodinium*. This parasite is also known as 'bitter crab disease', for its capacity to reduce both taste and texture of *Nephrops* and other crustaceans (Gunnarsson 2010), or as 'smoking crab disease', due to its ability to con-

vert host's organs into its own propagules. When complete, the free-swimming stage of the parasite then erupts from every aperture and joint, giving the prawn the appearance of smoking (Roberts 2007). During seasonal peaks, *Haematodinium* prevalence can reach as high as 70% (Field *et al.* 1992), with infection widely believed to lead to the death of the host (Stentiford and Shields 2005; Stentiford and Neil 2011). Seasons of high infection have therefore been associated with reductions in landings per unit effort and *Nephrops* burrow density (an accepted indicator of stock density, McLay *et al.* 2008), as well as considerable losses to fishermen who are forced to discard

high proportions of their catch that are heavily parasitized and therefore unmarketable (Field *et al.* 1998; Stentiford 2001; Beevers *et al.* 2007).

It has been proposed that overfishing in the Firth of Clyde may be encouraging the outbreak of *Haematodinium* through several mechanisms (Thurstan and Roberts 2010; Stentiford and Neil 2011). Parasites often modify host behaviour to increase the spread of infection. As infected prawns spend more time out of their burrows (Stentiford 2001; Stentiford and Neil 2011), there may be an increased chance of disease transmission between infected and uninfected prawns. When cod and other predatory fish were common in the Clyde, infected prawns would have been picked off quickly, limiting the spread of the parasite, but today there is little such control. Secondly, *Haematodinium* prevalence has been found to be highest at sites where *Nephrops* populations are made up of smaller-bodied individuals (Field *et al.* 1998; Stentiford 2001). Because fishing alters population size-structure, fishing may be increasing the prevalence of the disease by creating a shift towards a higher proportion of smaller-bodied, more susceptible, individuals within the population (Stentiford and Neil 2011).

The arguments above highlight current fishing practices in the Clyde as risky. If the *Nephrops* stock were to crash, the social consequences for Clyde fishermen would be dramatic as few species would be left to target. What is more, the value of trawled *Nephrops* has remained static since 1991, whilst the business costs of operating a vessel have steadily increased. In this market, fishers face the predicament of fishing for quantity rather than quality. Therefore, if landings were to drop, say because of disease or fishery restrictions, the trawl fleet will be highly susceptible to economic collapse (Combes 2007).

Lobster in the Northwest Atlantic

The Northwest Atlantic was once home to some of the world's richest fishing grounds for large predatory groundfish, particularly cod and haddock (Acheson and Steneck 1997; Jackson *et al.* 2001). However, over the past 30 years, fisheries within this region have experienced widespread collapse, and landings from fisheries targeting invertebrates such as sea urchins (*Strongylocentrotus droebachiensis*, Strongylocentrotidae), lobster (*Homarus americanus*, Nephropidae), snow crab (*Chionoecetes opilio*,

Oregoniidae) and shrimp (*Pandalus borealis*, Pandalidae) have come to dominate (Worm and Myers 2003; Frank *et al.* 2011) (Fig. 5). In addition to growing economic dependency on newly established invertebrate fisheries, we have also seen several new ecological states emerge throughout the entire Northwest Atlantic, what may well be the largest phase shift recorded to date as a direct consequence of overfishing.

In the Gulf of Maine, cod has been the single most valuable marine resource since the late 1880s. However, like many fisheries discussed in this study, fishing intensity and its impacts escalated over time. During the 1930s, new technologies enabled fishers to boost their catches by actively targeting spawning aggregations of coastal cod and haddock, but by 1949, these coastal stocks had become depleted (Steneck *et al.* 2004). Landings of cod and haddock were, however, maintained by targeting previously unexploited stocks further offshore between the 1950s and 1970s. Landings in the area then received another boost between the 1970s and 1990s due to further technological advancements and the establishment of the 200-mile exclusive economic zone. Both contributed to a temporary increase in species diversity of landings as fishers began to target new species such as monkfish (*Lophius americanus*, Lophiidae) and sea urchins. Despite the boost to landings, by 1992, stocks of predatory bottom fish experienced widespread collapse, and landings fell to just a tenth of what they had been in 1990 (Steneck and Wilson 2001, 2010).

In contrast, since the 1950s, landings of lobster have increased dramatically to the point that their value has surpassed all other harvested stocks in Maine, representing 80% of the total value of Maine's seafood landings, thereby making it one of the most important fisheries in North America (Steneck and Wilson 2001; Steneck *et al.* 2011). Following this success, the number of lobster pots in Maine has increased from around 300 000 in 1930 to well more than 3 million in 2000. Now, in 2011, more than 4400 commercial fishing vessels actively fish lobsters in coastal Maine (Department of Marine Resources 2012). Despite such intensive levels of fishing, population densities of lobster remain higher in Maine than in anywhere else in the world (Steneck and Wilson 2001; Steneck *et al.* 2011). With no sign of landings diminishing, it is no surprise that the Maine lobster fishery is widely regarded as successful and sus-

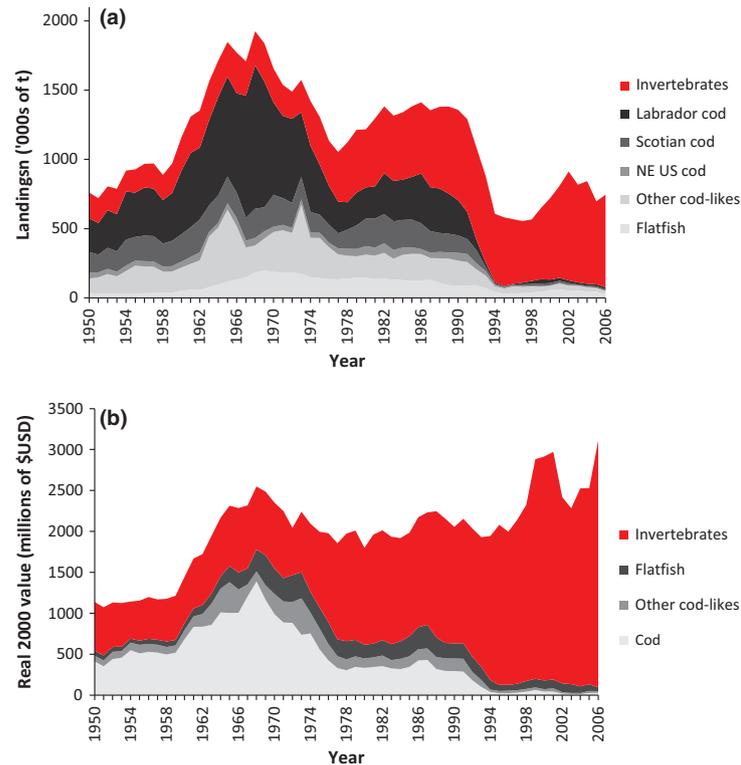


Figure 5 The rise of invertebrate fisheries in the Northwest Atlantic. Predatory groundfish fisheries have collapsed in the Northwest Atlantic triggering a dramatic shift in the value and composition of species landed. (a) Landings of several groups of species in the Northwest Atlantic between 1950 and 2006. Landings of cod split between the three large marine ecosystems. In all three regions, cod landings have almost ceased, and invertebrates now make up the majority of species landed. (b) The real 2000 adjusted value of several groups of species between 1950 and 2006. Invertebrate fisheries are now worth more than the finfish fisheries they replaced. Real 2000 value was obtained by multiplying the catch (by species) by the deflated ex-vessel price, adjusted by the Consumer Price Index. The group 'invertebrates' does not include oysters as this fishery had already boomed and collapsed by 1970. Data obtained from the Sea Around Us Project (www.seasaroundus.org).

tainably managed (Ostrom *et al.* 1994; Acheson and Steneck 1997; Steneck *et al.* 2011). Yet, although managers and fishers have indeed contributed to this success, there is a belief that the high abundance of lobster is more a result of them becoming ecologically 'released' from their overfished predators, allowing the population to expand in size and into new, relatively unprotected habitats from which they were previously excluded (Boudreau and Worm 2010). In addition, a high proportion of the lobsters' diet now comes from herring bait used in the trap fishery (Saila *et al.* 2002; Grabowski *et al.* 2009), creating an artificial trophic link between a pelagic fish and a benthic scavenger. Meaning, undersized lobsters receive a high-energy meal every time they are caught and released, thereby enhancing their growth (Saila *et al.* 2002; Grabowski *et al.* 2009).

This means that the Maine lobster fishery shares more characteristics with aquaculture and ranching (such as control of predators, provisioning of food and a greatly simplified food web) than most capture fisheries (Steneck *et al.* 2011).

Currently, lobsters represent more than 80% of the value of all fish and seafood landings in Maine (Steneck *et al.* 2011). Similar to our previous arguments, this means any future declines in lobster will have devastating social and economic consequences as we have effectively 'put all our eggs in one basket'. Furthermore, shallow ocean temperatures in the Gulf of Maine are steadily rising (Wanamaker *et al.* 2008), meaning lobsters may become increasingly stressed and more vulnerable to disease (Factor *et al.* 2006). For example, in the eastern Long Island Sound (just 200 km south of the Gulf of Maine), disease and

stresses related to increases in ocean temperature have resulted in more than a 70% decline in lobster abundance after a lethal disease outbreak during the unusually warm summer of 1998 (Castro *et al.* 2006; Glenn and Pugh 2006). Then, in 2010, fisheries managers proposed a 5-year moratorium on lobster fishing as lobsters were experiencing recruitment failure in response to warming sea temperatures (Steneck *et al.* 2011), which both lowered oxygen levels and increased the incidence of disease (Castro and Angell 2000; Castro *et al.* 2006). Recruitment failures as a result of climate change have also been observed in rock lobster fisheries in Tasmania (Pecl *et al.* 2009). If a similar epidemic were to occur in Maine, the effects would be more pronounced because lobster densities are higher than those in Long Island Sound, enhancing disease transmission (Steneck *et al.* 2011).

Ecological shifts have not been confined to the Gulf of Maine. The eastern Scotian Shelf has experienced similar phase shifts driven by the collapse of the benthic predatory fish community (Frank *et al.* 2005). Now, in a system where cod and other predatory bottom fish used to dominate, landings of northern shrimp and snow crab have increased to such an extent that their combined economic value exceeds that of the groundfish fisheries they replaced (Worm and Duffy 2003). Furthermore, it is thought that a number of measures designed to help the recovery of benthic fish are being hindered by the dramatic rise in forage fish and macroinvertebrates (a 900 and 200% increase in biomass, respectively), which may be outcompeting their former predators (Frank *et al.* 2005, 2011).

As well as impacting the species composition of landings, the decline in predatory groundfish has also been observed to cause shifts in seal populations, phytoplankton community composition and the prevalence of kelp forests (Frank *et al.* 2005). Kelp forests, in particular, dominated coastal ecosystems of the Northwest Atlantic for more than 4000 years (Steneck 1990; Jackson *et al.* 2001; Steneck *et al.* 2002), but from the mid-1960s to 1990, the overfishing of large predators triggered a dramatic increase in the populations of sea urchins and other herbivores, leading to widespread deforestation of coastal kelp forests (Steneck *et al.* 2004; Boudreau and Worm 2010). Under this new regime, grazing-resistant coralline algae came to dominate the benthos (Steneck 1982; Steneck and Dethier 1994) (Fig. 6), thereby reinforcing the



Figure 6 The shift from kelp forest to coralline algae. Between the 1960s and 1990s, coastal kelp forests in the Gulf of Maine were replaced by communities dominated by coralline algae due to intense grazing pressure from sea urchins. Picture taken in 1980 and reproduced with permission from Robert Steneck, University of Maine.

shift by replacing quality groundfish nursery habitat (i.e. the kelp) with new habitat suitable for sea urchin recruitment (i.e. coralline algae) (Steneck *et al.* 2004). This new ecological state persisted for 2–3 decades before a new fishery targeting the green sea urchin was established in 1987 (Vadas and Beal 1999). The fishery quickly depleted the sea urchin population from extensive coastal areas of Maine, allowing a return to a kelp-dominated state by the mid-1990s. This latest state looks so far to be stable, as the expansion in crustaceans appears to be preventing repopulation of sea urchins by feeding on their newly settling recruits (Steneck *et al.* 2004).

Can we 'farm' the open sea?

This study highlights several ecosystems that have undergone dramatic ecological shifts as a result of overfishing and other environmental changes. Controversially, some of these shifts have appeared to be positive from an economic perspective. Although biodiversity has been reduced, intensively fished systems can come to support important high-volume invertebrate fisheries, often capable of generating more economic value than the finfish fisheries they replaced. So the question remains is simplifying the seas a process that should be welcomed, as some have argued, improving the harvesting of resources like it does in agricultural systems on land?

Modern agriculture involves converting existing ecosystems into ones that can be controlled and reducing habitat heterogeneity and biodiversity to maximize the production of a small number of target crops or animals (Kareiva *et al.* 2007). Reducing biodiversity simplifies management, maximizes yield and allows for faster processing through automated planting and harvesting (Hooper *et al.* 2005). Marine capture fisheries are also based on generating economic profit from targeted species, and as with farming, fisheries too can be more profitable when the biodiversity of their catch is low (Diamond and Beukers-Stewart 2011). This is because fisheries rarely land all the species they catch. Instead, they are often governed by species-specific quotas, meaning that when a fisher's catch consists of a greater proportion of the target species, less time is spent sorting the catch and more of it can be landed, thereby generating greater profit. A simplified ecosystem should therefore provide a more predictable product, allowing fishermen to optimize their gear and techniques, and for seafood processors and retailers to streamline their supply chains. In many ways, these economic arguments are remarkably similar to those driving the dramatic expansion of the aquaculture industry which, over the past several decades, has been the fastest growing food production sector in the world (Bostock *et al.* 2010).

It is, however, widely recognized that monocultures are ecologically unstable. On land, crops and animals must be treated with a diverse array of chemicals (e.g. fertilizers, herbicide, pesticides, antibiotics, etc.) and biological controls (e.g. the introduction of predators and parasitoids) to maintain yields in the face of pests, weeds and diseases (Holt and Hochberg 1997; Palumbi 2001). Also, farmers often rely on a continuous supply of new crop varieties and strains as yields of successful, pest-resistant varieties are typically maintained for only 5–9 years before pests adapt to overcome them (Tilman *et al.* 2002). Similar methods are also used in aquaculture, but in the open sea, no such mechanisms exist for wild populations, meaning terrestrial analogies are misplaced (Roberts 2007). Maintaining low-diversity conditions in the marine environment for our long-term exploitation is therefore unlikely to be viable. Moreover, the transition from multispecies fisheries to high-volume single-species fisheries has largely been limited to crustaceans and molluscs. These organisms lay down protective shells made from

carbonate, a substance predicted to become increasingly scarce in the future as a result of increasing carbon dioxide levels and consequent ocean acidification (Sabine *et al.* 2004; Doney *et al.* 2009). In fact, many experimental studies show that molluscs and crustaceans suffer exceptionally high mortality and low recruitment at acidification levels predicted to occur by the end of the century (Gazeau *et al.* 2007; Kurihara 2008; Watson *et al.* 2009), meaning shellfish fisheries all over the world are badly exposed to risk if the organisms they target cannot adapt.

Finally, the economic benefits of simplification may in reality only be short term. As we have explored, simplification can result in ecosystems shifting to new states that are entirely undesirable and result in long-term losses, such as those observed in the Black and Baltic Seas. The ecological simplifying effects of overfishing also promote a loss in ecosystem services and can result in eutrophication, harmful algal blooms and large-scale invasions, which can affect target species and human well-being.

Can ecosystem change be reversed?

In the light of the problems discussed, it is important to know whether adverse ecosystem shifts can be reversed. Studies suggest they can. Meta-analyses reveal that the establishment of protected areas can restore ecosystems and biodiversity and often result in an increase in biomass, density and average body size of large predators and herbivores (Halpern and Warner 2002; Halpern 2003; Micheli *et al.* 2004). For example, the establishment of two marine reserves in New Zealand led to sea urchin-dominated barrens reversing back to macroalgal beds within 20 years (Shears and Babcock 2003). Evidence suggested that this was the result of an increase in the density and body size of snappers (*Pagrus auratus*, Sparidae) and rock lobsters (*Jasus edwardsii*, Palinuridae), the primary predators of sea urchins (Langlois and Ballantine 2005). Similarly, the designation of Mombasa Marine National Park in Kenya was followed by significant increases in predators of sea urchins and subsequent coral recovery after just 10 years of protection (McClanahan and Mangi 2000). Marine protected areas have also proven effective in large-scale industrial fisheries. In 1994, in the Gulf of Maine, three areas totalling 17 000 km² were closed to fishing gears that targeted ground-

fish or were damaging to their habitats, in an emergency response to the collapse of groundfish fisheries within the region (Murawski *et al.* 2000). In an area known as Georges Bank, haddock and yellowtail flounder (*Limanda ferruginea*, Pleuronectidae) increased between three- and fivefold within the first 5 years of protection (Murawski *et al.* 2000; Stone *et al.* 2004) and promoted recovery of the seabed through increasing the biomass and structural complexity of bottom habitats (Hermsen *et al.* 2003).

Equally though, there are many examples where protected areas have not managed to restore ecosystems and fish stocks. This is particularly true when they are not enforced or complied with (Pitcher and Lam 2010), but some even fail when compliance is absolute (Frank *et al.* 2005). In the Northwest Atlantic, for example, most Canadian stocks of Atlantic cod showed little or no signs of recovery despite the termination of direct fishing activity for over a decade (Hutchings 2001). How much this lack of recovery is down to the effects of continued prawn and scallop dredging on cod nursery grounds is unknown, but it seems likely in view of the experience we described for the Clyde ecosystem. Returning to the George's Bank closure, although haddock stocks are improving, cod is yet to show any signs of recovery (Mayo and Col 2006; Mountain and Kane 2010). Likewise, a protected area in Belize demonstrated good recovery of predatory reef fish, but only a weak response by herbivores (McClanahan *et al.* 2011). Correspondingly, there was little change in total herbivory and coral cover.

There are a diverse range of other management tools available. Enforcing the use of fishing gears that cause less damage to habitats and select for specific species, sizes and ages is one way to reduce exploitation and damage to ecosystems (Pitcher and Lam 2010). For example, after the ecological shifts in the Baltic Sea described earlier in this study, cod biomass trebled between 2005 and 2009, thought to be mainly driven by a ban on trawling, which led to a sudden reduction in fishing mortality (Cardinale and Svedäng 2011). Similarly, reducing fishing effort through reductions in quotas, total allowable catch and fishing capacity have all been shown to promote recovery in a number of fish stocks (Beddington *et al.* 2007; Worm *et al.* 2009). However, whilst such approaches may help restore the abundance of targeted species, they do not necessarily lead to the

recovery of biodiversity and the wider ecosystem (Pitcher and Lam 2010). In addition, any reductions made to fishing effort can cause social and economic instability as processing plant closures, unemployment and bankruptcy inevitably follow (Hilborn 2007a).

It has been heavily argued that protected areas and restrictions on fishing effort and fishing gears are not long-term solutions as they do not address the underlying causes behind overfishing (Beddington *et al.* 2007; Hilborn 2007a; Costello *et al.* 2008; Pitcher and Lam 2010). In 'open-access' systems, individuals lack secure rights to part of the quota, meaning fishermen often attempt to outcompete each other by attaining bigger vessels and better technology. Consequently, this leads to lobbying for ever larger quotas, excessive harvests and, eventually, the collapse of the stock (Costello *et al.* 2008). 'Dedicated access' systems, on the other hand, prevent the 'race to fish' by allocating individual rights to a quota or area to individual fishermen or communities (Hilborn 2007a). This guarantees fishers a certain proportion of the catch, thereby offering a sense of ownership, encouraging them to make more rational economic choices to manage their fishery resources more sustainably in the long term (Beddington *et al.* 2007; Pitcher and Lam 2010). Studies show that this approach has successfully reduced fishing effort and improved compliance and community participation in management processes (Johannes 1981; NRC 2003; Costello *et al.* 2008; Worm *et al.* 2009). In fact, greater involvement of fishermen and other stakeholders is commonly reported to result in more sustainable levels of exploitation, better distribution of power, reduced conflict and greater economic returns (Berkes 2007; Gutiérrez *et al.* 2007). However, there are cases where these approaches have not worked (Dulvy and Polunin 2004; Castilla *et al.* 2007; Chu 2008; Branch 2009), and there is little evidence for dedicated access management helping damaged ecosystems to recover (Costello *et al.* 2008).

Overall then, it is apparent that one management tool alone is not enough to prevent over-exploitation and subsequent ecosystem change. It is therefore widely agreed that a combination of managing fishing effort, fishing gears and establishing protected areas, all of which have received mutual consent from managers, fishermen and other stakeholders, will be most effective in achieving both fisheries and conservation objectives (Hil-

born 2007; Worm *et al.* 2009; Khan and Neis 2010).

Despite intervention, many over-exploited fish stocks and ecosystems simply never recover (Hutchings 2000, 2001; Hutchings and Reynolds 2004). What factors prevent recovery are largely unknown but are thought to include (see Hutchings and Reynolds 2004; Hooper *et al.* 2005; Hughes *et al.* 2005; Diaz-pullido *et al.* 2009) amongst others: (i) density-dependent effects (e.g. altered predator–prey ratios, recruitment failure through the Allee effect); (ii) local extinction of key functional groups; (iii) recovering functional groups not promoting return to a previous state (e.g. many reef-based herbivores will not eat late-succession macroalgae and therefore would not encourage the reef to return to a coral-dominated state, McClanahan *et al.* 2011); (iv) competition with/or predation by invasive species; (v) habitat alteration; (vi) life-history traits (e.g. fast-growing species such as herring are more likely to recover than long-lived species such as cod and halibut); and (vii) the overall reduction in biodiversity in simplified ecosystems, giving fishers less opportunity to switch to alternative taxa and therefore less likely to reduce their fishing effort (Worm *et al.* 2006). Whatever the reason, it appears that some ecosystems are altered to such an extent that they have crossed a threshold beyond which recovery to previous conditions may be impossible. The overall message from our research is clear; it would be easier for managers to maintain ecosystems in a more natural state than to try and repair them (Schiermeier 2002; Hughes *et al.* 2005; Worm *et al.* 2009).

Conclusions and perspectives

Recent papers (e.g. Hilborn 2007a, 2007b; Worm *et al.* 2009; Branch *et al.* 2011) argue that the global decline of fish stocks is slowing and that fisheries management is improving. However, these improvements are localized, confined to countries such as the USA, Australia, New Zealand and Iceland. Fishing grounds in Europe largely remain in a state of decline (Guénette and Gascuel 2012), and unassessed fisheries, which account for more than 80% of fisheries worldwide, have recently been argued to be in substantially worse condition than most assessed fisheries (Costello *et al.* 2012). We therefore argue that these improvements are not universal and that the per-

spective taken in this study better reflects the global state of fisheries and ecosystems. In addition, the above improvements come after many decades of decline, meaning it is too soon to know whether these early signs of recovery will be sustained.

Through overfishing, marine ecosystems worldwide have lost many of their natural populations of finfish, resulting in reduced biodiversity and significant ecological change. In a growing number of cases, these simplified ecosystems have come to support large invertebrate fisheries, often capable of generating more economic value than the fisheries they replaced. However, such changes are not a result of directed management, but rather a result of management failure, a failure to protect stocks of target species in the face of industry innovation and fisheries intensification.

Simplified ecosystems are only economically beneficial to one or two industry sectors and only in the short term, as low-diversity ecosystems are unstable, being more susceptible to sudden fluctuations in stock size, invasion and disease. From a wider societal perspective, ecosystem simplification makes little economic sense at all. The loss of functional groups can trigger dramatic ecosystem shifts to states that are both ecologically and economically undesirable, and often difficult and expensive to reverse. Further shifts could also leave fishers with few alternative species to turn to. In areas highly dependent on marine fisheries, this would have serious socioeconomic consequences. These changes occur because, unlike in terrestrial agricultural systems, there are no measures we can take to counter the ecological problems generated by simplification of food production systems in the open sea. All these arguments suggest that the transition from multispecies fisheries to simplified invertebrate fisheries has caused a global decline in biodiversity and ecosystem services, which is threatening global food security, rather than promoting it.

The lowered ecological and economic resilience of fisheries alone provides a strong reason for managers to avoid or reverse ecological simplification. When the wider economic costs of simplification are also taken into account (loss of ecosystem services, impacts on human well-being, etc.), it generates a compelling argument for a complete overhaul of present practice. We now need to work to implement management regimes that will promote recovery of complexity in food webs and habitats. This is why, we urgently need to shift to

a management system that incorporates extensive protected areas, reduces fishing intensity, eliminates or highly constrains use of habitat destructive and unselective fishing methods, promotes recovery in the abundance and variety of target and non-target animals, and helps restore ecosystem structure and function.

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