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Philopatry as a Tool to Define Tentative Closed Migration Cycles and Conservation Areas for Large Pelagic Fishes in the Pacific

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Abstract: Migrations of large pelagic fishes across the Pacific are usually inferred from tagging or genetic studies. Even though these techniques have improved over time, they still fail to demonstrate large transoceanic migrations, usually proposing 'routes' that do not cycle seasonally. The current study uses the concept of 'philopatry' in 11 large pelagic fish species, i.e., the tendency for animals to return to their natal site to reproduce. Tentative migration routes and maps emerge by applying this concept to the movements extracted through a comprehensive review of the literature on satellite and conventional tagging, and population and subpopulation linkages inferred from genetic and/or genomic studies. Moreover, when comparing these proposed migration routes and the mapped reconstructed catch (1950–2016, Sea Around Us) of each species in the Pacific, similarities emerge, reinforcing the accuracy of these migration cycles informed by philopatry. Finally, by superposing the migration routes of our 11 species, we identified areas of the Pacific that are part of the inferred migration routes of multiple species, leading to a discussion of possible 'blue corridors' that would protect the studied species' key migration routes and stocks, which are important for the fisheries, culture and nutrition of Pacific islanders.

Keywords: conservation priority; biodiversity; fisheries; tuna; billfish; migrations; temperature; philopatry; MPAs; high seas; blue corridors

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1. Introduction

Large marine pelagic fishes, such as tuna and billfish, are widely distributed, both within the 200-mile Exclusive Economic Zones (EEZs) of maritime countries and their overseas territories [1]. They undertake long-range migration and are very variable in their distribution and abundance [2]. However, the migratory routes of many large pelagic species are poorly or partially understood, which complicates fishery management.

Existing or proposed tools for the conservation of large pelagic fish include large-scale Marine Protected Areas (LSMPAs) and networks of MPAs that incorporate dynamic marine features such as primary productivity sites [1–5]. Additionally, well-enforced fishing regulations within EEZs can play an important role in the conservation of large pelagic fishes [6] and indeed represent a necessary initial step, even before the establishment of well-regulated MPAs. Most of the tuna and billfish are caught in the high seas by longliners and purse seiners [7,8]. However, until recently, few marine reserves had been implemented that included open ocean habitats [4,9]. There have also been more targeted attempts to protect large pelagic fish and other highly migratory species. Examples are the East Pacific Conservation Marine Corridor [10] or the sister sanctuaries established between the USA and the Dominican Republic to protect humpback whales [11].

Because understanding the movements of large marine pelagic fish is key to rebuilding their heavily diminished populations [1], conservation efforts need to consider the entire body of knowledge available on the migrations and movements of different species. Temperature is one key factor in the distribution and seasonal migration of fishes [12,13]; notably, it plays a key role in the global distribution patterns of tuna and billfish, with species richness peaking at intermediate latitudes in both hemispheres (10 to 35°) and declining near the equator and higher latitudes [14]. This is particularly true in the Pacific, where the highest species richness occurs between 20 to 35° North and South [14]. However, the key to unlocking an understanding of the seasonal migration of large pelagic fish is philopatry, i.e., the tendency for animals to return to their natal site to produce offspring [15–17]. This reproductive strategy implies an 'imprinting' of features of the natal site onto individuals, enabling them to readily identify a site favorable to the survival of their offspring [15–17]. This implies that fish migrations, for most of the individuals of a population, must involve a loop that completes an annual cycle.

Another important consideration when attempting to interpret data on tuna migration and spawning is that, contrary to the assumption that they would spawn in productive areas of the oceans so their larvae find abundant food, tuna prefer oligotrophic waters as spawning grounds [18–22], because of a lower abundance of larval predators [23].

Based on these three elements (i.e., the key role of temperature, philopatry and the tendency to spawn in oligotrophic waters), large-scale movements of tuna and tuna-like populations in 11 species of large pelagic fish in the Pacific Ocean are here integrated into plausible annual migration cycles. These species- and stock-specific cycles, defined by half-degree latitude x longitude spatial cells, were superposed to identify areas of the Pacific that appear to be parts of the migration pathway of multiple populations and species of large pelagic fishes. These areas may be considered of special concern, requiring special protection.

2. Materials and Methods

We selected large marine pelagic species based on their membership in functional groups defined by Christensen et al. (2009) [24], who classified species based on their taxonomic affinities, position in the water column, feeding habits and maximum size.

Of the species in the large pelagic functional group, we extracted species that are exploited both in the high seas and in the EEZs of countries with coastlines in the Pacific and that had high catches in the database of the Sea Around Us (www.seaaroundus.org, accessed on 30 November 2021 [25]), which includes data from the Food and Agriculture Organization of the United Nations (FAO, Rome, Italy), Regional Fisheries Research Organizations and other official and unofficial sources (see contributions in [26–28]), covering the years 1950 to 2018 [29,30]. The selected species are listed in Table 1.

An exhaustive literature review of the species in Table 1 was then undertaken to obtain information on the movements of large pelagics within the Pacific Ocean, concentrating first on well-documented trajectories through mainly tagging studies (with regular or satellite tags), then on spatial linkages inferred from genetic or genomic studies. These trajectories were mapped in the form of curved arrows. Assuming that philopatry would generate annual migration cycles, we traced tentative return trajectories in all cases where the existing literature failed to document a return to the start of a documented trajectory. This step involved a subjective element, whose impact we mitigated by simultaneously considering the catch maps available from the Sea Around Us website for the years 1950 to 2016 (the maps utilize a color-coded scale from low (blue) to high (red) catch).

Table 1. Major species of large pelagic fishes caught in the Pacific Ocean. The % refers to the amount that a species contributed to the total catch in the Pacific (EEZs and high seas, respectively) from 1950 to 2018 (extracted from the Sea Around Us database; www.seaaroundus.org, accessed on 3 September 2021). In the Pacific between 1950–2018, more than 4% of the total catch that occurred in its EEZs were large pelagic species, whereas more than 87% of the total catch in the high seas were large pelagic species. Note the 11 species in bold, which are the focus of the current study.

In Pacific EEZs (% Total Catch within EEZs)	In Pacific High Seas (% Total Catch within High Seas)
Katsuwonus pelamis (1.5)	***Katsuwonus pelamis*** (39)
Thunnus albacares (0.6)	***Thunnus albacares*** (24)
Thunnus obesus (0.2)	***Thunnus obesus*** (14)
Thunnus alalunga (0.2)	***Thunnus alalunga*** (6)
Scomberomorus commerson (0.2)	***Xiphias gladius*** (2)
Scomberomorus niphonius (0.2)	***Kajikia audax*** (0.8)
Coryphaena hippurus (0.08)	***Coryphaena hippurus*** (0.7)
Fistularia corneta (0.07)	***Thunnus orientalis*** (0.5)
Thunnus tonggol (0.06)	*Thunnus maccoyii* (0.1)
Euthynnus affinis (0.06)	***Acanthocybium solandri*** (0.08)
Thunnus orientalis (0.05)	***Istiompax indica*** (0.07)
Xiphias gladius (0.04)	***Istiophorus platypterus*** (0.03)
Kajikia audax (0.03)	-
Elegatis bipinnulata (0.03)	-
Istiompax indica (0.01)	-
Scomberomorus sierra (0.007)	-
Acanthocybium solandri (0.005)	-
Istiophorus platypterus (0.005)	-

The tentative migration routes identified by the arrow drawn as part of a review of the literature and the concept of philopatry were transposed onto maps of (seasonal or permanent) habitat uses. We use a grid that divided the waters of the world map into cells of half a degree of latitude and longitude. The maps were based on the cells covered by the length of these arrows, which connected the sections covered by the arrows with transitional spatial cells (Figure 1). This resulted, for stocks with wide, cross-Pacific distributions, in doughnut-shaped habitat use maps. For stocks with narrower distributions, this resulted in roughly circular habitat use maps, as it was assumed that the smaller, 'resident' stocks would inhabit their entire distribution range. The 11 individual maps that were thus created were then assembled (Figure 13) and digitized, and the $\frac{1}{2}$ degree cells were identified, which were part of the migration routes (i.e., the habitat) of each of our 11 species.

Finally, the superposition of the half-degree spatial cells, defined for each of the 11 bold species in Table 1 (*Katsuwonus pelamis*, *Thunnus albacares*, *Thunnus obesus*, *Thunnus alalunga*, *Thunnus orientalis*, *Xiphias gladius*, *Coryphaena hippurus*, *Kajikia audax*, *Istiompax indica*, *Acanthocybium solandri*, *Istiophorus platypterus*), generated a map in ArcGIS that defined areas of the Pacific used as a habitat by each selected species, leading to Figure 14, in which important areas for the conservation of large pelagic species in the Pacific are displayed.

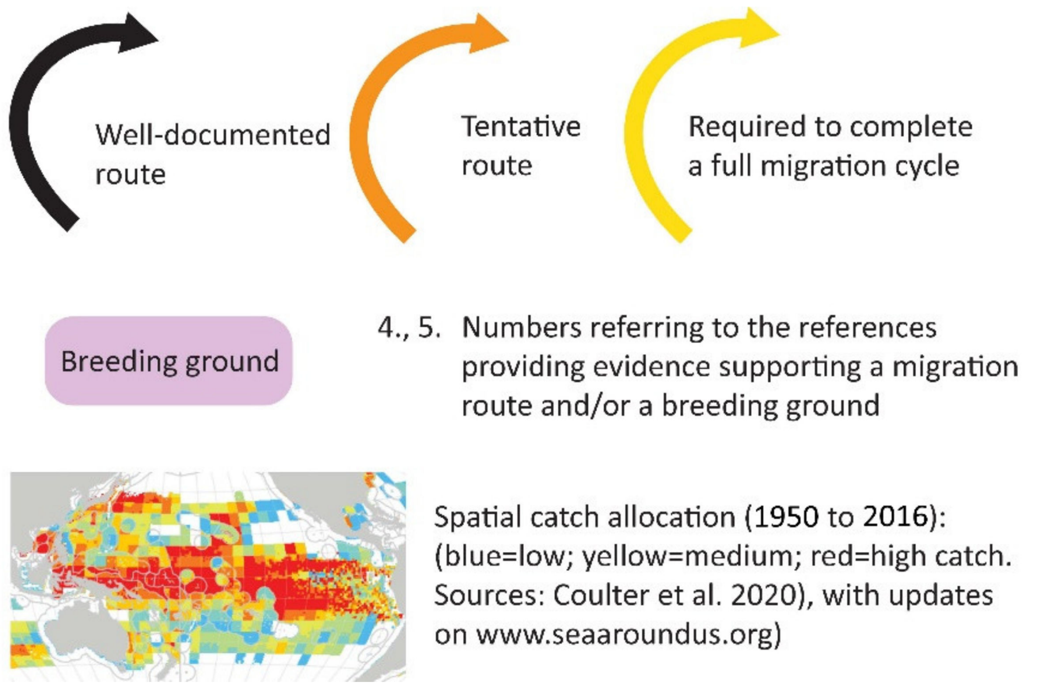

Figure 1. Key elements of the maps for the 11 studied large pelagic species. The arrows all have the same breadth, but the length and trajectories of the mapped curved arrows were drawn based on the literature and assuming that philopatry would generate annual migration cycles. The colors of the arrows represent the confidence level of the drawn trajectory. Black: all the available literature confirmed this route. Orange: there were discrepancies in the literature and the trajectory is partially supported by the concept of philopatry. Yellow: the available literature failed to document this trajectory and it is mainly based on the concept of philopatry (see text). The catch maps [28] available from the Sea Around Us website for the years 1950 to 2016 utilize a color-coded scale from low (blue) to high (red) catch and serve to mitigate the impact of subjective elements.

3. Results and Discussion

3.1. Large Pelagic Species Migrations

In the following, the results of the considerations and work described above are presented and discussed on a per species basis, then as a whole for all major pelagic fish species in the Pacific Ocean. Most of the suggested migration patterns match with the respective catch distribution map.

3.1.1. Skipjack (*Katsuwonus pelamis*)

Skipjack tuna (*Katsuwonus pelamis*) can be found between 40° N and 40° S [31,32], being more abundant in tropical and subtropical waters of the Pacific [32], within 20° N of the equator [33].

In what they claim is the first fishery-independent study of the horizontal and vertical habitat of skipjack tuna in the western Pacific Ocean, Kiyofuji et al. (2019) [34] show that 95% of its vertical distribution is above 115 m, i.e., shallower than the 18 °C thermocline. Thus, skipjack habitat distribution in the western part of the North Pacific is constrained between 18.8 °C and 28.2 °C [32,34]. The seasonal west–east movements of skipjack tuna thus appear to be a response to temperature [34].

Spawning tends to occur in waters with sea surface temperatures (SSTs) greater than 24 °C [33,35–40]. Events such as El Niño and La Niña impact skipjack distribution [18,38]; however, there is fidelity to spawning areas [38], i.e., philopatry. Figure 2 summarizes these considerations.

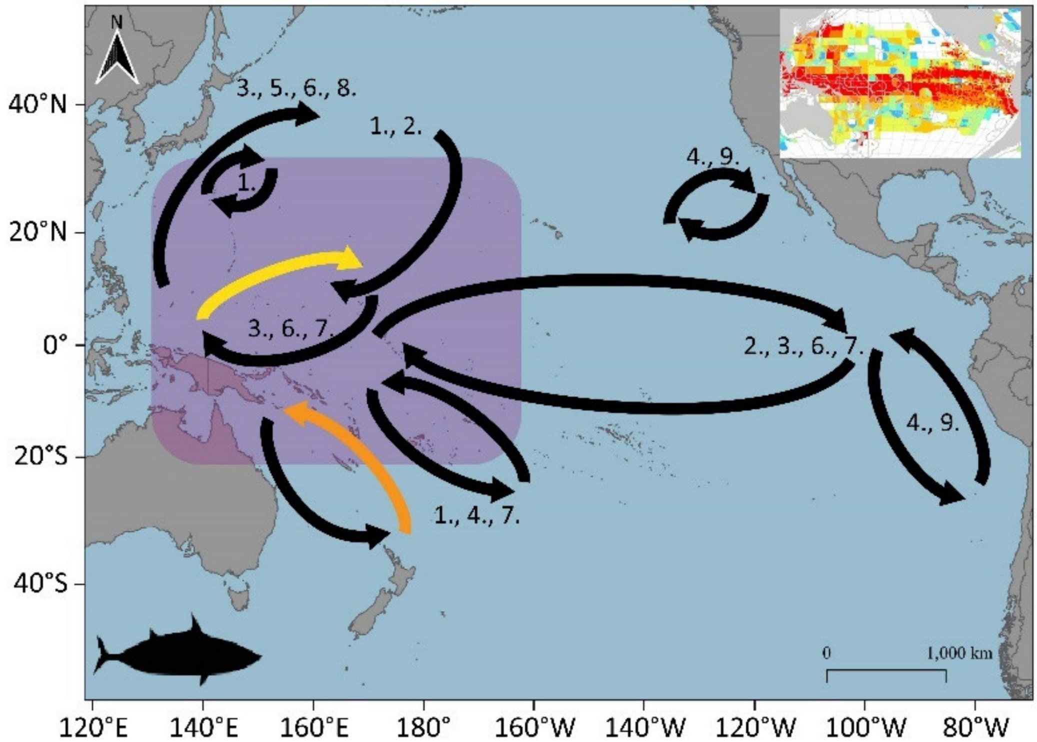

Figure 2. Tentative migration routes of skipjack (*Katsuwonus pelamis*) inferred from several sources (numbers adjacent to the arrows). This suggests six different stocks and substocks: a substock in the west of Japan and north of Papua New Guinea; a large central Pacific stock; substocks along the Peninsula of Baja California; along the coast of Ecuador, Perú and Chile; in the Coral Sea and Salomon Sea; and another adjacent to the last in Polynesian waters. Sources: (1) Kiyofuji et al. (2019) [34]; (2) Bell et al. (2013) [41]; (3) Harley and Williams (2013) [42]; (4) Fontenau and Hallier (2015) [43]; (5) Hernandez et al. (2019) [18]; (6) Vincent et al. (2019) [32]; (7) Lehodey et al. (1997) [44]; (8); Moore et al. (2020) [38] and (9) Prince and Goodyear (2006) [45]. The shaded purple area refers to breeding grounds [18,34]. The insert in the upper right corner shows the catch distribution of skipjack from 1950 to 2016 (blue: low; red: high catches [28]).

3.1.2. Yellowfin (*Thunnus albacares*)

In the western Pacific, adult yellowfin tuna (*Thunnus albacares*) can be found between 40° N and 40° S, with a narrowing of this range in eastern longitudes. Younger fish prefer warmer waters and thus have a more restricted latitudinal range [46]. According to Hernandez et al. (2019) [18], larvae are distributed between 23° N and 15° S, but other authors suggest a more limited distribution between 10° N and 5° S [35], supporting the idea of a continuous nursery ground between 10° N and 5° S [35]. The subadult tuna reaches further north, e.g., to Hawaii [47].

Southern and northern migration routes appear to exist [47], but overall, the migrations of this tuna in the Pacific are not well-understood. Moore et al. (2020) [38] believe in the notion of a Pacific-wide panmixia for yellowfin, while Bertrand (1999) [46] suggests the possibility of three different main stocks: one west of 170° W, one in the central Pacific, and one east of 120° W. Figure 3 summarizes this information.

3.1.3. Bigeye Tuna (*Thunnus obesus*)

Bigeye tuna in the Pacific Ocean belong to a population that is genetically distinct from those in the Atlantic and the Indian Ocean [52,53]. In the western Pacific, their distribution ranges from 45° N to 40° S, and from 40° N to 30° S in the eastern Pacific [46]. Adults move across a wide range of latitudes, while juveniles are found near the equator [46] and larvae mostly between 30° N and 20° S [18]. The wide distribution of the juveniles and adults around the equator shrinks towards the west [46], where juveniles have been observed in schools mixed with adult skipjack and juvenile yellowfin [46].

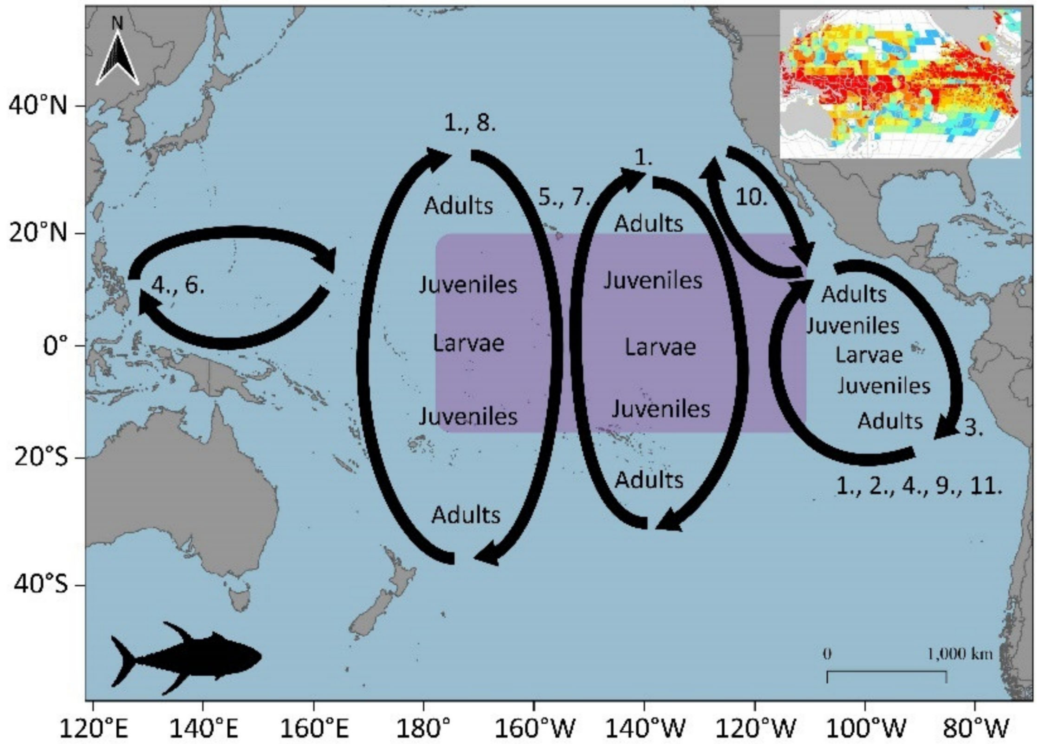

Figure 3. Tentative migration routes of yellowfin (*Thunnus albacares*) inferred from several sources (numbers adjacent to the arrows). This suggests the existence of three different stocks in the central Pacific and two substocks from the Bismarck Sea to the Philippine Sea and along the coast of Mexico. Sources: (1) Bertrand (1999) [46]; (2) Schaefer et al. (2011) [48]; (3) Harrison et al. (2018) [49]; (4) Fontenau and Hallier (2015) [43]; (5) Hernandez et al. (2019) [18]; (6) Itano (2000) [35]; (7) Moore et al. (2020) [38]; (8) Wells et al. (2012) [47]; (9) Prince and Goodyear (2006) [45]; (10) Block et al. (2011) [50] and (11) FAO (1994) [51]. The shaded purple areas refer to breeding grounds [18,35,38]. The insert in the upper right corner shows the catch distribution of yellowfin from 1950 to 2016 (blue: low; red: high catches [28]).

Bigeye can be found in cold and warm water between 9 and 28 °C with minimum dissolved oxygen levels of 1 mL·L^{-1} [46,54,55]. Climate projections indicate that the adult stock may decrease in the western and central Pacific but increase in the eastern Pacific [56].

The spawning grounds of bigeye tuna are along the equatorial strip during the whole year, with peaks in certain months [57]. There is a hypothesis suggesting the existence of a single stock in the Pacific [46]. However, other authors suggest the existence of an eastern and western stock [38,46,58]. Figure 4 summarizes these considerations.

3.1.4. Albacore (*Thunnus alalunga*)

This tuna is present in all three oceans between 40° N and 40° S, though with a lower abundance in equatorial waters [60], and occurs at depths down to 400 m [46]. The distribution of albacore in the Northern and Southern Hemispheres appears symmetrical. Adults spawn in tropical and subtropical waters, after which larvae and juveniles drift to higher latitudes in the north and south [36,60–63].

Larvae are more commonly observed around 20° N and S [18,60], while in the Northern Hemisphere, juveniles migrate into the productive waters of the Kuroshio and California Current Systems [46,62]. Figure 5 summarizes these considerations.

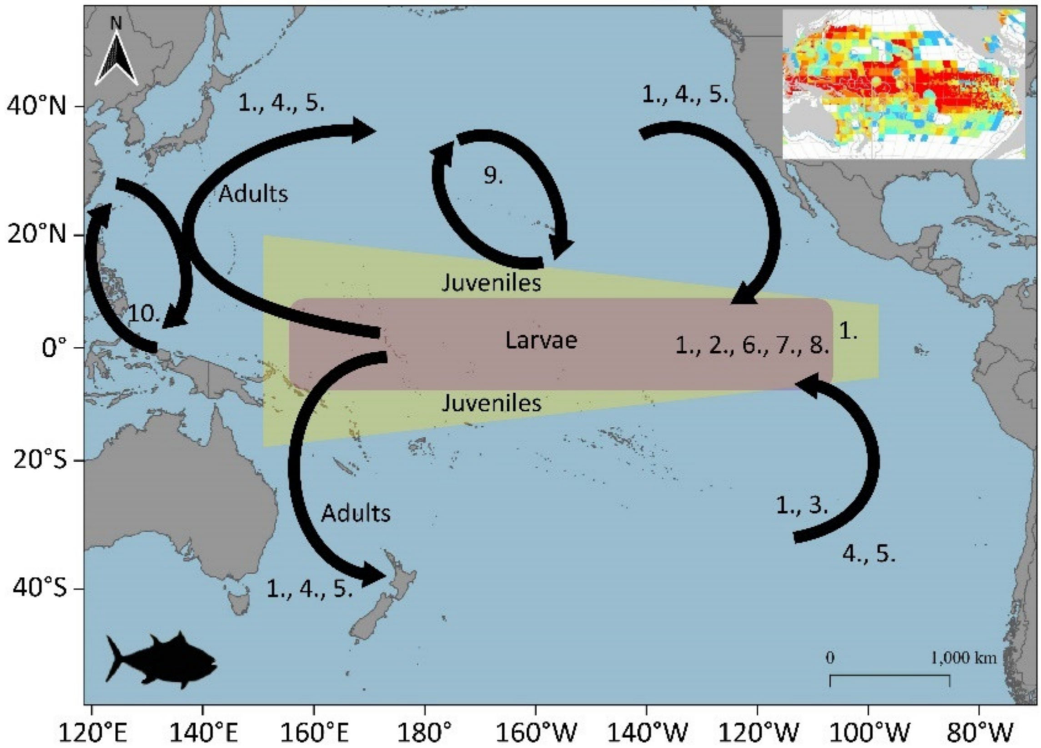

Figure 4. Tentative migration routes of bigeye (*Thunnus obesus*) inferred from several sources (see numbers adjacent to the arrows). This suggests two stocks, north and south of the equator, with spawning grounds throughout the Equatorial Pacific. Sources: (1) Bertrand (1999) [46]; (2) Harley and Williams (2013) [42]; (3) Fontenau and Hallier (2015) [43]; (4) Hernandez et al. (2019) [18]; (5) Schaefer and Fuller (2019) [40]; (6) Schaefer et al. (2005) [39]; (7) Zhu et al. (2010) [57]; (8) Moore et al. (2020) [38]; (9) Sibert et al. (2003) [59] and (10) Chiang et al. (2006) [53]. The shaded purple area refers to breeding grounds [38,39]. The pink and yellow shaded area refers to the main distribution area of larvae and juveniles, respectively. The insert in the upper right corner shows the catch distribution of bigeye from 1950 to 2016 (blue: low; red: high catches [28]).

Environmental factors such as temperature are responsible for these migrations; thus, Bertrand (1999) [46] proposed a temperature range for albacore between 15 and 22 °C. Adult albacore is reported to be caught most often in depths between 100 and 300 m; however, in the temperate waters of New Zealand, adult albacore is caught in waters shallower than 150 m. Research surveys suggest that juveniles are distributed in the upper 100–120 m and that fish tend to stay deeper during daylight hours [63].

3.1.5. Pacific Bluefin Tuna (*Thunnus orientalis*)

Pacific bluefin tuna (*Thunnus orientalis*) is one of the largest tuna species [66] and occurs across the Pacific [67,68], though mainly in the north [69], where it performs regular transpacific migrations [49,66].

The adults move to the western Pacific to spawn, and some adults make postspawning migrations to the South Pacific, but the early juveniles remain in the western Pacific. However, after their first year, some juveniles migrate to coastal waters off California to feed. Thus, the juveniles utilize both sides of the North Pacific Ocean, as do the adults [66,68,69]. However, there is not much information on Pacific bluefin tuna movements in the eastern Pacific [69]. Information is also scarce on their movements from the south coast of Japan to offshore areas and the pathways around New Zealand [66]. Figure 6 summarizes this information.

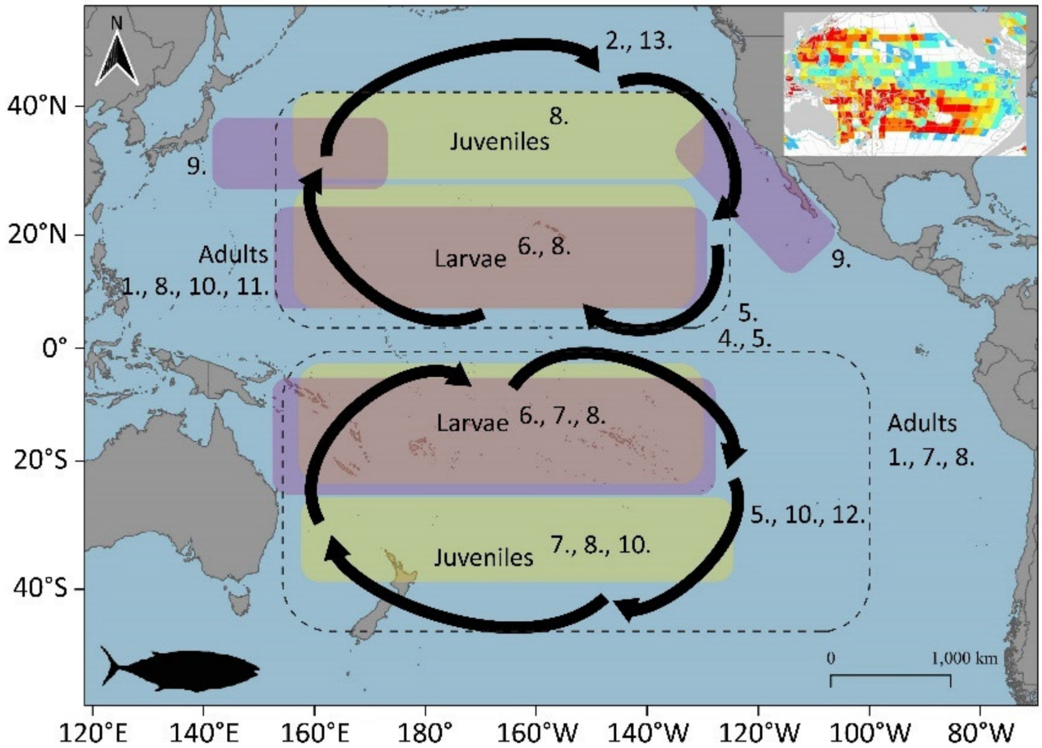

Figure 5. Tentative migration routes of albacore (*Thunnus alalunga*) inferred from several sources (see numbers adjacent to the arrows). This suggests two stocks, north and south of the equator. Sources: (1) Bertrand (1999) [46]; (2) Harrison et al. (2018) [49]; (3) Harley and Williams (2013) [42]; (4) Dhurmeea et al. (2016) [61]; (5) Farley et al. (2013) [36]; (6) Hernandez et al. (2019) [18]; (7) Murray (1993) [63]; (8) Lewis (1990) [60]; (9) Arnold (2001) [62]; (10) Childers et al. (2011) [64]; (11) Uosaki (2004) [65]; (12) Moore et al. (2020) [38]; (13) Block et al. (2011) [50]. The shaded purple areas refer to breeding grounds [36,38,62,64]. The pink and yellow shaded area refers to the main distribution area of larvae and juveniles, respectively. The insert in the upper right corner shows the catch distribution of albacore from 1950 to 2016 (blue: low; red: high catches [28]).

3.1.6. Swordfish (*Xiphias gladius*)

Swordfish (*Xiphias gladius*) has the widest distribution of all billfishes [73,74] and can be found in all three oceans [75] throughout temperate, subtropical and tropical regions, [76] mainly between 45° N and 45° S [73,74]. A study by Evans et al. (2014) [77] suggested that most of the individuals tagged spent the vast majority of their lifetime within the 15 and 45° S latitudinal range.

The gene flow of swordfish seems to have a U-shape, open in the western Pacific [76], which matches the suggested existence of two independent stocks, one northern and one southwestern stock [76,78,79]. Other genetic studies support a northeastern and southeastern stock differentiation in the Pacific [80,81]. Additionally, it appears that there is agreement as to the existence of two distinct stocks, northern and southern [80,81], although some authors suggest overlapping or exchange between these two stocks [82].

Spawning occurs between the equator and 30° N in the Northern Hemisphere during the boreal summer in the western and central Pacific. Spawning in the Southern Hemisphere occurs in the northeast of Australia during the austral summer [77]. There is a broad and quasi-continuous maturation–spawning region associated with the warm waters of the central-western intertropical band [83]. However, information is lacking about this species' spatial structure, spawning grounds, habitat preferences and population composition [75,77,84].

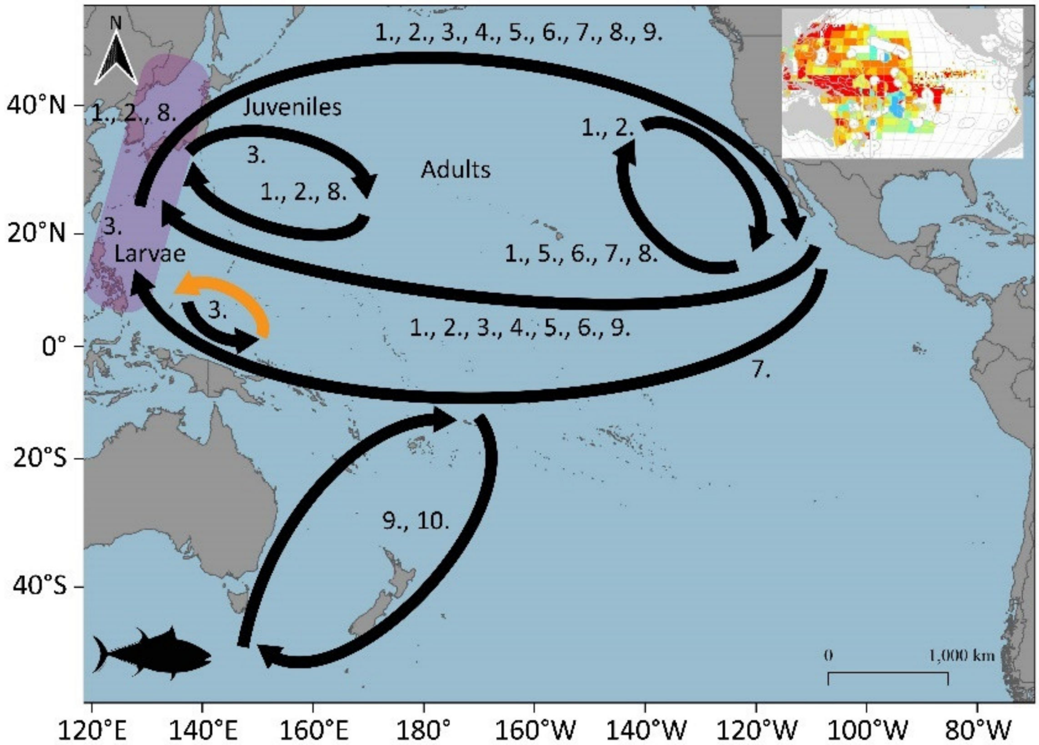

Figure 6. Tentative migration routes of Pacific bluefin (*Thunnus orientalis*) inferred from several sources (see numbers adjacent to the arrows). This suggests one stock in the North Pacific with three substocks and another stock in the south of the Pacific. Sources: (1) Boustany et al. (2010) [67]; (2) Secor (2015) [70]; (3) Block et al. (2011) [50]; (4) Harrison et al. (2018) [49]; (5) Itoh et al. (2003) [71]; (6) Kitaga et al. (2007) [69]; (7) Madigan et al. (2014) [68]; (8) Fujioka et al. (2015) [66]; (9) FAO (1994) [51] and (10) Fournier et al. (1990) [72]. The shaded purple area refers to breeding grounds [50,66]. The insert in the upper right corner shows the catch distribution of bluefin from 1950 to 2016 (blue: low; red: high catches [28]).

The study of Su et al. (2020) [75], based on fishery and remote sensing data with wide spatial coverage, demonstrated that sea surface temperature is the most important factor impacting swordfish spatial distribution. Abundance and distribution are generally associated with surface waters >18 °C and <30 °C [82]. Figure 7 summarizes these considerations.

3.1.7. Common Dolphinfish (*Coryphaena hippurus*)

Common dolphinfish (*Coryphaena hippurus*) is an epipelagic highly migratory species found across temperate, tropical and subtropical zones around the world [85–87] from 40° N to 40° S [73,88,89]. Diaz-Jaimes et al. (2010) [88] noted that, overall, there is a lack of genetic population studies covering the global distribution of dolphinfish.

Common dolphinfish migrate from the open ocean to nearshore [86,90,91] to reproduce, where they are mostly caught. Dolphinfish that escape fishing nets and survive spawning return offshore, and thus reduce their risk of predation by blue marlin, *Makaira nigricans* [90,92]. Environmental factors, such as sea surface temperature, fronts, chlorophyll concentrations [87,89,93,94] and surface currents [95], influence the migration patterns of common dolphinfish. Figure 8 summarizes these considerations.

It has also been reported that dolphinfish are strongly associated with floating macroalgae, drifting terrestrial plants and other flotsam [96]. Dolphinfish can tolerate low temperatures of around 16 °C [97] with a thermal preference of around 20 °C [98]. It is expected that the distribution of this species, due to climate change, is going to shift poleward [93]. These kinds of shifts are not properly addressed by most fisheries' management [99], which will affect fishers and other stakeholders.

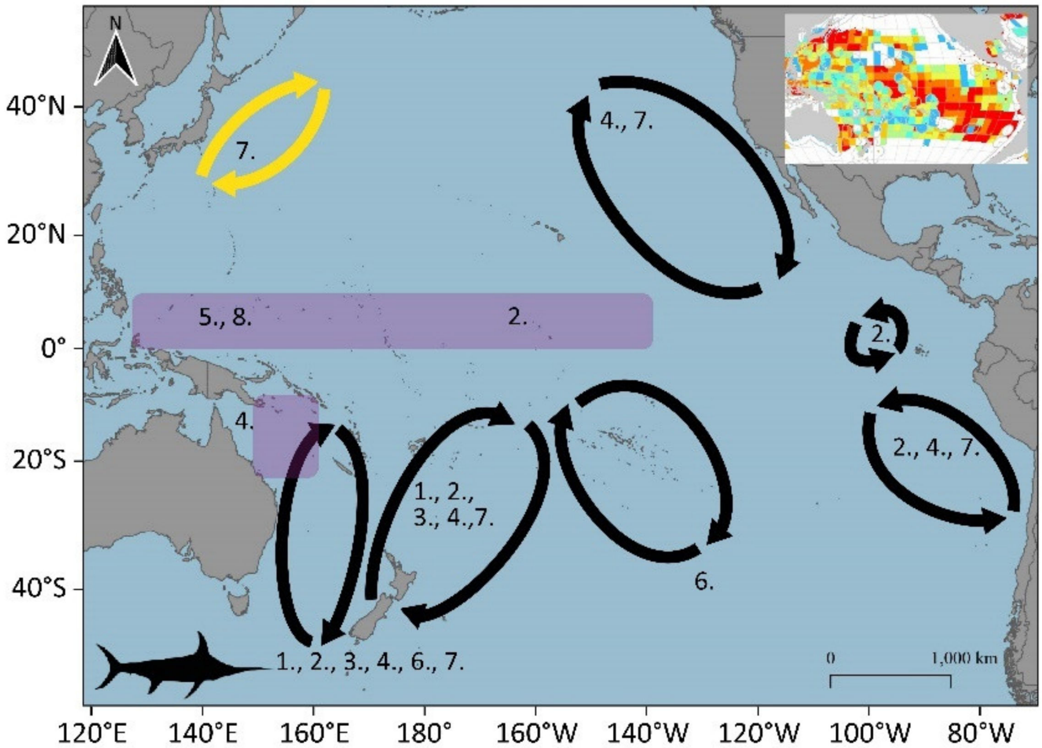

Figure 7. Tentative migration routes of swordfish (*Xiphias gladius*) inferred from several sources (see numbers adjacent to the arrows). There appears to be no consensus on the stock structure of swordfish in the Pacific. We present here one interpretation of the available data, suggesting a northern and a southern stock [76,77] with several substocks. Sources: (1) Davies et al. (2013) [79]; (2) Evans et al. (2014) [77]; (3) Evans et al. (2012) [76]; (4) Braun et al. (2015) [74]; (5) Reeb et al. (2000) [82]; (6) Harley and Williams (2013) [42]; (7) Su et al. (2020) [75] and (8) Kasapidis et al. (2008) [83]. The shaded purple area refers to breeding grounds [77,82,83]. The insert in the upper right corner shows the catch distribution of swordfish from 1950 to 2016 (blue: low; red: high catches [28]).

3.1.8. Striped Marlin (*Kajikia audax*)

Striped marlin (*Kajikia audax*) is one of the most widely distributed billfish [103,104], inhabiting the epipelagic zone throughout the Pacific basin [105]. Striped marlin can be found in the eastern Pacific between 45° N and 30° S and in the western Pacific between 45° N and 5° S [103,106]. The strip near the equator between 20–30° N and 20–30° S is less frequented [104,107,108], and many authors agree on a horseshoe-shaped distribution that occupies the whole Pacific Ocean [103,104,109–111]. However, a report by Kurashima et al. (2020) [112] indicates that "studies of movements in striped marlin have only been performed in the South Pacific and the North East Pacific. There is no long-term data [from pop-up satellite archival transmitting tags], and the longest case is 259 days" [112].

The distribution of striped marlin is related to environmental variables, especially with sea surface temperature [110,111,113]. Their optimum range is between about 20 and 25 °C [113]. As with other marine fishes, climate change predictions suggest a displacement of striped marlin to higher latitudes in the Pacific Ocean [110].

There are different spawning grounds based on the literature, for example, near the coast of Mexico [114], the east coast of Japan [104,115] or Hawaii [115]. Additionally, some areas are considered spawning grounds, such as the Coral Sea, around Fiji and south of French Polynesia [116]. Figure 9 summarizes these considerations.

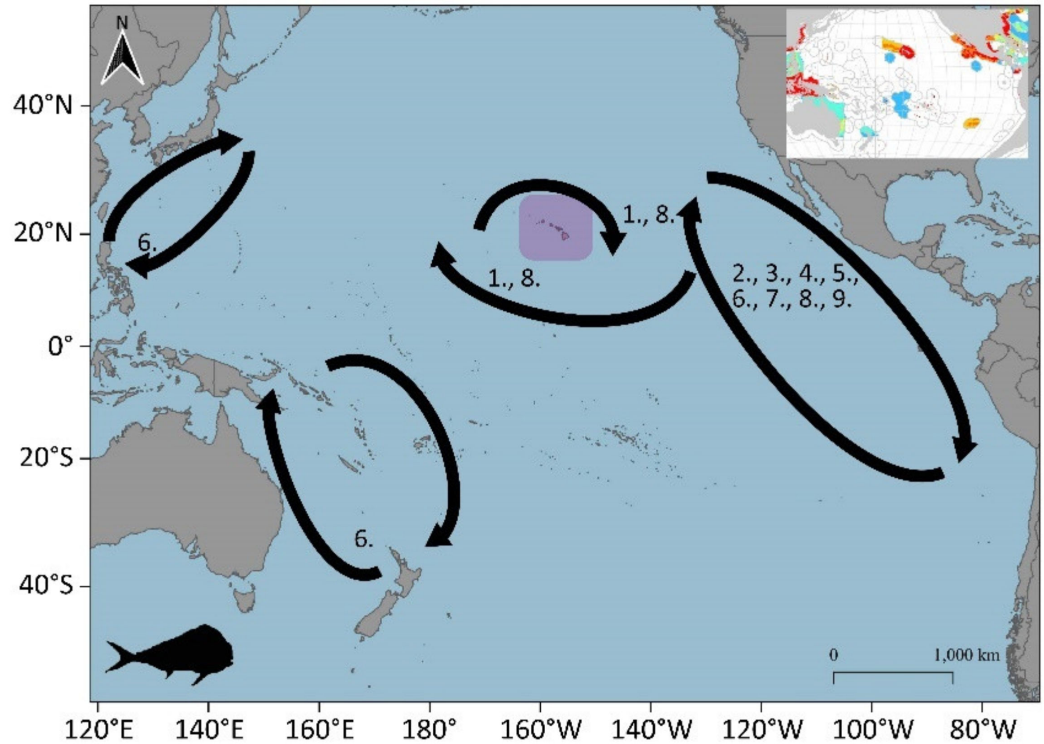

Figure 8. Tentative migration routes of common dolphinfish (*Coryphaena hippurus*) inferred from several sources (see numbers adjacent to the arrows). This distinguishes four strongly differentiated stocks in the eastern, central and northern Pacific [88]. Sources: (1) Uchiyama and Boggs (2006) [90]; (2) Lasso and Zapata (1999) [95]; (3) Flores et al. (2008) [94]; (4) Tripp-Valdez et al. (2010) [100]; (5) Torrejon-Magallanes et al. (2019) [87]; (6) Salvadeo et al. (2020) [93]; (7) Marin-Enriquez et al. (2018) [89]; (8) Kraul (1999) [101] and (9) Guzman et al. (2015) [102]. The shaded purple area refers to breeding grounds [90]. The insert in the upper right corner shows the catch distribution of common dolphinfish from 1950 to 2016 (blue: low; red: high catches [28]).

3.1.9. Black Marlin (*Istiompax indica*)

Black marlin (*Istiompax indica*) is a highly migratory species that is widely distributed in tropical and subtropical waters [74,122–124]. As in other billfish, the distribution of black marlin varies seasonally, with high densities in summer (in high latitudes) and in winter (in low latitudes) [74,125]. Black marlin often occurs in relatively high numbers in the East China Sea, northwest Coral Sea, Arafura Sea, Sulu Sea, Celebes Sea, around Taiwan, in northwestern Australia and off the coast of Panama [125,126]. Their migrations are correlated with SSTs of 25–28 °C [124,127]. It seems that this and other billfish species tend to visit continental margins and seamounts, where they are more exposed to human activities [128,129].

The trans-equatorial and trans-Pacific movements of black marlin [130], together with the fact that they do not form spawning aggregations [124], hinder the acquisition of knowledge about the distribution of this species. More detail-oriented research (temporal and spatial) is necessary to define the boundaries of spawning habitats [125]. In the absence of better information, some authors have suggested that the Pacific population of black marlin is genetically homogeneous [122,124,128,131,132]. Figure 10 summarizes this information.

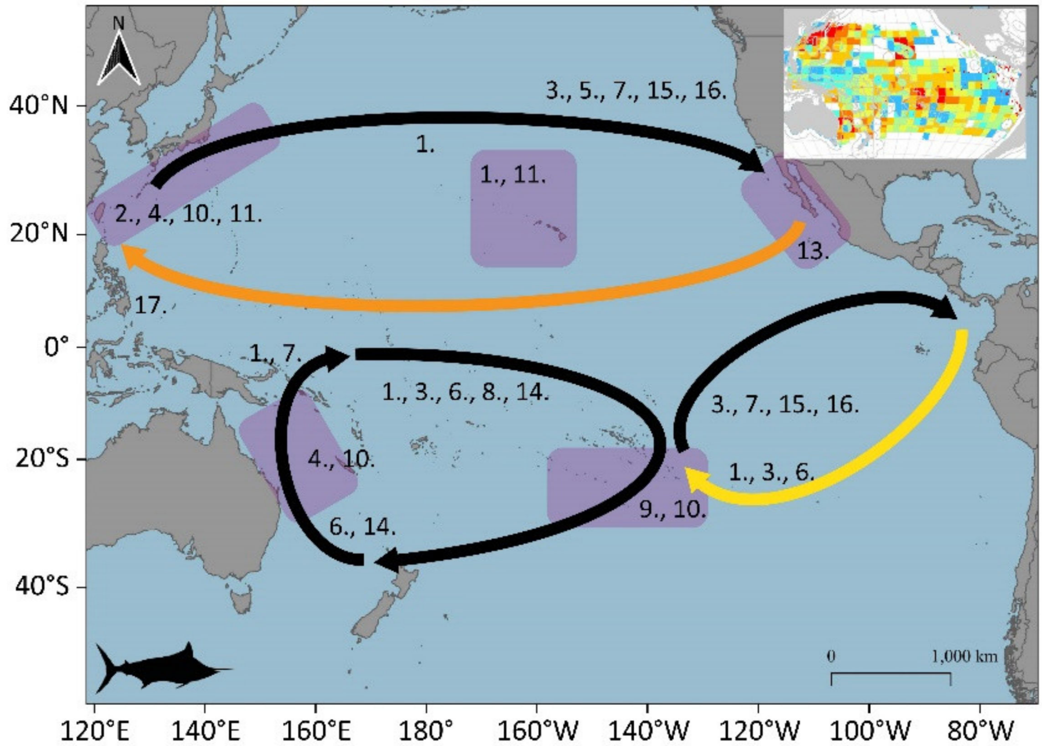

Figure 9. Tentative migration routes of striped marlin (*Kajikia audax*) inferred from several sources (see numbers adjacent to the arrows). This suggests the existence of three stocks: one across the entire North Pacific from Japan, the second occupying the southeast Pacific and the third in the southwest Pacific to French Polynesia. Sources: (1) Braun et al. (2015) [74]; (2) Humphreys and Brodziak (2019) [117]; (3) Acosta-Pachon et al. (2017) [118]; (4) Chang et al. (2018) [103]; (5) Domeier et al. (2019) [107]; (6) Holdsworth et al. (2009) [106]; (7) Lam et al. (2015) [105]; (8) Kopft et al. (2011) [119]; (9) Kopft et al. (2012) [116]; (10) McDowell and Graves (2008) [104]; (11) Piner et al. (2013) [115]; (12) Purcell and Edmans (2011) [109]; (13) Shimose et al. (2013) [120]; (14) Sippel et al. (2011) [108]; (15) Su et al. (2013) [110]; (16) Su et al. (2015) [111] and (17) Lien et al. (2014) [121]. The shaded purple areas refer to breeding grounds [104,115,117,120]. The insert in the upper right corner shows the catch distribution of blue marlin from 1950 to 2016 (blue: low; red: high catches [28]).

3.1.10. Wahoo (*Acanthocybium solandri*)

Wahoo (*Acanthocybium solandri*) is almost exclusively associated with surface waters, spending the vast majority of its time above the thermocline, but periodically diving to depths of up to 286 m [137,138]. The results of a tagging study conducted off the coast of California suggest that wahoo are subject to temperatures between 10 and 30 °C but tend to spend most of the time (98%) in waters above 22 °C [138,139]. They are typically solitary but can also be found forming small loose aggregations [140].

In addition to its targeted capture by small-scale fisheries, the wahoo is a highly prized game fish well-known to sport fishermen, and a common bycatch of purse seine, longline and troll fisheries targeting tuna and billfish species [141]. Historically, commercial catches have originated from the Atlantic Ocean. Since the late 1990s, however, the commercial fishery in the Pacific, especially the western and central Pacific, has also grown. Wahoo is not managed by Pacific Regional Fisheries Management Organizations (RFMOs) and most probably has two phenotypic stocks in the eastern and western Pacific [139,141]. Figure 11 summarizes these considerations.

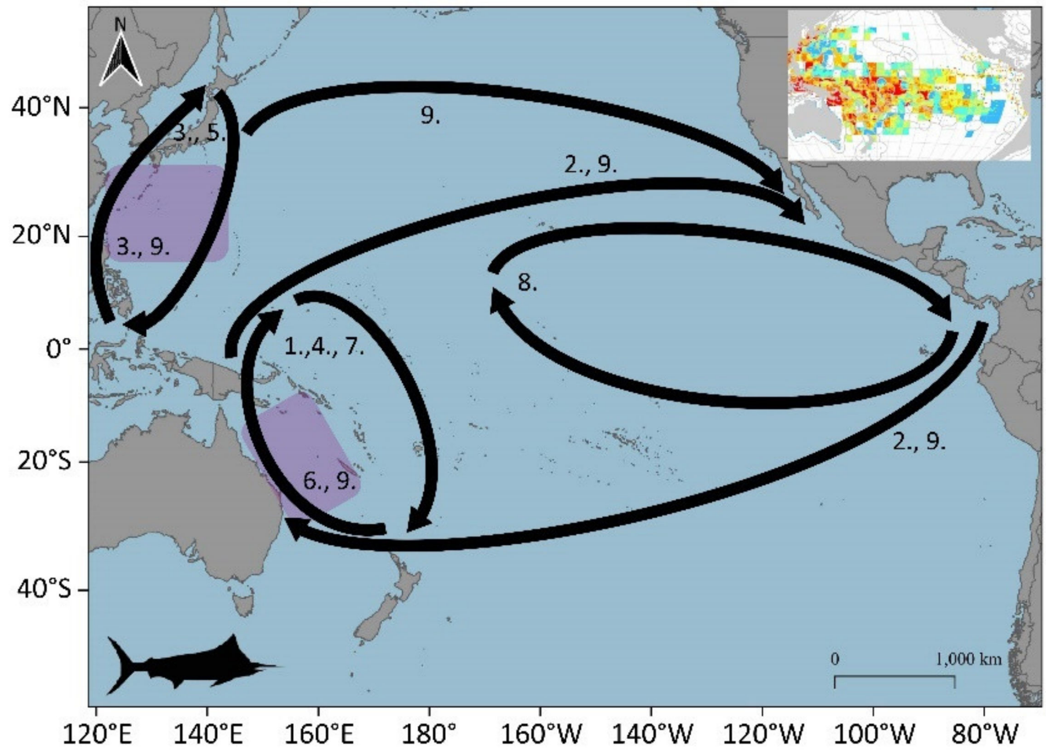

Figure 10. Tentative migration routes of black marlin (*Istiompax indica*) inferred from several sources (see numbers adjacent to the arrows). This suggests the existence of one stock throughout the whole basin that narrows towards the east and that may include three substocks. Sources: (1) Braun et al. (2015) [74]; (2) Ortiz et al. (2003) [130]; (3) Chiang et al. (2015) [125]; (4) Hill et al. (2016) [133]; (5) Sun et al. (2015) [124]; (6) Williams et al. (2016) [134]; (7) Williams et al. (2017) [135]; (8) Fachardi et al. (2018) [128] and (9) Williams (2018) [136]. The shaded purple areas refer to breeding grounds [125,136]. The insert in the upper right corner shows the catch distribution of black marlin from 1950 to 2016 (blue: low; red: high catches [28]).

3.1.11. Indo-Pacific Sailfish (*Istiophorus platypterus*)

Indo-Pacific sailfish (*Istiophorus platypterus*) are distributed in tropical and subtropical marine habitats worldwide [74]. This species is strongly associated with near-coastal waters over shallow continental shelves. As such, the highest catches are generally made in the extreme eastern and western areas of the equatorial Pacific Ocean. Indo-Pacific sailfish have a narrower thermal range than most other billfish species (18–30 °C) and will spend most of their time in 25–28 °C waters [14,147]. Pop-up satellite tagging studies have detected diel vertical migratory behavior as well as basking behavior at the surface during the day [147].

The population of Indo-Pacific sailfish in the Pacific Ocean is considered to form two genetically distinct stocks [148,149] without trans-Pacific movements [130]; according to the local RFMOs, there is one in the eastern Pacific and one in the western and central Pacific Ocean. Reliable assessments of the status of the eastern stock using management parameters are not possible due to the uncertainty associated with the region's catch data [148]. Figure 12 summarizes these considerations. The results of the Inter-American Tropical Tuna Commission's (IATTC) initial assessment conducted in 2013 suggest that there are significant levels of unreported catch. Similarly, no stock assessments currently exist for Indo-Pacific sailfish in the western and central Pacific Fisheries Commission (WCPFC) area [150]. Therefore, the status of Indo-Pacific sailfish across the Pacific remains uncertain.

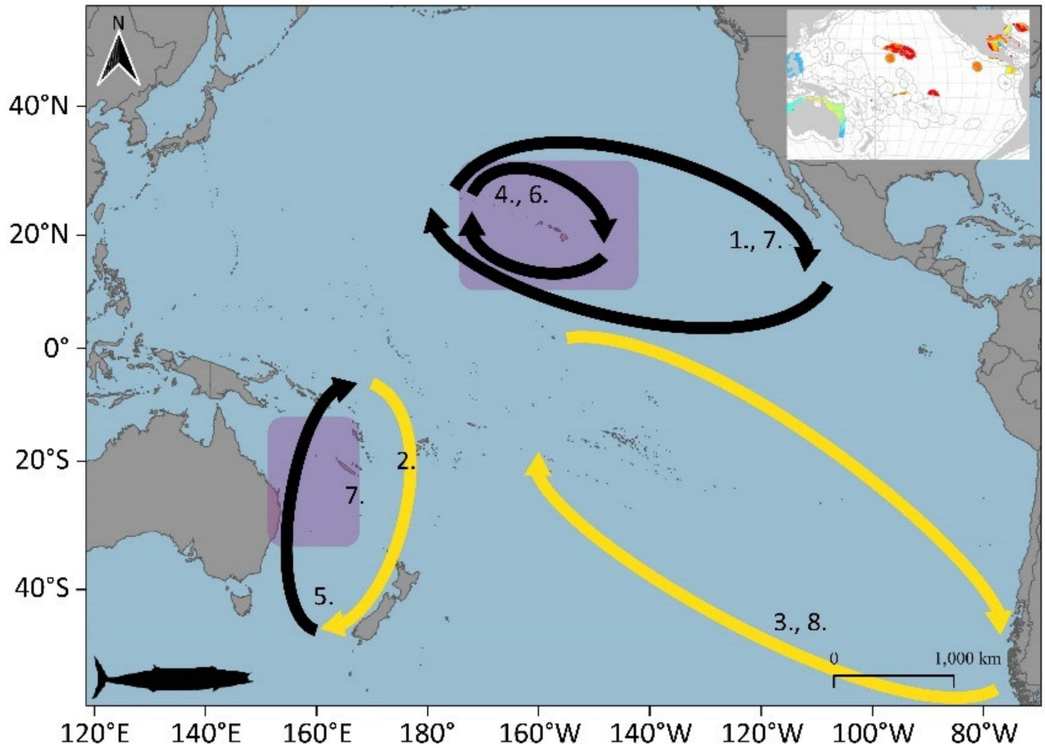

Figure 11. Tentative migration routes of wahoo (*Acanthocybium solandri*) inferred by several sources (see numbers adjacent to the arrows). This distinguishes two differentiated stocks in the eastern and western Pacific [139,141]. Sources: (1) Feeney and Lea (2016) [142]; (2) Gao et al. (2020) [139]; (3) Garber (2005) [143]; (4) Oyafuso et al. (2016) [144]; (5) Perelman et al. (2017) [145]; (6) Uchiyama and Boggs (2006) [90]; (7) Zischke et al. (2012) [141] and (8) Dawson and Irvin (2020) [146]. The shaded purple areas refer to breeding grounds [90,141,144]. The insert in the upper right corner shows the catch distribution of wahoo from 1950 to 2016 (blue: low; red: high catches [28]).

3.2. Potential Blue Corridors

The 11 panels of Figure 13 show the areas of the Pacific Ocean assigned as the habitat of various stocks of the large pelagic species that are the most exploited both in the high seas and in the EEZs of the Pacific and thus considered in the current study.

Figure 13 summarizes the habitat use maps in Figures 2–12, and it is a key step before obtaining Figure 14, which is based on the superposition of the stocks' distribution in Figure 13. This map fails to identify narrow 'blue corridors' as defined in Martin et al. (2006) [153] as channels or routes "of particular importance for the population exchange between locations and of importance for the maintenance biogeographical patterns of species and communities. [. . .]" [153]. However, the 'high traffic' areas in Figure 14 may still identify areas of great relevance to the 11 most important species in Table 1 and should be prioritized for protection.

Figure 14 suggests that the red and orange areas of the Pacific should be considered priority areas for protection, as they are used, in the course of their seasonal migrations, by all or nearly all of the large pelagic fishes considered in this study. In the Northern Hemisphere, there are three priority areas: the two 'very high priority areas' for conservation are between 10 and 30° N, one extending between 180 and 170° W and the other one between 170 and 130° W, while the 'high priority area' extends from 5 to 30° N, between 150° E and 110° W. In the Southern Hemisphere, there are also three priority areas from 5 to 35° S: the two 'very high priority areas' are between 150° E and 170° W and between 150 and 140° W, while the 'high priority area' is between 150° E and 130° W.

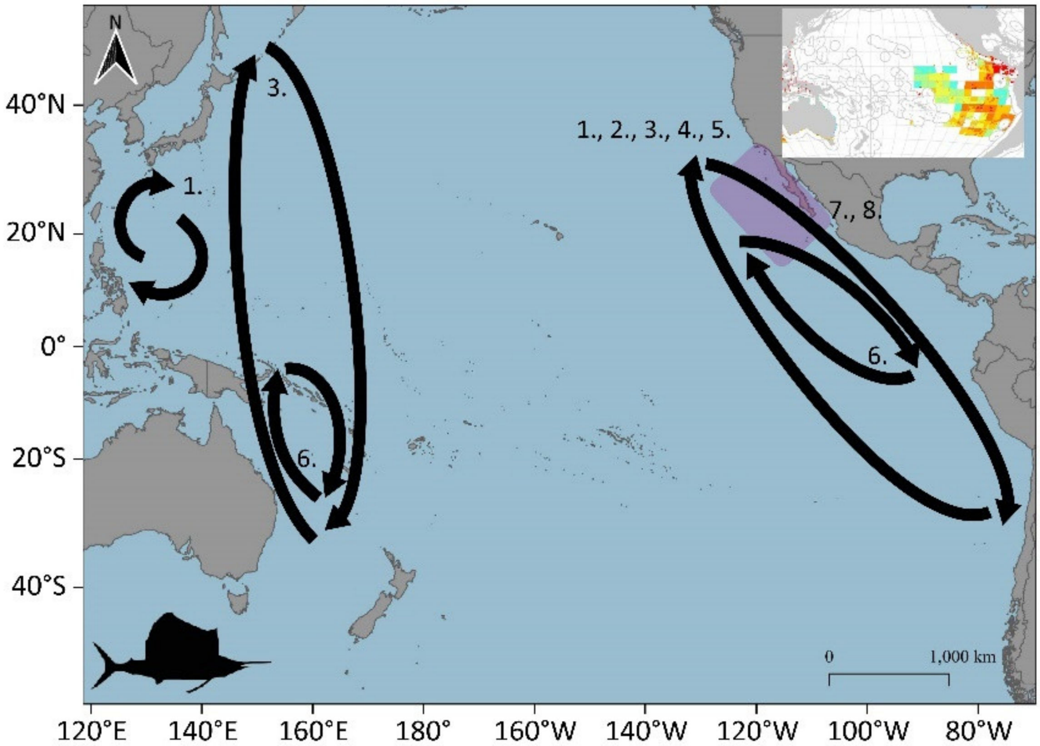

Figure 12. Tentative migration routes of Indo-Pacific sailfish (*Istiophorus platypterus*) inferred by several sources (see numbers adjacent to the arrows). This distinguishes two strongly differentiated stocks in the eastern and western Pacific [45,130,149]. Sources: (1) Braun et al. (2015) [74]; (2) Arizmendi Rodriguez et al. (2006) [151]; (3) Lu et al. (2015) [149]; (4) Prince and Goodyear (2006) [45]; (5) Rosas Alayola et al. (2002) [152]; (6) Ortiz et al. (2003) [130]; (7) Gonzalez-Armas et al. (2006) [114] and (8) Hernandez and Ramirez (1998) [31]. The shaded purple area refers to breeding grounds [31,114]. The insert in the upper right corner shows the catch distribution of common dolphinfish from 1950 to 2016 (blue: low; red: high catches [28]).

The creation of 'blue corridors' based on the red- and orange-coded priority areas would help protect large marine pelagic fishes, most of which have large distribution ranges. Blue corridors would increase the connectivity of habitats, leading to greater genetic exchange and enhancing species diversity and the populations of large pelagic species [154]. Boerder et al. (2019) [10] identified high-suitability habitats for the spatial management of albacore, bigeye, yellowfin, pacific bluefin, skipjack and swordfish, suggesting that conserving large pelagic species is possible, especially if such management includes strict fishery management measures [155]. This also requires making use of all available information on the ecosystems inhabited by large pelagic fishes, including the distribution of socio-economic benefits, impacts and their drivers [156,157].

Such information, together with time series of temperature and distributional data on food and nutrient availability under a changing climate, could help predict priority areas for the conservation of large pelagic fishes. For example, large pelagic fishes often aggregate around seamounts [158] and thermal fronts [3]. Further resources are needed to study and conserve such ridges, which normally "lie outside of national jurisdictions and are under threat from overfishing, plastic pollution, climate change, and potential deep-sea mining" [159]. Hooker et al. (2011) [160] present seven principles that are important for the effectiveness of MPA networks, which could be easily adapted for use in designing blue corridors in the Pacific. For example, using wildlife-habitat modeling and spatial mapping, incorporating life-history and behavioral data in habitat models and implementing an adaptive management approach would help in mitigating the effects of climate change.

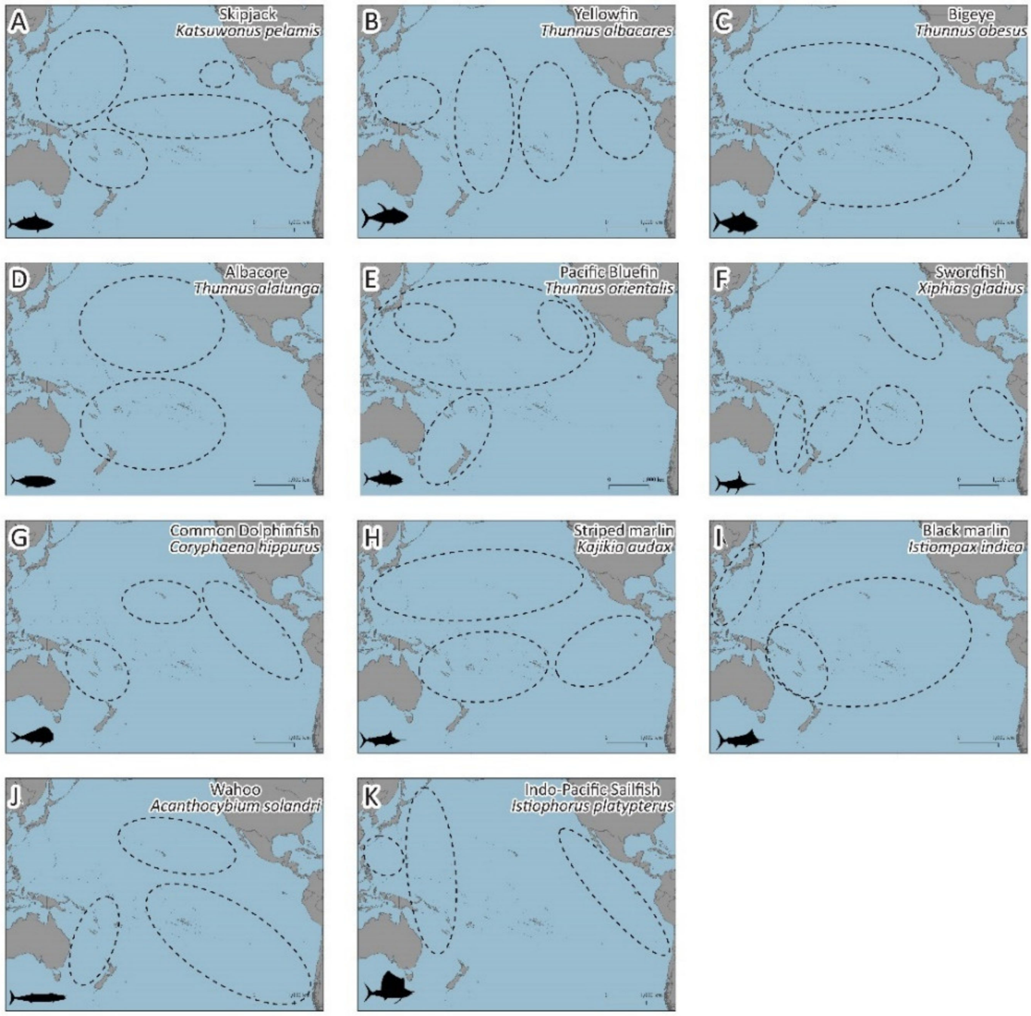

Figure 13. The areas of the Pacific highlighted with an ellipsoid are presumed to include the habitats of 11 species of large pelagic fishes. Based on the migration routes identified in the previous 11 maps, these ellipsoids may be seen as the distribution ranges of the stocks. The small ellipsoids within larger distribution areas or bigger ellipsoids refer to the habitats of the substocks identified in the previous maps. From (**A**–**K**): *Katsuwonus pelamis*, *Thunnus albacares*, *Thunnus obesus*, *Thunnus alalunga*, *Thunnus orientalis*, *Xiphias gladius*, *Coryphaena hippurus*, *Kajikia audax*, *Istiompax indica*, *Acanthocybium solandri*, *Istiophorus platypterus*.

Given the diffuse physical–biological interactions in pelagic systems [3], the variability of long-term environmental conditions [161] and our inability to precisely track large pelagic species, establishing buffer areas around the blue corridors should also be considered, if only to accommodate unforeseen migratory deviations of these species.

Next to a better understanding of the ecological cornerstones of well-designed blue corridors, governance and the inclusion of local stakeholders in their management are most important. In the Pacific, Polynesians and other islanders have a long history of resilience to environmental variability and unpredictability [162]. Future regulations and agreements within blue or migratory corridors may consider stricter regulations or partial bans of industrial fishing, while artisanal and subsistence fishing should be encouraged in the 12-mile territorial seas around islands. Given that there are still many remote areas in the Pacific that are not well-studied [162], the management of marine resources will benefit from more research focused on historically and culturally grounded conservation efforts, which would also address looming food security issues on many Pacific islands [163].

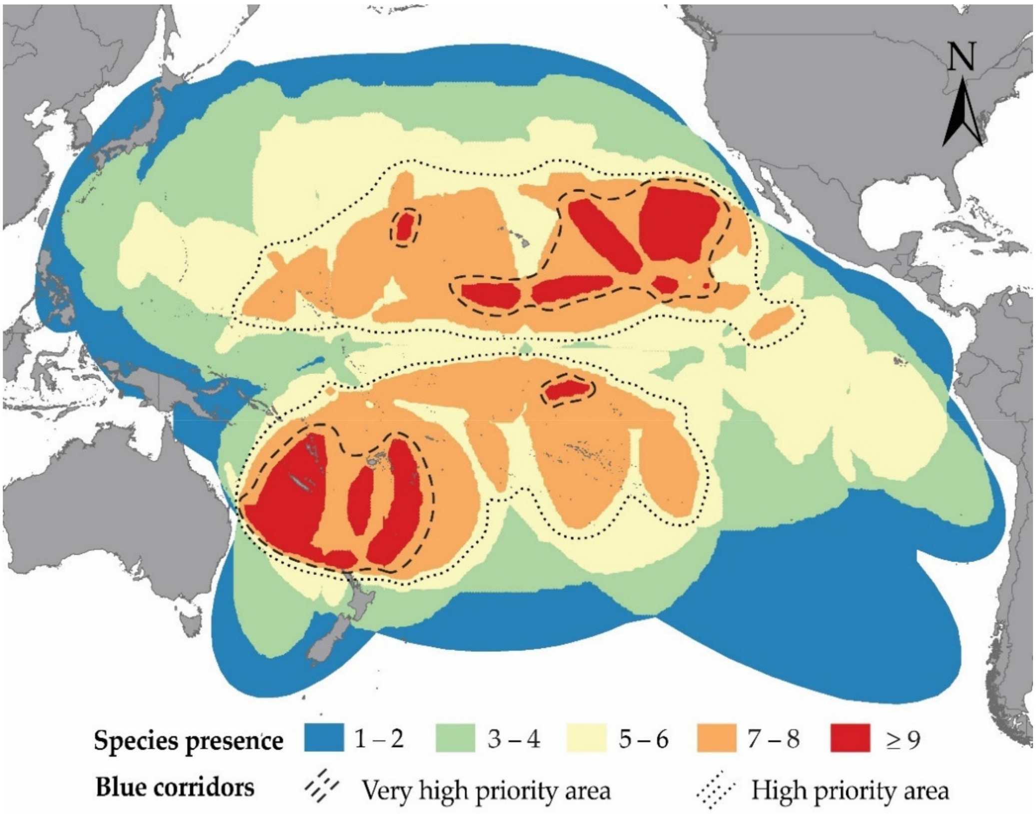

Figure 14. Habitat use maps for important large pelagic species in the Pacific, generated by superposing the habitat use maps of the different stocks (Figures 2–12 and their summarized version in Figure 13). 'Very high priority areas' for conservation contain nine or more of the studied species of large pelagic fish, while 'high priority areas' for conservation have five or more of the studied species of large pelagic fish.

4. Conclusions

This study assumes that philopatry should play a key role in identifying the horizontal movements of large marine pelagic species. Blue corridors are one of the measures that can rebuild stocks and boost fisheries [10], especially for tuna, which have very efficient respiratory and metabolic systems [164]. These tend to function best in young/small individuals in warmer water, and larger/older adults in deeper/cooler water. Thus, seasonal changes in water temperature can and often do drive seasonal migrations [12], although this is often not realized. However, given ocean warming, the effect of temperature on fish movements is now better perceived, and designing marine policy and model blue corridors based on temperature predictions due to climate change should be considered more often.

We focused on philopatry in conjunction with the mapped catch distribution of the Sea Around Us and several existing tagging and genetic sequencing studies to identify tentative migration routes. Based on the superposition of these maps, in the North Pacific, the very high priority areas for conservation are situated in the east, with some patches in the central and western Pacific, i.e., south and west of Hawaii. In the South Pacific, the high priority areas for conservation are mainly in the west, with a small patch north of French Polynesia. The recommended blue corridors, banning or reducing the industrial fishing of large pelagic species, should cover at least the "very high priority areas" for conservation (in red, Figure 14), and ideally also cover the "high priority areas" (in orange, Figure 14). Based on the presented assessment, the best-case scenario for conserving and rebuilding stocks would be an even larger and continuous blue corridor extending from 30° N to 40° S and from 160° E to 110° W of the Pacific.

In the future, the identification of the horizontal movements of large marine pelagic species and their conservation areas should also include population structure [165], as well as local and traditional knowledge. Understanding migration cycles and promoting the conservation efforts of large pelagic species is important for commercial and artisanal fisheries, indigenous cultures and marine ecosystems.

While international cooperation and development efforts in the Pacific have come a long way to protect marine resources, national and commercial interests (commercial shipping routes, fishing and military operations, deep-sea mining plans, etc.) contribute to a complex set of challenges for marine resources management [154,163]. Thus, strengthening governance and cooperation mechanisms are particularly important, along with conservation efforts to protect the fishery resources upon which many livelihoods rely [166]. Current examples of international organizations and prescribed concepts are Regional Fisheries Management Organizations (RFMOs), the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), the Convention on Migratory Species (CMS) and, in particular, the UN Convention on the Law of the Sea, allowing maritime countries to designate and use EEZs to manage coastal areas, from which over 90% of the world's marine catch originates [6].

The design and implementation of blue corridors in the Pacific, if they are to occur, will require various government and non-government entities, as well as local actors to cooperate. Our contribution to the required discussions is a review and interpretation, in light of philopatry, of the literature on the migration and population structure of 11 species of large pelagic fishes. We hope that this will be seen as a useful contribution to a discussion about the protection of large pelagic fishes in the Pacific, through MPAs, blue corridors or other space-based management measures.

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