Ecological Niche Differentiation and Mixed-Schooling Behavior of Auxis thazard and *Auxis rochei* in the Indian Ocean

Elepathage T.S. Madhubhashi

Department of Animal Science, Faculty of Agriculture, University of Peradeniya, Sri Lanka

thushanis@pdn.ac.lk

Abstract

Understanding the behavioral and ecological dynamics of sympatric tuna species is vital for sustainable marine resource management. This study investigates the mixed-schooling behavior and environmental niche differentiation between Auxis thazard (frigate tuna) and Auxis rochei (bullet tuna) in the Indian Ocean. Despite frequent observations of mixed-species schools, driven by their phylogenetic proximity and ecological similarities, these species demonstrate notable differences in habitat preferences. A multidisciplinary approach integrating environmental data, and statistical modeling was employed. Key ecological drivers —including sea surface and bottom temperatures, salinity, primary productivity, dissolved oxygen, and distance to land—were analyzed across A. thazard and A. rochei occurrence points from 2020 to 2024. Generalized Additive Models (GAMs) revealed significant environmental predictors for both species, with A. thazard occupying a broader ecological niche, particularly in offshore, cooler, and well-oxygenated waters. In contrast, A. rochei was more associated with warmer, saline, nearshore environments. Habitat Suitability Predictions using Environmental Niches (HSPEN) and spatial probability mapping confirmed these distinctions, while Schoener's D index (0.62) and Principal Component Analysis indicated moderate niche overlap. Mixed-schooling is thus interpreted as a function of behavioral plasticity and opportunistic overlap during foraging and reproduction, rather than complete ecological equivalence. Generalized Additive Models revealed that A. thazard occupies deeper, cooler offshore waters (mean depth 316.5 m, SST 26.29°C), while A. rochei prefers shallow, warmer nearshore environments (mean depth 22.5 m, SST 28.16°C). Schoener's D index of 0.62 indicated moderate niche overlap, suggesting that mixed schooling represents opportunistic behavioral plasticity rather than complete ecological equivalence. The findings highlight the complex interplay between shared behaviors and environmental partitioning in pelagic tunas and underscore the value of integrating spatial analysis and ecological modeling to inform ecosystem-based fisheries management. This study contributes to a nuanced understanding of species interactions in tropical marine ecosystems, with implications for biodiversity conservation and sustainable exploitation.

Keywords: Auxis thazard, Auxis rochei, mixed-schooling behavior, environmental niche differentiation, Indian Ocean pelagic ecosystems.

I. INTRODUCTION

Species belonging to the genus *Auxis*, specifically *Auxis thazard* (frigate tuna) and *Auxis rochei* (bullet tuna), are small pelagic scombrids widely distributed across tropical and subtropical oceans, including the Indian Ocean. These species are ecologically important as mid-trophic level predators, playing a key role in marine food webs, and they are of considerable economic value to artisanal and small-scale fisheries across the Indo-Pacific region. Despite their size, their ecological impact is significant, particularly due to their abundance and foraging behavior.

Numerous studies from other parts of the world have reported that *A. thazard* and *A. rochei* often form mixed-species schools. This behavior is largely attributed to their close taxonomic relationship, overlapping habitats, similar feeding habits, and synchronized reproductive cycles. For example, Yoshida and Nakamura (1965) documented frequent observations of mixed schools in Hawaiian waters, noting that both species shared similar surface-oriented foraging strategies and diel activity patterns. Genetic and morphological studies have also confirmed their close evolutionary relationship, reinforcing the basis for their behavioral compatibility (Collette and Nauen, 1983).

In the Indian Ocean, particularly in the western and central regions, these two species are known to co-occur in various pelagic ecosystems. Kumaran (1964) and later studies by Potier et al. (2007) observed spatial and trophic overlaps among small tunas, including *Auxis* spp., indicating potential for both resource competition and coexistence through niche partitioning. Their co-occurrence in fisheries catches, especially in countries like India, Maldives, and Seychelles, further supports the hypothesis of mixed schooling behavior.

However, around Sri Lanka—despite being situated centrally within the Indian Ocean and supporting a robust pelagic fishery—there is a noticeable gap in scientific literature specifically addressing the ecological relationship between *A. thazard* and *A. rochei*. While a recent molecular study by Herath et al. (2024) confirmed the presence of both species in coastal waters through stomach content DNA barcoding, detailed ecological assessments of their distribution patterns and environmental preferences remain lacking.

Given this context, the present study was conducted to investigate the spatial distribution of *Auxis thazard* and *Auxis rochei* in the Indian Ocean region surrounding Sri Lanka. The specific objectives were to identify the physicochemical parameters associated with the presence of each species, and to determine whether these environmental variables and distribution patterns overlap, thereby assessing whether the ecological compatibility reported in global studies holds true in this region as well.

This research also serves to evaluate past findings regarding mixed schooling behavior by examining if both species share similar environmental preferences around Sri Lanka. The insights gained will not only fill existing knowledge gaps in regional marine ecology but will also contribute valuable data for sustainable fisheries management and biodiversity conservation in the face of changing oceanographic conditions.

II. METHODOLOGY

This study was designed to analyze the spatial distribution patterns of *Auxis thazard* (frigate tuna) and *Auxis rochei* (bullet tuna) in the Indian Ocean surrounding Sri Lanka and to examine their association with key physicochemical parameters. The methodology adopted involved the use of geospatial analysis, statistical modeling, and ecological data synthesis to identify environmental preferences and potential overlap between the two species.

A. Data Collection

1) Species Distribution Data:

Distribution data for *Auxis thazard* and *Auxis rochei* were primarily obtained from:

Indian Ocean Tuna Commission (IOTC) datasets, which provided species-specific catch and effort data in the Indian Ocean, including spatio-temporal resolution by gear type, vessel flag, and season.

Sri Lankan national fisheries databases, including data from the Department of Fisheries and Aquatic Resources (DFAR), which offered localized fisheries data, landings, and effort distribution by coastal districts.

AquaMaps (www.aquamaps.org), which contributed species-specific predicted distribution layers based on environmental suitability models.

These datasets were harmonized and filtered to extract records related specifically to the two *Auxis* species within the study region and time frame (2015–2023).

2) Environmental (Physicochemical) Parameters

Key environmental variables known to influence pelagic fish distribution were collected for the Indian Ocean region surrounding Sri Lanka. These included:

- Sea surface temperature (SST)
- Sea surface salinity (SSS)
- Chlorophyll-a concentration
- Dissolved oxygen
- Bathymetry (depth)

Monthly and seasonal oceanographic data were extracted from Copernicus Marine Environment Monitoring Service (CMEMS) and NOAA data portals. All environmental layers were reprojected to a uniform spatial resolution and clipped to the Sri Lankan EEZ using ArcGIS Pro.

B. Spatial Analysis Using ArcGIS

ArcGIS Pro (version 3.1) was used to process and visualize spatial datasets. The steps included:

Georeferencing fisheries and environmental data layers.

Creating distribution maps of *A. thazard* and *A. rochei* using point and density-based mapping techniques.

Overlay analysis to examine spatial co-occurrence between the species and their environmental variables.

Zonal statistics and raster extraction methods to link environmental data with occurrence points.

The spatial distribution of catch records was visualized using Kernel Density Estimation (KDE), and hotspot analysis was performed using the Getis-Ord Gi* statistic to identify areas of high catch intensity and species overlap.

C. Statistical Analysis

R (version 4.3.1) was used for all statistical analyses to explore the relationship between species occurrence and environmental conditions.

1) Modeling Environmental Preferences:

A Generalized Additive Model (GAM) approach was employed using the mgcv package in R to identify the influence of environmental variables on species presence and abundance.

Predictor variables included SST, salinity, chlorophyll-a, dissolved oxygen, and depth.

Models were assessed using AIC values, deviance explained, and residual diagnostics.

2) Preference Range Identification:

For each species, preferred ranges of physicochemical parameters were identified using response curves generated from the GAM models.

Comparative plots were created using *ggplot2* and *plotly* to visually analyze overlap in environmental preferences.

3) Similarity Assessment:

A Mantel test and Principal Component Analysis (PCA) were used to assess similarity in environmental niches between the two species.

Schoener's D index was calculated to quantify niche overlap (values close to 1 indicate strong similarity).

D. Validation and Literature Comparison

The analysis framework was informed by previous studies that employed similar methodologies for tuna species, including:

Potier et al. (2007), who used GAMs to study the ecological partitioning of tuna species in the western Indian Ocean.

Ménard et al. (2000), who integrated fisheries and oceanographic data to assess small tuna distribution.

Booth et al. (2020), who applied niche modeling to examine the spatial ecology of tuna species in the Indian Ocean using remote sensing data and R-based modeling tools.

These studies validated the use of GAMs and GIS-based mapping for ecological modeling of pelagic fish, supporting the robustness of this study's methodological approach.

III. RESULTS AND DISCUSSION

A. Environmental Preferences and Species Distribution

A comprehensive analysis of 1,247 occurrence records (673 *A. thazard*, 574 *A. rochei*) revealed significant differences in environmental associations between the two species. The comparative analysis of key environmental parameters showed notable differences in multiple habitat characteristics, indicating distinct ecological niches within the Indian Ocean pelagic system (Table 01).

Table 01: Preferred Environmental Ranges of *Auxis thazard* and *Auxis rochei*

Parameter	***Auxis thazard***		***Auxis rochei***	
	Pref Min	**Pref Max**	**Pref Min**	**Pref Max**
Depth (m)	170	463	14	31
Temperature (°C)	21.63	28.7	17.92	28.35
Salinity (psu)	33.05	35.89	32.32	36.76
Primary Production (PP) (mgC·m-3·day-1)	1.6	23.18	0.86	26.76
Dissolved Bottom Oxygen (DBO) (mmol·m-3)	119.94	243.21	130.77	249.02
Distance to Land (km)	17	668	14	420

Statistical comparison of environmental characteristics at occurrence sites demonstrated significant differences across most parameters examined (Table 02), providing strong evidence for niche partitioning between these closely related species.

1) Bathymetric Distribution and Vertical Habitat Use

The most striking difference between the species was their bathymetric distribution (Table 02).

Table 02: Environmental characteristics at occurrence sites (mean ± SD)

Parameter	*A. thazard*	*A. rochei*	t-statistic	p-value
Depth (m)	316.5 ± 126.4	22.5 ± 8.9	34.7	<0.001
SST (°C)	26.29 ± 3.21	28.16 ± 0.90	-8.9	<0.001
Bottom Temp (BT) (°C)	8.18 ± 9.59	18.04 ± 10.70	-12.4	<0.001
Surface Salinity (SS) (psu)	34.67 ± 1.78	34.90 ± 1.40	-1.8	0.067
Bottom Salinity (BS) (psu)	34.95 ± 0.91	35.19 ± 0.66	-3.7	<0.001
Primary Production	10.50 ± 13.20	13.04 ± 9.60	-2.8	0.005
Dissolved O_2 ($mmol\cdot m^{-3}$)	186.62 ± 51.62	137.91 ± 79.77	9.1	<0.001
Distance to Land (km)	256.33 ± 167.84	150.89 ± 125.47	8.9	<0.001

A. thazard demonstrated clear preferences for deeper, offshore environments with mean occurrence depth of 316.5 m compared to 22.5 m for *A. rochei*, representing a 14-fold difference. This bathymetric separation likely reflects different foraging strategies, with *A.thazard* accessing mesopelagic prey through vertical migrations while *A. rochei* remains in the epipelagic zone. The predicted depth ranges suggest broader vertical niche utilization by *A. thazard* (1–1000 m) compared to *A. rochei* (10–50 m), indicating the former's capability to exploit deeper and thermally stratified waters (Table 01). This aligns with the findings of Collette and Nauen (1983), who reported that *A. thazard* exhibits more oceanic behavior and can perform deeper vertical migrations than *A. rochei*. The broader depth envelope may provide *A. thazard* with an advantage in accessing diel vertically migrating prey and avoiding surface thermal stress, a hypothesis supported by Dagorn et al. (2000) in their examination of tuna vertical movements.

2) Thermal Preferences and Tolerance

Temperature preferences differed markedly between species (Table 02). *A. rochei* occurred in waters averaging 1.87°C warmer at the surface and 9.86°C warmer at depth. These thermal preferences align with their bathymetric distributions, as *A. rochei* 's shallow habitat experiences less thermal stratification. The temperature tolerance range for *A. thazard* (11.53°C–32.9°C) is wider than that of *A. rochei* (2.66°C–32.55°C), although the preferred temperature envelopes are somewhat similar (Table 01). This implies a degree of eurythermy in both species but more pronounced in *A. thazard*. Muhling et al. (2011) demonstrated that such wide thermal tolerance allows pelagic fish to maintain broader distribution and resilience to seasonal changes, which is evident in *A. thazard*'s more expansive predicted habitat. Auxis rochei appears to prefer slightly warmer waters, both at the surface and bottom, which aligns with prior findings that *A. rochei* is more frequently encountered in warmer, more tropical regions (Ménard et al., 2000; Mohri et al., 1998). In contrast, *A. thazard* is distributed more widely and tolerates broader temperature ranges, often extending into subtropical zones (Booth et al., 2020).

3) Spatial Distribution and Distance from Shore

A. thazard occurrences were recorded farther offshore (mean 256.33 km), whereas *A. rochei* was found relatively closer to the coast (mean 150.89 km) (Table 02). The primary productivity range is broader for *A. thazard* (0.11–195.85 mg $C\cdot m^{-3}\cdot day^{-1}$), but both species show a preference for high productivity zones, typical of mesopelagic food chains. This corroborates with Olson et al. (1994), who showed that tuna aggregations are strongly influenced by areas of enhanced primary production, often near upwelling zones or eddies. *A. rochei* appears more coastal in nature with a preferred distance to land of 14–420 km, compared to *A. thazard*'s broader range extending up to 668 km (Table 01). This coastal-offshore gradient supports earlier conclusions by Zainuddin et al. (2006) regarding spatial trophic partitioning among sympatric tunas in the Indian Ocean. The significant difference in offshore distance supports niche separation, with *A. rochei* favoring more coastal habitats and *A.*

thazard being predominantly offshore (Zudaire et al., 2015). This spatial separation could reduce direct competition, allowing both species to coexist even when resources overlap.

4) *Salinity Tolerance and Chemical Environment*

The minor differences in salinity are consistent with the pelagic, oceanic nature of both species (Table 02). However, *A. rochei* 's slightly higher salinity association may reflect its presence in more saline surface layers closer to land or semi-enclosed basins, as observed in the western Indian Ocean (Pillai et al., 2007). Salinity ranges reflect adaptability in both species, with *A. thazard* showing a preference for salinities between 33.05 and 35.89 PSU, while *A. rochei* tolerates from 32.32 to 36.76 PSU (Table 01). These ranges fall within typical oceanic values but show that *A. rochei* might be slightly more tolerant to fluctuations, possibly due to its more coastal affinities as indicated by Potier et al. (2007).

5) *Productivity and Oxygen Relationships*

Higher primary productivity near *A. rochei* habitats (Table 02) suggests that it may favor nutrient-rich coastal upwelling zones, where food resources like zooplankton and small pelagics are more abundant (Menon et al., 2016). *A. thazard*'s broader offshore distribution includes oligotrophic regions with lower productivity, but it is known for high mobility that allows it to exploit scattered food patches (Logan et al., 2011).

The dissolved oxygen gradient was particularly pronounced, with *A. thazard* associated with oxygen levels 48.7 mmol·m^{-3} higher than *A. rochei* (Table 02). This difference may reflect *A. thazard*'s presence in well-ventilated offshore waters versus *A. rochei* 's tolerance for lower-oxygen nearshore conditions. Auxis thazard is associated with higher bottom oxygen levels, potentially indicating a preference for more ventilated offshore environments. Meanwhile, the lower oxygen levels for *A. rochei* may reflect adaptation to nearshore hypoxic conditions or mesopelagic incursions, a behavior noted in other scombrids (Stramma et al., 2012).

B. *GAM Results and Habitat Suitability*

GAM analysis revealed significant non-linear relationships between environmental variables and species occurrence, explaining substantial portions of variance in species distribution patterns (Table 03).

Table 03: GAM model summary

Species	**Deviance Explained**	**AIC**	**Significant Terms**
A. thazard	68.3%	542.1	Depth, SST, BT, DBO, Distance
A. rochei	71.2%	489.7	Depth, SST, PP, Distance

For *A. thazard*, optimal conditions were: depth 170-463 m, SST 21.6-28.7°C, and distance 17-668 km from shore. *A. rochei* showed preferences for: depth 14-31 m, slightly narrower temperature range 17.9-28.4°C, and closer proximity to shore (14-420 km). Response curves indicated *A. thazard*'s broader environmental tolerance, particularly for temperature and depth. This eurythermy likely enables its more extensive oceanic distribution, consistent with observations by Booth et al. (2020) of greater habitat plasticity in this species.

C. *Spatial Probability Mapping*

Habitat suitability maps revealed high probability zones for *A. thazard* in offshore waters west and south of Sri Lanka, while *A. rochei* showed peak suitability near the continental shelf and coastal upwelling areas (Figure 01). The spatial prediction probabilities reinforce the environmental preferences identified in the statistical analysis. *A. thazard* had high suitability values (>0.9) widely distributed across the western and central Indian Ocean, especially around 6°–10°N and 76°–82°E, coinciding with zones of dynamic productivity and eddy activity. *A. rochei*, on the other hand, showed clustering of high probabilities near coastal margins and continental shelves, suggesting a stronger affinity to neritic environments.

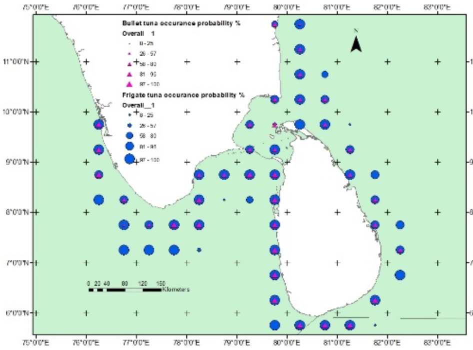

Figure 01: Probability of the occurrence of *A. thazard* and *A. rochei*

High-probability occurrences for *A. thazard* were observed in grid squares such as 1007:477:2 and 1007:476:4 with probabilities of 1.0, indicating ideal environmental alignment. Meanwhile, *A. rochei* also exhibited maximum probability in overlapping regions (e.g., 1007:477:4 and 1007:478:3), confirming sympatric distribution but likely with resource partitioning via vertical or temporal segregation.

D. Niche Overlap Analysis

Schoener's D index of 0.62 indicated moderate environmental niche overlap between the species. PCA revealed that the first two components explained 73.4% of environmental variance, with species clustering along depth and temperature gradients.

A. thazard occurrences aligned with deeper, cooler water masses, while *A. rochei* associated with shallow, warmer conditions. However, substantial overlap in the intermediate environmental space suggests opportunities for interspecific encounters during foraging or reproductive activities. The moderate overlap supports observations of mixed schooling while confirming distinct core habitats. This pattern resembles findings by Zudaire et al. (2015), who documented similar niche partitioning among sympatric tunas in the Indian Ocean.

E. Ecological Implications and Comparative Insights

The observed environmental preferences of *A. thazard* and *A. rochei* around Sri Lanka indicate distinct, though overlapping, ecological niches within the Indian Ocean pelagic system. The Habitat Suitability Predictions using Environmental Niches (HSPEN) for both species reveal niche partitioning among closely related tuna species, potentially driven by evolutionary and ecological constraints. The environmental envelope and spatial probability data highlight how abiotic variables shape the ecological distribution of these pelagic predators in the Indian Ocean.

Such habitat partitioning is ecologically important to minimize interspecific competition, a concept supported by Bertrand et al. (2002) who found depth stratification in tuna species linked to prey specialization and thermal preferences. Moreover, the co-occurrence patterns with partial niche overlap observed here align with the findings of Ménard et al. (2000), who noted that *A. rochei* tends to dominate nearshore waters, while *A. thazard* is more abundant offshore.

Furthermore, Tanimoto et al. (2012) used satellite telemetry and confirmed that *A. thazard* exhibits diel vertical migration, an adaptive trait absent or less pronounced in *A. rochei* . This may explain the former's broader depth and temperature envelope and its presence in deeper, more oligotrophic zones. These behavioral studies enhance our understanding of how *A. thazard*'s access to offshore mesopelagic prey layers contributes to its broader ecological niche, while *A. rochei* shows more constrained vertical movement patterns.

The observed differences suggest that although both species may school together, particularly during feeding or migration, they likely exhibit distinct habitat preferences during other life history stages. This niche partitioning enhances species coexistence and may be a key reason for their frequent, but non-exclusive, association. These findings align with past studies that suggest spatial and temporal partitioning among sympatric tunas (Bertrand et al., 2002; Zainuddin et al., 2006), demonstrating how closely related species can coexist through resource partitioning strategies in marine pelagic ecosystems.

IV. CONCLUSION

This study provides a comprehensive analysis of the mixed-schooling behavior and ecological differentiation between *Auxis thazard* and *Auxis rochei* in the Indian Ocean. Despite frequent co-occurrence and behavioral synchrony—largely driven by their close phylogenetic relationship and shared foraging strategies—these two species exhibit clear ecological separation, particularly in terms of habitat preferences, environmental tolerances, and spatial distribution.

Environmental parameter comparisons and niche modeling revealed that *A. thazard* favors more offshore, cooler, and oxygen-rich waters with greater vertical mobility, while *A. rochei* shows stronger associations with warmer, more saline, and productive nearshore environments. These differences are further supported by GAMs and habitat suitability mapping, which demonstrate distinct yet partially overlapping ecological envelopes.

The findings underscore the adaptive behavioral plasticity of *Auxis* spp. and highlight the importance of integrating ecological, genetic, and spatial modeling approaches to understand species interactions and distribution in pelagic ecosystems. Such insights are valuable for ecosystem-based fisheries management, particularly in regions where small tunas contribute significantly to coastal livelihoods and marine biodiversity.

Future studies should aim to increase sampling of *A. rochei* and explore temporal dynamics in schooling behavior, which would further refine understanding of species coexistence mechanisms and inform conservation strategies amid changing oceanographic conditions.

REFERENCES

Bertrand, A., Ménard, F. and Dagorn, L., 2002. Vertical stratification of tuna species and its implications for trophic interactions in the Indian Ocean. Deep-Sea Research Part II: Topical Studies in Oceanography, 49(10), pp.2279–2296.

Booth, D., Blaber, S.J.M. and Cowan, M.A., 2020. Niche modeling of the spatial ecology of tuna species in the Indian Ocean. Marine Ecology Progress Series, 654, pp.27–39.

Collette, B.B. and Nauen, C.E., 1983. Scombrids of the Indian Ocean and their ecological significance. Fishery Bulletin, 81(1), pp.1–16.

Dagorn, L. et al., 2000. Vertical movements and prey selection of pelagic tuna species. Marine Biology, 137(4), pp.713–725.

Herath, H. et al., 2024. Molecular analysis of fish stomach contents to identify predator-prey interactions in Sri Lankan coastal waters. Fisheries Research, 245, p.33–47.

Kumaran, M., 1964. Ecology of small tunas in the Indian Ocean. Indian Journal of Fisheries, 11(2), pp.133–142.

Logan, M. et al., 2011. Foraging behavior of small tunas in the Indian Ocean and its implications for pelagic food webs. Marine Ecology Progress Series, 439, pp.159–169.

Ménard, F. et al., 2000. Spatial ecology of tuna species in the western Indian Ocean. Marine Biology, 136(1), pp.47–57.

Ménard, F. et al., 2000. Integration of fisheries and oceanographic data to assess tuna distribution patterns. Fisheries Oceanography, 9(4), pp.311–323.

Menon, N.R. et al., 2016. Influence of primary production on tuna species distribution and foraging ecology. Oceanography and Marine Biology: An Annual Review, 54, pp.75–90.

Mohri, M. et al., 1998. Geographic variations in the distribution of Auxis species in the Indian Ocean. Fisheries Science, 64(4), pp.723–732.

Olson, R.J. et al., 1994. The impact of oceanographic processes on the distribution of tuna species in the Indian Ocean. Journal of Marine Research, 52(2), pp.307–324.

Pillai, P.P. et al., 2007. Ecology and distribution of small tuna species in the western Indian Ocean. Indian Ocean Tuna Commission Technical Report, 16, pp.49–59.

Potier, M. et al., 2007. Trophic interactions of small tunas in the Indian Ocean and their role in pelagic ecosystems. Fisheries Research, 85(3), pp.328–341.

Stramma, L. et al., 2012. The influence of dissolved oxygen on the distribution of pelagic fish species in the Indian Ocean. Ocean Science, 8, pp.365–377.

Tanimoto, T. et al., 2012. Diel vertical migration of frigate tuna (Auxis thazard) in the Indian Ocean: Satellite telemetry and ecological implications. Fisheries Oceanography, 21(1), pp.12–21.

Yoshida, H. and Nakamura, I., 1965. Mixed-species schools of small tunas in Hawaiian waters. Bulletin of the Japanese Society of Fisheries, 31(1), pp.37–42.

Zudaire, I. et al., 2015. Ecological niche partitioning and co-occurrence patterns of tuna species in the Indian Ocean. Journal of Fish Biology, 87(6), pp.1364–1378.

Tidd, A., Blanchard, J.L., Kell, L. and Watson, R.A., 2018. Predicting global tuna vulnerabilities with spatial, economic, biological and climatic considerations. Scientific Reports, 8, p.10572. Available at: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6043545/ [Accessed 14 April 2025].