










Near-global spawning strategies of large pelagic fish

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Understanding the spawning strategies of large pelagic fish could provide insights into their underlying evolutionary drivers, but large-scale information on spawning remains limited. Here we leverage a near-global larval dataset of 15 large pelagic fish taxa to develop habitat suitability models and use these as a proxy for spawning grounds. Our analysis reveals considerable consistency in spawning in time and space, with 10 taxa spawning in spring/summer and 9 taxa spawning off Northwest Australia. Considering the vast ocean expanse available for spawning, these results suggest that the evolutionary benefits of co-locating spawning in terms of advantageous larval conditions outweigh the benefits of segregated spawning in terms of reduced competition and lower larval predation. Further, tropical species spawn over broad areas throughout the year, whereas more subtropical and temperate species spawn in more restricted areas and seasons. These insights into the spawning strategies of large pelagic fish could inform marine management, including through fisheries measures to protect spawners and through the placement of marine protected areas.

Large pelagic fish, such as tuna and billfish, are key species in marine food webs¹. They are important socioeconomically, supporting valuable fisheries in subtropical and tropical national waters and in the high seas². These fisheries provide income and food for many countries, particularly island nations of the Global South^{2,3}. Many large pelagic fish also play important ecosystem roles in carbon cycling through predation, diel vertical migration, and sinking of feces and carcasses⁴. Their high mobility, migrating across vast ocean expanses and traversing both national boundaries and the high seas, presents challenges for their effective fisheries management and

conservation. A deeper understanding of their life history—including how these species reproduce in time and space—could ultimately aid their management.

Life history strategies of pelagic fishes are highly variable and can be inferred from co-variation in traits, such as body size, longevity, growth rates, and fecundity. In scombrid fishes (tunas, bonitos, mackerel), most life history variation is explained by traits describing body size, swimming speed, and reproductive schedule, with body size being the most influential⁵. At one end, opportunistic strategists, such as tropical tunas (e.g., skipjack tuna - *Katsuwonus pelamis*), have a fast

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life history strategy. These species are often small to medium in size, grow rapidly, mature early, and have short life spans. At the other end, periodic strategists (e.g., Atlantic bluefin tuna - *Thunnus thynnus*) predominantly inhabiting temperate waters have a slow life history. These species are often large in size, grow slowly, mature late, and have long life spans, leading to slower population turnover^{5–7}. Similarly, billfishes such as marlin, spearfish (Istiophoridae) and swordfish (Xiphiidae), also have a slow life history strategy because they are large bodied, late-maturing and slow-growing⁸.

Fundamental to the life history strategy of large pelagic fish is their spawning strategy in time and space. Tropical scombrid species with a fast life history generally have a longer spawning season than subtropical and temperate scombrids with a slow life history⁵. Although, it is unknown whether this trend is followed more generally by other large pelagic fish. By contrast, there is much more limited information on the extent of spawning grounds of large pelagic fish in relation to life history variation. Muhling et al.⁹ interestingly noted the tendency for three bluefin tuna species with slow life histories to spawn in spatially restricted spawning grounds. A synthesis of the spawning strategy in time and space of large pelagic fish could provide valuable insights into evolutionary processes governing spawning. Many species tend to return to one or several natal grounds to spawn at similar times each year. For example, some spawning grounds host aggregations of multiple large pelagic fish species, such as off North-west Australia for skipjack and Southern bluefin tuna, and off Japan for skipjack and Pacific bluefin tuna^{10–12}. This co-location of spawning is despite these species having contrasting life history strategies. The extent to which this strategy of co-location of spawning in space and time is prevalent among a broader suite of large pelagic fish taxa remains unknown.

The best data on near-global spawning dynamics is restricted to key commercial tuna and billfish species, with limited information for other non-targeted species. Multiple studies have found restricted temperature preferences for large pelagic fish, suggesting co-location of spawning. Reglero et al.¹³ found that seven tuna species preferred spawning in warm waters and Schaefer¹⁴ found that tuna species spawn in waters >24 °C. Muhling et al.⁹ suggested that tuna larvae tend to be found within narrower temperature windows than adults, suggesting that there could be considerable overlap in larval distributions. Reglero et al.¹³ also found that most tuna spawned in waters of intermediate values of mesoscale activity from eddies, supporting the triad hypothesis of Bakun (2006)¹⁵ that links favorable spawning areas to the physical environment, and suggests that co-location might be a valuable strategy. This evidence for common environmental drivers of many species and the co-location of their spawning in time and space indicates that large pelagic fish could exploit advantageous environmental conditions for adults and larvae^{9,16}.

There could also be substantial evolutionary benefits for large pelagic fish species if their spawning is segregated in time and space. This could reduce density-dependent food limitation and thus competition for food by adults, potentially increasing spawning and enhancing recruitment¹⁷. Such segregated spawning could also enhance the food availability for developing larvae, reduce egg and larval cannibalism by conspecifics, and decrease predation on eggs and larvae by other large pelagic fish species and invertebrates, all of which could lead to an increase in survivorship, a major factor limiting recruitment¹⁸. Therefore, both strategies—species either segregating or co-locating spawning in time and space—could have evolutionary benefits for large pelagic fish species.

A deeper understanding of the variation in life history strategies of large pelagic fish could provide the foundation for their improved management. For example, if many species co-locate their spawning in time and space, then this could be used in fisheries management to help avoid harvesting spawning females and to elucidate stock structure^{19,20}. Detecting co-located spawning grounds, could also

inform the location of marine protected areas (MPAs) or other effective area-based conservation measures (OECMs). Although debates persist on the potential benefits of MPAs for highly migratory fish species^{21,22} and challenges exist in protecting such species throughout their long migrations²³, species such as tunas and billfish are likely to receive some benefit from the protection of their spawning areas. As countries seek to meet the Global Biodiversity Framework target of conserving 30% of land, waters and seas by 2030²⁴, knowledge of the spawning areas of commercial and non-commercial species are likely to be valuable, especially considering the lack of data available for pelagic ecosystems²⁵.

Assessing the spawning strategies in time and space is complicated by the paucity of available data. Collecting spawning data during field surveys is labor-intensive and expensive. It usually involves sampling individual females to assess gonadal state or eggs and larvae from the water column and is sometimes complemented by local knowledge and observations²⁶. Realized spawning areas—defined by the presence of eggs—are difficult to identify because they are patchy and ephemeral, particularly for highly migratory species²⁷. For these species, the presence of larvae is often used as an indicator of spawning events⁹. Larval data and habitat suitability models can then be used to identify potential spawning times and locations²⁸. Most data on the larvae of large pelagic fish species are collected from one-off surveys, involve individual species, cover local-to-regional scales, and use different methods²⁹. A notable exception is the extensive dataset of Nishikawa et al.³⁰, which provides an unprecedented window into the spawning strategies of large pelagic fish species. This data set spans 40°N to 40°S at 1° × 1° resolution, includes seasonal data collected during surveys from 1956 to 1981, and has 63,017 samples collected with similar methods. The seminal work of Reglero et al.¹³ on environmental requirements for spawning habitats also used the Nishikawa et al.³⁰ observations and other data sets at a coarser resolution (5° × 5°) and investigated seven tuna species. However, they did not assess spawning seasonality, nor did they address the question of the co-location of spawning by different species.

Here we leverage previously digitized^{30,31} larval data as a proxy for spawning to answer questions about the generality of spawning strategies—over time and space—for 15 taxa of large pelagic fish of both commercial and non-commercial value. We match these larval data with environmental variables from Earth System Model (ESM) outputs to build larval habitat suitability models and thus identify potential seasonal larval hotspots in the Indian and Pacific Oceans. To provide insights into spawning strategies, we assess the degree to which larvae for multiple species are segregated versus those that are co-located in hotspots across time and space. We investigate how consistent these spawning patterns are across hemispheres and across a slow-fast continuum of life history strategies⁵. Finally, we test the influence of latitude—specifically, whether the spawning season of large pelagic fish is longer³ and their spawning grounds are more restricted spatially⁹ at higher latitudes than those at lower latitudes. This work could help inform conservation and sustainable use of these large pelagic fish, through informed fisheries management measures and protected area placement.

Results

Larval habitat suitability

Using larval habitat suitability models for the pelagic fish taxa based on Boosted Regression Trees (BRTs, see Methods), the optimal models (Area Under the receiver operator Curve, AUC > 0.80; Supplementary Table 1) showed that high-probability areas of larval occurrence across the 15 taxa were mostly located in the tropics and subtropics of the Western Pacific and the Eastern Indian Oceans (Figs. 1–4). However, the BRTs showed notable similarities and differences in the spatio-temporal distributions of different species of larvae (Figs. 1–4). For example, habitats conducive to skipjack (Fig. 1a–d) and yellowfin tuna

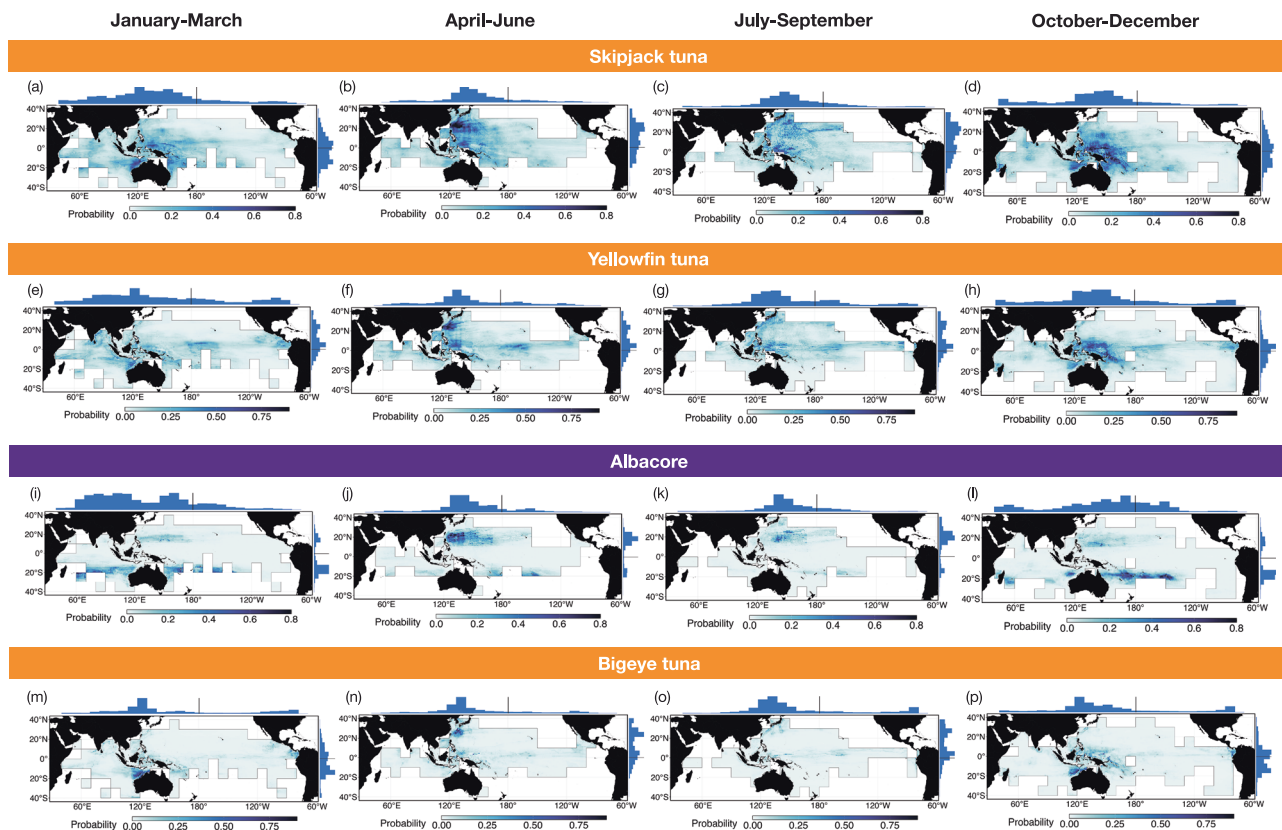


Fig. 1 | Seasonal larval suitability maps for. **a–d** skipjack tuna; **(e–h)** yellowfin tuna; **(i–l)** albacore; and **(m–p)** bigeye tuna. Taxa are categorized according to life-history strategy (“fast” are in orange, “slow” are in purple, and “unknown” are in

black; Table 1). Relative mean probabilities across longitude and latitude are shown on the top and right of each panel, respectively. Seasons are January–March, April–June, July–September, and October–December.

larvae (Fig. 1e–h) were concentrated across the Indo-Pacific, particularly in the Northwestern Pacific in boreal spring/summer, and east of Papua New Guinea and northwest of Australia in austral spring/summer. Suitable habitats for Southern bluefin tuna larvae (Fig. 2m–p) were concentrated off Northwest Australia in austral spring/summer, whereas suitable habitats for larval Pacific bluefin tuna were in the East China Sea in boreal spring/summer. Shortbill spearfish (Fig. 3e–h), albacore (Fig. 1i–l), and blue marlin (Fig. 4e–h) showed a similarly wide distribution, with larvae mostly around 20°N and 20°S in the Pacific, but also in the Indian Ocean off Northwest Australia. Suitable habitats for sailfish (Fig. 4i–l) and frigate tuna (Fig. 2a–d) were concentrated in the Indo-Pacific region and off Japan, as well as the equatorial Eastern Pacific. The sauries (Fig. 2i–l), however, were confined to the extremities of the modeled region—25–40°N in boreal winter/spring and 25–40°S west of South America in austral winter/spring.

Biophysical drivers of larval suitability

Despite spatial differences in larval habitats for each taxon, we found prominent similarities in their ranges of suitable biophysical environments, and this varied little across seasons. Most of the larvae were found in warm surface waters (Supplementary Fig. 1). The tropical tunas (e.g., skipjack and yellowfin tunas) preferred warmer waters than the temperate tunas (e.g., Southern and Pacific bluefin tunas). Most larval taxa generally preferred temperatures >25 °C, especially yellowfin and skipjack tunas, albacore, shortbill spearfish and blue marlin. However, slender tuna was generally found between 20 and 25 °C, sauries observed in waters <25 °C, and frigate tuna had a broad temperature range, but with the greatest presence in waters >25 °C. Probabilities of larval occurrence were higher for most taxa in waters of moderate large-scale flow activity (generally <5 m² s⁻²) measured using mean kinetic energy (see Methods). However, some taxa, like

frigate tuna and sailfish were found across broad ranges of mean kinetic energy (Supplementary Fig. 2). Probabilities of larval occurrence were generally higher in areas with: pH levels between 8.1 and 8.2 (Supplementary Fig. 3, except for sauries and frigate tuna found across broader ranges of pH levels); lower concentrations of chlorophyll-a (<0.2 g m⁻³; Supplementary Fig. 4), nitrate (<5 mmol m⁻³; Supplementary Fig. 5), phosphate (<0.5 mmol m⁻³; Supplementary Fig. 6), and ammonium (<0.4 mmol m⁻³; Supplementary Fig. 7); higher salinities (>30 ppt; Supplementary Fig. 8); weak thermal (<0.01 °C km⁻¹; Supplementary Fig. 9) and salinity (<0.001 ppt km⁻¹; Supplementary Fig. 10) gradients; and dissolved oxygen levels from 6.0 to 8.0 mg L⁻¹ (Supplementary Fig. 11, except for frigate tuna found in broad ranges of dissolved oxygen concentrations). Probabilities were also higher in regions with surface mixed layer depths of ~50 m (Supplementary Fig. 12), in areas ~500 km from the nearest coastline (Supplementary Fig. 13), and in mean water depths of 0–6 km (Supplementary Fig. 14).

Seasonality

Mean probabilities of larval occurrence varied seasonally, but often with similar patterns in both hemispheres (Fig. 5). Three seasonal patterns were clear: spring/summer peaks, winter/spring peaks, and little seasonality. The most common seasonality was a spring/summer peak in the mean larval probability (Fig. 6) for albacore, striped marlin, and sailfish in both hemispheres. Peaks in warmer months for skipjack tuna, yellowfin tuna, bigeye tuna, and blue marlin were more evident in the northern hemisphere. Although Pacific bluefin tuna and swordfish larvae were mostly observed in the northern hemisphere and Southern bluefin tuna larvae in the southern hemisphere, all three species also followed a spring/summer pattern. Other species exhibited a winter/spring peak, including larvae of sauries, which had higher mean larval probabilities during winter/spring in both hemispheres. Frigate and

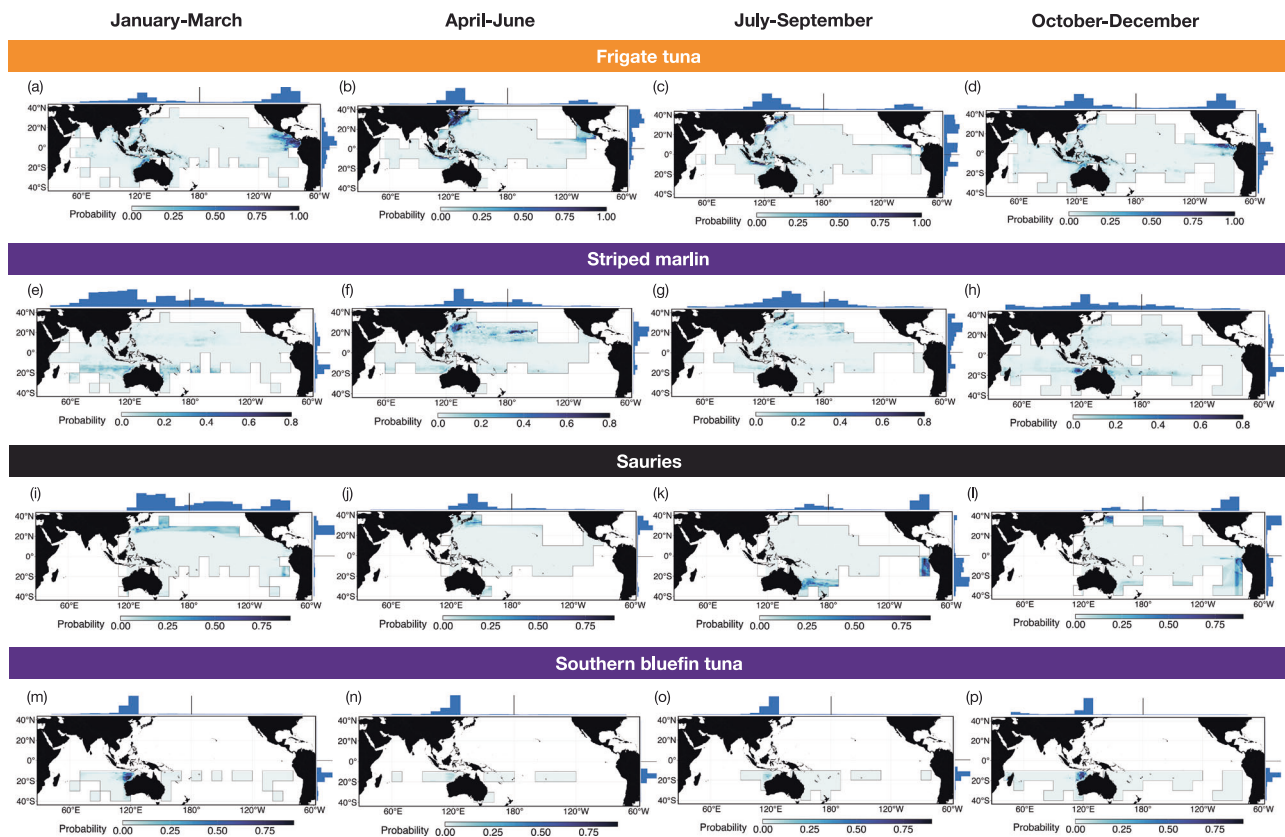


Fig. 2 | Seasonal larval suitability maps for. **a–d** frigate tuna; **e–h** striped marlin; **i–l** sauries; and **m–p** Southern bluefin tuna. Taxa are categorized according to life-history strategy (“fast” are in orange, “slow” are in purple, and “unknown” are in

black; Table 1). Relative mean probabilities across longitude and latitude are shown on the top and right of each panel, respectively. Seasons are January–March, April–June, July–September, and October–December.

slender tuna larvae exhibited the same pattern but only for the northern and southern hemispheres, respectively. Some species displayed little seasonality, such as longfin escolar and shortbill spearfish.

Spatiotemporal life-history and interhemispheric patterns

Spatial and temporal spawning patterns across hemispheres were revealed by evaluating the relationship between the Spatial Aggregation Index and Seasonality Index (see Methods) for each taxon (Fig. 6; F -statistic (25 degrees of freedom) = 11.14, $p = 0.002649$, $r^2 = 0.28$, 95% confidence intervals = [0.20, 1.19]). Some taxa spawned seasonally but were spatially dispersed, such as striped marlin and swordfish. Frigate tuna exhibited spatially aggregated spawning patterns with little seasonality. Finally, spawning patterns of Pacific and Southern bluefin tunas were both spatially aggregated and seasonal. The Spatial Aggregation and Seasonality Indices were strongly related to the latitudinal preference of taxa. There was a significant positive relationship between the Spatial Aggregation Index and the mean latitude across taxa (Fig. 7a; F -statistic (25 degrees of freedom) = 11.8, $p = 0.002014$, $r^2 = 0.32$, 95% confidence intervals = [0.71, 4.26]); considering each hemisphere separately for each taxon). Thus, tropical taxa (e.g., yellowfin tuna, skipjack tuna and bigeye tuna) generally had dispersed spawning areas, whereas subtropical and temperate taxa (e.g., sauries, slender tuna, Pacific bluefin tuna, and Southern bluefin tuna) had more tightly aggregated areas. There was an even stronger relationship between the Seasonality Index and mean latitude across taxa (Fig. 7b; F -statistic (25 degrees of freedom) = 32.42, $p = 0.000006266$, $r^2 = 0.56$, 95% confidence intervals = [0.11, 1.10]). Thus, tropical taxa (e.g., yellowfin tuna, skipjack tuna and bigeye tuna) spawned broadly throughout the year, while subtropical and temperate taxa (e.g., Pacific bluefin tuna, slender tuna, sauries) exhibited more concentrated spawning periods. Generally, taxa found across both hemispheres had

similar values for both Spatial Aggregation and Seasonality Indices in each hemisphere.

We found clear relationships between the Spatial Aggregation and Seasonality Indices and major taxonomic groups as well as with different life history strategies (Table 1). Tuna spawning areas are more spatially aggregated than billfish (Fig. 8a), whereas the degree of seasonality of tuna spawning was more variable than billfish (Fig. 8b). Further, we observed similar degrees of spatial aggregation between slower- and faster-growing taxa (Fig. 8b), but slower-growing taxa generally had greater seasonality in their spawning than faster-growing ones (Fig. 8d).

Larval hotspots

We did a Principal Component Analysis (PCA) based on the habitat suitability model outputs (i.e., probabilities of occurrences of each taxon) to identify the primary seasonal larval hotspots (see Methods). We used the first two PC axes and found similarities and differences in spatiotemporal patterns among taxa and between hemispheres (Fig. 9). Areas with high PC scores reflect areas with high probabilities of occurrences across different taxa, signifying potential larval hotspots. Also shown are the correlations of the PC axes across the taxa, where high, positive correlations correspond to taxa likely spawning in areas with positive PC scores and high, negative correlations corresponding to taxa likely spawning in areas with negative PC scores. In the northern hemisphere, there were high PC1 (Principal Component 1) scores in boreal spring/summer, particularly in the East China Sea south of Japan (Fig. 9c, e). In the southern hemisphere, high PC1 scores were found off Northwestern Australia in austral spring/summer (Fig. 9a, g). We observed generally high, positive correlations between PC1 scores and many taxa (red grids on the left in Fig. 9), indicating that these taxa could have co-located spawning in areas of high PC1 values.

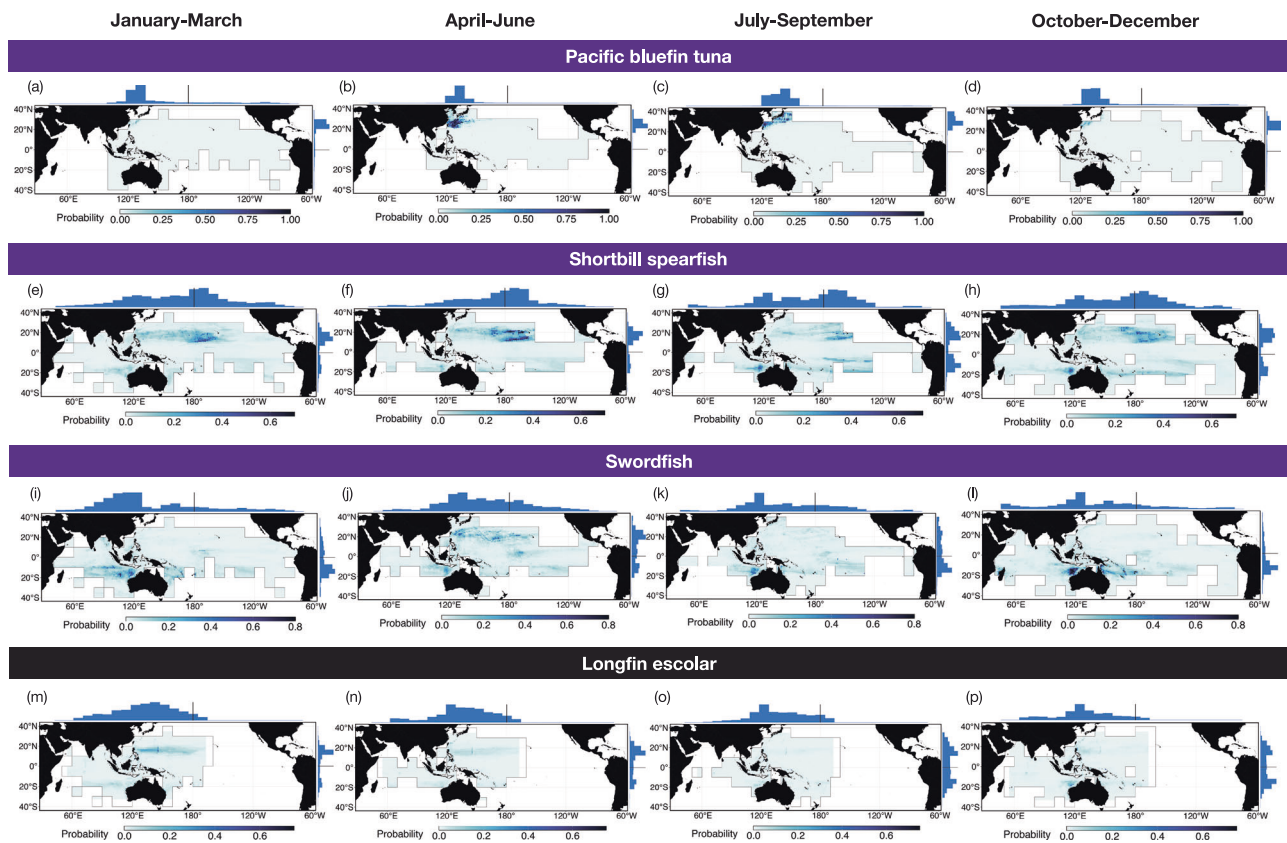


Fig. 3 | Seasonal larval suitability maps for. a–d Pacific bluefin tuna; **e–h** shortbill spearfish; **i–l** swordfish; and **m–p** longfin escolar. Taxa are categorized according to life-history strategy (“fast” are in orange, “slow” are in purple, and “unknown” are in

black; Table 1). Relative mean probabilities across longitude and latitude are shown on the top and right of each panel, respectively. Seasons are January–March, April–June, July–September, and October–December.

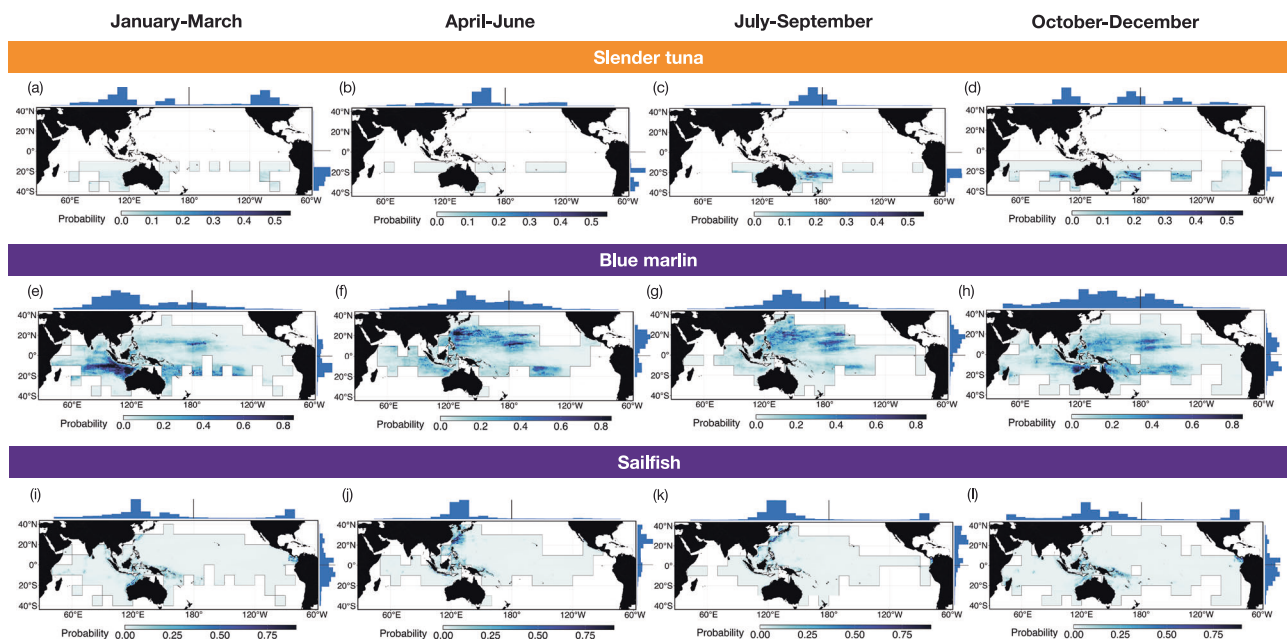


Fig. 4 | Seasonal larval suitability maps for. a–d slender tuna; **e–h** blue marlin; and **i–l** sailfish. Taxa are categorized according to life-history strategy (“fast” are in orange, “slow” are in purple, and “unknown” are in black; Table 1). Relative mean

probabilities across longitude and latitude are shown on the top and right of each panel, respectively. Seasons are January–March, April–June, July–September, and October–December.

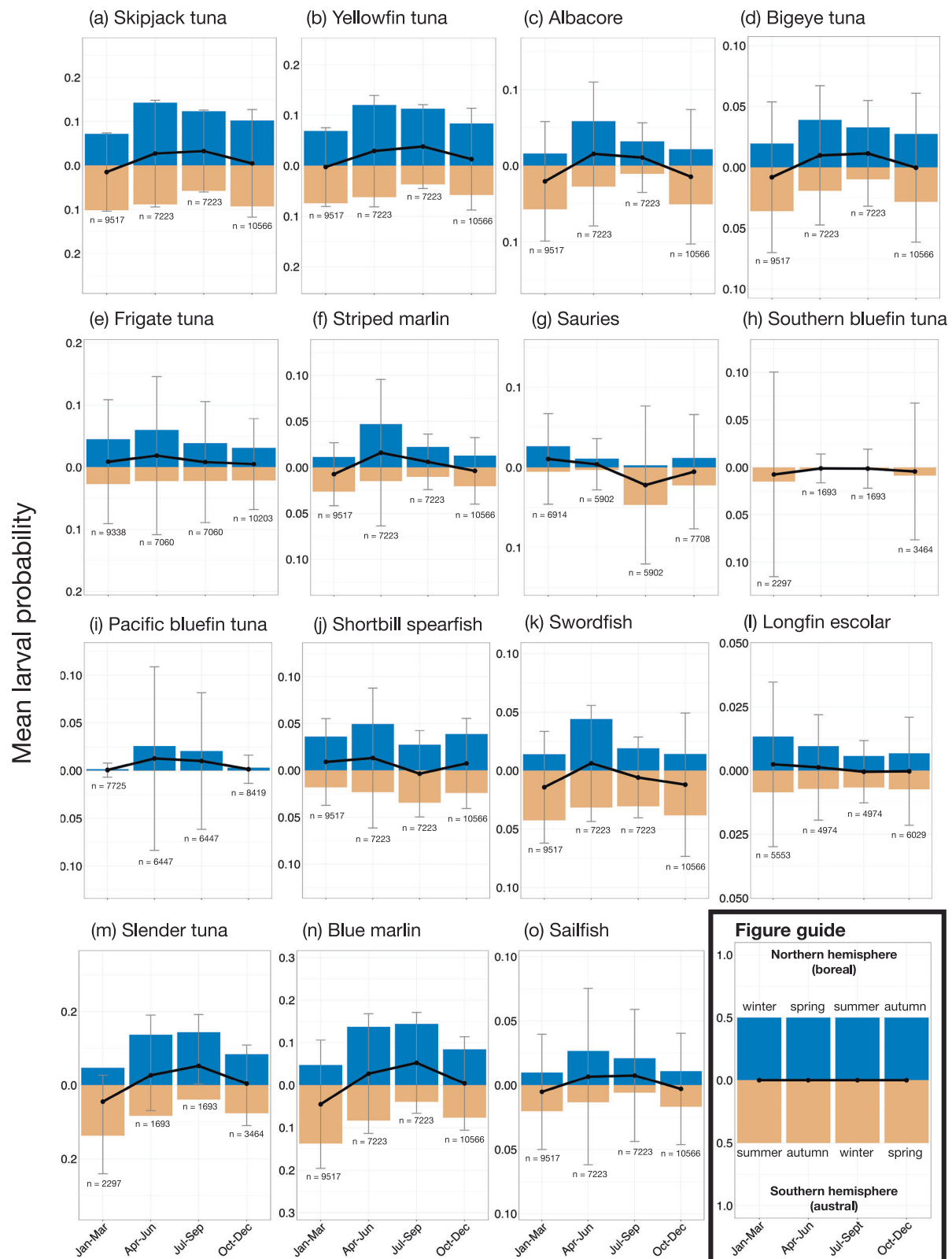


Fig. 5 | Seasonality of mean larval probability for. a skipjack tuna; **b** yellowfin tuna; **c** albacore; **d** bigeye tuna; **e** frigate tuna; **f** striped marlin; **g** sauries; **h** Southern bluefin tuna; **i** Pacific bluefin tuna; **j** shortbill spearfish; **k** swordfish; **l** longfin escolar; **m** slender tuna; **n** blue marlin; and **o** sailfish. The bars represent the mean larval probability for 15 fish taxa across the

northern (blue, above) and southern (orange, below) hemispheres. Points represent the overall global mean \pm SD. Note that a taxon will be found in a different number of grid squares in each hemisphere, so the global mean will not generally be the average of the mean of the probabilities in each hemisphere. Sample sizes across taxa (n) per season are also reported.

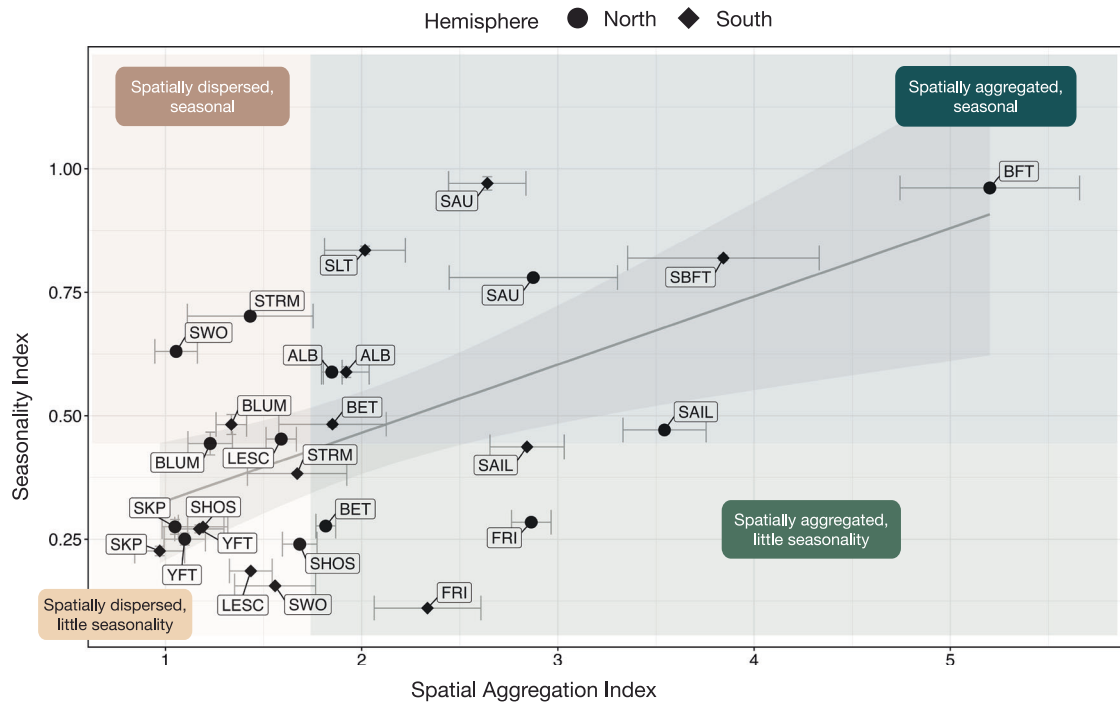


Fig. 6 | Relationship of Spatial Aggregation Index and Seasonality Index across taxa. This relationship (F -statistic (25 degrees of freedom) = 11.14, $p = 0.002649$, $r^2 = 0.28$, 95% confidence intervals = [0.20, 1.19]) is assessed using a two-sided linear model. Data points are by taxon for each hemisphere (North Hemisphere points are shown as circles and South Hemisphere points are shown as triangles): SKP skipjack tuna, YFT yellowfin tuna, ALB albacore, BET bigeye tuna, FRI

frigate tuna, STRM striped marlin, SAU sauries, SBFT Southern bluefin tuna, BFT Pacific bluefin tuna, SHOS shortbill spearfish, SWO swordfish, LESC longfin escolar, SLT slender tuna, BLUM blue marlin, and SAIL sailfish. Data are presented as the mean values \pm SEM of the calculated Spatial Aggregation Index (x-axis) against the Seasonality Index \pm SEM for each taxon (y-axis; See Methods). Quadrants are defined using the medians of the indices.

Thus, spawning of skipjack tuna, yellowfin tuna, blue marlin, and swordfish were consistently co-located across seasons, although swordfish did not follow the general pattern in boreal summer.

PC2 revealed spatial patterns unobserved in PC1. Positive PC2 scores revealed hotspots in the eastern tropical Pacific in boreal autumn and winter (Fig. 9b, h), north and east of Papua New Guinea in austral spring (Fig. 9h), and south of Japan in boreal winter to summer (Fig. 9b, d, f). Frigate, yellowfin, and bigeye tuna were most strongly positively correlated with PC2 across all seasons indicating that these taxa co-occur in the PC2 hotspots. Negative PC2 scores were observed in latitudinal bands at $\sim 20^\circ\text{N}$ and $\sim 20^\circ\text{S}$ across seasons in the western to central Pacific, but this extended to the Southern Indian Ocean in austral summer, which appear to be larval hotspots for taxa like albacore and shortbill spearfish across seasons, striped marlin in austral summer, and blue marlin in boreal spring.

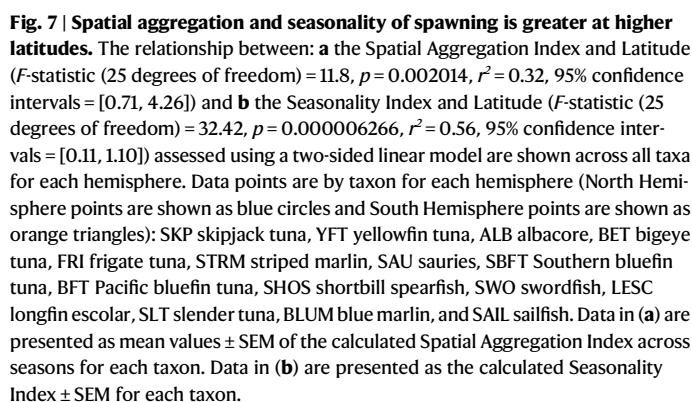
Discussion

This study reveals interhemispheric larval hotspots for 15 ecologically and commercially important pelagic taxa at ocean-basin scales. Based on the largest synthesis of larval data for large pelagic fish, we found evidence for spawning synchrony amongst large pelagic fish, with ten taxa spawning in spring/summer, two in winter/spring, and only three with little seasonality. We also found hotspots were often co-located across taxa, with nine taxa spawning extensively off Northwest Australia (tuna: skipjack, yellowfin, albacore, bigeye, and Southern bluefin tunas; billfish: blue marlin, striped marlin, shortbill spearfish, and swordfish), nine taxa off Japan (tuna: skipjack, yellowfin, bigeye, frigate, and Pacific bluefin tunas; billfish: striped marlin, sailfish, blue marlin, and swordfish), and seven in a broad band around 20°N and 20°S (tuna: albacore and slender tuna; billfish: blue marlin, striped marlin, swordfish, and shortbill spearfish; others: sauries). We found that tropical taxa spawn over broader areas throughout the year,

whereas subtropical and temperate species spawn in more restricted areas and seasons. Species with slower growth were more seasonally restricted compared to species with faster growth. Considering the vastness of the ocean area where these large pelagic fish can spawn, these results suggest considerable co-location of spawning in time and space, rather than taxa predominantly segregating their spawning. This implies that the evolutionary benefits of spawning in similar areas and at similar times likely outweighs the additional competition and predation that co-locating their spawning in time and space would generate.

The reliability of larvae as a proxy for spawning

We assume that larval data can be used to understand spawning, but this depends on factors such as the age of larvae sampled³⁰ and local currents³². Although the age of sampled larvae is unknown, the concurrence between the observation-derived predictions of larval hotspots in the current work and independent spawning studies provides some confidence that Nishikawa larval data can offer insights into spawning strategies. For example, Southern bluefin tuna are known to spawn off Northwest Australia¹² and across the tropical southeast Indian Ocean³³; skipjack, yellowfin, and bigeye tunas spawn east of the Philippines³⁴; Pacific bluefin tunas spawn between the Philippines and Japan³²; skipjack tuna spawn in the tropical Eastern Pacific Ocean¹⁴; blue marlin in the northwestern to central Pacific Ocean³⁵; and tuna larvae have been reported north of Madagascar³⁶. Further, our findings on the timing of peak larval presence broadly agree with current information on the timing of spawning of large pelagic fish from the region of this study, specifically on the tunas and billfish whose spawning information are known. For instance, bigeye tuna spawning peaks in the Pacific Ocean from spring through to early autumn both in the northern³⁷ and southern^{37,38} hemispheres. Peak Southern bluefin tuna spawning is in spring and summer^{37,39}. Striped marlin spawning



The co-location of spawning in many large pelagic fish could be driven by their shared environmental preferences. Consistent with other studies, we found that most of the fish larval taxa preferred warmer temperatures (25–29 °C)²⁸, while sauries and slender tuna prefer cooler

By contrast, productivity is more strongly seasonal and predictable in temperate regions^{52,53}. In these more eutrophic temperate regions, nutrient concentrations vary substantially throughout the year, with predictable seasonal productivity pulses driven by large-scale and reliable shifts in large-scale weather patterns such as movements of atmospheric pressure systems^{52,54}. These predictable productivity pulses at higher latitudes⁵¹ (Mann and Lazier 2006) make a periodic spawning strategy more advantageous, where large pelagic fish spawn in recurrent productivity hotspots at particular times of year.

Enhanced knowledge of spawning locations and behavior can help support fisheries management. Specifically, identifying spawning grounds can help elucidate stock structure⁵⁵ and thus improve

Table 1 | Taxonomic, life-history and sampling information of the 15 large pelagic fish taxa

Common name	Species ^a	Family	Oceanic environment ^b	Life-history strategy ^b	Number of presences ^c
Skipjack tuna	<i>Katsuwonus pelamis</i>	Scombridae	Tropical	Fast	1695
Yellowfin tuna	<i>Thunnus albacares</i>	Scombridae	Tropical	Fast	1327
Albacore	<i>Thunnus alalunga</i>	Scombridae	Subtropical	Slow	539
Bigeye tuna	<i>Thunnus atlanticus</i> , <i>Thunnus obesus</i>	Scombridae	Subtropical	Fast	476
Frigate tuna	<i>Auxis rochei</i> , <i>Auxis thazard</i>	Scombridae	Tropical	Fast	415
Southern bluefin tuna	<i>Thunnus maccoyii</i>	Scombridae	Temperate	Slow	105
Pacific bluefin tuna	<i>Thunnus orientalis</i> , <i>Thunnus thynnus</i>	Scombridae	Temperate	Slow	104
Slender tuna	<i>Allothunnus fallai</i>	Scombridae	Tropical, Subtropical, Temperate	Fast	75
Blue marlin	<i>Makaira Mazara</i> , <i>Makaira nigricans</i>	Istiophoridae	Cosmopolitan	Slow	1697
Shortbill spearfish	<i>Tetrapturus angustirostris</i> , <i>Tetrapturus pfluegeri</i>	Istiophoridae	Tropical, Subtropical, Temperate	Slow	556
Swordfish	<i>Xiphias gladius</i>	Xiphiidae	Tropical, Subtropical, Temperate	Slow	517
Striped marlin	<i>Kajikia albida</i> , <i>Kajikia audax</i>	Istiophoridae	Temperate	Slow	362
Sailfish	<i>Istiophorus platypterus</i>	Istiophoridae	Cosmopolitan	Slow	215
Longfin escolar	<i>Scombrobrax heterolepis</i>	Scombrobracidae	Tropical, Subtropical, Temperate	Unknown	204
Sauries	<i>Cololabis saira</i> , <i>Scomberesox saurus</i>	Scomberesocidae	Temperate	Unknown	166

^aSpecies names are italicized.^bInformation from: Juan-Jordá et al.⁵.^cInformation from: Buenafe et al.³¹.

assessments⁵⁶, reduce the likelihood that particular stocks are overfished⁵⁷, and potentially aid understanding of stock-specific responses to climate change^{58,59}. Spawning grounds can also be incorporated directly into area-based fisheries management⁶⁰ to protect spawning adults⁶¹. Such measures can help rebuild depleted fish stocks and improve overall stock resilience^{9,62}.

The co-location of spawning of many taxa of large pelagic fish could inform where fishing could be restricted during spawning periods⁶³. This is especially critical for highly migratory species managed by Regional Fisheries Management Organizations (RFMOs) whose jurisdictions span regions of international waters across both hemispheres. Although the use of spatial management measures by RFMOs remains rare⁶⁴, implementing pelagic closures around spawning aggregations could be an effective tool in fisheries management⁶⁵. Targeted fishing closures in spawning grounds of overfished or declining fish stocks—such as the bigeye tuna in the western and central Pacific Ocean⁶⁶, the striped marlin in the western and central northern Pacific Ocean⁶⁷, and albacore in the South Pacific Ocean⁶⁸—could help rebuild populations and increase stock resilience. Current efforts, however, are limited. For example, there is only a single Conservation Management Measure (CMM 2023-01) in the Western and Central Pacific Fisheries Commission with a spatiotemporal component for either target or non-target species. This Conservation and Management Measure for bigeye, yellowfin and skipjack tuna includes a ban on setting fish aggregating devices in the high seas between 20°N and 20°S in the western and central Pacific Ocean from July to mid-August, with a further one month ban for most countries. The measure does not mention protection of spawning aggregations as a rationale for the closure⁶⁹.

Information on spatiotemporal variation could also contribute to the development of general theoretical considerations to inform appropriate and targeted fisheries management approaches for specific taxa. For example, taxa with spatially aggregated spawning grounds that had little seasonality—such as frigate tuna—might benefit more from permanent spatial closures than taxa that spawn over a more dispersed area⁷⁰. However, taxa that are temporally aggregated but spatially dispersed—such as striped marlin and swordfish in the

northern hemisphere—could benefit more from seasonal closures of some areas in their potential spawning grounds⁷⁰. Conversely, taxa that are both spatially and temporally aggregated—such as Pacific bluefin tuna and Southern bluefin tuna—could benefit from seasonal spatial closures, dynamic time-area, or event-triggered fisheries closures⁷¹. Such time-area closures are likely to have fewer benefits for taxa that are both spatially and temporally dispersed, such as skipjack and yellowfin tuna. For these species, traditional management measures such as input (e.g., gear restrictions) or output controls (e.g., quotas) may be more beneficial.

Harnessing spawning information in biodiversity conservation

Identifying spawning grounds for multiple pelagic fish species could inform and enhance conservation measures. For example, the criteria for Ecologically or Biologically Significant Areas in the Convention on Biological Diversity emphasizes the role of critical life history stages, particularly for threatened species, in identifying key conservation areas⁷². The cross-taxa spawning hotspots could be integrated into the design of fisheries closures as part of fisheries management strategies⁶⁵. Such closures could provide benefits beyond commercially valuable fish species, including non-target biodiversity. When such closures deliver long-term conservation benefits beyond their primary purpose related to fisheries management, these closures could potentially qualify as OECMs⁷³. Further, these spawning areas could inform the design of MPAs. While the effectiveness of MPAs in conserving highly migratory tuna species is debated²¹, protecting their spawning areas from intense fishing is likely to yield conservation benefits^{74,75}. Incorporating larval hotspots in the design of MPAs could potentially lead to increases in fish biomass and associated ecosystems services such as food provisioning^{57,76}. It could also increase the resilience of tuna and billfish fisheries⁶¹, and provide broader biodiversity protection to less-monitored non-target populations.

Caveats

This study has several caveats. First, fish larvae were not identified through genetic analyses, so some misidentification is possible for species that are more difficult to identify morphologically. Second, the

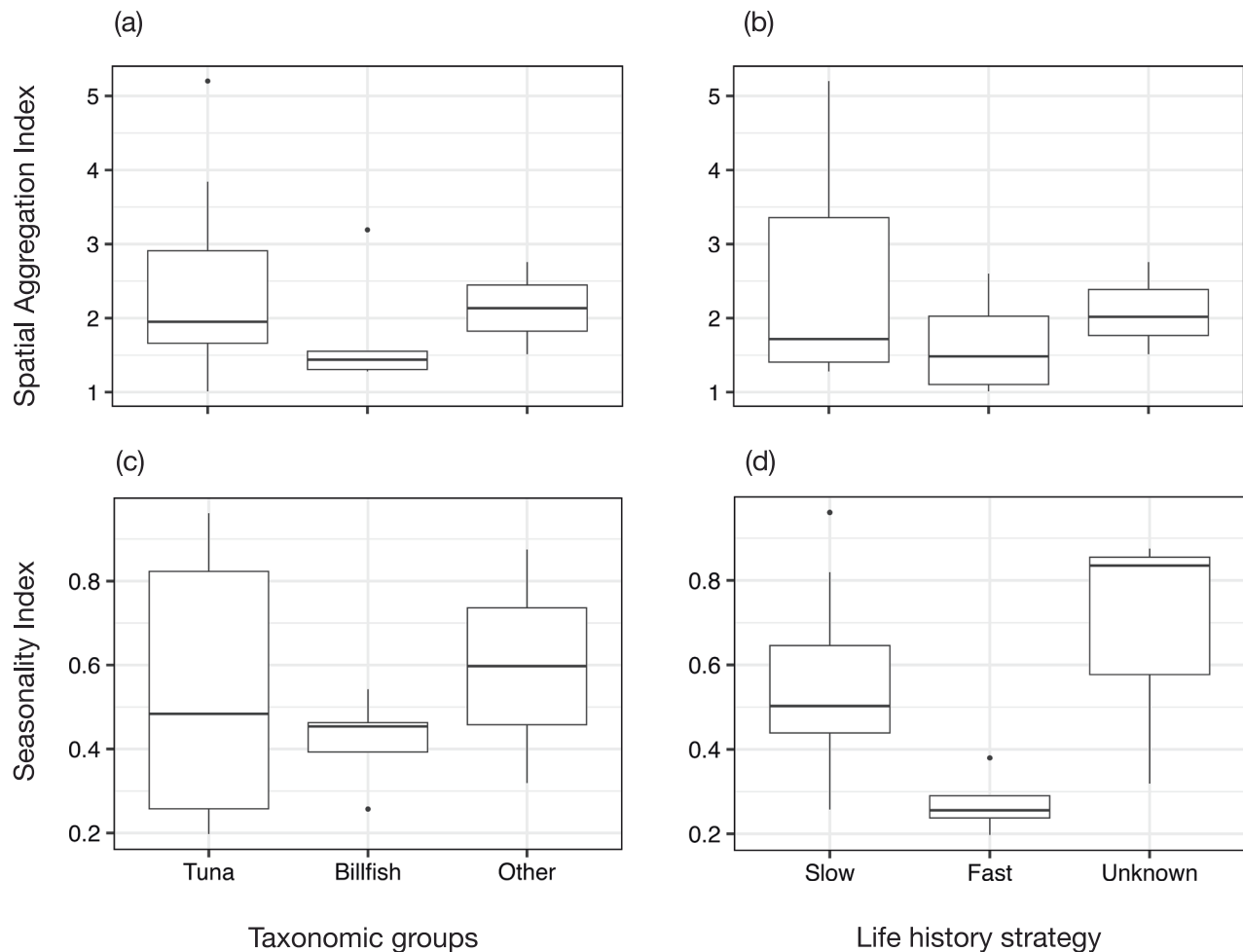


Fig. 8 | Variation in spatial aggregation and seasonality of spawning. **a–c** across taxonomic groups (Tuna: $n = 8$; Billfish: $n = 5$; Other: $n = 2$, where n represents the number of taxa in this category) and **b–d** across life history strategies (Slow: $n = 8$; Fast: $n = 4$; Unknown: $n = 3$, where n represents the number of taxa in this category).

Variation in the means of the two indices across taxa is illustrated using box plots with bounds from 25th (Q1) to 75th (Q3) percentiles, a solid line indicating the median, and whiskers extending to $\pm 1.5 \times$ Interquartile Range (IQR). Outliers are represented as points beyond the whiskers.

status of the exploited fish stocks could have influenced the observed spatiotemporal spawning patterns. Some species could have suffered declines in abundance before or during the period of sampling⁷⁷. For example, fishing activities during the sampling period (1956–1981) of the Nishikawa dataset led to range contractions in several species, including blue marlin, sailfish, Southern bluefin tuna, skipjack tuna, and striped marlin⁷⁸. Notably, areas of range contractions identified in Worm and Tittensor⁷⁸ overlap with areas of low probabilities of occurrence for the sailfish and skipjack tuna BRT models. However, 10 out of the 15 taxa in our study were not listed as highly exploited⁷⁸. These larval distributions are a historical record of spawning grounds under the stock status at the time, providing a valuable reference for current and future comparisons.

Third, while BRTs are a robust approach for building habitat suitability models, it has its limitations. For example, habitat suitability models built using BRTs may detect interactions among predictors better than other methods but are prone to overfitting due to the sequential fitting of the model⁷⁹. Additionally, BRTs can also have problems when extrapolating to areas where the relationship between response and predictors is unknown. To minimize these problems, we have: (1) balanced the number of trees, tree complexity, and learning rate of the models, as well as including a bag fraction that introduces stochasticity to decrease overfitting⁷⁹; and (2) restricted the extrapolation of the models to $10^\circ \times 10^\circ$ grid cells with at least 5% of its area having sampling data. However, there is still the

potential for overfitting of non-causal predictors when using BRTs. Thus, the role of environmental drivers in explaining larval distributions should be interpreted with some caution, as should the use of the predictions for climate-impact studies.

Fourth, we used output from ocean models from OMIP2 instead of observations such as satellite data¹³ or in-situ data recorded during tows. Although model outputs have greater uncertainty than observations⁸⁰, it was not possible to obtain observations for environmental variables in the 1956–1981 period. OMIP2 models had the best temporal overlap with the larval dataset compared to other environmental databases available. Fifth, the spatial resolution of the calculated mean kinetic energy is 1° , which might not adequately reflect finer-scale local mixing processes. Thus, relationships between species occurrence and mean kinetic energy should be interpreted with caution. Last, we built the models using only a single dataset, and many taxa had relatively few positive records, resulting in low probabilities of occurrence, and some had too few positive records where the BRTs did not converge (e.g., little tuna, bonitos). Subtle seasonal patterns and habitat preferences could therefore have been missed in these taxa.

Concluding remarks

We found that large pelagic fish exhibit diverse spawning strategies in both location and timing. Generally, species in tropical regions spawn broadly across time and space, whereas those in subtropical and

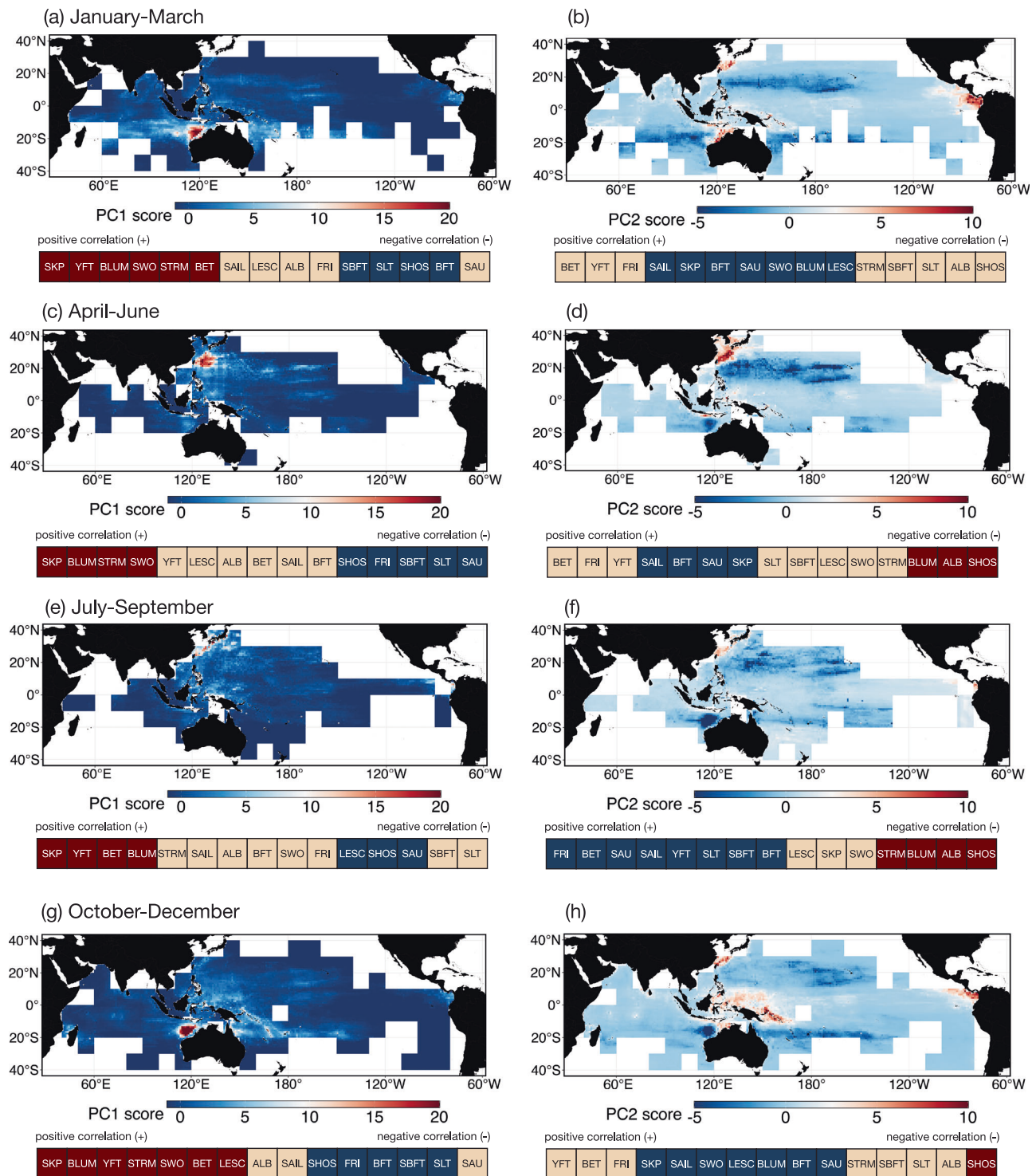


Fig. 9 | Seasonal hotspots based on Principal Component Analysis (PCA). **a, b** January–March ($r^2_{PC1} = 0.30$; $r^2_{PC2} = 0.14$); **c, d** April–June ($r^2_{PC1} = 0.30$; $r^2_{PC2} = 0.17$); **e, f** July–September ($r^2_{PC1} = 0.22$; $r^2_{PC2} = 0.15$); and **g, h** October–December ($r^2_{PC1} = 0.31$; $r^2_{PC2} = 0.14$). The left column shows PC1 scores (**a, c, e, g**) and the right column shows PC2 scores (**b, d, e, h**). Below each panel is a

summary of the correlation of the PC axes with the seasonal probability maps of each taxon. Grids of taxa are color-coded depending on the absolute value of their Spearman correlation coefficients: high are red (≥ 0.6 or ≤ -0.6); moderate are cream (0.3 to 0.6 or -0.6 to -0.3); and low are blue ($-0.3 \geq$ and ≤ 0.3).

temperate regions spawn over a narrower time window and in more localized areas. Further, many large pelagic fish taxa co-locate their spawning in time and space. These spawning hotspots—south of Japan in the East China Sea, in the eastern tropical Pacific Ocean north and south of the equator, and off Northwest Australia—could inform the development of area-based management tools. These areas have the

potential to deliver multiple benefits for fisheries and conservation. These benefits include improving fisheries management approaches, increasing fish biomass of commercially important species, and achieving conservation outcomes for overfished species. Such measures could enable fisheries to contribute more actively towards achieving globally agreed societal goals. With less than five years

remaining to achieve the target of protecting 30% of the oceans by 2030²⁴, the cross-taxa larval hotspots identified in this paper provide critical information to guide the development of MPAs and OECMs, particularly in data-poor and under-protected areas beyond national jurisdiction.

Methods

Preparing seasonal historical larval and environmental data

A $1^\circ \times 1^\circ$ grid from 40°N to 40°S was created spanning the Indian and Pacific Oceans and all data were resampled into this grid. The digitized catch per unit effort (CPUE) categories from the Nishikawa data³¹ were converted to presence-absence data (i.e., CPUE categories >0 were considered presences) because there were few sampling points with categories >1 (Supplementary Fig. 15). Following Nishikawa et al.³⁰, we defined seasons as one month delayed from standard calendar seasons (i.e., boreal summer is July–September and austral summer is January–March). Historical climate data for the following surface predictors were downloaded from the Ocean Model Intercomparison Project Phase 2 (OMIP2)⁸¹: (1) temperature ($^\circ\text{C}$); (2) oxygen (mol m^{-3}); (3) pH; (4) chlorophyll-a (mmol m^{-3}); (5) salinity (ppt); (6) mixed layer thickness (m); (7) nitrate (mmol m^{-3}); (8) phosphate (mmol m^{-3}); (9) ammonium (mmol m^{-3}); (10) zonal (east-west) velocity (m s^{-1}); and (11) meridional (north-south) velocity (m s^{-1}) (Supplementary Fig. 16–26). OMIP2 outputs are the result of six simulation cycles of a 61-year forcing dataset (1958–2018), resulting in 366-year simulation outputs. While the Nishikawa dataset runs from 1956 to 1981, we prepared the mean, seasonal layers of each surface predictor through 1963–1981 from the last simulation cycle of the OMIP2 ensemble members (Supplementary Table 2), removing the first five years of the simulation cycle to account for the possible overshoot from the previous simulation cycle⁸². Using the temperature and salinity data, we calculated broad-scale thermal ($^\circ\text{C km}^{-1}$; Supplementary Fig. 27) and salinity (ppt km^{-1} ; Supplementary Fig. 28) gradients using VoCC R package⁸³. We calculated mean kinetic energy ($\text{m}^2 \text{s}^{-2}$) as a proxy for large-scale surface flow dynamics⁸⁴, using zonal (u) and meridional (v) geostrophic velocities (Supplementary Fig. 29):

$$MKE = \frac{1}{2} (u^2 + v^2) \quad (1)$$

The mean depth layer was prepared using the current gridded, sub-ice bathymetric dataset of General Bathymetric Chart of the Oceans (GEBCO; Supplementary Fig. 30)⁸⁵. The distance of each grid cell to the nearest coastline was calculated using the `rnatuarearth`⁸⁶ and `sf`⁸⁷ R packages (Supplementary Fig. 31). Finally, we combined larval and environmental data to prepare seasonal datasets following the Nishikawa data (i.e., January–March, April–June, July–September, and October–December).

We intersected all layers with the grid to provide response and predictor values in each of the 15,551 cells of $1^\circ \times 1^\circ$. Values of predictors for each cell were assigned based on geographic location and time period (for seasonal environmental predictors). Each grid cell inherited the nearest known value for the predictors. Larval and environmental data described were prepared with the same resolution. All analyses were done in the R statistical computing environment (version 4.4.3)⁸⁸ and the Climate Data Operators (CDO) software⁸⁹. Packages used to analyze the data are available in Supplementary Table 3. All output from habitat suitability models is available at Bue-
nafe et al.⁹⁰.

Building historical habitat suitability models

Many different techniques can be used to build habitat suitability models⁹¹, including Generalized Additive Models for larval habitat suitability models^{13,92}. However, Boosted Regression Trees (BRTs)—a machine learning technique—are generally more powerful at

detecting interactions between predictors⁷⁹. Since our aim was to describe seasonal, historical larval hotspots, we used BRTs to build the habitat suitability models rather than other techniques. BRT models were built using the `dismo` R package⁹³. Predictors in the BRTs were oceanographic and biophysical drivers that have been identified as characterizing potential spawning locations of fish larvae in previous studies: (1) longitude^{94,95}; (2) latitude^{94,95}; (3) season¹³; (4) mean surface temperature^{28,95}; (5) mean surface dissolved oxygen⁹⁶; (6) mean surface pH⁹⁷; (7) mean surface chlorophyll-a^{28,45,95}; (8) mean surface salinity^{28,94}; (9) mean mixed layer thickness⁹⁵; (10) mean surface nitrate concentration⁹⁸; (11) mean surface phosphate concentration⁹⁸; (12) mean surface ammonium concentration⁹⁸; (13) broad-scale thermal gradients^{28,45}; (14) broad-scale salinity gradients²⁸; (15) mean kinetic energy⁴⁸; (16) mean depth⁹⁵; and (17) distance to the nearest coastline⁹⁵. While many of the predictors covary, BRTs, as do any other modeling approaches, are robust to a moderate amount of covariation⁷⁹.

We used the presence-absence data (i.e., 1 – presence; 0 – absence) of the following fish taxa as the response: (1) skipjack tuna (*Katsuwonus pelamis*); (2) yellowfin tuna (*Thunnus albacares*); (3) albacore (*Thunnus alalunga*); (4) bigeye tuna (*Thunnus obesus*); (5) frigate tuna (*Auxis rochei* and *A. thazard*); (6) Southern bluefin tuna (*Thunnus maccoyii*); (7) Pacific bluefin tuna (*Thunnus orientalis*); (8) slender tuna (*Allothunnus fallai*); (9) blue marlin (*Makaira nigricans*); (10) shortbill spearfish (*Tetrapturus angustirostris*); (11) swordfish (*Xiphias gladius*); (12) striped marlin (*Kajikia audax* and *K. albida*); (13) sailfish (*Istiophorus platypterus*); (14) longfin escolar (*Scombrobrax heterolepis*); and (15) sauries (*Cololabis saira*, *C. adocetus*, and *Scomberesox saurus*). We categorized these taxa according to their oceanic environment⁹⁹ and life-history strategy⁵ (Table 1). We also reported the number of presences of each taxon from 40°N – 40°S as reported in Nishikawa et al.³¹. All taxa had the same number of samples ($n = 13,275$) in the Nishikawa dataset (i.e., CPUE for each taxon was measured in all the samples). As each taxon was modeled using individual BRTs, models for taxa that were more common (i.e., larvae were present in more samples) were more robust than for species that were relatively rare (i.e., taxa that had more zeros) (Table 1). Although the larval dataset has information on three more taxa (little tuna, bonitos, and black marlin), the BRTs did not converge for these taxa because of too few presence data.

The BRT method combines regression trees with boosting, an ensemble learning method, iteratively aggregating individual weak learners to a final strong learner⁷⁹. We built the models using cells with presence/absence data in our domain ($n = 6,166$), dividing them into an 80–20 train-test split. Using the training data, we executed a grid search to determine the configuration of hyperparameters that would yield the optimal model for each taxon (i.e., model with the highest Area Under the receiver operating Curve, or AUC, of the testing data). We ran the grid search across this range of different hyperparameters: (i) tree complexity (i.e., interaction depth): 1 or 2; (ii) learning rate: 0.005 to 0.01 in increments of 0.001; and (iii) bag fraction: 0.5 or 0.75. We reported the optimal model for each taxon by employing a five-fold cross-validation to search for the optimal number of trees while ensuring that each BRT was built with at least 1000 trees (Supplementary Table 1)⁷⁹. Using the optimal models, we presented the seasonal habitat suitability maps of each taxon (i.e., 15 taxa \times 4 seasons = 60 maps).

To increase the confidence in the models, we overlaid a $10^\circ \times 10^\circ$ grid onto the Indian and Pacific Oceans. We then only retained $1^\circ \times 1^\circ$ grid cells found within the larger $10^\circ \times 10^\circ$ cells that had at least 5% of its area covered by $1^\circ \times 1^\circ$ sampling cells. By doing so, we restricted the extrapolations to areas relatively close to where larvae were sampled. We also restricted the resulting habitat suitability maps of each taxa to their respective adult distributions. The range of the adult distributions are defined using predicted occurrences from AquaMaps

(probabilities of species occurrence ≥ 0.01 are considered as presences¹⁰⁰). Because not all taxa were identified to the species-level in Nishikawa et al.³⁰, we followed Buenafe et al.³¹ and calculated the mean of the adult probabilities of species occurrence of the species listed within each taxon. Spatial dependence among grid cells was not considered in the models.

Describing interhemispheric seasonality and spatiotemporal aggregation

To visualize interhemispheric seasonality across taxa, we calculated the mean probabilities for each season in each hemisphere. As a measure of spawning seasonality, we defined the “Seasonality Index” for each taxon in each hemisphere as the standard deviation (across seasons) of the mean probabilities. Higher Seasonality Index values indicate greater seasonality in spawning. As a measure of spatial aggregation in spawning, we defined the “Spatial Aggregation Index” for each taxon in each hemisphere as the mean (across seasons) of the coefficient of variation (i.e., standard deviation over the mean) of the probabilities. The coefficient of variation scales the standard deviation with the different magnitudes of probabilities for each taxon. Higher Spatial Aggregation Index values indicate greater aggregation in spawning (i.e., less uniformly distributed). The Seasonal Index and the Spatial Aggregation Index are compared across taxonomic groups and life-history strategies (Table 1). We assessed the relationship between the Seasonality and Spatial Aggregation Indices across taxa. Further, we quantified the relationships of the indices across different predictors, such as latitude (specifically, the absolute value of latitude), taxonomic groups, and life history strategies (Table 1). These relationships were quantified by fitting linear models for the different responses (typically, the indices) and predictors (latitude, taxonomic groups, life history strategies) (Supplementary Table 4).

Identifying historical larval hotspots

To summarize the major spatial patterns in larval distribution, including the high-probability areas common to multiple taxa (i.e., larval hotspots), we performed a Principal Component Analysis (PCA) for each season on the probability of occurrence for all larval taxa. The input matrix for each season comprised the 15 larval taxa (as columns) and the resulting probabilities for each of the grid points from the BRTs (as rows). The PCA was performed on the correlation matrix of this input matrix. The first two PC axes explained 35% of the total variance (Supplementary Fig. 32), suggesting that the identified patterns explained a substantial proportion of the larval distribution patterns across taxa, although there remains considerable unexplained variation. Grid cells with high PC scores reflect areas with high probabilities of occurrences across different taxa and are thus potential larval hotspots. Information on how to perform and interpret PCA can be found in Legendre and Legendre¹⁰¹. We also calculated the Spearman correlation coefficient between the individual seasonal larval maps and each of the first two PCA axes to determine the relationship between each taxon and the major seasonal patterns of larval distribution.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The environmental, oceanographic and larval data used to run the models are available in the Zenodo database (<https://doi.org/10.5281/zenodo.14745329>)⁹⁰. The model outputs generated in this study have been deposited in the Zenodo database (<https://doi.org/10.5281/zenodo.14745329>)⁹⁰.

Code availability

The up-to-date code used to generate the data, run all analyses, and create the figures and plots are available in the GitHub repository (<https://github.com/SnBuenafe/LarvaDistModels>) and archived in the Zenodo database (<https://doi.org/10.5281/zenodo.14745329>)⁹⁰.

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K.C.V.B., I.M.S., J.D.E., J.M. and A.J.R. worked on the preliminary data for the article. K.C.V.B., S.N., J.D.E., and A.J.R. refined the final models. K.C.V.B., S.N., K.L.S., J.D.E., J.F. and A.J.R. contributed substantially to the analyses. K.C.V.B., S.N., K.L.S., D.C.D., J.D.E., J.F., I.M.S., P.G.D., A.D., K.J.T.E. and A.J.R. contributed substantially to the discussion of the

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Competing interests

The authors declare no competing interests.

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