



Review Article

A review of the impacts of fisheries on open-ocean ecosystems

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Open-ocean fisheries expanded rapidly from the 1960s through the 1980s, when global fish catches peaked, plateaued and possibly began to decline. While catches remain at best stagnant, fishing effort globally continues to increase. The likelihood of ecosystem impacts occurring due to fishing is related to fishing effort and is thus also expected to be increasing. Despite this rapid growth, ecological research into the impacts of fisheries on open-ocean environments has lagged behind coastal and deep-sea environments. This review addresses this knowledge gap by considering the roles fisheries play in controlling the open-ocean at three ecological scales: (i) species (population or stock); (ii) biological community; and (iii) ecosystem. We find significant evidence for top-down control at the species and community scales. While evidence of ecosystem-level impacts in the open-ocean were not explicit in the literature, we provide examples of these impacts in several marine pelagic systems and encourage further research at this ecological scale. At the species level, fishing can reduce abundance, and alter physiology and life history traits, which, in turn, affect the functional role of the species within the biological community. Fishing may also induce changes to open-ocean community trophodynamics, and reduce biodiversity and resilience in open-ocean ecosystems. Our ability to manage open-ocean ecosystems has significant implications for provisioning of ecosystem services and food security. However, we posit that the monitoring required to assure the sustainability of open-ocean ecosystems is not being undertaken, and will require coordination with the Global Ocean Observing System, industry, and academia.

Keywords: community, ecosystem, fisheries, fisheries management, fishing impacts, open-ocean, pelagic.

Introduction

The world's oceans are experiencing an unprecedented level of biotic exploitation, which is altering the abundance and population structure of many species, transforming the composition of biological communities, and threatening the integrity and resilience of entire marine ecosystems (Pauly *et al.*, 1998; Jackson *et al.*, 2001; Bellwood *et al.*, 2004; Daskalov *et al.*, 2007). Over the last few decades, a growing body of evidence has accumulated, demonstrating these impacts at different trophic levels and across a wide range of taxa and marine ecosystems. Most fisheries impacts in coastal zones were well described by the turn of the century (Dayton *et al.*, 1995; Jennings and Kaiser, 1998), and our understanding of impacts on similarly static, deep-sea habitats have also been well documented (Koslow *et al.*, 2000; Clark, 2001; Roberts, 2002) and have been reviewed recently (Clark *et al.*, 2016). However, there remain knowledge gaps regarding the

potential impacts of biotic exploitation on open-ocean ecosystems. The dynamism, distance from land and sheer scale of these ecosystems have limited the capacity of researchers to study their ecology and the species that comprise them, let alone monitor changes induced by anthropogenic stressors. These gaps in understanding limit our ability to manage and conserve these ecosystems and, if not addressed promptly, may result in permanent structural or compositional changes to these ecosystems, which in turn jeopardize their functionality and thus their ability to provide ecosystem services.

Historically, marine fisheries have operated near coastal areas, mainly because of the elevated biological productivity of coastal systems and our reduced ability to store and transport fish from distant waters (Pauly *et al.*, 2005; Swartz *et al.*, 2010). However, this spatial pattern of fishing changed dramatically after onset of the industrial revolution (Swartz *et al.*, 2010). Improvements in

locomotion and refrigeration, among other factors, allowed for the expansion of fisheries in terms of fishing capacity, fishing effort and spatial extent (Swartz *et al.*, 2010). Prior to many of these technological advancements, many open-ocean ecosystems had been sheltered from growing commercial fisheries exploitation. However, between 1950 and 1990, landings from areas beyond national jurisdiction (ABNJ) (i.e. the majority of the open-ocean) more than quadrupled to over 80 million tonnes (Merrie *et al.*, 2014). New global fishing catch reconstruction estimates suggest that historical catches have been even higher and the declines since the peak have been even greater (Pauly and Zeller, 2016). While catches have stagnated since 1990, fishing effort has continued to increase, doubling between 1990 and 2010 (Anticamara *et al.*, 2011; Merrie *et al.*, 2014). According to FAO estimates, 6366 fishing vessels from 40 flag states, fish for open-ocean species in the high seas (HSVAR, 2016). The average catch of these fisheries in the first decade of the century was 10 million tonnes, which is equivalent to ~12% of the total average marine fisheries catch (Sumaila *et al.*, 2015). Catches in pelagic fisheries in ABNJ are dominated by large and medium pelagics which account for 82.69% of total pelagic catches; where tuna species dominate the catches for large pelagics and menhaden lead medium pelagic catches (Figure 1). The majority of the taxa in those functional groups are managed by tuna RFMOs, and the vast majority of those catches (88% of the tuna species) come from purse seine, longline, and pole and line fisheries. We do not directly address potential impacts from trolling (6% of large pelagic catches) or trawling (<6% of large pelagic catches) activities by tuna RFMOs.

The stagnant catch trend and decreasing catch per unit effort trend in ABNJ over the last 20 years have been caused, at least in significant part, by overfishing (Merrie *et al.*, 2014). Migratory and straddling stocks¹ spend a significant proportion of their life cycle in ABNJ (Harrison, 2012) and are particularly vulnerable to overfishing, mismanagement and illegal, unreported, and unregulated (IUU) fishing, due to the difficulty of managing their entire range and ensuring the compliance of all parties harvesting such stocks (Maguire, 2006). On-going difficulties in managing these stocks calls into question the once accepted notion of marine fish stock inexhaustibility, particularly that of wide-ranging pelagic species. A recent report by the United Nations Environment Programme (UNEP) and the Convention on Migratory Species (CMS) reinforces this notion of the vulnerability of highly mobile species, reporting that 36% of the 153 migratory or potentially migratory chondrichthyan fishes are threatened with extinction; though this proportion could be larger, as a further 27% of the taxa are data deficient (Fowler, 2014).

Implementing measures to abate the negative impacts of fisheries on wide-ranging oceanic species will require advancements in the international management frameworks for these species as well as improvements in the understanding of their ecological function within oceanic systems. We are currently at a point of convergence between growing availability of long-term multispecies catch datasets for open-ocean systems and a more robust framework for ecosystem-level mass balance models, which together allow for a comprehensive assessment of the knowledge gaps regarding the ecological impacts of fisheries on open-ocean

ecosystems. These advancements have come together at a time when the international policy arena is orienting its attention towards improving the governance of ABNJ^{2,3}. A review of the impacts and efficacy of current fisheries management regimes are underway at the United Nations, as are negotiations over a new legally-binding, international instrument for the conservation and sustainable use of biodiversity beyond national jurisdiction (BBNJ).

Here, our objective is to address a major knowledge gap in our understanding of anthropogenic impacts of fishing on the open-ocean, which we hope will help inform the review of the United Nations Fish Stocks Agreement (UNFSA) and the BBNJ negotiations. Toward that end, we synthesize the current state of knowledge on the effects that open-ocean fisheries have at three distinct ecological scales: (i) species (population or stock); (ii) biological community, and (iii) ecosystem. Managing marine ecosystems across multiple scales—from stock to ecosystem—is essential for their long-term health and resilience (Hunt and McKinnell, 2006), and is a basic tenant of ecosystem-based fisheries management (Francis *et al.*, 2007). Before doing that, we broadly review differences in the control mechanisms of open-ocean ecosystems and define open-ocean species, communities and ecosystems.

Top-down versus bottom-up control: complementary mechanisms

The notion that changes in the upper trophic levels of an oceanic system can lead to ecosystem-wide changes differs from the traditional view that bottom-up control (in the form of resource dependence) is the main factor shaping the structure and composition of these ecosystems (Cushing, 1975; Aebischer *et al.*, 1990; Verity and Smetacek, 1996; Strong and Frank, 2010; Mulder *et al.*, 2012). This view is strongly reinforced by a body of literature which demonstrates bottom-up control of the biological community in various marine systems around the world; among the most relevant of these examples are empirical demonstrations of positive relationships between fisheries captures and levels of primary productivity (Chavez *et al.*, 2003; Ware and Thomson, 2005; Chassot *et al.*, 2007).

A subset of these examples argue against the potential for top-down control of open-ocean pelagic systems, due to a lack of conclusive examples (Steele, 1998; Steele *et al.*, 1998). Among the main arguments are: (i) high species diversity can buffer changes in trophodynamics of open-ocean systems; (ii) the opportunistic character and dietary plasticity of most pelagic predatory species may result in prey switching that dampens the trophic cascades; (iii) the high level of connectivity in these systems may buffer against local depletions; (iv) the dynamism, heterogeneity and patchiness of primary productivity reduces the likelihood of disrupting trophic linkages at any particular location, as feeding is more opportunistic; and (v) the potential dominant role of

²Preparatory Committee established by General Assembly resolution 69/292 “Development of an international legally-binding instrument under the United Nations Convention on the Law of the Sea on the conservation and sustainable use of marine biological diversity of areas beyond national jurisdiction” (28th March to 8th April, 2016).

³Review Conference on the Agreement for the Implementation of the Provisions of the United Nations Convention on the Law of the Sea of 10 December 1982 relating to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks (23rd to 27th May, 2016).

¹Straddling stocks are stocks of fish such as Pollock, which migrate between, or occur in both, the economic exclusive zone (EEZ) of one or more states and the high seas” (UNAtlas, 2010).

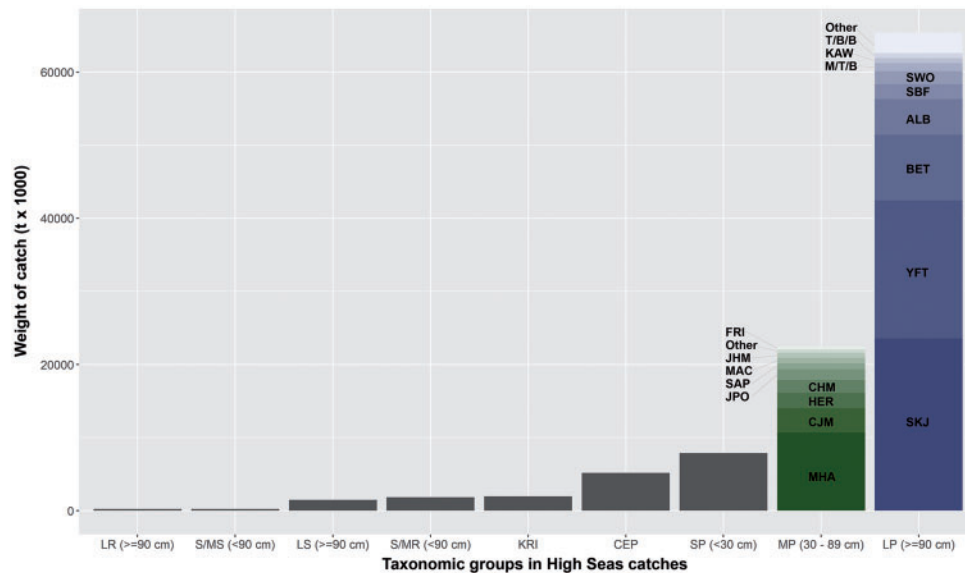


Figure 1. Total catch of the nine pelagic functional groups caught in areas beyond national jurisdiction from 1950 to 2010. The data was aggregated across the 17 high seas regions in the Sea Around Us catch reconstruction database (Pauly and Zeller, 2015). LR(≥ 90 cm) = Large Rays (≥ 90 cm); S/MS(< 90 cm) = Small to medium sharks (< 90 cm); LS(≥ 90 cm) = Large Sharks (≥ 90 cm); S/MR(< 90 cm) = Small to medium rays (< 90 cm); KRI = Krill; CEP = Cephalopods; SP(< 30 cm) = Small Pelagics (< 30 cm); MP (30–89 cm); LP(≥ 90 cm) = Large Pelagics (≥ 90 cm). The Medium and Large Pelagics are further broken down into the taxonomic groups which account for $< 95\%$ of their biomass. Large Pelagics: SKJ = *Katsuwonus pelamis*; YFT = *Thunnus albacares*; BET = *Thunnus obesus*; ALB = *Thunnus alalunga*; SBT = *Thunnus maccoyii*; SWO = *Xiphias gladius*; M/T/B = Mackerels/tunas/bonitos; KAW = *Euthynnus affinis*; T/B/B = Tunas/bonitos/billfishes. The 37 taxonomic groups which individually represented less than 1% of the biomass caught in this functional group were aggregated in “Other”. Medium Pelagics: MHA = *Brevoortia tyrannus*; CJM = *Trachurus murphyi*; HER = *Clupea harengus*; CHM = *Scomber japonicus*; JPO = Jacks/pompanos; SAP = *Cololabis saira*; FRI = *Auxis thazard*; MAC = *Scomber scombrus*; JHM = Jack/horse mackerels. The 42 taxonomic groups which individually represented less than 1% of the biomass caught in this functional group were aggregated in “Other”.

gelatinous carnivores in these systems also reduce the top-down pressure of fishing on the biological community as these organisms are not harvested (Larkin, 1979; Mills, 1995; Steele, 1998; Jennings and Kaiser, 1998; Link, 2002). This perspective has fostered the belief that fishing cannot exert top-down trophic control in these systems. Here, we review evidence for top-down control on open-ocean ecosystems and encourage a more holistic view where both bottom-up and top-down controls are accepted.

We consider this approach to be necessary given the growing evidence of the impacts that climate change may be having on pelagic communities, through changes in a system’s primary productivity (Ware and Thomson, 2005; Frederiksen *et al.*, 2006) or disruption of the timing of ecological events, which may alter the phenological patterns of marine species (Edwards and Richardson, 2004). This more holistic approach is not novel; work by Brander (2007) or Lam *et al.*, (2016) highlights how the interaction between climate change and fishing can negatively affect the maintenance of global seafood production. Corroborating this approach, reviews of regime shifts recorded in Northern Hemisphere pelagic ecosystems by Möllmann and Diekmann (2012) and Beaugrand *et al.* (2015), identified multiple drivers (including fishing and climate change) as the potential cause of shifts in ecosystem state.

Open-ocean species, communities, and ecosystems

In setting the stage for this review, we broadly define open-ocean species in terms of their ecology and life history traits, open-ocean communities in terms of their composition and

trophodynamics and open-ocean ecosystems according to their spatiotemporal distribution, dynamics, and biophysical characteristics.

Different approaches can be taken when defining what constitutes an open-ocean species. The Russian ichthyologist Nikolai Parin established a three category ecological classification for open-ocean fish based on the proportion of the species’ life history that is spent in the open-ocean zone: (i) those species which spend the entirety of their life cycles in the open-ocean (permanent residents); (ii) those species which spend only a part of their life cycle in the open-ocean; and (iii) those species which occasionally spend time in the open-ocean, spending most of their time near coastal waters but occasionally moving offshore to feed (Pepperell and Harvey, 2010). This same approach can be applied to other taxonomic groups such as sea turtles, where certain species (e.g. Loggerhead sea turtles) have oceanic developmental stages in their life cycles (Zug *et al.*, 1995; Bolten, 2003), while others (e.g. flatback sea turtles) have more coastal distributions and lack an oceanic stage, thus venturing into the open-ocean environment much less frequently (Walker and Parmenter, 1990; Limpus *et al.*, 1995). For the purpose of this review, we define open-ocean species as the combination of all three of Parin’s categories.

Given the scope of this paper, our definition of an open-ocean community is limited to open-ocean nekton, which are the species most directly affected by open-ocean fishing. The composition of this community is highly dynamic and heterogeneous across space and time, as many open-ocean species are migratory and shift their range throughout the year. A 2006 FAO report on

the state of migratory and straddling stocks identified up to 226 highly mobile open-ocean species (Chondrichthyes and Osteichthyes), while the aforementioned CMS and UNEP report identified 153 migratory or potentially migratory chondrichthyan fishes (Maguire, 2006; Fowler, 2014). It is important to note that scientific information on the composition of open-ocean marine food webs is scarce and is largely based on fisheries catch records and fisheries observer programs, which are not homogenous across space, time or fisheries. In recent years, however, there have been improvements in the collection of this type of ecosystem-level data, as in the case of observer programs in the Pacific Ocean basin (Colléter *et al.*, 2015).

There is currently no widely accepted, official definition of what constitutes the open-ocean environment. The spatiotemporal variability of oceanographic boundaries in all three spatial dimensions (particularly the vertical dimension) and the lack of structural features to delineate habitats within the pelagic open-ocean, complicate the delineation of this definition. Moreover, in the vertical dimension, the structuring of the physical and chemical properties of the open-ocean water column are dynamic across space and time and have been shown to be different between ocean basins. For these reasons, we opted for a clear-cut definition of the open-ocean environment based on bathymetric and oceanographic principles.

The continental shelf break provides a horizontal boundary for an oceanic system which, although it can interact with continental shelf ecosystems, has distinct communities. Thus, we define the open-ocean as extending beyond the continental shelf break (generally delineated as 200 m in depth), and encompassing the entire water column. The biological productivity and connectivity of the upper kilometer of the water column are key elements for setting the vertical boundaries of the open-ocean environment (Angel, 2003), and this zone encompasses most oceanic diel vertical migrations and the community. Below the mesopelagic zone, the biomass of pelagic organisms generally decreases by a factor of ten (Angel and Baker, 1982). Considering these factors together with the near total lack of studies on the impact of fisheries on the bathypelagic and abyssopelagic zones, we loosely draw the vertical boundary for this study at 1000 m.

Below we use these three ecological scales (species, communities, and ecosystems) to enumerate evidence of top-down control over open-ocean ecosystems by fisheries. These impacts can result from direct stressors such as mortality derived from target and non-target catch, or indirect stressors, such as changes in trophodynamics, life history traits or biodiversity.

Species-level impacts (direct)

Declines in abundance

While the improvements in the health of stocks within the Exclusive Economic Zones (EEZs) of coastal states such as the United States, Iceland or Australia are positive trends that should be acknowledged, open-ocean species are never found within only one EEZ (Murawski *et al.*, 2007). Rates of overfishing and the per cent of overfished stocks are greater for straddling stocks (64%) under multinational management than those under national management (28.8%) (FAO, 2014). A 2010 assessment of the 48 fish stocks managed by the world's 18 Regional Fisheries Management Organizations (RFMOs) concluded that 67% of these were either overfished or depleted, all of which are open-ocean species (Cullis-Suzuki and Pauly, 2010); these are

consistent with the FAO (2014) estimates for straddling stocks mentioned above. Specific examples abound: according to the International Scientific Committee of Tuna and Tuna like Species in the North Pacific Ocean, Pacific bluefin tuna population (*Thunnus orientalis*) has declined by 97.4% (ISC Pacific Bluefin Tuna Working Group, 2016). The latest stock assessments for the West and Central Pacific stock of big eye tuna (*Thunnus obesus*) and southern bluefin tuna (*Thunnus maccoyii*) indicate spawning stock biomass declines of greater than 80 and 90%, respectively (CCSBT, 2014; Harley *et al.*, 2014). While a number of reviews have shown very strong declines across top predators in pelagic systems (Baum *et al.*, 2003; Myers and Worm, 2003; Baum and Myers, 2004; Ward and Myers, 2005), these reports have been strongly rebutted for assumptions regarding their use of data, small sample sizes, or the reliability of spatial catch-per-unit-effort to infer trends in biomass (Walters, 2003; Burgess *et al.*, 2005; Maunder *et al.*, 2006). However, other methods, including ecosystem models and analyses of trade data, have also identified declines of >2 orders of magnitude in top predators due to fishing pressure (Clarke *et al.*, 2006).

At the species level, the greatest exploitation-induced threat that any given species can face is extinction: local, ecological, or commercial (McCauley *et al.*, 2015). Although there are no known examples of ecological extinctions in the open-ocean, there is strong evidence of very high depletion of oceanic predatory fish species, such as sharks, tunas, and billfishes (Cox *et al.*, 2002; Hutchings *et al.*, 2010). A frequent explanation for the lack of examples of ecological extinctions of open-ocean target species is that the economical extinction of a stock precedes its ecological extinction, which leads to a decrease in pressure on the stock. However, this assumption fails to account for dynamics in multi-species fisheries, such as pelagic longline fisheries. Multispecies fisheries may target more abundant, lower-value species to generate the majority of the income within the fishery, but continue to take the more depleted, high-value species opportunistically. Thus, such fisheries allow for the parallel exploitation of rarer species, which are at densities below their bioeconomic equilibrium (Gordon, 1954); below which point single-species fisheries would normally cease to operate (Branch *et al.*, 2013). Unlike generalist species, which will shift the composition of their diet based on the relative abundances of prey (Smout *et al.*, 2010), humans see value in rarity and will continue exploiting depleted species as long as they are economically profitable (Courchamp *et al.*, 2006; Branch *et al.*, 2013); this is the case of the United States pelagic longline fishery where the main target species are swordfish (*Xiphias gladius*), big eye tuna (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*), but which still catches Atlantic bluefin tuna (*Thunnus thynnus*).

Impacts of size-based targeting: stock structure and recruitment

Selectivity in many marine fisheries extends past species preferences to the population level, leading to the asymmetric exploitation of stocks by age class, maturity status, behaviour, or morphology; all of which may act as selection pressures towards certain life history traits (Heino and Godø, 2002; Sharpe and Hendry, 2009). Any changes to these life history traits will affect the population's dynamics and structure, which in turn control factors such as abundance, growth rate or demography (Law and Grey, 1989; Conover and Munch, 2002; Jorgensen *et al.*, 2007).

Older age classes in fish populations are much more susceptible to fishing pressure, even at moderate levels than those of younger age-classes (Garcia *et al.*, 2012). Sibert *et al.* (2006) used long-term tuna fisheries catch data from the Pacific to determine that, from 1950 to 2004, fish larger than 175 cm decreased from 5% to 1% of the total population. The uneven exploitation of the larger individuals within fish populations has changed the age-class structure of many open-ocean populations, making them more vulnerable to fluctuations in inter-annual recruitment rates (Hsieh *et al.*, 2006). The age-structure of catches of *Thunnus orientalis* illustrate how biased fisheries harvest towards adult individuals has resulted in the age-truncation of the stock, where most of the catch (~90%) belongs to sexually immature age classes of 0–2 years (ISC Pacific Bluefin Tuna Working Group, 2016). These age-truncated stocks are more susceptible to experiencing booms and busts in recruitment, which makes them more vulnerable to stock collapses (Rochet and Benoît, 2011). The targeted exploitation of older age classes in open-ocean species may also lead to the loss of geographic substructure of populations, making them more vulnerable to environmental variability (Berkeley *et al.*, 2004; Ottersen *et al.*, 2006). Further, it can reduce the average reproductive potential of the population (Birkeland and Dayton, 2005; Anderson *et al.*, 2008)—as older age classes are more fecund (Denney *et al.*, 2002).

Unfortunately, it is uncommon for fisheries to record data on the size distribution of their catch since the initiation of fishing, particularly for species that are not of high commercial interest (Jackson *et al.*, 2001). The importance of recording these parameters is reflected in studies such as Ward and Myers (2005), which shows that continuous fishing of open-ocean predatory species can lead to reductions in their average body mass, which has implications to their life histories and ecological roles. They demonstrated that 11 of the 12 predatory species assessed experienced reductions in body mass between 29 and 73%. Changes in average body mass is one of the many alterations in life history traits or phenotypic characteristics attributed to fisheries exploitation (Walsh *et al.*, 2006; Sharpe and Hendry, 2009). Fishing may also reduce the age and size at maturation of exploited stocks (Rochet, 1998; Law, 2000; Jorgensen *et al.*, 2007). Although the causality of these changes is still contested—whether triggered by fisheries-induced genetic changes or environmental changes (Kuparinen and Merilä, 2007; Garcia *et al.*, 2012)—a study which analysed these trends in 143 fishing time series (from 37 separate stocks) asserts that the changes in maturation are highly correlated, and can be attributed to increases in fishing pressure (Sharpe and Hendry, 2009).

Impacts of size-based targeting: demographic changes

The traditional management approach of highly mobile oceanic species through single-stock assessments rarely consider the spatiotemporal information about stock connectivity and population structure and may thus obscure some of the ecological impacts of their exploitation. While catch metrics of a species may be steady across time in a fishery, not accounting for the spatial location of the catch may be masking local extinctions, range contractions, or structure-level effects in the stocks (Taylor *et al.*, 2011; Worm and Tittensor, 2011; Goethel *et al.*, 2012). Worm and Tittensor (2011) used multidecadal catch datasets to address the range-abundance relationship in stocks of 13 exploited marine predators and demonstrated range contractions in 9 of the 13 species

of tuna and billfish assessed, mostly along the edge of the ranges. Interestingly, they also quantified range expansions in two of the species (skipjack tuna (*Katsuwonus pelamis*) and sailfish (*Istiophorus platypterus*)), which may be a result of changes in the trophodynamics in their communities—such as predatory release, which we discuss later in this review. However, the range expansions of these two species were not replicated across ocean basins, highlighting the necessity of spatially discrete assessments on a regional basis.

Changes in range may also result from the asymmetric exploitation of populations. Oceanic species such as Atlantic swordfish (*Xiphias gladius*), exhibit differences in their ranges at different stages of their life cycle, where adult individuals display larger ranges. Thus, if particular age classes are targeted more heavily, changes in the realized niche of the species could take place (Neilson *et al.*, 2014). This asymmetric exploitation of the older age-classes across open-ocean taxa may also be removing the age-classes that are more physiologically tolerant, which could be leading to range contractions along the latitudinal edges of the range, where temperatures may only be tolerated by those age-classes.

Dulvy *et al.* (2003) suggest that dispersal and geographic range size play a role in regulating the risk of extinction of wide-ranging marine species, where large geographic ranges add an extra layer of ecological resilience by reducing their catchability at low densities. However, certain highly migratory species display dense annual aggregations on feeding and breeding grounds. This is the case of *Thunnus thynnus*, which congregate in northern part of the Gulf of Mexico and coastal waters in the Mediterranean to spawn; this life history trait can lead to heavy exploitation of even highly vagile stocks (Block *et al.*, 2001; Fromentin and Powers, 2005). Together with the truncation of stock age-structure, the loss of geographic substructure within populations makes them more susceptible to climate-induced alterations (Marshall and Browman, 2007) and genetic changes addressed below.

Impacts of size-based targeting: genetic changes

Another significant—yet more cryptic—impact on target and non-target species, comes in the form of genetic changes which, in the context of this review, we address as potential impacts given the lack of consolidated evidence of fisheries-induced genetic impacts on open-ocean species. The earliest evidence of induced variations in genetic traits in fish originated in aquaculture programs and experiments; these were induced in a short temporal window of just a few generations (Gjedrem, 1983; Garcia *et al.*, 2012). In wild fisheries, evolutionary changes may be induced by selecting against certain life history traits, through high selectivity towards size and age, and by removing large proportions of the population (Stokes and Law, 2000). For example, in the last half century, 26 harvested stocks of tunas and their relatives have been halved (Juan-Jordá *et al.*, 2011; see “Declines in abundance” section for further details).

Fishing-induced genetic changes can increase the risk of extinction and decrease the rate of recovery of overfished stocks (Olsen *et al.*, 2004; Walsh *et al.*, 2006). There are three main types of genetic change: alteration of sub-population structure, decrease in genetic variation and selective genetic changes (Allendorf *et al.*, 2008). Populations may be comprised of spatially discrete breeding groups (sub-populations) that, unless characterized

genetically, will be erroneously managed as a single, genetically homogenous population. For example, there is evidence that migratory species such as *Thunnus thynnus* show sub-population structure, which is not reflected in their management strategies (Fromentin and Lopuszanski, 2013). This lack of consideration of the genetic stock structure may not only be translating into reductions in genetic diversity at the population level, but also the sub-population level (Allendorf *et al.*, 2008).

There are two main ways to assess this variation: heterozygosity and allelic diversity. Reductions in heterozygosity of a population can be quantified through its effective population size, which is affected by factors such as demography, sex ratios and fecundity. By reducing the effective population size, selective fishing can thus exacerbate the loss of genetic variation (Allendorf *et al.*, 2008). On the other hand, loss of allelic diversity can be caused through high rates of both targeted or non-selective exploitation (Ryman *et al.*, 1995). Reductions in allelic diversity due to fishing pressure may also reduce the species' ability to adapt to changing climatic conditions and represents one way in which fisheries and climate (i.e. top-down and bottom-up controls on the system) may act synergistically on populations of marine species (Soule and Wilcox, 1980; Brander, 2007). While species can theoretically maintain levels of genetic heterozygosity during population bottlenecks, allelic diversity can be severely reduced in such events (Allendorf, 1986). Given very limited genetic research on open-ocean species, we can only address this as a potential impact of fishing pressure, likely of increasing relevance as the abundance of a species decreases.

Bycatch and other sources of inadvertent mortality

The impacts of fisheries on open-ocean species can extend beyond those taxonomic groups targeted commercially, through the unintentional catch of other taxa that is either unused or unmanaged; this catch is defined as bycatch. Pelagic longline fleets primarily targeting billfish and tuna are the most widespread fisheries in open-ocean systems (Worm *et al.*, 2005) and the source of most pelagic discards across ocean basins, together with midwater pelagic trawling and purse seining (Cook, 2003; Kelleher, 2005). Bycatch in open-ocean fisheries can incur high mortality rates and have been implicated in the collapse of many sea turtle (Wallace *et al.*, 2010), seabird (Anderson *et al.*, 2011), marine mammal (Lewison *et al.*, 2014), and shark (Dulvy *et al.*, 2008; Oliver *et al.*, 2015) populations. For example, bycatch of Pacific loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) turtles in pelagic longline gear have played a key role in the severe (>80% and >95%, respectively) declines in the nesting populations of these species over 20–30 years (Spotila *et al.*, 2000, Limpus and Limpus, 2003; Lewison *et al.*, 2004). Further, all 22 species of albatross and 19 of 21 oceanic elasmobranchs are listed as at least *Near Threatened* by the IUCN with bycatch cited as the main threat (Robertson and Gales, 1998; Dulvy *et al.*, 2008; Anderson *et al.*, 2011; IUCN, 2015).

Quantifying the global estimates of bycatch in the open-ocean remains a challenge due to lack of data (Alverson *et al.*, 1994; Kelleher, 2005). Gilman *et al.* (2014) estimated that two thirds of RFMO fisheries targeting open-ocean species lack adequate observer coverage, which is a basic requirement to obtain robust bycatch estimates. While global bycatch estimates are useful for starting the discussion on the impacts of bycatch of open-ocean species, taxa-specific studies for the main bycatch taxonomic

groups do exist: sea turtles, seabirds, marine mammals, and sharks (Wallace *et al.*, 2010; Anderson *et al.*, 2011; Molina and Cooke, 2012; Lewison *et al.*, 2014; Oliver *et al.*, 2015).

Open-ocean species have wide spatiotemporal distributions which can overlap significantly with the range of one or more pelagic fishing fleets (Block *et al.*, 2011). In a recent publication, Queiroz *et al.* (2016) quantified an 80% spatial overlap between the distributions of six species of oceanic shark and that of two longline fishing fleets, and noted how both sharks and fishermen were tracking similar biophysical cues in the marine environment. Given the high overlap, on-board monitoring of fisheries catch and bycatch must be comprehensive across fishing fleets, gear types and marine regions (Birdlife International, 2004; Queiroz *et al.*, 2016).

Just like highly mobile sharks, many of the open-ocean seabird species threatened with extinction, such as albatrosses and petrels, are wide-ranging species whose distributions overlap greatly with those of marine fishing fleets worldwide (Birdlife International, 2004). Mortality due to interaction with longline gear has been cited as a critical threat to these species (Klaer and Polackech, 1997; Brothers *et al.*, 1999; Tuck *et al.*, 2001). However, seabird bycatch mitigation measures have resulted in strong declines in seabird bycatch rates in many longline fisheries over the last decade (Gilman *et al.*, 2005). Similarly, sea turtle bycatch mitigation has also seen advances over the last two decades, though with more limited success than with seabird bycatch mitigation (Gilman *et al.*, 2006).

Quantifying the degree to which these pelagic species interact with fishing gear in the open-ocean is a very challenging issue given the small amount of information available on the distributions of both the animals and fishing fleets at high spatiotemporal resolutions; but as seen in Queiroz *et al.* (2016), improvements in tracking and vessel monitoring data are allowing for these types of inferences. This issue is catalysed by the low observer coverage and low bycatch reporting rates across open-ocean fisheries (Gilman *et al.*, 2014) and is not unique to seabirds, marine mammals, sea turtles or sharks, as a much wider spectrum of open-ocean species are caught as bycatch and are rarely reported or considered in the management strategies.

Other impacts of non-targeted catch

Other more cryptic sources of indirect or unaccounted mortality include pre-catch losses, which occur when an organism is caught and killed by fishing gear, yet it is not commercialized for reasons such as depredation by predatory species (Hernandez-Milian *et al.*, 2008), or simply because the catch or bycatch falls from the gear before it is hauled (Gilman *et al.*, 2014). Another source of mortality that is regularly unaccounted for in fisheries management and population models is that of post-release mortality, whereby specimens that are caught in fishing gear are released alive, but because of post-release stress and/or injuries, may later die (Gilman *et al.*, 2005; Campana *et al.*, 2009). Not accounting for these sources of mortality may lead to underestimation of bycatch mortality which can, in turn, compromise the quality of population models for those species (Gilman *et al.*, 2005; Coggins *et al.*, 2007; Molina and Cooke, 2012).

Understanding the post-release mortality of specimens that are discarded alive is of major importance, as it may otherwise lead to underestimations of bycatch-induced mortality (Coggins *et al.*, 2007, Molina and Cooke, 2012). A 2009 study used archival

satellite pop-up tags to quantify the mortality rate of one of the most frequently discarded fish species in marine open-ocean longline fisheries: blue sharks (*Prionace glauca*) (Campana *et al.*, 2009). They concluded that while all healthy sharks survived, over a third of those that were injured died within a few days/weeks, which, according to Skomal and Mandelman (2012) may be the result of disturbances in their behaviour or physiology. These findings on post-release mortality raise fundamental questions about true mortality rates of discarded species and how these may affect both stock-level and ecosystem-level models.

Another less acknowledged source of indirect mortality is the death by starvation of young individuals if the parent(s) on which they depend for feeding is killed. For example, if an adult albatross from a breeding pair is killed, the chick may starve to death and it may take years before the other adult albatross procreates again (Tasker and Becker, 1992; Brothers, 1995; Gilman *et al.*, 2005). Given their life history strategies, seabirds, and marine mammals may be more vulnerable to this type of indirect impact.

Community-level impacts (indirect)

Most of the impacts of fishing at the community level concern the trophic relationships and are tightly linked with changes at the species level. Changes in the trophic dynamics of the system are caused by: changes in species abundance, alterations of species size, and behaviour, and changes in the growth and reproductive rates of populations. The community-level impacts come in the form of imbalances in the trophic control mechanisms of the community, where the trophic pressure, feeding rate, or dietary composition of species have changed as a direct or indirect result of fishing pressure on open-ocean species. Top-down trophic control of prey abundance by higher trophic level organisms (Paine, 1980) can propagate across multiple trophic levels and is generally characterized by opposing changes in biomass from one trophic level to the next. This asymmetric trophic imbalance is known as a *trophic cascade* (Pace *et al.*, 1999).

Trophic cascades

In the last two decades, there has been a growing body of scientific literature which addresses the role of top-down trophic processes in defining the composition and structure of marine communities and how marine fisheries may be triggering changes in these dynamics (Cury *et al.*, 2000; Worm and Myers, 2003; Ainley *et al.*, 2007; Nicol *et al.*, 2007; Polovina and Woodworth-Jefcoats, 2013). Top-down trophic control of marine community composition, in the form of trophic cascades, has been demonstrated in variety coastal marine systems (Jackson *et al.*, 2001; coral reefs, Bellwood *et al.*, 2004; rocky intertidal ecosystems, Menge, 2000; kelp forests, Estes and Palmisano, 1974; and reviewed across coastal ecosystems, Pinnegar *et al.*, 2000; Steneck and Sala, 2005). However, detecting and characterizing these changes in open-ocean biological communities has proven to be a challenge. Data availability is the main factor limiting any effort to evaluate the impacts of fisheries on the integrity of marine populations, biological communities, and ecosystems (Colléter *et al.*, 2015), and explains why our understanding of open-ocean impacts has lagged behind coastal ecosystems (Webb *et al.*, 2010). Further, open-ocean pelagic food webs are highly dynamic and heterogeneous in composition, making them especially challenging to model in space and time. Despite the paucity of data and obstacles to model development, ecosystem-level models have

begun to reveal community-level impacts of marine fisheries on open-ocean communities (Kitchell *et al.*, 2002; Hinke *et al.*, 2004; Kitchell *et al.*, 2006; Polovina and Woodworth-Jefcoats, 2013). We review these models and the evidence for community-level impacts in open-ocean ecosystems below.

One of the best-studied regions for the impacts of fisheries on open-ocean communities is the Pacific Ocean basin, where a series of ecosystem mass-balance models have been assembled for this purpose. Hinke *et al.* (2004) reviewed the impact of commercial tuna fisheries in two published oceanic food-web modelling studies in the Eastern Tropical Pacific (ETP) and Central North Pacific (CNP) ecosystems. Although similar in terms of their biological structure, these systems differ in their fishery histories and in the composition of their target and bycatch species (Cox *et al.*, 2002; Olson and Watters, 2003). Based on the mass balance models, Hinke *et al.* (2004) concluded that increases in catch by the pelagic tuna fisheries (both purse-seine and longline gears) had similar impacts on the food-web structure in both systems: fishery-induced reductions in the top predators were followed by increases in the biomasses of lower trophic levels (Hinke *et al.*, 2004). The impacts of both fishing gear types were stronger in the upper trophic levels (particularly longline fisheries), while the purse-seine fishery seemed to have a more profound impact on the abundance of intermediate trophic levels.

Further empirical and model-based evidence for mesopredator releases in oceanic systems caused by declines in apex predator guilds is becoming plentiful (Carscadden *et al.*, 2001; Cox *et al.*, 2002; Ward and Myers, 2005). However, it is important to note that certain studies have not found such evidence, or only limited evidence of trophic cascades. This is the case of Botsford *et al.* (1997) and Pace *et al.* (1999), who made some of first comprehensive assessments of the potential impacts of marine fisheries. Both studies reviewed the potential trophic cascade in the Bering Sea stemming from fisheries-induced fluctuations in the abundance of pink salmon (*Oncorhynchus gorbuscha*) (Shiomoto *et al.*, 1997). However, the evidence was weak and was only statistically significant between two trophic levels (Shiomoto *et al.*, 1997). A report by the Western and Central Pacific Fisheries Commission recently demonstrated decreasing abundance trends in pelagic Hawaiian waters for five species of trophic level 4.0 or higher and increasing trends for four species of trophic level 3.9 or lower (Allain *et al.*, 2012). In another ecosystem modelling study of the Central North Pacific, Kitchell *et al.* (2006) assessed changes in community structure as a result of increases in fishing mortality of different predatory species (billfishes, sharks and tunas). They found that the removal of billfishes and sharks led to weak effects on the structure of the Central North Pacific marine community, suggesting that top predators in open-ocean systems may not always be keystone species. Increasing the fishing mortality of yellowfin tuna (*Thunnus albacares*), however, led to rapid changes in the trophic structure of the system, which was attributed to their role as both predator and prey. Nonetheless, they concluded that none of the predatory taxa were indispensable for the functioning of the ecosystem, as the dietary composition and range of many of the predators overlapped (Kitchell *et al.*, 2006). This question of the “keystoneness” of species in oceanic environments was partly addressed in a recent study, which quantified the keystone role of species in marine communities through three different indices in over 100 *Ecopath with Ecosim* (EwE) models; 19 of which were oceanic models (Valls *et al.*, 2015). Keystone species were identified in five of the models, however, only one of the models

belonged to an open-ocean ecosystem (Kitchell *et al.*, 2002); this model identified blue marlin (*Makaira nigricans*) as a keystone species in the Central Pacific Ocean. The limited evidence together with the opportunistic nature of feeding behaviour in the open-ocean suggests a limited role for keystone species in this environment.

The concurrent exploitation of multiple species, as seen in Kitchell *et al.* (2006), makes it more difficult for ecosystem modellers to discern the trophic mechanisms shaping the biological community. Perhaps with the exception of the pole and line fishery, most open-ocean pelagic fisheries are multispecies fisheries, which target different trophic levels simultaneously. The interaction between different fisheries targeting different trophic levels in the same ecosystem may offset fishery-induced trophic imbalances in the community (Andersen and Pedersen, 2010). In the CNP, it was demonstrated that the purse-seine fishery reduced the abundance of skipjack tuna, however, parallel declines in big eye tuna (*Thunnus obesus*), one of its natural predators, resulted in a partial predatory release on skipjack, which reduced the overall impact of fisheries on the community structure (Cox *et al.*, 2002). The simultaneous exploitation of different trophic levels may thus mask the trophic effects associated with declines of upper trophic level predators, which does not imply that there is no impact on the community, but that the depletion across trophic levels is not destabilizing.

In the context of a trophic cascade, declines in body size of apex predators can result in body sizes of lower trophic level taxa either being maintained or increased (Ward and Myers, 2005). A reduction in the average body size of a predatory species reduces the size ratio between predator and prey and can thus reduce the magnitude of the top-down trophic control that the predator exerts on the system (Woodward *et al.*, 2005). Animal body size is also positively correlated with parameters such as longevity and trophic status, and negatively correlated with factors such as the rates of growth and turnover of a species. Thus, changes in body size of species may affect the trophic interactions of the species, which in turn affect the stability and rate of propagation of trophic control mechanisms through the system (Emmerson and Raffaelli, 2004; Woodward *et al.*, 2005).

Recent studies have highlighted how these fishing-induced trophic imbalances caused by the heavy exploitation of predatory species may increase the abundance of commercially valuable fish species, thus allowing for the creation or expansion of fisheries that target these lower trophic level released prey (i.e. cultivation effects) (Brown and Trebilco, 2014). While the concept of fisheries benefiting from large-scale biomanipulation is not new (Brander, 2010; Lindgren *et al.*, 2010), caution must be exercised, as the food-web impacts of fishing may also lead to the proliferation of commercially unattractive species (Brown and Trebilco, 2014); as shown by Ward and Myers (2005) with the increase in pelagic stingray (*Dasyatis violacea*) abundance; an elasmobranch species of low commercial value (Báez *et al.*, 2015). Additional research demonstrates the proliferation of species of low economic interest for which no fisheries have been created (Carscadden *et al.*, 2001; Daskalov, 2002; Walters and Kitchell, 2001).

Non-consumptive effects

Decreases in the abundance of predatory species may also be causing changes in the behavioural dynamics of open-ocean

communities, which indirectly affect the trophodynamics. These are known as “non-consumptive”, “trait-mediated” or “risk” effects. Given that prey respond to the presence of predatory species through a series of traits aimed to reduce mortality, the reduction in top-down predator pressure may cause behavioural changes that propagate to other species groups in the community (Peacor and Werner, 2008). In certain cases, non-consumptive effects can also induce changes in prey growth and development (Peckarsky *et al.*, 2008). Better understanding of these dynamics may help explain top-down trophic controls in open-ocean systems (Baum and Worm, 2009).

Ecosystem-level impacts

Healthy marine ecosystems provide a series of services which maintain the functionality of the system and provide for a variety of societal needs, which include the provision of protein and micronutrients for millions of people worldwide (Holmlund and Hammer, 1999; Postel *et al.*, 2012). Fisheries mismanagement, overfishing, bycatch, and IUU fishing not only threaten the availability of food for millions of people, but may also lead to irreversible changes in the integrity and state of marine ecosystems and the ecosystem services they provide. Fisheries are thus considered a key industry in addressing food security concerns (Godfray *et al.*, 2010; FAO, 2014). Our understanding of the ecosystem-level impacts of biotic exploitation in coastal systems is very developed. Studies have shown that the impacts of fisheries exploitation range from alterations in primary productivity and changes of the physical environment, such as coastal erosion (Estes and Duggins, 1995), to changes in both ecosystem structure and function at large spatial scales (Dulvy *et al.*, 2004). In the case of coastal reef systems, it has been demonstrated that the overharvesting of higher trophic level species has led to profound changes in ecosystem structure and function (Dulvy *et al.*, 2004). Because the ecosystem-level impacts in offshore oceanic fisheries are less well studied, inferences from studies of similar systems must pave the way for new research avenues.

Changes in ecosystem-state and biodiversity

In the open-ocean, where the water column generally lacks physical habitat, changes at the ecosystem level are mostly expressed as transitions between alternative states of the ecosystem. These “regime shifts” affect both the system’s dynamics and functionality (Scheffer and Carpenter, 2003; Daskalov *et al.*, 2007; de Young *et al.*, 2008; Beaugrand *et al.*, 2015). In the marine realm, this concept was first applied to describe synchronicities between climatological and fish stock indices in coastal ecosystems (Steele, 2004; Wooster and Zhang, 2004) and since then, it has been used to describe general disruptions of ecosystem structure and function (Möllmann and Diekmann, 2012). Although regime shifts can be induced through anthropogenic stressors, most of the studied regime shifts in pelagic marine systems have been triggered by large scale climatological processes, which have led to structural changes in the functioning of the biological community (Hare and Mantua, 2000; Möllmann *et al.*, 2009). This review focuses on the role that a top-down anthropogenic stressor—in this case, open-ocean fisheries—can play in triggering regime shifts in open-ocean ecosystems and how they may interact with other drivers such as climate to reach these tipping points or stability thresholds.

A shift between ecosystem states depends on two main factors: the magnitude of the perturbation (whether anthropogenic or

natural, biotic or abiotic) that drives the shift, and the current condition of the ecosystem when the perturbation takes place, a concept known as the “size of its attraction basin” (Scheffer *et al.*, 2001; Scheffer and Carpenter, 2003; Möllmann and Diekmann, 2012). Based on this concept, there is an inverse relationship between the integrity of the ecosystem and the magnitude of the stressor which would lead to a regime shift: where a weak stressor may cause a regime shift in a “stressed” system and a much larger stressor would be needed to have the same effect on a “healthy” system (Möllmann and Diekmann, 2012). Stressed systems, where reductions in biodiversity or changes community structure have taken place, will have a smaller attraction basin, which translates to a reduction in the levels of perturbations that they can withstand, i.e. its resilience. Ample evidence from studies in pelagic, non-oceanic systems supports the claim that regime shifts are more likely to occur when the resilience of an ecosystem is diminished by actions such as the reduction of biodiversity, removal of functional groups of species, or trophic levels from a biological community (Folke *et al.*, 2004; Worm *et al.*, 2006).

Different studies have concluded that commercial fishing is the main driver of long-term loss of diversity in open-ocean predators across all ocean basins in addition to reductions in oceanic predator abundance and size (Worm *et al.*, 2005; Ward and Myers, 2005). While some of these studies have been criticized (reviewed in Banobi *et al.*, 2011), those critiques question the magnitude of the declines in the abundance of species, not the impact of loss of biodiversity on the system. Given the connection between fisheries and biodiversity loss in open-ocean ecosystems, it is unsurprising that fisheries exploitation has also been implicated in regime shifts in pelagic systems (Daskalov *et al.*, 2007; Möllmann *et al.*, 2009).

Worm *et al.* (2006) alleged that these losses in marine biodiversity could compromise the ability that marine ecosystems have to provide ecosystem services such as seafood provisioning. Over the last 60 years the biodiversity of open-ocean predators across all ocean basins has declined between 10 and 50%; these trends coincide with increases in fishing pressure, while no trend was found between these changes in diversity and major decadal changes in oceanography during the study period (1960s–1990s) (Worm *et al.*, 2005). It is noteworthy that the declines in tuna and billfish diversity were more pronounced in intensely fished tropical areas, where species richness and density had a strong inverse relationship with fisheries catch values from the 1950s until the early 2000s (Worm *et al.*, 2005).

Evidence of regime shifts in pelagic systems

No fishing-induced regime shifts have been identified in open-ocean ecosystems as defined by this paper. However, a number of very large pelagic ecosystems (e.g. enclosed seas and continental shelves) have encountered regime shifts, and are reviewed here to illustrate the potential for regime shifts to happen in dynamic pelagic systems. Although there is a lack of empirical evidence of abrupt ecosystem-level oceanic changes induced solely by fishing, heavy fisheries exploitation may be gradually corroding the resilience of the system by reducing its biodiversity and restructuring its biological community; making it more vulnerable to regime shifts when exposed to changes in climate. However, the relationship could be reversed if climatological factors push the system towards a tipping point, which is reached by the top-down pressure of fisheries.

Subsequent studies have evaluated the community-level trophic changes that have taken place in the Eastern Scotian Shelf ecosystem along with the collapse of the stock of Atlantic cod (*Gadus morhua*), to assess the ecosystem-level changes in the Eastern Scotian Shelf from 1960 to 2002 (Choi *et al.*, 2004, 2005). The analysis revealed ecosystem changes of the system during the 1970s and 1990s, and identified that changes in variables related to the abundance of upper trophic level species and conditions of these, such as size and body mass, were the principal explanatory elements of the ecosystem changes in the 1990s (Choi *et al.*, 2005). The author, however, stated that the fishery-induced changes could not explain the ecosystem shift alone. Further multivariate analysis demonstrated that climatological changes between the mid-1970s and late 1980s and between the late 1980s and late 1990s, in the form of changes in water temperature or oceanic front positions, interacted with the fisheries-induced ecological effects and led to the regime shift of the system. Kenny *et al.* (2009) reached similar conclusions in the North Sea, where the authors interpreted that abiotic changes, in the form of an abrupt water temperature increase by the late 1980s, catalysed the shift in ecosystem state, which had most likely been started by the interaction of intense fishing pressure and gradual sea surface warming (Beaugrand, 2004). The state shifts described by the authors (1983–1993 and 1993–2003) involved a change in the control mechanisms for the pelagic stocks, from top-down (fishery) control prior to the shift, to bottom-up (climatological) control after the regime shift (Kenny *et al.*, 2009).

The Black Sea ecosystem has undergone profound ecological changes since the 1970s, and may be a good indicator of how the cumulative impacts of biotic, abiotic, and anthropogenic stressors can lead to several shifts in states in large pelagic systems (Daskalov *et al.*, 2007; Oguz and Gilbert, 2007). Although the Black Sea is almost an entirely land-locked basin, which does not fulfil all the requirements of what we define as an open-ocean ecosystem, we find that its characteristics (e.g. average depth of 1253 m and holopelagic community) are similar enough to that of open-ocean marine ecosystems to be used as a comparative example. From 1960 to 2000, the Black Sea experienced multiple regime shift episodes that were triggered by fisheries exploitation, changes in its biological community, climatological events, and eutrophication (Oguz and Gilbert, 2007). The depletion of pelagic stocks caused a trophic cascade in the ecosystem, which together with abiotic changes in the system (nutrients and temperature), led to a regime shift in the early 1970s. Carnivorous plankton became a dominant taxonomic group until the pelagic fish populations recovered during the late 1990s. Their recovery acted together with a reversal of the climatic state and reductions in nutrient loading, to revert the system to its original “low production” regime state (Oguz and Gilbert, 2007).

Restoring the state of a system to that prior to a regime shift is a challenging objective. Not only is it unlikely that an ecosystem is able to return to its original state, but also studies show that adjusting the sources of external pressure (e.g. fishing) to the levels prior to the shift, will be costly and insufficient to restore the biotic balance (Möllmann and Diekmann, 2012). Different studies indicate that restoring the ecosystem balance would require a reduction of external pressures at much more pronounced levels than the original levels that led to the regime shift which, in terms of fisheries, would imply significant socio-economic impacts (Suding *et al.*, 2004; Möllmann and Diekmann, 2012).

Discussion

All types of marine systems, including coastal, open-ocean and deep sea ecosystems, can be subject to the three types of fisheries-induced ecological impacts discussed in this paper. The way these impacts are manifested across ecosystems and the recovery rates of the systems vary. Species-level impacts from fisheries in open-ocean ecosystems are (or are likely to be) the same as those impacts on coastal or deep sea ecosystems. Evidence for community level impacts that mimic coastal and deep sea ecosystems also exists in open-ocean ecosystems, though much longer time-series have been required to identify them. The major difference between the systems comes in the form of ecosystem-level impacts. In oceanic ecosystems, these take the form of changes in biological community structure, composition, and dynamics and no evidence of impacts on the abiotic environment have been identified to date. On the other hand, the ecosystem level impacts on coastal and deep sea ecosystems can result in the deterioration of physical habitat such as (tropical or cold-water) coral reefs or result in biochemical changes in the fluid environment (Jackson *et al.*, 2001) in addition to population, community, and ecosystem-level impacts.

Beyond differences in impacts to coastal, deep sea and oceanic ecosystems, there are difference in governance that directly influences our ability to monitor, understand, and manage impacts. Unlike nationally managed coastal fisheries, deep sea, and oceanic fisheries cross jurisdictional boundaries and are largely managed through international agreements. Among its many mandates, the 1982 UN Convention on the Law of the Sea (UNCLOS) requires Parties to cooperate in the establishment of regional or subregional fisheries management organizations, intended for the conservation and management of living resources within jurisdictional waters and the high seas (Part VII, Section 2, Article 118) (UNCLOS, 1982). UNCLOS entered into force in 1992 and by 1995 had been built on by the UNFSA (1995). The UNFSA promoted the conservation and management of straddling and highly migratory fish stocks through an ecosystem-based approach (UNFSA, 1995: *General Principles—Article 5*), exercised both within and beyond the 200 nm jurisdictional boundary of coastal states. The components of the ecosystem approach are derived from the mandate in the UNFSA, and laid out specifically in a FAO technical report (Garcia *et al.*, 2003) and the Code of Conduct for Responsible Fisheries (FAO, 1995; UNFSA, 1995). The mandate includes requirements for monitoring and managing impacts not just on target species, but to “species belonging to the same ecosystem or associated with or dependent upon the target stocks” (FAO, 1995; UNFSA, 1995).

Although an ecosystem approach to fisheries has been incorporated into the mission of many RFMOs, Gilman *et al.* (2014) found that up to five of the 17 RFMOs do not work towards mitigating their impacts on non-target fish species and non-fish species, while the rest undertake actions with different success rates. While some tuna-RFMOs have expanded their management efforts to account for impacts on other species groups such as sharks, the current, single-stock assessment approach that dominates RFMO management does not account for impacts on non-target species and the marine biological community as a whole. Gilman *et al.* (2014) further estimated that only one third of the bycatch problems are addressed through legally binding measures and that over two thirds of RFMO fisheries lack adequate observer coverage.

This lack of observer coverage feeds into a more general problem that underlies why it has taken so long to identify impacts of fisheries on open-ocean ecosystems: the limited number of complete and reliable multispecies fisheries catches time series. In this manuscript, we have demonstrated the importance of long-term multispecies catch datasets and stock assessments for understanding not just population-level impacts on target and non-target taxa, but also to parameterize community-level mass-balance models to demonstrate community and ecosystem-level impacts of fishing on the open-ocean. However, such datasets are based on observer monitoring programs which are still absent in many RFMOs. At least one RFMO with competency for pelagic species had no observer coverage as of 2013 (Gilman *et al.*, 2014). As monitoring strategies improve across RFMOs, more pressure should be placed on fishing nations, which have the responsibility of submitting high quality observer data so that RFMOs can do their job effectively. Further attention will have to be placed on the spatial coverage of observer programs of each fishing nation. The biases in taxonomic identification and spatial coverage across fisheries and RFMOs contribute and widen some of the current knowledge gaps about fisheries impacts on certain species. In a recent study on the global trends of shark bycatch, Molina and Cooke (2012) highlighted the regional and taxonomical bias found in 103 papers on shark bycatch, and noted that the South Atlantic, South Pacific, and Indian Oceans and commercially unimportant shark species (such as species of the order Hexanchiformes and Orectolobiformes) were underrepresented in the shark bycatch literature.

If long-term multispecies monitoring programs are not established, we will continue to remain blind to the broader ecological impacts of fisheries on open-ocean ecosystems and at risk of failing to recognize early warning signals of trophic cascades or fisheries-induced regime shifts. To ensure the sustainability of open-ocean fisheries, the extent and thematic coverage of observer programs must be increased and include non-target species, as well as other forms of monitoring such as community-level modelling efforts and genetic sampling. Genetic monitoring of harvested wild populations is the most powerful method of tracing genetic changes induced by exploitation (Allendorf *et al.*, 2008).

A number of challenges to effective monitoring of open-ocean ecosystems by RFMOs exist. Competency for the management of species in a single ocean basin can be divided among RFMOs, leading to shared management of resources and impacts. Strongly coordinated monitoring by RFMOs of a shared ecosystem is essential. While RFMOs clearly have a duty to monitor ecosystem components beyond target species, even strong coordination among RFMOs is unlikely to be sufficient to monitor species, community, and ecosystem level indicators given current budgets. There is a strong need for enhanced cooperation between organizations with competency for managing open-ocean ecosystems and large-scale biodiversity monitoring programs like the Global Ocean Observing Systems (GOOS). Similarly, the analytical requirements related to monitoring of ecosystem impacts go beyond the capacity of the RFMOs and may require collaborations with industry and academic institutions. The current barriers to such collaborations are largely constructed from lack of funding, poor communication on all sides, and data availability. Only by increasing coordination within RFMOs, cooperation between RFMOs and other competent organizations, and collaboration

between RFMOs, industry, and academia will begin to be able to appropriately monitor, and thus, manage open-ocean ecosystems.

The cost of mismanaging open-ocean biological resources extends from the ecological dimension into the socioeconomic dimension. Evidence indicates that reversing the ecological impacts of regime shifts would be more costly in socioeconomic and management terms than applying a precautionary approach, which would prevent the shift in ecosystem state by avoiding trophic imbalances and loss of biological diversity (Suding *et al.*, 2004; Möllmann and Diekmann, 2012). Moreover, given that in 2013 fish represented 17% of the global intake of animal protein (FAO, 2016), the social cost of unhealthy open-ocean ecosystems in the terms of food security is too high to ignore. With human population estimates exceeding 8 billion in 2025 and reaching up to 9.7 billion in 2050, it becomes incontestable that the management of marine fisheries and their impacts in the open-ocean over the next few decades will have implications in both ecological and human dimensions worldwide (FAO, 2016).

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