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Not all who wander are lost: Improving spatial protection for large pelagic fishes

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ABSTRACT

Spatial protection measures have become ubiquitous in fisheries management and marine conservation. Implemented for diverse objectives from stock rebuilding to biodiversity protection and ecosystem management, spatial measures range from temporary fisheries closures to marine protected areas with varying levels of protection. Ecological and economic benefits from spatial protection have been demonstrated for many reef and demersal species, but remain debated and understudied for highly migratory fishes, such as tunas, billfishes, and pelagic sharks. Here we summarize the spatial extent of fisheries closures implemented by the tuna RFMOs as well as marine protected areas worldwide, which together cover ~15% of global ocean area. We furthermore synthesize results from modeling and tagging studies as well as fisheries-dependent research to provide an overview of the efficacy and benefits of present spatial protection measures for large pelagic fishes and their associated fisheries. We conclude that (1) many species with known migration routes, aggregating behavior, and philopatry can benefit from spatial protection; but (2) spatial protection alone is insufficient and should be integrated with effective fisheries management to protect and rebuild stocks of highly migratory species. We suggest tailoring spatial protection to the biology of large pelagic fishes, including improved protection for aggregation sites and migration corridors. These features currently appear to be an important—yet overlooked— opportunity to safeguard depleted and recovering stocks and protect pelagic biodiversity. New remote-sensing tools that track pelagic fishes and fishing vessels may provide timely support for improved spatial management in waters that were previously difficult to observe.

1. Introduction

Motivated in part by explicit international conservation targets, the last two decades have seen a large increase of ocean area placed under some form of spatial protection [1]. While most countries have committed to specific marine protection goals (e.g., 10% of national waters), spatial protection initiatives are highly varied and include both large-scale fisheries closures aimed at safeguarding heavily fished stocks as well as marine protected areas (MPAs) designed to protect marine biodiversity more broadly [2]. The rapid pace of MPA establishment in particular has gained much attention, especially due to the creation of very large MPAs (> 100,000 km^2) in recent years [3,4] (Fig. 1). Here, fisheries closures are defined as spatially discrete management measures that restrict certain gears or fleets for defined amounts of time to aid with the management of fish stocks [5]. MPAs, in contrast, are designed to achieve long-term conservation of biodiversity on a broader scale [6]. Although the conservation of biodiversity is a primary objective [2], MPAs are often also expected to benefit nearby fisheries by increasing local fish abundance, biomass, and larval supply. Yet most empirical examples of such 'spillover' effects focus on small, nearshore MPAs and non-migratory species such as lobster [7,8], clams [9], scallop [5] and reef fishes [10–14]. In contrast, potential benefits of closed areas for highly mobile large pelagic fishes such as tunas, billfishes, and pelagic sharks, have received less scientific attention, mostly because their highly migratory nature presents a substantial challenge for the design, implementation, and evaluation of such initiatives. Note, however, that despite similar limitations, spatial protection strategies have been studied and discussed in some detail for migratory sea birds [15–18] and turtles [19,20]. Available studies demonstrate the importance of spatial protection during vulnerable life stages such as nesting and breeding periods, as well as for juveniles to reduce interactions with fisheries [15,17]. In this paper, we are interested in exploring whether similar benefits of targeted spatial protection may occur for highly migratory fishes, and how existing spatial protection measures could be improved to maximize possible benefits for those stocks and associated fisheries.

Fisheries for highly migratory species now support some of the world's largest seafood markets and also play a vital role in ensuring the socio-economic stability and food security of many low-income and small island nations [21,22]. As these fisheries extend across multiple national waters and the high seas, cohesive multilateral governance of the fisheries targeting these species is essential. At present, 18 major

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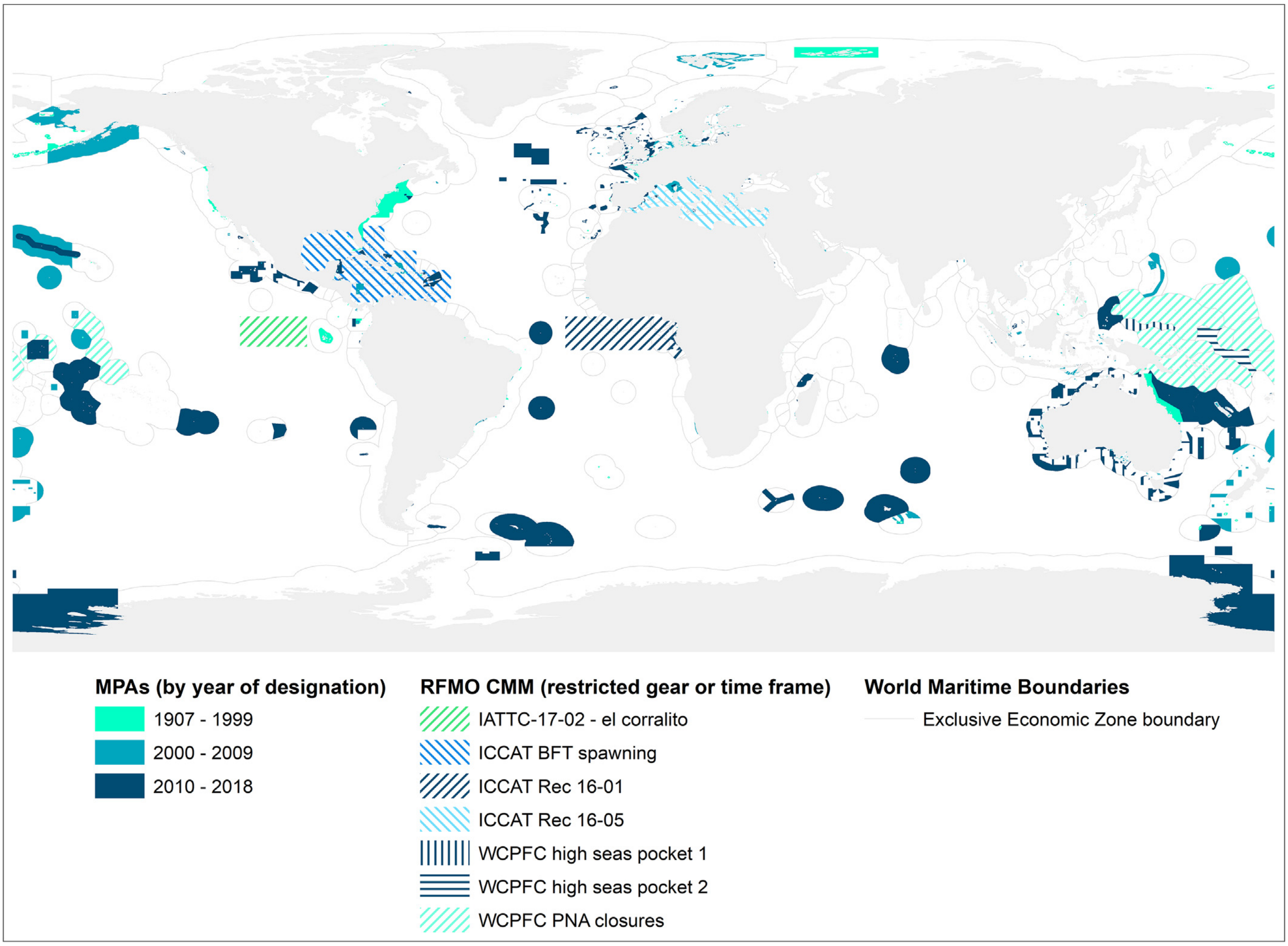

Fig. 1. Locations of MPAs and fishery closures around the world. Marine protected areas (MPAs, solid patterns) are color coded by year of establishment as reported by the World Database on Protected Areas in 2018 (www.protectedplanet.net). Active spatial Conservation and Management Measures (CMMs, hatched patterns) implemented by Regional Fisheries Management Organizations (RFMOs) are typically seasonal or gear specific closures. The temporary closure of the entire IATTC Convention Area in the Eastern Tropical Pacific (IATTC 17-02) is not included; it was classified as a fisheries management measure rather than a closure as it comprises the whole convention area. Marine protected areas shown here cover about 7.6%, and RFMO CMMs cover about 7.4% of total ocean area. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Regional Fisheries Management Organizations (RFMOs) exist around the globe, out of which five are responsible for the management of the world's tuna stocks. Fishing pressure for highly migratory species under RFMO management has proven hard to monitor and control due to a variety of factors: variable biological characteristics of target species [23,24], competing fishing interests [25–27], unequal conservation burdens between nations in the global North and South [28,29], limited transparency in decision making [30], as well as incomplete monitoring of fishing activity [31–33].

Complementing the efforts of RFMOs, multilateral international agreements (e.g. *Convention on International Trade in Endangered Species of Wild Fauna and Flora [CITES], Convention on Migratory Species [CMS]*) also seek to promote improved management and conservation of certain pelagic fishes, mostly through regulation of trade. Likewise, the UN General Assembly in 2015 called for an amendment to the UN Convention on the Law of the Sea (UNCLOS) to explicitly address the conservation and sustainable use of marine biological diversity of areas beyond national jurisdiction (Resolution 69/292). Since then, spatial protection and management strategies (including MPAs) have been identified as a key topic for discussion (see http://www.un.org/depts/los/biodiversity/prepcom.htm).

The analyses presented in this paper are thought to support these efforts and highlight options for improved spatial protection of pelagic fishes. We address the following questions: (1) is improved protection of migratory species warranted? (2) how suited different are pelagic species for spatial protection given their particular life history and management attributes? (3) what is the current global coverage of spatial protection measures for these species? (4) what are the documented benefits of current protection measures? and (5) how can the degree of spatial protection be improved?

We focus herewith on major commercially targeted highly migratory species (Table 1) including the tropical and temperate tunas (*Thunnus* and *Katsuwonus* genera), billfishes (swordfish [*Xiphias gladius*], marlins [*Istiophoridae* family]) and pelagic sharks (such as mako [*Isurus* sp.], great white [*Carcharodon carcharias*], thresher [*Alopias* spp.], silky [*Carcharhinus falciformis*], and blue shark [*Prionace glauca]*). The unifying characteristics of this diverse group of species is that they are highly mobile, undertake long-distance horizontal movements through the pelagic environment, are currently exploited by commercial fisheries, and are collectively managed through RFMOs.

2. Methods

We amalgamated available information from peer-reviewed and

Table 1
Characteristics of major commercial species discussed in this study. IUCN red list status categories: CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened, LC = least concern. Suitability for spatial management was assessed based on the specific life history attributes of each species.

Species	Defined migratory routes	Aggregation	Philopatry	RFMO harvest control rules	Targeted spatial management	Stock assessment	IUCN red list status*	Suitability for spatial management
Southern bluefin tuna (*Thunnus maccoyii*)	✓	✓	✓	✓	✗	✓	CR	High
Atlantic bluefin tuna (*Thunnus thynnus*)	✓	✓	✓	✗	Western Stock	✓	EN	High
Pacific bluefin tuna (*Thunnus orientalis*)	✓	✓	✓	✗	✗	✓	VU	High
Bigeye tuna (*Thunnus obesus*)	✗	✓	✗	Pacific stocks	Pacific stocks	✓	VU	Medium
Common thresher shark (*Alopias vulpinus*)	✗	✓	✓	✗	California	some (NOAA)	VU	Medium
Shortfin mako shark (*Isurus oxyrinchus*)	✗	✗	✓	✗	national shark sanctuaries	✓	VU	Medium
Silky shark (*Carcharhinus falciformis*)	✗	✗	?	✗	national shark sanctuaries	some	VU	Medium
Albacore tuna (*Thunnus alalunga*)	✓	✓	✓	North Atlantic stock	Mediterranean	✓	NT	High
Yellowfin tuna (*Thunnus albacares*)	✗	✓	✗	Pacific stocks	Pacific stocks	✓	NT	Medium
Blue shark (*Prionace glauca*)	?	✓	✓	✗	national shark sanctuaries	✓	NT	Medium
Skipjack tuna (*Katsuwonus pelamis*)	✗	✓	✗	Pacific and Indian Ocean stocks	Pacific stocks	✓	LC	Medium
Swordfish (*Xiphias gladius*)	some	✗	✓	✗	✓	✓	LC	Medium

*refers to global status, as listings may vary for regional stocks.
Key sources: [34–40].

grey literature regarding the use of spatial closures for large pelagic fishes. Key search terms on Google Scholar used alone and in combination included: *Marine protected areas, marine reserves, spatial management, protection for highly migratory species/tunas/sharks, large pelagics, fisheries closures,* and *benefits of protection*. We reviewed the extracted papers and key references within them. Available information on current MPA coverage was extracted from databases such as protectedplanet.net and MPAtlas.org. Information on RFMO-led spatial conservation and management measures (CMMs) was derived from the respective RFMO websites in order to quantify the current extent of spatial closures for large pelagic fishes at the multi-national level.

3. The case for improved protection

Large pelagic fishes are regionally abundant and of high commercial value; yet a long life span and high age at maturity can render some species vulnerable to overexploitation [41]. Many populations of large tuna species have been depleted to 10–25% of their virgin spawning biomass (SSB_0) [42–45], some with extreme depletion (i.e., > 95%) such as observed in Pacific bluefin tuna (*Thunnus orientalis*) [46]. In addition to changes in abundance, the spatial ranges of all three bluefin tuna species appear to have shrunken significantly since 1960 [47]. Recent assessments suggest five of seven billfish stocks in the Atlantic Ocean are overfished [43] and, in the western and central Pacific Ocean, striped marlin (*Kajikia audax*) has been subject to overfishing since 1977 [48]. Of five assessed Indian Ocean billfish stocks, only swordfish is considered healthy [164]. Furthermore, global range contractions have been observed for black (*Istiompax indica*), striped, and white marlin (*Kajikia albida*), as well as sailfish [47].

The case for improved oversight and protection appears even more pressing for pelagic sharks, with about half of them classified as threatened [49,50]. Like billfishes, these species are susceptible to high mortality from incidental capture in tuna longline fisheries [51,52], yet they are also targeted directly to meet the demand of a lucrative market for their fins and other products such as meat and liver oil [50,53,54]. Given the high degree of unreported catch, as well as noted incidents of illicit shark fishing in protected waters, much of the world's shark catch is contextualized as illegal, unreported, or unregulated (IUU), which poses significant challenges to conservation [55–57].

4. Suitability for spatial protection

The suitability of highly migratory species for spatial protection has been extensively probed by modeling studies and, to a lesser extent, by empirical observation. We consider results from these two approaches in turn and highlight species life history traits that may affect their suitability for spatial protection.

Multiple modeling studies have suggested that highly mobile fish stocks within a system that includes closed areas appear more resilient to collapse, and fisheries yields are higher over time, when contrasted with a scenario that lacks spatial protection [58–61]. These benefits are predicted to be especially pronounced where fishing morality is difficult to control, IUU fishing prevails, or fisheries are mismanaged [62]. For example West et al. [58] and Apostolaki et al. [61], both showed with single-species population models that yields of the target species, population persistence, as well as resilience to overexploitation were higher in a modelled environment containing a protected area than without spatial protection.

Closed areas and MPAs may thus serve as buffers against overexploitation under the precautionary principle [63,64]. Yet, not all species discussed here are equally suited for spatial protection, mainly due to variation in their distribution and behavior, including philopatric behavior and site fidelity (Table 1), migration along fixed pathways, and aggregation for spawning. In the following we discuss how such life history variables may affect the efficacy of spatial protection measures.

4.1. Distribution and behavior

The suitability for spatial protection of any species relates to its spatial distribution and how this distribution changes over time. Individuals of any given species are neither randomly, nor homogenously distributed through time and space: Responses to environmental heterogeneity as well as inherent behavioral differences are assumed to govern the distribution of individual fishes [65]. This could include, for example, variations of movement rates of individual tuna [66]. While some fish disperse over wider areas or travel farther distances, others remain closer to areas where they have hatched, or return to aggregate in breeding, nursing, and feeding areas such as specific coastal regions or around hydrographic or bathymetric features such as seamounts [67,68]. It is thus well understood that the vulnerability of large pelagics to fishing pressure varies with both location and life stage [69,70] and movement patterns and behavior strongly influence the response of pelagic fishes to particular management and conservation measures [71]. The reduction of area-specific threats especially in frequently used habitats might therefore lead to disproportional benefits relative to the size of the protected area [69]. This is particularly important as predictable aggregations are often preferentially targeted by fisheries, rendering the targeted species more vulnerable to overfishing [68].

According to a majority of modeling studies simulating the effects of spatial protection, a species' movement rate within and between habitats is identified as a key variable—the higher their mobility, the lower the predicted efficacy of spatial protection fixed in space [61,72]. An empirical example of this process concerns bigeye tuna (*Thunnus obesus*) in the Central Pacific [73] (discussed below); however, such field studies are not common as dedicated spatial management exists for only 7 out of 40 stocks of major commercial tunas and billfishes examined by Pons et al. [24].

In addition to movement rates, the type of movement and the stage of life at which it occurs [74] further influence the effects of spatial protection on migratory species. These include diffusive movement, dependence on home ranges, and density-dependent and independent movements, the latter including adult and ontogenetic migrations [72]. The degree to which species movement and aggregation patterns are predictable in space and time plays a major role in determining their suitability for protection (Table 1).

For example, Atlantic (*Thunnus thynnus*), Pacific, and southern bluefin tuna (*T. maccoyii*) return to well-defined spawning and feeding areas each year via known migratory routes [42,46,75]. Likewise, for bigeye tuna in the Pacific Ocean, spawning and feeding movements within restricted home ranges are quite well known [76]. For predictable cases like these, "targeted" closures [77] such as a closure in the Gulf of Mexico for Atlantic bluefin tuna, may be effective in protecting vulnerable life stages in defined areas such as spawning sites.

This strategy, however, may not be as suitable for opportunistic spawners, such as yellowfin tuna (*Thunnus albacares*), which are less bound to particular locations [78]. Likewise, skipjack tuna (*Katsuwonus pelamis*) are not known to follow predictable spawning or feeding migration patterns, and changing environmental conditions are thought to play a primary role in driving their dynamic movement patterns [79]. A modeling study of the Chagos MPA in the Western Indian Ocean demonstrated the importance of design and scale of spatial protection for such "unpredictable" fish species [59]. This MPA was found to have little effect on skipjack tuna stocks due to strong seasonal variations of habitat conditions that drive stocks into and out of the MPA. In contrast, a much larger hypothetical fisheries closure covering large parts of favorable habitat for skipjack tuna was predicted to stabilize spawning stock biomass (SSB) and yield higher catches over a 20-year especially compared to a contrasting scenario without any closure [59].

4.2. Philopatry and site fidelity

Philopatry is the tendency to return to certain areas repeatedly, which increases the value of spatial protection for such areas. Strong philopatric behavior has been demonstrated for many pelagic fishes. For example, Chapman et al. [80] reviewed more than 80 publications for residency and site fidelity in 31 shark species, including at least 6 migratory species. Based on tagging studies as well as DNA analyses, different philopatric behaviors, e.g. feeding site fidelity, were identified in large pelagic sharks such as tiger sharks (*Galeocerdo cuvier*) and great white sharks [80]. Often found at predictable locations, e.g. in South Africa and Australia [81], great white sharks exhibit repeated homing behaviors to specific places on fixed routes [82]. For example, an offshore region in the central Northeast Pacific is frequently visited by Californian great white sharks, followed by homing behavior to very specific coastal sites [82]. The same areas can be frequented by multiple species, as seen in Cleveland Bay, Australia, which is used as a communal nursery area by eight different species of the Carcharhinidae (requiem sharks) and Sphyrnidae (hammerhead sharks) [83]. Similar repeated returns to specific nursery areas in the North Atlantic were shown for oceanic blue sharks [84].

Site fidelity, aggregation, and restricted movement patterns were also described for several tuna species such as Atlantic bluefin tuna, with an eastern stock that spawns in the Mediterranean Sea and a western stock that returns annually to spawn in the Gulf of Mexico—with stock mixing in both these sites as well as on foraging grounds [85]. Similarly, Pacific bluefin tuna have specific spawning grounds in the East China Sea and the Sea of Japan [86]. Southern bluefin tuna spawn off Java in the Indian Ocean, with juveniles (2–5 years old) undertaking seasonal migrations to the Great Australian Bight, New Zealand or South Africa, and older fish dispersing widely throughout the southern hemisphere from 50 to 30°S [87].

While some individuals leave and return, others remain in the same region throughout their lives: Some populations of yellowfin, skipjack, and bigeye tuna exhibit such restricted ranges [88–90]. Around the Hawaiian Islands, for example, yellowfin tuna were found to have displacement distances of only 50 km [91,92] as well as high retention rates with 91% of sub-adult yellowfin in the Hawaiian Islands originating from a known spawning ground there [90]. Populations like these appear to be ideal candidates for spatial protection measures.

5. Current spatial protection measures

According to our analysis, unilaterally established MPAs and RFMO fishery closures targeting large pelagic fishes now cover nearly 15% of global ocean surface, in approximately equal proportions (Fig. 1). This means that collectively more than 50 million km^2 of ocean area are under some spatial management that could potentially benefit large pelagic fish stocks.

As of the beginning of 2019 MPAs cover about 7.6% of global ocean surface area and range from small, coastal MPAs to large, offshore area of up to 2 million km^2. Fisheries closures, both seasonal and permanent time-area or gear-specific closures currently cover about 7.4% (Fig. 1). Although some of these measures date back several decades, most have been established since the early 2000s. While MPAs are typically fixed in space and permanent and usually declared by individual countries within their exclusive economic zone (EEZ), fisheries closures are also multilateral and managed at RFMO level, more dynamic and may be adapted to changing conservation objectives over time [69,72,93].

In the following we discuss documented effects of both spatial fishery closures and MPAs on large pelagic fishes differentiating unilateral, national protection measures from multilateral, RFMO-led measures while highlighting a number of empirical case studies (Table 2).

Table 2
Selected empirical examples documenting benefits of spatial closures on large pelagic fishes. See text for details.

Type	Area	Time frame	Documented benefits	Sources
Large-scale MPA	Galápagos Marine Reserve	since 1998	elevated yellowfin tuna catch rates close to reserve, increased yellowfin and skipjack productivity in and around reserve	Boerder et al. [94]; Bucaram et al. [95]
MPAs	Various (87 sites worldwide)	since 2006	increased biomass and diversity of large pelagic fishes	Edgar et al. [96]
MPA Networks with strong fisheries management	Florida, Bahamas, U.S. Virgin Islands	1993–2008	only Caribbean countries with large sharks abundant	Ward-Paige et al. [97]; Graham et al. [56]
EEZ-wide shark sanctuary	Shark Sanctuaries (15 countries)	since 2009	reduced shark fishing and slower shark population declines	Ward-Paige & Worm [57]
Unilateral fisheries closure	Baja California billfish closure	1977–1980, 1984–1985	22% increase of striped marlin abundance	Squire & Au [98]; Jensen et al. [99]
Unilateral fisheries closure	US Atlantic swordfish closures	since 1999	reduction of swordfish bycatch contributed to stock rebuilding	NMFS [100]
IATTC closure	Purse seining and *'el corralito'* closures	since 2004	reduction of fishing mortality (primarily bigeye tuna)	Xu et al. [101]
WCPFC restriction	FAD closure	since 2008	reduction of juvenile bigeye tuna bycatch	Hanich et al. [102]; SPC-OFP [103]
ICCAT closure	Mediterranean swordfish closure	since 2011	reduction of total catch of adult and juvenile swordfish	ICCAT [104]

5.1. Unilateral measures

Some targeted spatial protection measures to specifically protect vulnerable aggregations and life stages of pelagic fishes have been implemented domestically. Here we focus on well-studied MPAs first, followed by unilateral fisheries closures.

One of the first large-scale MPAs to include large pelagics was the Galápagos Marine Reserve (GMR). Established in 1998 by the Ecuadorian government, the 133,000 km^2 MPA protects the unique marine biodiversity of the Pacific island chain and also includes a presumed tuna nursery [105]. Commercial tuna fishermen are aware of positive reserve effects on targeted tuna stocks and preferably fish close to the reserve boundaries to maximize benefits [105], achieving higher catch rates compared with surrounding areas [94]. On-board observer and Automatic Identification System (AIS) vessel tracking data indicated that four times more purse seine sets for tuna were deployed within 20 km from the reserve boundaries compared to the rest of the study area (400 km) between 2011 and 2015 [94]. In addition, since 1990 catch, effort and catch-per-unit-effort (CPUE) distributions in the wider area have shifted closer to the reserve boundaries where overall declining catch trends of the three major tuna species appeared to be buffered by spillover of adult fish from the reserve [94,95]. Impacts of the reserve were most pronounced for yellowfin and skipjack tuna, which showed increased productivity both inside and around the GMR [95].

The GMR is an example of an MPA that is large (> 100 km^2), old (> 10 years), reasonably well-enforced, and in an isolated location. More generally, such areas have been shown to have predictable conservation benefits for larger fish (> 25 cm), which increase both in abundance and diversity, according to a comprehensive meta-analysis of 87 MPAs worldwide [96]. Effects were especially pronounced for sharks (including pelagic species such as *Sphyrna* spp.) which doubled in abundance across all MPAs and increased up to 20-fold in areas that had all of the above-mentioned features.

Protected areas in combination with improved fisheries management might also be important in allowing larger shark species to persist in Florida, the Bahamas, and the US Virgin Islands, in notable contrast to the remainder of the Caribbean [97]. Electronic tagging studies confirmed that established MPAs in Florida and the Bahamas provide protection to great hammerhead (*Sphyrna mokarran*) and tiger shark populations, but hardly cover the range of bull sharks (*Carcharhinus leucas*) [106].

In addition to MPAs, fisheries closures can provide similar benefits for large pelagic fishes. Mexico established a series of closures for longline fisheries in Baja California between 1977-1980 and 1984–1985 to reduce commercial fishing mortality of billfishes. From a stock reduction analysis model based on data from the Japanese longline fishery in the area, Jensen et al. [99] confirmed earlier observations [98] documenting increases of abundance of striped marlin up to 22% in relation to the closures. Presently, striped marlin in the eastern Pacific is not believed to be overfished or subject to overfishing although there is uncertainty around available catch data for fisheries targeting this species [107].

Likewise, since 1999, the United States National Marine Fisheries Service (NMFS) has implemented a series of unilateral time-area closures on the U.S. Atlantic coast to manage domestic tuna, shark, and swordfish fisheries. These closures have reduced bycatch and contributed to the recovery of the Atlantic swordfish stock [100] although other billfishes such as the Atlantic white marlin continue to be overfished [108]. On the Pacific coast, the entire U.S. EEZ is now closed to industrial pelagic longlining for tunas and swordfish— a measure that is also meant to reduce bycatch of common thresher shark, sea turtles, and marine mammals. Drift gillnetting for swordfish and sharks is prohibited in certain parts of the U.S. EEZ in order to reduce bycatch of these and other coastal species [109] and recently California legislators moved toward phasing out the use of this gear entirely (Senate

Bill No. 1017).

Shark sanctuaries are another unilateral management measure being adopted by countries that aim to maintain large shark populations, often for ecotourism. As of end of 2018, seventeen countries have established shark sanctuaries in parts or the whole of their EEZ, covering nearly 20 million km^2. Commercial and sometimes also subsistence fishing for sharks is typically prohibited in these areas, as is retention, possession, and trade of bycaught sharks [57]. A global survey analyzing the observations of 438 divers from 38 countries indicated that shark sanctuaries showed less pronounced shark population declines, fewer observations of sharks being sold on markets, and lower overall fishing threats compared to non-sanctuary countries [57]; yet their effectiveness in rebuilding depleted shark populations remains uncertain due to difficulties in monitoring and enforcement [110] as well as bycatch mitigation [111].

Some unilateral management measures target known aggregation and spawning sites for highly migratory species, such as tuna spawning areas included in the Galápagos Marine Reserve in Ecuador and the Phoenix Islands Protected Area in Kiribati. Likewise, some fisheries closures include spatial management regulations to protect aggregations such bluefin tuna spawning grounds in the Gulf of Mexico and the Mediterranean Sea (Fig. 1 and Table 1) and in the abovementioned U.S. longline closures to protect juvenile swordfish. Underwater geomorphological features such as seamounts and ridges tend to aggregate pelagic fishes, and have become a recent focus of spatial protection [112]. Several MPAs such as the Charlie-Gibbs and Josephine Seamount MPAs in the North Atlantic, and the SGaan Kinghlas-Bowie Seamount MPA off the Pacific coast of Canada have been specifically designed to protect such features, and the communities that they harbor. However, the management of large pelagic fishes is often not a primary objective in these MPAs. In another attempt to expand unilateral protection measures to known migratory routes, the Cocos-Galápagos Migratory Pathway between the Galápagos Islands and the Cocos Island Marine Reserves has been discussed as a possible candidate for improved spatial protection of a variety of sharks, rays, and turtles, especially in the light of intense legal and illegal fisheries in the wider area [113,114]. While these areas are subject to some regulations by RFMOs (see below and Fig. 1), establishment and enforcement of spatial closures remains a challenge, particularly on the high seas.

5.2. RFMO measures

In addition to unilateral spatial management and MPA establishment, four of the five tuna RFMOs have also included spatial closures as a tool for managing heavily fished target stocks. The earliest record of this includes temporary closures to purse seining for yellowfin tuna in the Inter-American Tropical Tuna Commission's (IATTC) Yellowfin Regulatory Area from 1966–1978 and 1999–2001 (Table S 1). These closures were primarily implemented to constrain fishing effort on yellowfin tuna and their applicability for other tunas such as bigeye were deemed less successful given initial challenges with determining an appropriate total allowable catch (TAC) for this species and the relatively low catch of bigeye tuna by purse seiners at the time [115].

Since 1993, the International Commission for the Conservation of Atlantic Tunas (ICCAT) has prohibited directed fishing for Atlantic bluefin tuna on their Gulf of Mexico spawning grounds [116], though independent research suggests that incidental catch of this species was occurring through the mid-2000s [85]. Although this CMM is the oldest RFMO-led closure still in place today, its success remains unknown due to a high degree of uncertainty around the state of the stock as a whole [117]. Furthermore, given additional uncertainty around the exact spawning location of the eastern Atlantic bluefin tuna stock, no additional spatial protection for this species exists in the Mediterranean Sea. Although spawning sites of both Pacific and southern bluefin are also known, no spatial measures specific to these areas have been adopted by the respective RFMOs.

ICCAT, IATTC, and the Western and Central Pacific Fisheries Commission (WCPFC) all have spatial measures in place as part of larger fisheries management plans for the key tuna stocks under their jurisdictions: skipjack, yellowfin, and bigeye tuna. Given the high degree of juvenile tuna bycatch incurred through the use of fish aggregating devices (FADs), fishing on these structures has been prohibited in specifically defined areas during certain months of the year by both ICCAT and the WCPFC (Fig. 1). WCPFC members have also adopted increasingly stricter spatial management measures over the last decade, largely in conjunction with the fishing regulations laid out by Parties to the Nauru Agreement countries with regard to access to their EEZs [102]. Due to concerns over elevated fishing mortality of juvenile bigeye tuna, a variety of closures to purse seining with FADs were adopted as part of CMM 2008-01 with explicit requirements that fishing states refrain from transferring effort from these closures to other fishing areas. These measures were largely successful in substantially reducing bycatch of juvenile bigeye tuna [103]. Despite this, economic losses were minimal as the reduction in volume was offset by the higher value of larger individuals landed as more fishing occurred by sets on free schools, which catch larger fish [103]. Since their original implementation, there has been a temporary extension of these FAD closures and, presently, overfishing of the bigeye tuna stock in the Western Central Pacific is not occurring [118].

The IATTC has arguably the most extensive spatial management measures: a three-month closure to all industrial purse seining within the Convention Area, as well as a one-month spatial closure in a region known as *el corralito* during the fall (Fig. 1). Variations of both measures were first adopted by IATTC members in 2004 and have since been expanded both spatially and temporary (i.e., 59 days in 2010 to 72 days at present). These closures aim to reduce fishing mortality primarily of bigeye tuna and, in combination with other management measures, are believed to have met their objectives between 2005 and 2009 [101]. However, overcapacity of the Eastern Tropical Pacific purse seine fleet remains a challenge and the bigeye tuna stock is currently subject to overfishing [101].

The Indian Ocean Tuna Commission (IOTC) has implemented two spatial management measures for target tunas, although neither of these are still active. While these measures were adopted to decrease effort on bigeye and yellowfin tuna, they did not appear sufficient for achieving these aims, likely as a result of uncertainty around stock dynamics as well as a redistribution of fishing effort outside of closed areas [119].

Swordfish is the only billfish species for which spatial management measures have been adopted at the RFMO level. Directed fishing and retention of this species is prohibited in the Mediterranean Sea for three months annually. As a result of the establishment of the first version of this CMM in 2011 by ICCAT, there was a significant reduction in total swordfish catch as well as a 50% decrease in the volume of juveniles caught relative to the 2000s. As the majority of juvenile swordfish bycatch occurs during the fall, an additional two-month closure to the Mediterranean albacore tuna (*Thunnus alalunga*) longline fleet was established in 2016 and the effectiveness of this new measure will be evaluated in the near future [104].

6. Improving spatial protection of pelagic fishes

The continued proliferation of MPAs and spatial closures at both the national and RFMO level suggests spatial management is increasingly seen as a valuable complement to other measures used to control fishing mortality of tunas and other large pelagic fishes. The evidence compiled in this paper further supports such a notion. In the following, some considerations regarding target species, area design, management, and policy concerning improved spatial protection of large pelagic fishes are discussed.

6.1. Species considerations

It is noteworthy, that all spatial RFMO measures discussed here were developed solely for commercial target species (i.e. tunas and swordfish). Consequently, there is room for improvement when it comes to adopting spatial measures to mitigate bycatch of non-commercial species and ensure the sustainable management of non-target pelagics under RFMO jurisdiction, including most sharks. Determining areas of special concern for both target and associated bycatch species would be an important step in developing comprehensive spatial management measures for these species [70].

For target species, of the four tuna species identified in Table 1 as having a high suitability for spatial management, specific area-based fishing measures exist for only two: albacore (Mediterranean stock) and Atlantic bluefin tuna (western stock). Yet, the effectiveness of the closure for western bluefin tuna spawning in the Gulf of Mexico is debatable since bycatch of these species in other fisheries continues (Table S 1) and the closure to albacore tuna fishing was devised as a means of addressing swordfish bycatch, not albacore tuna mortality. Bearing these circumstances in mind, both southern and Pacific bluefin tuna, as well as Atlantic bluefin tuna may benefit from stronger targeted spatial management measures. Since these species exhibit philopatry, it seems that improved protection of known spawning sites could be highly beneficial.

6.2. Design considerations

A number of design criteria apply when considering improved spatial protection measures for large pelagic fishes. The size of a closed area that achieves effective protection is related to dispersal and migration distances at different ages and can vary between 40 and 85% of the full range of a stock closed for species with medium to high dispersal rates [120]. Where detailed data are available for spatial planning, a trade-off between protected area size and area closed to fisheries can be achieved through networks of several smaller, well-placed and adequately spaced protected areas, specifically taking adult dispersal distances and larval connectivity into account [74,121]. However, in this context, enforcement plays a critical role, as multiple smaller reserves have a higher boundary-length to area ratio that can be infringed upon [122]. Thus, for remote and often data-poor pelagic areas, larger closures may be more efficient to increase fisheries benefits as well as stock rebuilding [122,123].

Where mobility is high, or where species distributions and migratory routes shift with changing environmental conditions [124,125] dynamic closures may be more effective than static measures, both for target and bycatch species management [126,127]. Models also show that dynamic closures tailored to species' presence and absence reduce the cost to fisheries substantially by limiting the fraction of time and area that is subjected to a closure [126,128]. Empirically, dynamic closures have been successful in reducing bycatch of threatened species such as North Atlantic right whales (*Eubalaena glacialis*) [129,130] or loggerhead sea turtles (*Caretta caretta*) [131]. Likewise, dynamic closures have been applied with some success in an effort to reduce bycatch of southern bluefin tuna off eastern Australia [132,133].

Compared to individuals exhibiting higher mobility, 'lazy' semi-resident fish with low movement rates may be favored by spatial protection [134,135]. Though unstudied in the field so far, selection towards fish with increased residency might positively affect stock sizes and size at maturation [135] within a protected area but may potentially negatively affect 'spillover' of fish into adjacent areas, stock connectivity, as well as genetic resilience to environmental changes [136]. Both should ideally be taken into consideration in the planning of protected areas.

Spatial protection of large pelagics in general, and dynamic protection measures in particular, often require a substantial data base on which decisions can be based. These include proper species life history and movement data, for example through tagging studies, ideally for multiple species [137]. Likewise, the intensity and distribution of fishing effort needs to be known to assess the effectiveness of spatial protection measures. Here, novel satellite-based tools such as multi-sensor remote sensing and tracking systems (e.g. Synthetic-Aperture Radar [SAR], Vessel Tracking System [VMS], and Automatic Identification System [AIS]) can help to improve our knowledge for marine spatial planning and management, especially in previously poorly observed high seas areas [33,138–140]. These tools provide a window into large and remote areas, enabling the tracking of movement of vessels and the analyses of their behavior such as fishing [3,138], observation of fleets around spatial closures [141] and large-scale fleet dynamics [142], as well as other human use patterns such as the transshipment of catch at sea [143,144]. Increasingly publicly available, these datasets can aid in improving the visibility and transparency of fishing activities around the world, and thus help to address policy and enforcement gaps and challenges [3,33].

6.3. Management considerations

The potential benefits of spatial closures for fisheries are thought to be influenced strongly by the state of fisheries management in surrounding areas. For example, positive effects of spatial closures on fish stocks and catches outside of closures are likely less pronounced when surrounding fisheries are already well-managed [58,62,145,146]. In these cases, the value of lost catch due to area closure is likely not outweighed by benefits of the protected area to target fisheries, especially if total fishing effort is kept constant. Note, however, that other benefits, for example on sensitive bycatch species or habitats, are independent of this. At the same time lost catch from a protected area is less likely to be a serious issue for large pelagic fishes as their range usually exceeds the closed areas and they can be caught elsewhere [58]. Moreover, if overfishing occurs and the gradient of fish abundance from inside to the outside of a protected area is large, fish stocks and associated fisheries might benefit significantly from larval and adult spillover [120,147,148].

Following the establishment of a large closure, an appropriate reduction of fishing effort or fishing capacity is deemed essential to avoid a 'squeeze factor', whereas the same amount of fishing is concentrated in a smaller fishable area [60], potentially affecting other species and habitats [149]. For example, in response to the closures of high seas areas between the Pacific Island EEZs in the Western Central Pacific, purse seining effort for skipjack and bigeye tuna simply redistributed to EEZs surrounding the closures and no beneficial effect of the closures on bigeye tuna was detectable [73]. Likewise, around Cocos Island National Park, several target species such as the scalloped hammerhead shark (*Sphyrna lewini*) decline despite spatial protection, largely due to remaining fishing pressure both inside and outside the protected areas [113,114]. Hence, spatial protection alone may not be enough: Adequate combination of spatial protection and improved fisheries management is most likely to produce intended positive effects. On this note, Ward-Paige et al. [97] observed that several large pelagic sharks such as tiger, silky, and bull sharks were more frequently sighted in areas with low human population density, well-regulated fisheries, or enforced marine reserves.

While is clearly advantageous to combine spatial protection measures with improved effort controls, this is not always achievable. In these cases, adjustment of output controls such as TACs might be an alternative. Pons et al. [24] found that enforced TACs in combination with minimum size regulations and spatial closures yielded good benefits in rebuilding major commercially exploited tuna and billfish stocks. For bigeye tuna, for example, a combination of closed areas for certain gear types (longlines) as well as fisheries management measures (prohibition of the use of FADs) was effective to increase adult biomass due to a simultaneous reduction of fishing mortality of both sexually mature adults in longline fisheries and juveniles in purse seine fisheries on FADs [73]. However, ecosystem and population dynamics models generally suggest strongest effects of spatial closures when fisheries management controlled for (eliminated) displaced fishing effort, amounting to 10–25% increase of adult biomass over the entire range of Pacific bigeye tuna [73].

For some species, conventional fisheries management tools such as catch and gear restrictions might suffice for adequate management [146]. This potentially applies for highly target-specific fisheries with little bycatch [150], and for species where information on predictable aggregations or migratory patterns is lacking (Table 1). However, even for those species protected areas can buffer against management uncertainties [123,151], such as those caused by limited knowledge, uncertain enforcement, or environmental change [64]. The weaker and more uncertain fisheries management is, the more important spatial protection may become as a management tool [152]. For example, in situations where conventional fisheries management tools such as catch controls are not applicable, spatial protection might be the easiest, cheapest and most effective means to achieve similar benefits [150].

6.4. Practical policy considerations

The uptake, modification, and retention of CMMs related to spatial management at the RFMO level suggests that states see value in the use of these tools as a complement to other national and multilateral management strategies for highly migratory species. Still, it appears that most of these measures have been developed largely as a means of buffering against increasing fleet capacity or a way of mitigating the impact of a specific gear (i.e. FADs) rather than to explicitly protect certain species or life history stages.

It is worthwhile to note that the ability of RFMO member states to collectively designate specific management areas may be limited. As expressed in the UN Fish Stocks Agreement, RFMO legislation may not infringe upon the sovereign right of the nation state to access and utilize the resources of their EEZ. In the case of migratory fishes, whose ranges often extend across multiple EEZs, the conservation burden associated with closing an area for protection may be disproportionately borne by one country if the area occurs within their waters, but all fishing countries benefit from its implementation. For example, in the case of both southern and Pacific bluefin tunas strong leadership and commitment from Indonesia and Japan is required as spawning locations for these fish fall within their domestic waters. Subsequently, ensuring this disparity is equitably addressed through other legislation is vital such that all countries equitably bear the cost of management.

Furthermore, while the unilateral establishment of large marine protected areas is increasing, an understanding of the relationship between these MPAs and independently established multilateral fishery closures appears limited. This is surprising given that both MPAs and fisheries closures cover significant and almost equal fractions of the global ocean, and both can target – at least in part – the spatial protection of highly migratory species. To this end, research and resources directed at evaluating the benefits and shortcomings of existing areas should complement the design and designation of new areas. Going further, the potential of establishing linkages in the form of migratory corridors through the high seas between existing MPAs (e.g., Cocos Island and the GMR) should be a focus of future work, especially in the context of the ongoing UN negotiations on biodiversity beyond national jurisdiction.

7. Conclusion and next steps

While close to 15% of global ocean area is now under some form of targeted spatial management (Fig. 1 and Table S 1) and many pelagic fishes appear suitable for spatial production based on their life history (Table 1) the effects of these measures on large pelagics are documented in comparatively few case studies (Table 2) and may be difficult to generalize. Yet, their propensity to aggregate, as well as the defined migratory patterns and philopatry observed in many species suggest that highly migratory species can benefit from targeted, well-designed spatial protection, especially in spawning or nursery areas or around geomorphological features that aggregate species such as seamounts and thermal fronts, as well as for critical life stages such as juvenile fish. Additionally, spatial protection can be more beneficial where stocks are overfished or subject to high bycatch rates. In conjunction with effective, transboundary fisheries management regimes, spatial protection measures can provide additional benefits in terms of increased habitat quality, increased resilience to stock collapse, insurance against management errors, and protection of non-target species and associated biodiversity. Next to unilateral spatial protection measures, RFMO member states have implemented spatial management for several highly migratory target species, although the degree to which vulnerable life stages and aggregation areas are protected appears still low. Therefore, significant potential for improving spatial protection measures for these migratory fishes still exists and requires better institutional cooperation between organizations involved in the establishment and management of both MPAs and large-scale fisheries closures.

Conflict of interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

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