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Global habitat predictions to inform spatiotemporal fisheries management: Initial steps within the framework

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ABSTRACT

Tuna Regional Fishery Management Organizations (tRFMOs) are increasingly interested in spatiotemporal management as a tool to reduce interaction rates with vulnerable species. We use blue shark (*Prionace glauca*) as a case study to demonstrate the critical first steps in the implementation process, highlighting how predictions of global habitat for vulnerable life stages can be transformed into a publicly-accessible spatial bycatch mitigation tool. By providing examples of possible management goals and an associated threshold to identify essential habitats, we show how these key areas can represent a relatively low percentage of oceanic area on a monthly basis (16–24% between 50°S and 60°N), yet can have relatively high potential protection efficiency (∼ 42%) for vulnerable stages if fishing effort is redistributed elsewhere. While spatiotemporal management has demonstrable potential for blue sharks to effectively mitigate fishing mortality on sensitive life stages, we identify inherent challenges and sequential steps that require careful consideration by tRFMOs as work proceeds. We also discuss how our single-species framework could be easily extended to a multispecies approach by assigning relative conservation risk before layering habitat model predictions in an integrated analysis. Such broader application of our approach could address the goals of tRFMOs related to reducing the ecosystem effects of fishing and pave the way for efficient fisheries co-management using an ecosystem-based approach.

1. Introduction

Overfishing is the foremost cause of population declines for sharks at a global scale [23,24]. The intrinsic vulnerability of sharks to exploitation warrants precautionary management [35,43], even for species or populations that are comparatively more resilient to intensive fishing. Highly-migratory pelagic sharks are primarily caught as bycatch in commercial longline fisheries targeting billfishes or tunas [19,47,48], and dynamic spatial management (i.e. spatiotemporal management) offers a promising avenue to redistribute fishing effort away from areas and/or periods of higher bycatch risk [33,45,7]. In particular, there is increasing interest among tuna Regional Fishery Management Organizations (tRFMOs) in spatiotemporal management as a tool to reduce interaction rates of tuna and billfish fisheries with vulnerable shark species (e.g. [44]).

There are only a few examples of successful implementation of spatiotemporal management so far ([18]; although see [34,30,31]). A major initial challenge for highly-mobile pelagic species, given their seasonally-driven migrations and wide distributions, involves characterising their ecological niche at the basin and global scales, in the vertical, horizontal and temporal dimensions. Only after seasonal distribution patterns and associated environmental conditions are identified, can the areas associated with a high probability of species presence be accurately predicted in space and time from current or future environmental conditions [40]. Recently, there have been substantial gains in the derivation of reliable ocean data products, where satellite-derived physical data are assimilated with observational data to characterise ocean conditions at high vertical and horizontal resolutions (e.g. [21,53,57]). Similarly, there have been major advances in the use of electronic tags for understanding precisely how animals such as sharks utilise ocean environments [14]. For species that undertake frequent vertical diel migrations [3], environmental predictors can now be derived at various depths (e.g. currents to describe fronts or eddies, mixed layer depth). This presents a major opportunity to advance understanding of species-environment interactions, habitat use, and distribution [10,40,58], resulting in increased knowledge of their ecological niches and the environmental conditions associated with higher probability of species presence [22,4,55].

However, using a species' habitat suitability to minimise catch rates within an applied management context requires several additional and potentially controversial steps for tRFMOs (Fig. 1). First, it is necessary to define explicit management and conservation goals related to the life stages targeted for a species' protection, as well as to agree on the thresholds for occurrence and/or mortality that will be used. Second, preferred habitat must be identified, which involves mapping relevant environmental conditions and delineating areas associated with high, medium and low frequencies of species occurrence to meet the predefined management goals. Third, independent presence or abundance data for the species and for the distribution of fishing effort by fleets should be overlaid with habitat suitability. This would quantify risk to the species as well as potential socio-economic impacts on fleets (e.g. [36]). Fourth, a range of mitigation strategies (with potentially divergent goals and thresholds) need to be assessed through simulation analyses to compare mitigation efficiency (i.e. to minimise risk and socio-economic impact relative to conservation goals and identify an optimal management strategy). Fifth, effective communication mechanisms will need to be implemented to help inform the fleets on more or less suitable and/or risky areas to fish within a usable time-frame (e.g. through online platforms in real time or quasi-real time and direct emails to the vessels, or through capacity building workshops). This sequence of activities would be logical during implementation, although we recognize that progress could occur in parallel for multiple steps and that it would be optimal to engage with industry participants via workshops throughout the process. Ideally, each individual step should involve an iterative or continuous adaptive process where new information could be used to improve models, or refine management/conservation goals and implementation frameworks. Finally, a formal management strategy would need to be negotiated and adopted at the tRFMO level, and revisited periodically as new information becomes available (Fig. 1). The diverse steps of this process argues strongly for an incremental approach, where practical tools describing habitat suitability are made available immediately to stakeholders to potentially incentivize voluntary effort redistribution while formal management processes are developed.

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This work evaluates one such practical tool of habitat suitability as a starting point in the framework for spatiotemporal management of pelagic fisheries. It is not yet possible to work through all of the steps identified above because fishing effort data on the high seas are not yet available at sufficient spatial resolution (1 by 1 degree resolution or better) to allow explicit comparison with environmental information. This precludes the development and evaluation of different spatiotemporal management scenarios at spatial scales that are relevant to tRFMOs. Although there is an example using primarily 5 by 5 degree data [11], management at this spatial scale would result in substantial lost opportunity for individual fleets as one 5 by 5 degree square at the equator represents an area in excess of 300,000 km^2. The low resolution of fishing effort data also means that it is not yet possible to determine how much overlap exists between blue shark habitats and the locations most commonly targeted when fishing tuna, swordfish and billfishes. However, substantial progress towards a useable framework can still be made in the interim. The aim of this work is to demonstrate how a practical management tool can be derived from predicted global habitat as a first step towards the effective spatiotemporal management of pelagic sharks. We use blue shark (*Prionace glauca*) as a case study because it is commonly intercepted as bycatch and is considered near-threatened at a global level, with varying regional status (Supplementary Information). These two characteristics of blue shark suggest that spatiotemporal management could help maintain or improve population status and become an important tool to advance the overall economic and ecological sustainability of global fishing practices [25,41,54].

Developing this case study allowed us to identify and explore the challenges inherent to the spatial management of highly migratory pelagic species, largely due to their life histories and ecology coupled with the characteristics of available data to identify habitat suitability (both occurrence data and environmental characteristics). Such challenges would be universal for other highly mobile large pelagic species and will require careful consideration by tRFMOs intending to implement spatiotemporal management for vulnerable species. Looking forward, we show how information from targeted as well as bycatch species could be combined into a truly multi-species evaluation of spatial distribution and fleet overlap. Such spatiotemporal tools would represent substantial progress towards the implementation of an ecosystem approach to fisheries management (EAFM).

2. Methods

The basis of our bycatch mitigation tool was an Ecological Niche Model (ENM; [22]) that characterised habitats for different life stages of blue shark at a global level (Supplementary Information). This habitat model addressed the common limitations identified by Melo-Merino et al. [40] for ENMs for widely distributed marine species. Specifically, (1) substantial effort was made to ensure equivalent temporal and spatial resolution of observational (daily and < 50 km accuracy) and environmental data (daily at 1/24° resolution or weekly at 1/12° resolution) so that environmental predictors were at the same scale as the presence data for blue shark when predicting habitat [22]; (2) the model included consideration of the species' feeding ecology to delineate suitable habitat, which is expected to be more accurate for species that can tolerate a wide range of abiotic conditions (e.g. [9,2]); and (3) several environmental predictors considered the vertical dimension of the water column, allowing suitable habitat to be predicted individually for surface waters (epipelagic layer; ≤ 100 m) as well as at depth (mesopelagic layer; > 100 m). The model accurately predicted habitats for each life stage of blue shark, with 86–99% of validation observations falling within or closer than 50 km (and 68–94% of validation observations fell within 10 km) of favorable habitat [22]. This demonstrates that the ENM can appropriately characterize the occurrence of different sexes and life stages of blue shark over space and time, and can thus be used as the basis for our bycatch mitigation tool.

2.1. Spatial bycatch mitigation tool

To use the ENM to delineate potential areas to protect specific life stages, we first needed to define the sex and life stages of interest for management, and then define habitat suitability thresholds for those life stages. Ideally, tRFMOs would make these decisions, taking into account different perspectives and risk tolerances from stakeholders to define a consensual set of (operational) management and conservation targets. Objectives could be to protect the reproductive capacity of a population and to minimise exploitation on the most vulnerable life stages, as determined by population dynamics modelling. Elasticity analyses for

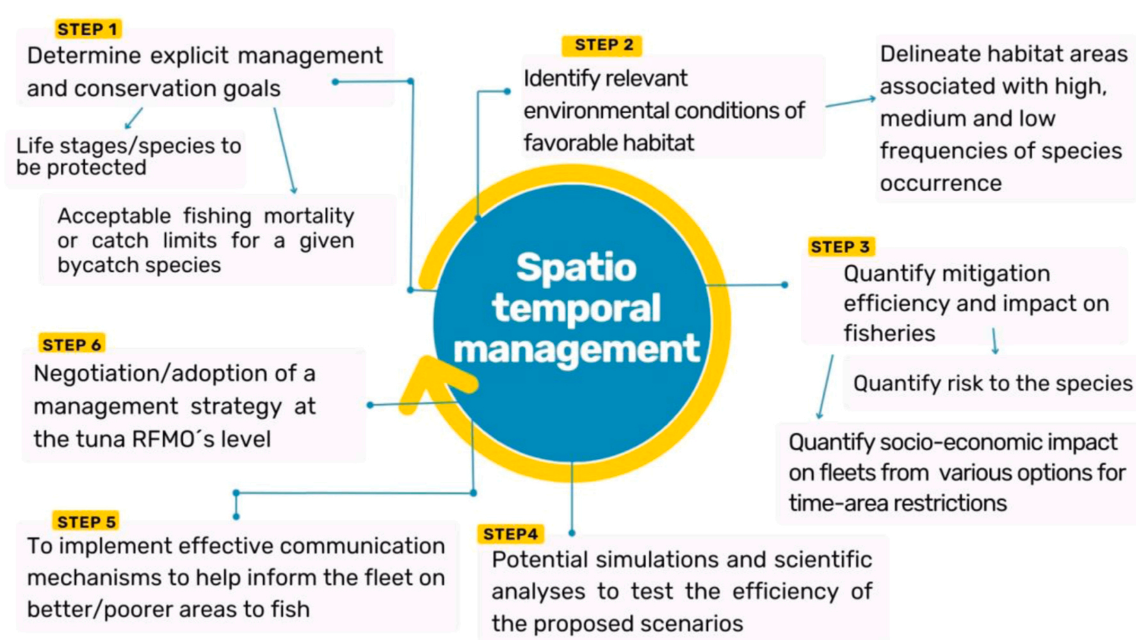

Fig. 1. A schematic of the steps required to develop and implement spatiotemporal management for bycatch mitigation by tuna Regional Fisheries Management Organizations.

sharks indicate that all juvenile females have equal contribution to population growth rates (unlike teleost fishes) and young mature female age classes have higher reproductive value than older reproducing adult females by virtue of their higher abundance, making the protection of these life stages particularly important [17]. For blue sharks, large juvenile females (LJF) may be particularly vulnerable to exploitation in longline fleets characterised by dome-shaped selectivity [13]. Furthermore, stable isotope studies (δ13 C models and trophic position) suggest that male and female blue sharks segregate their main feeding areas [56], so it is likely possible to target spatial protection measures on the female component of the population. We developed our example for small juveniles (SJ), large juvenile females (LJF) and adult females (AF) in combination (SJ=30–125 cm fork length (FL) of both sexes, LJF=125–180 cm FL large juvenile females, AF=180–330 cm FL adult females).

To quantify the amount of oceanic area having a high, medium or low frequency of blue shark occurrence, habitat suitability thresholds were required. We evaluated multiple suitability levels to define three habitat categories for blue shark, representing essential, fringe and low/non-habitat areas (e.g. essential habitat above 50%, 60%, 70% and 80% suitability; Supplementary Information). The example that we discuss in the results uses > 70% and 40%–70% frequency of occurrence to delineate essential and fringe habitats, respectively. All other locations (< 40% frequency of occurrence) were considered to be habitat of low value or unsuitable for blue sharks (Table 1). Using different threshold values and/or including consideration of different life stages would influence the amount of area contained in each category (Supplementary Information), demonstrating the importance of predefined management objectives.

Our spatial management tool generates habitat suitability maps based on the abiotic and biotic predictors from the blue shark ENM. Daily habitat predictions from 2015 to 2018 were combined to generate monthly mean predictions in order to account for seasonal variability in habitat suitability during recent years. The three ontogenetic stages (SJ, LJF and AF) were given equal weight to generate the integrated habitat maps of essential, fringe and non-suitable habitat areas for each month from the ENM. While it would be ideal to generate real-time predictions or short-term forecasting for informing spatial management options for fisheries [33], this was not yet possible from the blue shark ENM. We relied on the monthly averages because it was too time-intensive to align the predictions of mesopelagic micronekton (the variable used as a feeding proxy to identify suitable habitats in deep water within the ENM) at the temporal and spatial resolution plus time period of the other data products in real time. While real-time projections would capture inter-annual variability in climactic conditions, mean conditions encompassed areas in which the species was commonly observed over multiple recent years.

The spatial management tool differentiates among the three habitat categories (essential, fringe, and low/non-suitable) for two fishing depths (surface: ≤ 100 m, deep: >100 m) to produce five habitat categories where different mitigation measures could be evaluated (Table 1). In an operational context, these habitat maps were intended to delineate areas in which fishing effort could be minimised (essential habitat), reduced (fringe habitat) or redirected to (low or non-suitable habitat areas) in order to optimally reduce capture rates, and therefore mortality, on the vulnerable life stages of blue shark. Because the ENM differentiates between surface and deep feeding habitats, we were able to discuss implications of any redistribution of fishing effort for both shallow-set (i.e. within the top 100 m of the water column) as well as deep-set (> 100 m) longline gear. Because our spatial management tool was specific to blue shark, we did not demonstrate if low/non-suitable habitats were associated with sufficient target species biomass to sustain viable fisheries. The ways in which our framework could be extended to evaluate overlap between target and bycatch species' habitats are discussed below in Section 4.4.

Table 1
Categorization of foraging habitat in relation to the frequency of occurrence of favourable habitat for blue sharks within two depth layers (CHLmin is the daily surface chlorophyll-a level that horizontally differentiates surface from deep blue shark habitats; Supplementary Information). Thus, suitable surface habitat has moderate productivity while suitable deep habitat is associated with low-productivity surface environments.

Foraging habitat (frequency of favorable occurrence)			***Surface** habitat*	***Deep** habitat*
Low or non-habitat		**< 40%**	**CHL ≥ CHLmin**	**CHL < CHLmin**
Core habitat	**Fringe habitat**	**40–70%**		
	Essential habitat	**≥ 70%**		

2.2. Potential Benefit of Spatiotemporal Management

To assess the potential conservation benefits to blue shark resulting from a potential redistribution of fishing effort, we calculated the percentage of observations of blue shark presence from the ENM model validation data (Supplementary Information) that fell within each habitat category (essential, fringe and low/non-suitable habitat). Only areas within the main latitudinal bounds of the known distribution of blue sharks (from 50° South to 60° North latitude) were considered, thus excluding the Arctic and Antarctic regions that are unsuitable for the species. These percentages can be interpreted as follows: if all longline fishing was hypothetically outside of the areas representing essential habitat (e.g. above 70% occurrence) in a given month, any blue shark known to be present within those areas at those times would have been protected (i.e. not susceptible to capture). In other words, the percentage of the validation data within each habitat category represents the potential conservation benefit to the population from a redistribution of longline effort. The greatest conservation benefit to blue shark populations would be realised in a scenario where longline effort was excluded from essential habitats. To quantify the potential loss in fishing opportunity relative to the potential conservation benefit, we compared the percentage of global ocean area (between 50° South and 60° North latitude) within essential habitat with the protection efficiency of these essential habitats. In an ideal scenario, the former percentage (lost fishing opportunity) would be small and the latter (conservation benefit) would be large.

3. Results

3.1. Patterns in global habitat suitability

Predicted locations of essential, fringe and low or non-suitable habitat areas for both shallow (≤ 100 m) and deep (> 100 m) foraging habitats of blue shark showed seasonal differences. A comparison of representative months (Fig. 2; see all months in the Supplementary Information, Figures S1-S3) demonstrates that essential and fringe foraging habitats of blue shark in surface waters include substantial coastal and slope areas as compared to deep-water foraging habitats which are located mostly in warmer offshore waters, particularly in the Northern Hemisphere. The surface habitat in February was concentrated along the Western coasts and slopes of North and South America, Europe and North Africa, the northern extent of the Indian Ocean, and approximately along the 30° and 50° latitude range in both hemispheres (Fig. 2a; left panel). By May, the shallow habitats became more concentrated along 40° N and 40° S latitudes (Fig. 2b; left panel) and they extended northward beyond 40° N and S latitude, encircled Australia and South Africa, and encompassed equatorial areas in August (Fig. 2c; left panel). August and September represent the warmest period in the northern hemisphere, coincident with preferred habitat shifting northward. At the equator, the increase in favourable habitat from May to August reflects the switch from deep habitat to surface habitat associated with surface productivity fronts. By November, the spatial

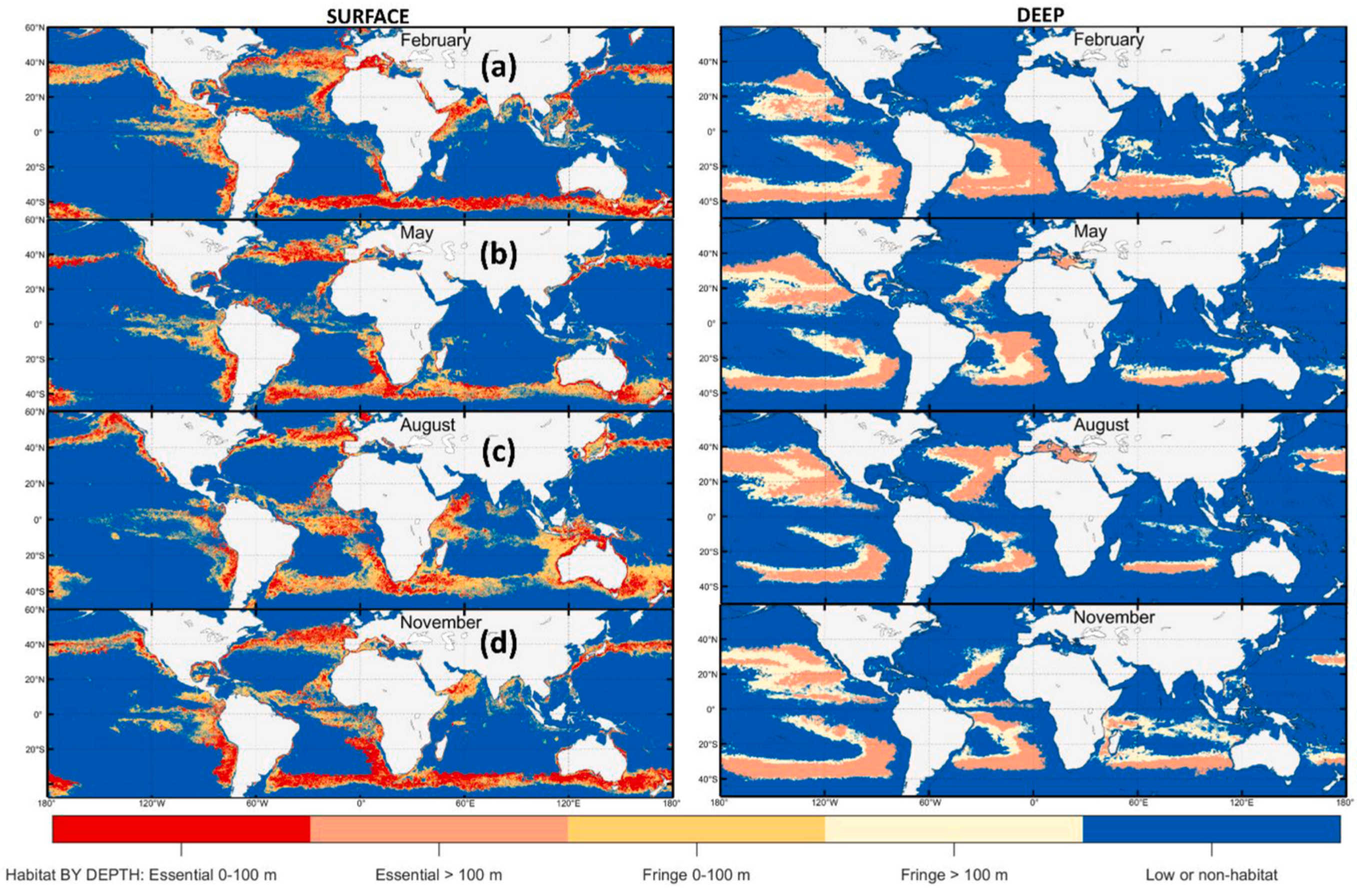

Fig. 2. Seasonal variability in essential, fringe and low/non-suitable habitat areas for vulnerable life stages (small juveniles, large juvenile females and adult females) of blue shark, predicted from an Ecological Niche Model (ENM) of global habitat. Left panels for February (a), May (b), August (c) and November (d) represent shallow (≤ 100 m) habitats, while right panels represent deep (> 100 m) habitats. Note that no overlap exists between the shallow and deep habitats predicted from the ENM. Latitudinal extremes occur in February and August, while May and November are intermediate between the extremes.

distribution of shallow essential habitat was similar to predictions from February (Fig. 2d; left panel). Conversely, essential habitats for blue sharks in deeper water were more broadly distributed offshore, particularly in the Southern Hemisphere. In February, essential habitats in deep water were concentrated from 5° to 40° S latitudes (Fig. 2a; right panel). By May, these had shifted to include substantial areas in the North Pacific and North Atlantic (Fig. 2b; right panel). In August, essential habitats in deep water became primarily distributed in the northern hemisphere (from 10° to 40° N latitudes; Fig. 2c; right panel), yet had shifted back to the Southern Hemisphere by November (Fig. 2d; right panel). For both habitat layers, the locations of fringe habitats were directly adjacent to essential habitat, and seasonally changed in a similar manner. The geographic location of the boundary between essential and fringe habitats largely depended on the threshold values used to delineate habitat suitability categories, given that mean environmental conditions in the ENM change gradually over space and time. This is why we evaluated multiple options for thresholds (Supplementary Information).

Even though the spatial distributions of essential habitats vary seasonally in latitude, the overall percentage of area in each habitat suitability category at a global scale remained fairly similar over the course of the year (Fig. 3). The percentage of total area represented by essential and fringe monthly habitat (above 70% and 40% suitability, respectively) at all depths from 50° S to 60° N ranged from 16% to 24% and 22–25%, respectively (the sum of the two depth-linked curves of each habitat in Fig. 3). Considering habitat at all depths, 50–61% of total area from 50° S to 60° N had a low frequency of occupancy by the vulnerable classes of blue shark in any month and/or represented non-suitable habitat areas (i.e. having an occurrence frequency below 40% for the assessed life stages). If shallow and deep habitats were considered independently, the seasonal percentage of low or non-suitable habitat area ranged from 75% to 82% for the surface layer and 76–81% for the deep layer (Fig. 3). Overall, the absence of overlap between surface and deep blue shark habitat means that only a small amount of total area from 50° S to 60° N would be considered for mitigation, representing a monthly range of 6–9% and 10–15% of essential habitat in the surface and deep layer, respectively (Table 2), as well as 11–16% and 8–14% for fringe habitat in the surface and deep layer, respectively. Note that these percentages remained relatively consistent by month at a global scale (Fig. 3), yet seasonally shifted in spatial location (Fig. 2). In other words, the geographical locations that fisheries might avoid would be different each month, but the total amount of area being avoided would remain largely consistent throughout the year.

3.2. Bycatch mitigation tool

To enable tRFMOs, industry and other stakeholders to make practical use of the predicted suitable habitats (essential, fringe and low/non-suitable) as a spatial management tool, we have archived them as a freely available Google Earth map (Google Earth Pro 6.2.1.6014 (beta, October 5, 2011); available for download at: https://fishreg.jrc.ec.europa.eu/web/fish-habitat). This open-source format allows users to zoom in to any area of interest for each monthly habitat map (as illustrated in Fig. 4). It is important to keep in mind that suitable blue shark habitat, as predicted in the ENM, would only be found in one layer

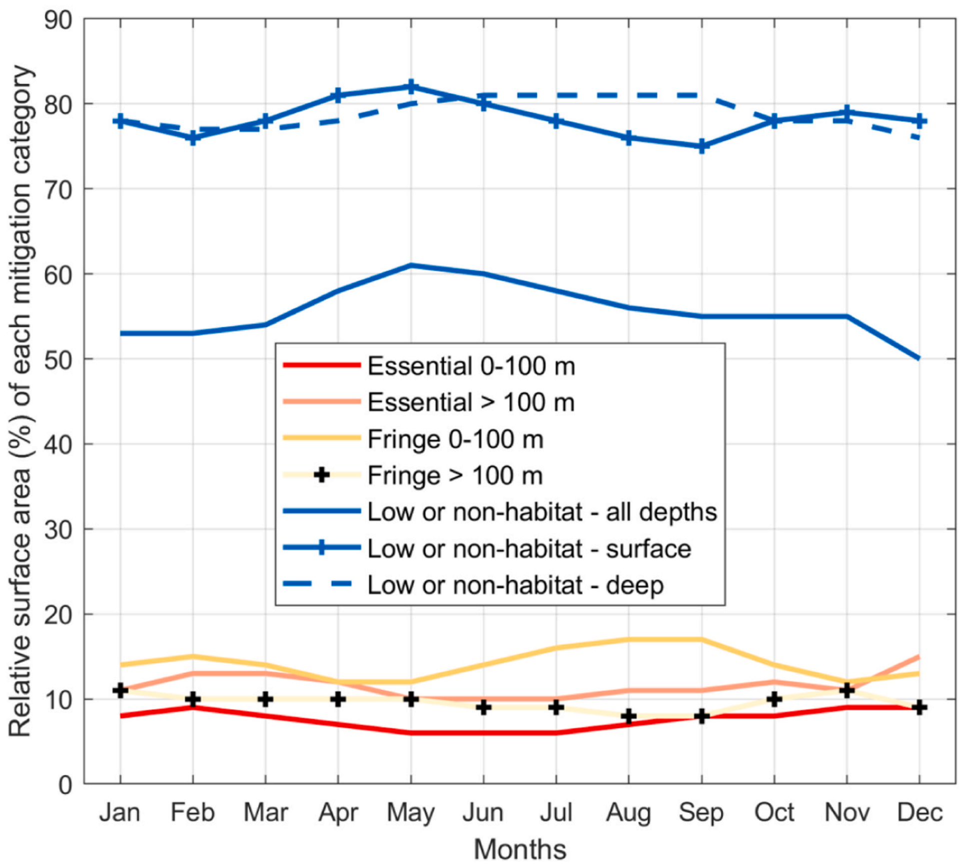

Fig. 3. Seasonal variability in the amount of essential, fringe and low/non-suitable habitat areas between 50° South and 60° North latitude for vulnerable life stages of blue shark (small juveniles, large juvenile females and adult females). Predictions are given separately for shallow (≤ 100 m) and deep (> 100 m) habitats.

Table 2
Summary of potential protection efficiency for each life stage and the resulting overall loss in longlining opportunities from avoiding essential habitat areas. Protection efficiency represents the proportion of validation data on blue shark presence [22] within low/non habitat, fringe and essential areas. Lost opportunity represents the percentage of essential habitat area within 50° South and 60° North latitude.

FORAGING HABITAT (frequency of favorable occurrence) vs Validation data	*LOW (≤ 40%)*	*FRINGE (40–70%)*	***ESSENTIAL (≥ 70%)***	**Monthly ocean surface of essential habitats (three combined classes from 50°S–60°N):**
Small juveniles (total N = 25,563)	*24.5%*	*35.3%*	***40.2%***	**Shallow = 6–9%**
Large juvenile females (total N = 26,366)	*38.8%*	*19.1%*	***42.1%***	**Deep = 10–15%**
Adult females (total N = 15,594)	*36.9%*	*21.2%*	***41.9%***	**All depths = 16–24%**

(shallow or deep) at any specific place and time, so both habitat layers are combined in a single habitat map. This also means that mitigation efforts could be specific to depth, because essential habitat in deep water would not preclude setting shallow-set gears (e.g. shallow-set pelagic longline targeting swordfish) and vice versa (e.g. deep-set longlines for tunas). In terms of potential conservation benefit, 40–42% of the validation observations for each of the vulnerable life stages fell directly within essential areas (essential surface and essential deep habitats combined; Table 2). This represents approximately 28,000 records of independent presence data out of a total of 67,563. A large proportion of the vulnerable life stages of blue shark may not experience exploitation pressure if fishing was shifted outside of essential areas. While we recognize that the majority of the population would remain vulnerable to bycatch, spatiotemporal management for such a widely-distributed and adaptable species is unlikely to ever approach 100% unless fishing were to be prohibited entirely. Thus, we consider the potential conservation benefit for blue shark to be high if fishing were shifted outside of essential areas.

4. Discussion

Our blue shark case study offers concrete initial progress towards spatiotemporal management of widely distributed, vulnerable pelagic fishes. Our spatial management tool is quite novel in that it considers the frequency that vertically-separated habitats are occupied within seasonal habitat suitability predictions at a global scale. This means we have extended the current framework used for spatiotemporal management in other fisheries (e.g. hake nurseries in the Mediterranean Sea - https://fishreg.jrc.ec.europa.eu/web/fish-habitat) to widely distributed, highly mobile pelagic sharks. Starting from explicitly defined goals (target life stages and thresholds for occurrence), we quantified the amount and distribution of biologically relevant habitats for blue sharks on a seasonal basis at a global scale. We then evaluated the potential protection efficiency of essential and fringe habitats for this species in a hypothetical scenario where all fishing effort is redistributed to other areas. Future work should involve simulation analyses to test the efficacy of redistributing various percentages of effort based on the actual distribution of global longline fleets, once effort data at suitable resolution become available. Such simulations should also evaluate whether

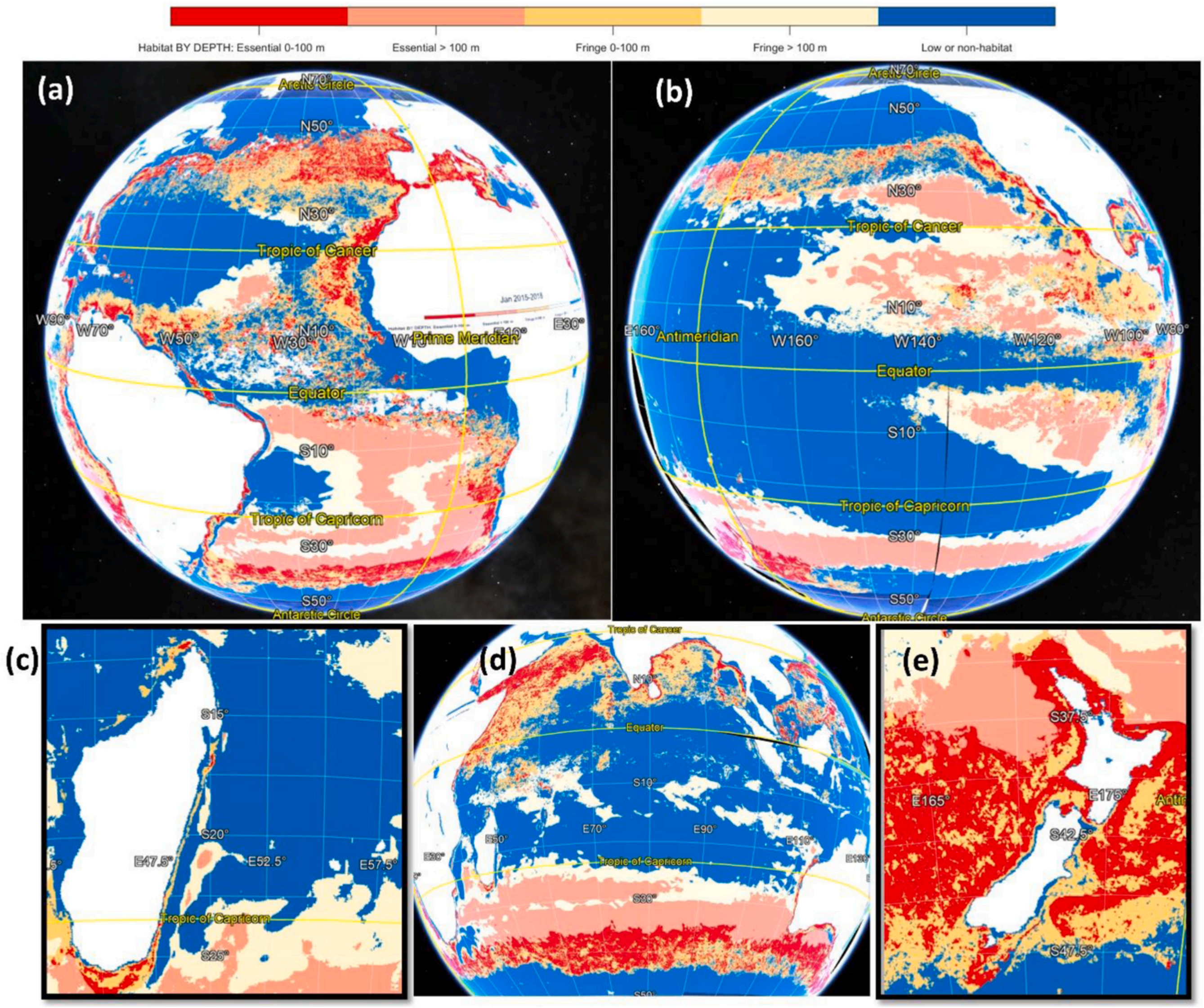

Fig. 4. Static views from the Google Earth platform of the Bycatch Mitigation Tool for vulnerable life stages of blue sharks (available at: https://fishreg.jrc.ec.europa.eu/web/fish-habitat) for January 2015–2018. The panels show: (a) the Atlantic Ocean, (b) the eastern Pacific Ocean, (d) the Indian Ocean and a more precise view on (c) Madagascar and (e) New Zealand areas. The habitat suitability categories are the same as described in Table 2.

effort redistribution effectively results in an increase in fishing intensity on blue shark within fringe areas. Considerations related to economic viability of the fishery is discussed in Section 4.4 below.

4.1. Suitability of the ENM for spatiotemporal management

The Ecological Niche Model underlying our spatial predictions offers various advantages relative to other analytical approaches. First, this ENM was observation-based at a global scale and deterministic (i.e., centered on a feeding proxy defined by productivity fronts or mesopelagic micronekton) rather than reliant on commonly used, regional statistical approaches such as Generalized Additive Mixed Models (GAMM; [40]). When predicting into the future, a large-scale deterministic method is better suited for areas that are not well-sampled, or when biotic and abiotic predictors (i.e. environmental conditions) may have shifted from historical ranges due to climate change [5]. Second, statistical models focus on getting the best possible fit between observations and environmental variables to characterise ecological processes, yet these relationships can be problematic when trying to extrapolate over a different range or spatial domain [16,8]. Spatial biases in the distribution of fishing effort (e.g. [12,39]) are well-known and lead to substantial variability in sampling intensity over the range of a globally-distributed species such as blue shark. Thus, statistical fits have the potential to exclude suitable habitats, particularly if fishery-dependent sampling missed areas of high density of non-target (bycatch) species. In addition, progressive warming at a global scale [20] may further alter the range of abiotic conditions experienced by blue sharks at particular locations on a seasonal basis, shifting their distribution outside of historical ranges. Incorporating complementary data from electronic tagging and using a deterministic model (such as ours) improves the identification of habitat from fishery-dependent data, especially in more extreme conditions [22].

Additionally, the ENM incorporated proxies for shark feeding behaviour derived from modelled (e.g. mesopelagic micronekton) and observed (satellite-derived productivity fronts) outputs that allowed habitat suitability to be assessed in both the vertical and horizontal dimensions. Consequently, our spatial management tool could differentiate between shallow and deep habitat suitability for actively foraging blue sharks. This feature could be very useful for managing longline fleets that can change their area of operation or fishing strategy to target species at different depths [29]. For example, fleets typically use either shallow-set gear to primarily target swordfish or deep-set gear to primarily target tunas [6]. Explicitly considering depth when defining and testing potential bycatch mitigation measures reduces the potential global surface area targeted for restrictive management. However, this ENM does not account for behaviours other than foraging when predicting habitat suitability. For example, species such as blue shark may periodically occupy surface waters for thermal compensation even when actively foraging at depth [4], or may access different habitats for reproduction [38] or predator avoidance [42]. While it would likely be possible to quantify a behaviour-related variable from dive depth data recorded by electronic tags to better evaluate blue shark ecology, the challenge in the ENM would be to find a corresponding environmental metric that could be used as a proxy (such as mesopelagic micronekton). In addition, predicting essential deep habitats in the ENM was more uncertain than for shallow ones, particularly because set depth was not available as a covariate with captures and because feeding at depth in oligotrophic surface areas does not preclude blue shark spending time in the surface layer to warm up. This uncertainty suggests that effort redistribution out of deep areas (i.e. moving geographical location) may benefit blue shark more than bycatch mitigation using shallow-set gear within essential deep-water habitats (i.e. remaining in the same place but fishing with shallow-set gear only).

Within the ENM, incorporating the feeding proxy to delineate shallow and deep habitats meant that it was not possible to account for interannual variability in habitat suitability. In other words, future spatiotemporal management for blue shark based on this ENM could not be in real-time but had to be based on mean environmental conditions. One of the main benefits of real-time management (also called dynamic ocean management) is that the area targeted for mitigation can be substantially smaller relative to static spatial closures [31,45]. While the realised conservation benefit of mitigation based on this ENM may be somewhat greater with higher temporal resolution (e.g. weekly, in near real-time), the distribution of suitable habitat for blue sharks was markedly different by month (Fig. 2). This suggests that the distribution of suitable habitat was primarily related to seasonal patterns and characteristics of the water column, rather than interannual variability. However, allowing for climate change and understanding its influence in the ENM is an important future research goal. Interannual variability may increase in the future as warming progresses [5]. Yet this should not overshadow the need to use biologically-relevant environmental variables to predict suitable habitat. The mean absolute trend of foraging habitat by month for each blue shark size and sex class (2003–2018) already provides useful insights of the current effects of climate change on the seasonal distributional of blue shark (Supplementary information of [22]).

4.2. Practical applicability of the bycatch mitigation tool

If fishing effort were to be redistributed, the greatest benefit to blue sharks would be realised if fisheries avoided essential habitats (reddish colours in Figs. 2 and 4) and redirected effort to the low or non-suitable habitat areas at all depths (blue colour in Figs. 2 and 4). Fringe habitats represent a larger total area which was associated with a lower potential for species protection and higher expected costs for fisheries in terms of missed opportunities. However, seasonal changes in the spatial distribution of essential suitable habitats demonstrate specific regulatory challenges associated with spatiotemporal management of widely distributed, highly mobile species. While the total amount of the global oceans potentially targeted for the application of spatiotemporal management may be small, essential habitats were not distributed evenly relative to national Exclusive Economic Zones (EEZ). This would mean that a mitigation strategy could disproportionately affect fisheries in countries with essential habitats concentrated inside their EEZs, affecting either national and coastal fleets, or distant-water fleets with an agreement to fish within an EEZ. Taking surface essential habitats as an example, these encompassed the vast majority of several countries' EEZs during the months when fisheries are expected to be most active, such as during the summer and fall along the Pacific coast of North America (Fig. 2a-d; left panels). For smaller coastal vessels, displacement of effort to low or non-suitable habitat areas farther offshore may not be a viable option, given safety concerns and operational costs [52]. Thus, we expect that our web-based tool will be most useful for highly mobile fleets operating on the high seas. A more equitable distribution would require some type of mechanism for compensation for lost opportunity by disadvantaged countries. Similarly, vessel configurations and characteristics may complicate any switches from shallow- to deep-set longline gear and would preclude changing gear types from longline to purse seine. Beyond any extra equipment costs, implementation would be imperfect because it is difficult to ensure that all longline hooks are above or below a specific depth threshold [6]. Other socioeconomic considerations such as market opportunities for different products or fishing quotas may further limit a fleet's flexibility. Equitable management must ensure that national fleets do not disproportionately bear the conservation burden in terms of lost opportunity, effort redistribution, or food and job securities. These complexities emphasise the need to consider factors beyond habitat suitability when developing/evaluating the goals underlying spatiotemporal management strategies for globally distributed marine species [1,27]. Ultimately, it may be necessary to use a Management Strategy Evaluation [46] to better elucidate trade-offs between different spatial mitigation strategies.

Providing the spatial habitat suitability predictions as a scalable and publicly accessible web-based application means that multiple users can immediately make use of the information. Hopefully, these results will make the decision-making process more practical and efficient, and will meaningfully inform discussion about the use of spatiotemporal management measures to reduce bycatch of vulnerable species, including sharks. Our intention was also to facilitate the fishing industry's ability to evaluate the likelihood of encountering sensitive stages of blue shark when choosing their fishing locations and gear set depths. Accessible tools increase the transparency and dissemination of information, thus favouring dialog and trust [28,37]. While there will always be the argument that such open-source information could be misused to target blue sharks in a more efficient way, we consider it relatively unlikely that fleets on the high seas will try to optimise their fishing strategy relative to blue sharks, potentially at the expense of other target species. Various economic and logistical drivers and pre-existing regulations, such as distance to port, licensing requirements for specific fishing grounds, ability to catch target species, and/or feasibility of gear adaptations will continue to shape vessels' fishing strategies and thus the seasonal distribution of effort [52]. All concern could be alleviated by producing aggregate maps that are a product of several species and/or size classes from which no individual species distribution could be inferred, suggesting that a multi-species approach would be preferable.

4.3. Synthesis

We have placed our results within the context of the steps required to develop and implement spatiotemporal management for bycatch mitigation by tRFMOs (Fig. 5) to highlight key information, remaining gaps, and considerations related to future implementation. We defined explicit management goals for blue sharks by focusing on the conservation of small juveniles, large juvenile females and adult females (Step 1, Fig. 5). We extracted favourable environmental conditions for each life stage from a global ENM, and combined predictions within a spatial management tool to map essential, fringe and low/non-habitat areas in shallow and deep habitats (Step 2, Fig. 5). Using the ENM validation data, we demonstrated that there was the potential for spatiotemporal management to benefit the species if fishing effort was moved outside of essential shallow and essential deep habitats. These two categories combined accounted for low percentages of relative ocean coverage (monthly ocean area from 50° S to 60° N ranged from 16% to 24%), indicating that spatial mitigation could potentially be restricted to

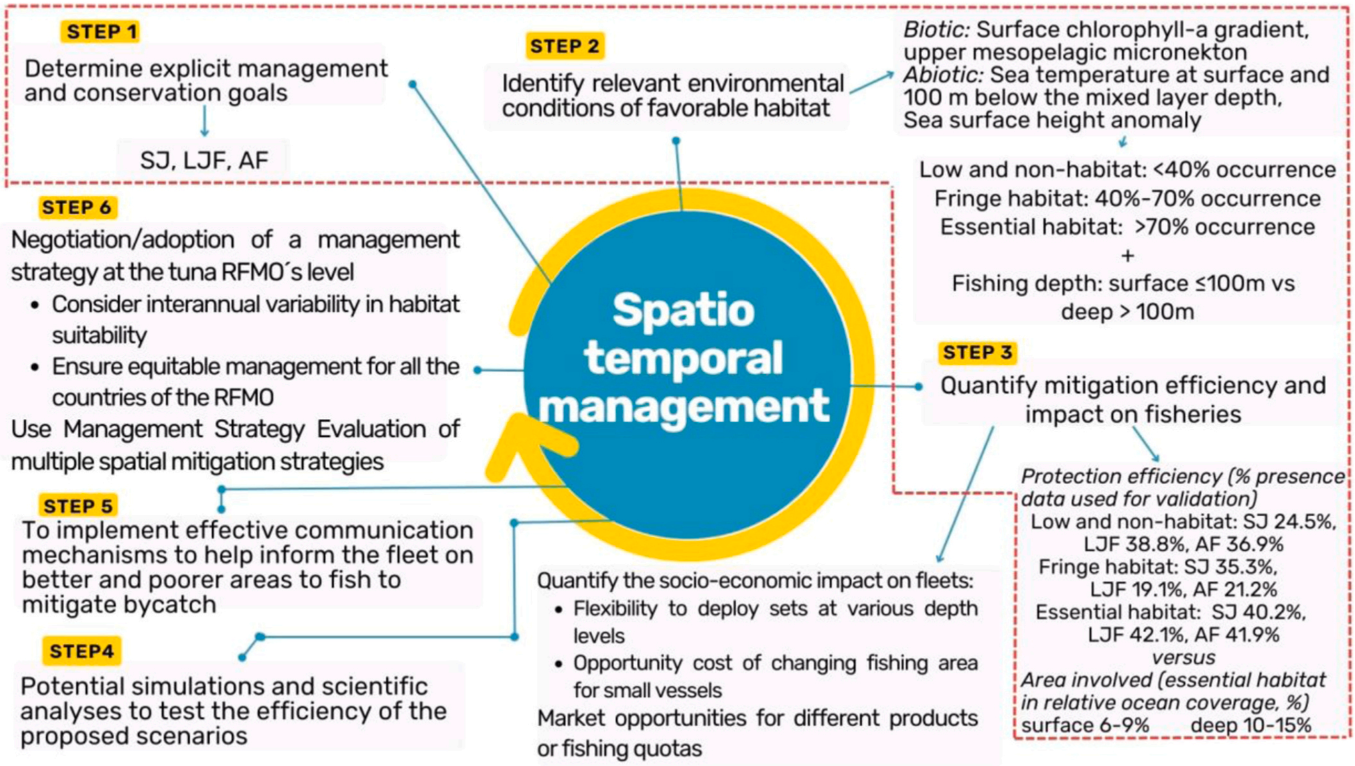

Fig. 5. Summary of the results of this case study and their application to the development of spatiotemporal management by tuna Regional Fishery Management Organisations. The habitat modelling considered: SJ - small juveniles, LJF - large juvenile females, AF - adult females. The red dashed line indicates the steps covered by the present paper.

comparatively small areas (especially considering the more reliable shallow essential habitat only from 6% to 9%) while still achieving substantial conservation benefits (about ~42% protection efficiency for all depths essential habitat; Step 3, Fig. 5). We recognize that 16–24% of the ocean surface from 50° S to 60° N represents large areas that would unlikely be the spatial extent considered for strict time-area restrictions. Management may alternatively decide for less restriction and protection efficiency, such as for the 80% threshold for essential habitat (leading to 10–14% surface area and about 24–34% estimated protection depending on life stages, see Table S1 in Supplementary Information). Nevertheless, this comparison demonstrates clear potential for spatiotemporal management to benefit blue sharks, thus validating the need for further work. Prior to further evaluation, there is a need to quantify the ability of fleets to implement technical mitigation strategies (e.g. to change gear set depth) and any socio-economic impacts (e.g. opportunity costs). It will be particularly important to quantify how effort redistribution may influence the economic viability of high seas fisheries. Assessment of future mitigation scenarios will depend on the availability of anonymized, high-resolution data on fishing effort (preferably at or lower than 1 by 1 degree resolution) that can be overlaid with habitat predictions (Step 4, Fig. 5; although see an example mostly using 5 by 5 degree resolution data in [11]). Consensus and open communication will be key during the development and assessment of management scenarios, and may be facilitated by open-source access to scientific tools (Step 5, Fig. 5). Negotiations prior to adoption will need to consider equitability among fleets, conservation objectives for blue shark, and logistical/operational constraints when evaluating efficacy (Step 6, Fig. 5).

4.4. Towards ecosystem-based co-management

Several of our results strongly support the need to develop spatiotemporal management in a multi-species context. Multi-species habitat modelling would remove any concerns surrounding potential misuse of species-specific predictions, and would more accurately account for conservation objectives in a multi-species fishery context (e.g. maintain fishing opportunity and minimise bycatch). Our spatiotemporal bycatch mitigation tool can be easily extended into a multi-habitat, multi-species approach (Fig. 6) once the underlying species-specific ENMs become available. Similar to the manner in which information was combined from multiple life stages in our blue shark case study, the habitat characteristics of any number of target, unwanted and/or species of conservation concern could be overlaid to identify areas in which it would be optimal to minimise, reduce, or redistribute fishing effort to achieve pre-agreed targets (e.g. [31]). The ensemble habitat maps would identify areas that represent the optimal trade-off amongst this suite of pre-agreed management objectives, similarly categorised into areas of high, medium and low priority for bycatch mitigation. Given that multispecies fisheries are highly adaptive when faced with regulatory changes, a multi-species approach would better mitigate any unintended displacement of effort and/or changes to targeting practices that would undermine management objectives for the broader ecosystem [1]. A multi-species framework would also operationalize the Ecosystem Approach to Fisheries Management (EAFM) or ecosystem-based management in tRFMOs. This extension relies on the future development of ENMs for each species to be included in the multi-species framework. A priority for future research could be species that are regularly intercepted by global fisheries but are already subject to no-take measures (e.g. thresher, hammerhead and mako sharks).

As in our case study, initial work for tRFMOs would be to define the main species and/or life stages that are targeted, unwanted, and protected. Prior to any modelling, it would be ideal to develop measurable and broadly acceptable objectives within a formal decision tool for bycatch management [28]. Different weighting factors for the intersection of habitats for each category would be set based on the pre-agreed management objectives and priorities, accounting for the

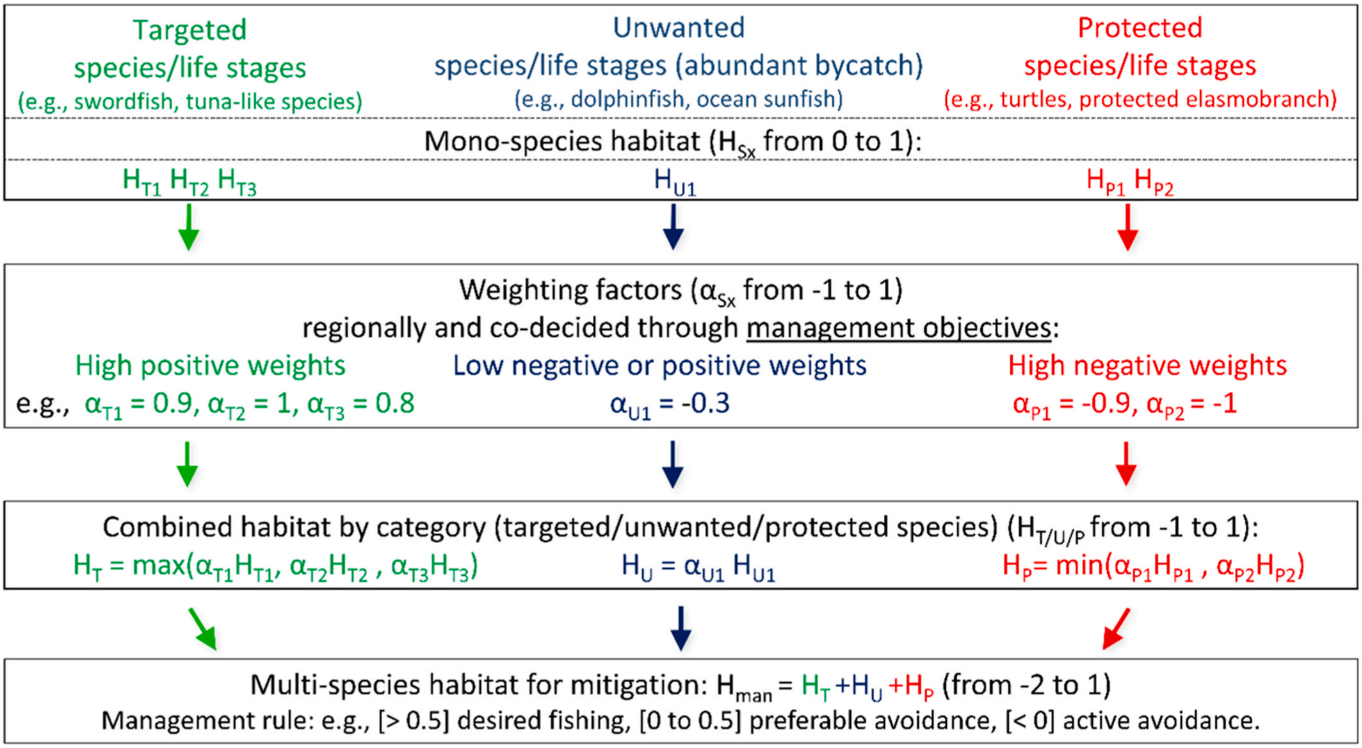

Fig. 6. Conceptual framework of a multi-species (targeted and protected) habitat product for optimising simultaneous management objectives. Identified habitat of any number of species or life stages could be associated with a species-specific weighting factor and combined into a multi-species habitat product to identify optimal areas for restrictive management.

vulnerability status of the species. Note that the categorization of each species could differ for shallow and deep habitats. Protected species should be fully avoided by longline gear. Within these three categories (targeted, unwanted, and protected), habitat suitability predictions for each species/life stage would be associated with a weighting factor that represents the desired balance between catching targeted, unwanted and protected species. As an example, areas associated with high frequencies of target species catch would likely have large positive weights (e.g. 0.9–1), representing the objective to maintain high catch rates on target species. Unwanted species could be given lower negative weight (e.g. −0.3), depending on either: (1) the estimated vulnerability of the species or (2) its role in the broader ecosystem, to avoid instability or even ecosystem regime shifts [50]. Species of extreme conservation concern could be assigned large negative weights (e.g. −0.9 to −1), operationalizing the objective to completely avoid important habitats associated with these species. We recognize that setting these weights could be complex in practice, because the chosen value represents the perceived relative importance of each species and these perceptions would differ among stakeholders. Ideally, these weights should be informed by management priorities, as well as vulnerability and ecosystem analyses to ensure the stability of their functioning in marine ecosystems. They should be decided through consensus (co-management) to facilitate compromise and acceptance.

Weighted habitat predictions would then be combined for each cell and time period (e.g. month/season) for each of the species categories. When there are multiple targeted, unwanted or protected species, the maximum of the absolute (positive or negative) weighted habitat value could be used to keep track of the species' essential habitat in the final management tool (see example in Fig. 6). The habitat suitability predictions for the species ensemble would result from the sum of the combined habitat by category (targeted species, unwanted and protected) with negative levels for the unwanted and protected species. This ensemble bycatch mitigation product would therefore map: (1) areas where targeted species are likely more present and unwanted/protected species are likely less present, representing desirable fishing grounds, and (2) areas where bycatch of unwanted and protected species are likely to occur together with a lower or more uncertain presence of the targeted species, representing areas to be avoided by the fisheries. If catch limits do not exist for a given species, the tRFMO may also decide to include a buffer zone or intermediate management status (such as 'preferable avoidance'; Fig. 6) to further geographically separate the desired fishing grounds from areas that should be actively avoided, noting that this buffer may contain the most uncertainty. A vertical dimension to the management scheme could also be included provided the information was available for the species of interest, as in our case study on blue sharks.

5. Conclusions

One of the most exciting research directions stemming from recent developments in oceanographic modelling are the novel ways to characterise space use and distribution patterns for marine species [10,51]. Further advances in ENM for marine fishes open new avenues for the development of tools to support global decision-making and EAFM [49]. While acknowledging that suitable habitats for a cosmopolitan and generalist species like blue shark are varied and may encompass large amounts of the global oceans [15,26], we demonstrate that there is still high potential to use these habitat dynamics to identify priority areas for bycatch mitigation. Looking forward, substantial effort is being made through tRFMOs to characterise fishing effort at higher spatial resolution so that spatiotemporal management options can be meaningfully evaluated (e.g. [32]). Our spatial bycatch mitigation tool and associated framework for ecosystem-based management offers a concrete basis for future discussions, supporting conservation and fishery sustainability objectives (and their trade-offs) and strengthening governance of the high seas. Widespread implementation of such an approach would support the need to safeguard biodiversity as enshrined in major regulations such as the UN Convention for Biological Diversity and the EU

Common Fisheries Policy (CFP; EU Regulation No 1380/2013).

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CRediT authorship contribution statement

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Declaration of Competing Interest

All authors are national science delegates or have participated in international advisory processes through Regional Fisheries Management Organizations.

Data Availability

The habitat tool is publicly available; link is in the manuscript

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.marpol.2024.106155.

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