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# Role of tunas in the Western and Central Pacific Ocean: Evidence from a mass-balanced model

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## ABSTRACT

Tunas represent one of the most economically and ecologically significant marine taxa worldwide. The Western and Central Pacific Ocean (WCPO) accounts for approximately 58% of global tuna harvests annually. Using data from the 2023 High-Seas Fishery Resources Survey in the WCPO, the role of tuna species in ecosystem dynamics was assessed through the Ecopath with Ecosim modeling framework. Eighteen functional groups were delineated based on shared ecological characteristics. Biomass estimates derived from *in situ* observations were complemented with literature-sourced parameters to maximize model robustness. Monte Carlo simulations were employed to analyze the impact of input uncertainty on key model-derived indices. Modeled trophic levels ranged from 1.00 to 4.50. A comparative analysis with 2007 baseline data revealed a decline in trophic positions for tunas and other apex taxa such as sharks, swordfish, and pelagic stingrays. Tuna species exhibited the highest keystone index and relative total impact, underscoring their central structuring role in pelagic food webs. Mixed trophic impact analysis identified widespread negative interactions exerted by tunas, especially on larval fish populations. The WCPO system demonstrated a total system throughput (TST) of 6 912.24 $t \cdot km^{-2} \cdot year^{-1}$, substantially exceeding the 2002 estimate of 4 846.58 $t/km^2$/year. The low system omnivory index (0.27) and these overall ecosystem characteristics suggested that the WCPO ecosystem is currently disturbed to a low extent and lead to a relatively stable system compare with other studies. Sensitivity analysis highlighted strong model dependence on biomass and production-to-biomass (P/B) ratios across functional groups. These findings refine current understanding of pelagic food web architecture in the WCPO and provide a quantitative foundation for implementing ecosystem-based fishery management strategies in high-seas environments.

**Keywords:** Ecopath; Ecosystem model; Ecological network analysis; Tunas; Western and Central Pacific Ocean

## INTRODUCTION

Tunas represent one of the most economically and ecologically critical marine taxa, significantly underpinning global pelagic fisheries. Within this context, the Western and Central Pacific Ocean (WCPO) has long served as a major center for tuna exploitation and currently ranks among the most intensively fished marine ecosystems worldwide (Langley et al., 2009). Recent assessments by the Western and Central Pacific Fisheries Commission (WCPFC) indicate that fisheries operating in this region supply approximately 58% of the annual global tuna harvest (WCPFC, 2024). As the designated Regional Fisheries Management Organization (RFMO) responsible for the stewardship of highly migratory species in the WCPO, the WCPFC regulates fisheries primarily targeting tuna species within the genus *Thunnus* and swordfish (*Xiphias gladius*), placing this institution at the center of global tuna governance.

Historical catch statistics highlight the scale and pace of tuna exploitation. Notably, Food and Agriculture Organization (FAO, 2022) records demonstrate that worldwide tuna landings increased from approximately 600 000 metric tons in 1950 to more than 7.39 million metric tons by 2015, corresponding to approximately 16% of total global marine capture production over this period. This sustained expansion



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reflects both technological advances and the growing reliance of global seafood markets on pelagic resources. Ecologically, tunas occupy high trophic positions, typically exceeding trophic level (TL) 4.0 and exert strong top-down control on prey assemblages, thereby shaping energy transfer and community structure across open-ocean food webs. Their frequent occurrence as both targeted catch and incidental bycatch further amplifies their systemic influence. Despite this prominence, recent decades have witnessed considerable declines in the abundance of key tuna species, including bigeye tuna (*Thunnus obesus*), driven largely by the rapid expansion and spatial reach of distant-water fisheries (Griffiths et al., 2019). These declines will compel management agencies to focus on tunas' role within ecosystems and implement stringent regulatory measures. In this regard, sustained and systematic evaluation of ecosystem structure and function in the WCPO is increasingly recognized as a prerequisite for effective management. Implementation of long-term systematic monitoring of the WCPO ecosystem structure and functional characteristics would enable: (1) enhanced understanding of ecosystem dynamics in this marine region; (2) establishment of baseline references for developing precautionary conservation measures by RFMOs including WCPFC; (3) provision of technical support and empirical data to facilitate ecosystem-based fisheries management approaches.

Ecosystem modeling frameworks such as Ecopath with Ecosim (EwE) play a central role in advancing ecosystem-based fisheries management. Grounded in thermodynamic principles and mass-balanced trophic exchange among living groups, these models offer a quantitatively robust platform for evaluating marine ecosystem structure, energy flow, and ecological function (Mace, 2001; Wang et al., 2025). Beyond mass-balanced trophic representation, these models have facilitated exploration of complex ecological processes, including species interactions, environmental variability, and structural shifts across trophodynamic networks (Chen et al., 2025; Ma & Li, 2024; Plagányi, 2007). Within this framework, EwE has been widely applied in marine ecosystem research due to its accessibility and relatively modest data requirements, while also contributing to interdisciplinary domains including water resource management and climate change assessment (Zhang et al., 2017). Over the past several decades, ecosystem models have served as core analytical tools for evaluating ecosystem function, stability, and response to disturbance. However, despite the global proliferation of such models, applications within the WCPO—a key region for global tuna production—remain limited, largely due to insufficient empirical data. This data gap has constrained the implementation of scientifically sustainable fisheries management strategies in this region. However, the research on the ecosystem models of the WCPO and the structure and function of its ecosystems is still insufficient (Allain et al., 2007), which limited our understanding on the trophic structure of WCPO and the role of tunas in it.

To address this gap, an Ecopath model was developed for the WCPO based on data collected during high-seas surveys conducted by the research vessel "*Songhang*" of Shanghai Ocean University, supplemented with published literature. The primary objectives of this study were to: (1) compare current ecosystem characteristics with historical benchmarks to assess structural change and vulnerability to disturbance; (2) quantify the ecological role of tunas within this pelagic food web; and (3) generate a scientifically grounded reference for ecosystem-based fisheries management in this region. Besides, whether the survey data can enhance the quality of the ecosystem model and minimize the uncertainty is one of our interests.

## MATERIALS AND METHODS

### Sampling area and data sources

The study was conducted in the WCPO (129°E–138°E and 11°N–19°N) (Figure 1). Field investigations were carried out aboard the research vessel "*Songhang*", which has a gross tonnage of approximately 3 000 t. A total of 50 evenly distributed stations were designed for squid jigging surveys, among which seven stations were additionally sampled using pelagic trawling. The fine-mesh pelagic trawl measured 434 m×97.1 m and featured a single capsule structure with a cod-end mesh of 40 mm (stretched). At each trawling station, sampling was conducted over a duration of approximately 1–2 h at a trawling speed of 3–4 knots. Trawling depths ranged from 50 m to 150 m. All captured organisms, primarily fish and cephalopods, were classified and counted, and the total weight of each species was recorded on-site.

### Ecopath model

The Ecopath modeling framework conceptualizes an ecosystem as a network of functional groups, each comprising taxa that share similar ecological roles. Based on thermodynamic principles, the model quantifies energy flow and conducts trophic network analysis to evaluate ecosystem structure and function (Plagányi, 2007). Functional groups may include species with comparable ecological behavior, life history traits, or economic relevance. To ensure ecological completeness, the model includes all key components necessary to capture major pathways of energy transfer within the system (Christensen & Pauly, 1992; Heymans et al., 2016). Ecopath operates under a mass-balance approach, requiring input parameters such as biomass (B), production-to-biomass ratio (P/B), consumption-to-biomass ratio (Q/B), ecotrophic efficiency (EE), and diet composition for each functional group (Christensen et al., 2005; Heymans et al., 2016; Lucey et al., 2020; Taghavimotlagh et al., 2021). The core model is constructed using the following mass-balance equation:

$$B_i \times \left(\frac{P}{B}\right)_i \times EE_i = \sum_{j=1}^{n} B_j \times \left(\frac{Q}{B}\right)_i \times DC_{ji} + Y_i + BA_i + E_i \qquad (1)$$

where $B_i$ and $B_j$ are the biomasses of functional groups $i$ and $j$, respectively; $(P/B)_i$ is production rate of group $i$, typically approximated by its total mortality rate; $(Q/B)_i$ is the consumption rate of group $i$; $EE_i$ is the ecotrophic efficiency of group $i$; $DC_{ji}$ is the proportion of group $i$ in the diet of predator group $j$; $Y_i$ is the catch; $BA_i$ is the biomass accumulation rate for group $i$; and $E_i$ is the net migration rate.

### Functional groups

Eighteen functional groups were defined for the WCPO ecosystem based on shared ecological traits, including habitat depth and trophic behavior. *Thunnus alalunga*, *T. albacares*, and *T. obesus* were aggregated into a single "Tunas" group due to their ecological similarity. The functional groups included one detritus group (particulate organic matter, POM), one primary producer group (phytoplankton), one zooplankton

group, 11 fish groups, one cephalopod group, and three crustacean micronekton groups. Detailed group compositions are provided in Table 1.

**Basic input parameter quality**

Biomass estimates for functional groups were derived from 2023 field surveys, published literature, and relevant studies conducted in the WCPO and adjacent regions. The swept area method (Gulland, 1971) was used to estimate the biomass of most fish groups based on trawl survey data from the WCPO in 2023. Tuna biomass was estimated using the most recent report from the International Scientific Committee (ISC, 2023). Biomass values for phytoplankton, zooplankton, and detritus were sourced from previously published studies (Supplementary Table S1). Due to gear selectivity issues related to mesh size, anchovy biomass —considered underestimated in the trawl survey—was estimated using the Ecopath model (Christensen et al., 2005) assuming an EE of 0.95.

Q/B ratios were estimated using an empirical formula based on caudal fin morphology (Palomares & Pauly, 1989), with data obtained from FishBase (https://www.fishbase.org) or other relevant sources. P/B ratios were primarily derived from literature. For some functional groups with incomplete data, P/B and Q/B ratios were inferred assuming a production-to-consumption ratio (P/Q) of 0.3, following the approach of Christensen et al. (2005). Diet composition data were obtained from recent stomach content analyses conducted in the WCPO or adjacent areas. Quantitative diet data (wet weight) were used when available; qualitative descriptions were used when necessary. EE, representing the fraction of production utilized within the living food web for each functional group,

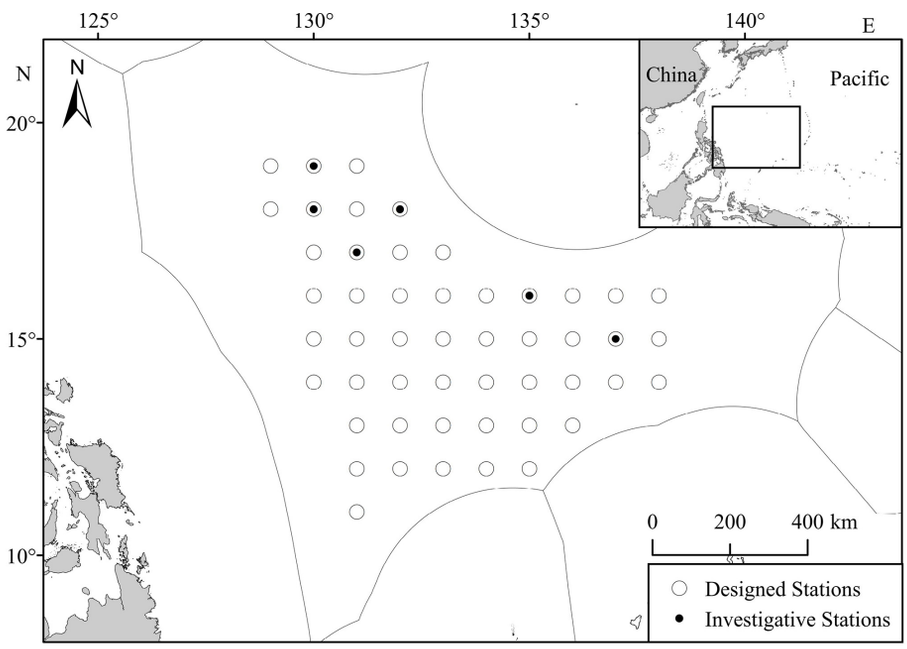


**Figure 1 Spatial distribution of fishery trawl sampling stations in the Western and Central Pacific Ocean**

Stations were located at 130°E, 19°N; 130°E, 18°N; 131°E, 17°N; 132°E, 18°N; 135°E, 16°N and 137°E, 15°N.

**Table 1 Species composition of functional groups defined in the Western and Central Pacific Ocean ecosystem model**

| Group name | Main species composition |
|---|---|
| Sharks | *Alopias pelagicus*, *A. superciliosus*, *Isurus paucus*, *Prionace glauca* |
| Swordfish | *Xiphias gladius* |
| Tunas | *Thunnus alalunga*, *T. albacares*, *T. obesus* |
| Pelagic stingray | *Pteroplatytrygon violacea* |
| Large pelagic fishes | *Brama brama* |
| Large mesopelagic fishes | *Cubiceps pauciradiatus*, *Nesiarchus nasutus*, *Nemichthys scolopaceus* |
| Small mesopelagic fishes | *Diplophos* sp., *Lestrolepis intermedia*, *Xenolepidichthys dalgleishi* |
| Small pelagic fishes | *Acanthuridae* sp., *Decapterus lajang* |
| Anchovy | *Engraulis japonicus*, *Encrasicholina* sp. |
| Lantern fish | *Bolinichthys longipes*, *Diaphus perspicillatus*, *Symbolophorus evermanni* |
| Larval fish | Leptocephalus, Tuna larvae |
| Decapoda | *Euphausia mutica*, *E. nana*, *E. pacifica*, *E. recurva* |
| Stomatopoda | *Harpiosquilla harpax* |
| Other crustaceans | Amphipoda |
| Cephalopoda | *Sthenoteuthis oualaniensis* |
| Zooplankton | Copepoda, Ostracoda |
| Phytoplankton | *Dinophysis* sp., *Navicula* sp., *Thalassiosira* sp. |
| Detritus | Particulate organic matter (POM) |

was estimated by the model. Complete input data and parameter sources are detailed in Supplementary Tables S1 and S2.

**General ecosystem indices**

Mixed trophic impact (MTI) analysis was applied to quantify the net positive or negative effects among all functional groups in a trophically balanced ecosystem (Christensen et al., 2005; Ulanowicz & Puccia, 1990). MTI was derived from an $n \times n$ interaction matrix, where $i$ and $j$ represent the interactions between impacted group $i$ and impacting group $j$:

$$MTI_{ij} = DC_{ij} - FC_{ij} \quad (2)$$

where $DC_{ij}$ is the contribution of group $i$ to the diet of group $j$ and $FC_{ij}$ represents the feeding proportion of group $i$ as a predator on $j$.

Additionally, several ecological indices were used to assess the overall structural and functional state of the WCPO ecosystem (Christensen et al., 2005; Odum, 1969): (1) total system throughput (TST, $t \cdot km^{-2} \cdot year^{-1}$), total exports, total respiration, and total biomass were used to characterize ecosystem size; (2) net system production (NSP), total primary production/total respiration (TPP/TR), and total primary production/total biomass (TPP/TB) were used to judge ecosystem maturity; and (3) system omnivory index (SOI) was used to assess food web complexity.

**Ecopath quality and sensitivity analysis**

Pre-balance (PREBAL) diagnostics offers a suite of diagnostic tools grounded in ecological and fisheries principles to evaluate the reasonableness of input data and verify the ecological viability of key parameters prior to model balancing. This approach provides a critical foundation for model balancing and subsequent analysis (Heymans et al., 2016; Link, 2010). Specifically, PREBAL was implemented to examine P/B ratios to confirm their ecological consistency—such as the expectation that predator P/B ratios remain lower than those of prey groups. Biomass typically declines with increasing trophic level, and when plotted on a log scale, the slope of biomass across functional groups arranged by trophic level is expected to decrease by approximately 5%–10% (Link, 2010). In accordance with the second law of thermodynamics, PREBAL also verifies that the P/Q ratio falls within the ecologically acceptable range of 0.1 to 0.3 (Christensen et al., 2005; Darwall et al., 2010).

Uncertainty associated with model input parameters was quantified using a pedigree index that assigns parameter-specific error ranges based on a semi-quantitative ordinal score of data quality (Christensen et al., 2005; Funtowicz & Ravetz, 1990). For each functional group, input parameter sources were assigned quality scores, each corresponding to a predefined confidence interval (CI) spanning ±10% to ±90%. These default CIs were derived from the pedigree tables reported by Christensen et al. (2005) and were used to generate parameter-specific pedigree indices for biomass, P/B, and Q/B (Supplementary Table S3). Based on these CIs, uncertainty levels of 10%, 25%, and 40% were applied to biomass, P/B, and Q/B, respectively, following Morissette (2007) (Supplementary Table S4).

A Monte Carlo resampling approach was implemented to assess the impact of uncertainty in biomass, P/B, and Q/B on model-derived ecosystem indices, including TST, total production (TP), net primary production (NPP), TPP/TR, and TPP/TB. Input parameters were randomly sampled from uniform distributions bounded by [(1−uncertainty level)×original input value, (1+uncertainty level)×original input value]. Corresponding model projections were then estimated and compared, with a total of 1 000 iterations performed. Since changes in input parameters could lead to an unbalanced situation, only resampled values that satisfied the model's balance conditions (based on EE<1) were selected for subsequent analysis (the range, proportion, and CV of successful test parameters were recorded simultaneously). Then we calculated the range of the model-derived indices through uncertainty analysis. Impacts were assessed as changes (relative bias) to model-derived ecosystem indices:

$$RB = \frac{Y_{\text{monte carlo}} - Y_{\text{base}}}{Y_{\text{base}}} \cdot 100\% \quad (3)$$

where $RB$ is the relative bias for each index, $Y_{\text{monte carlo}}$ is the index value derived from the randomly resampled model parameter set, and $Y_{\text{base}}$ is the index value derived from the originally defined parameter set.

In this study, the Ecopath model for the WCPO was constructed using Ecopath with Ecosim v6.6.8 (Christensen et al., 2005). Spatial mapping of survey stations was conducted with ArcMap v10.8. Parameter sensitivity analysis results were visualized using the ggplot2 package in R v4.3.2 (R Development Core Team, 2025). Parameter sensitivity analysis was primarily performed using the Rpath package in R (Wickham, 2016).

## RESULTS

**Food web structure and trophic level (TL) characteristics**

The TL of defined functional groups ranged from 1.00 to 4.50 (Table 2). Tunas occupied a high trophic position of 4.19, ranking third among all groups, below sharks (4.50) and swordfish (4.38). All fish functional groups demonstrated TL values exceeding 3.00, with anchovy representing the lowest fish trophic position at 3.02. Several non-fish groups, including Stomatopoda and Cephalopoda, also presented TL values above 3.00, indicating roles as secondary consumers within the food web. Organisms at the second trophic level were primarily represented by zooplankton, Decapoda, and other crustaceans (Figure 2).

All functional groups exhibited EE values below 1.00. Tunas displayed a moderate EE of 0.45. The lowest EE values were observed in swordfish (0.02), detritus (0.03), large pelagic fish (0.04), and larval fish (0.11). The remaining groups showed EE values above 0.30, with Cephalopoda exhibiting the highest value of 0.97.

Omnivory index (OI) values across functional groups ranged from 0.01 to 0.83. Stomatopoda exhibited the highest OI (0.83), followed by large mesopelagic fish (0.78), Decapoda (0.60), Cephalopoda (0.59), and small mesopelagic fish (0.55). In contrast, all other groups had OI values below 0.30. Tunas showed a notably low OI of 0.07, indicating a relatively narrow trophic niche compared to most other groups.

In the Ecopath framework, keystone species are defined as groups with relatively low biomass but disproportionately high structural influence on the food web, where fluctuations in their abundance significantly affect the biomass distribution of other species and overall ecosystem dynamics. Keystone species were identified using the keystone index and relative total impact, with values generally close to or exceeding zero.

**Table 2 Input parameters for functional groups in the Ecopath model of the Western and Central Pacific Ocean ecosystem**

| No. | Group name | Trophic level | Biomass (t/km$^2$) | Production/biomass (/year) | Consumption/biomass (/year) | Ecotrophic efficiency | Catch (t/km$^2$) | Omnivory index |
|---|---|---|---|---|---|---|---|---|
| 1 | Sharks | 4.50 | 0.0097 | 0.30 | 3.00 | 0.51 | 0.0015 | 0.17 |
| 2 | Swordfish | 4.38 | 0.0036 | 0.40 | 5.00 | 0.02 | 0.0043 | 0.08 |
| 3 | Tunas | 4.19 | 0.0109 | 1.24 | 15.57 | 0.45 | 0.0046 | 0.07 |
| 4 | Pelagic stingray | 4.16 | 0.0005 | 0.75 | 2.50 | 0.51 | 0.0002 | 0.09 |
| 5 | Large pelagic fishes | 4.02 | 0.3800 | 1.59 | 5.30 | 0.04 | | 0.17 |
| 6 | Large mesopelagic fishes | 4.13 | 0.0075 | 0.45 | 1.50 | 0.88 | | 0.78 |
| 7 | Small mesopelagic fishes | 3.06 | 0.8700 | 5.62 | 35.00 | 0.42 | | 0.55 |
| 8 | Small pelagic fishes | 3.02 | 0.1081 | 10.00 | 60.00 | 0.91 | 0.0000 | 0.01 |
| 9 | Anchovy | 3.02 | **0.6507** | 2.96 | 9.87 | 0.95 | 0.0000 | 0.01 |
| 10 | Lantern fish | 3.03 | 0.5352 | 3.20 | 10.00 | 0.63 | | 0.02 |
| 11 | Larval fish | 3.04 | 0.0218 | 2.10 | 8.00 | 0.11 | | 0.01 |
| 12 | Decapoda | 2.83 | 2.4951 | 2.56 | 12.05 | 0.92 | 0.0000 | 0.60 |
| 13 | Stomatopoda | 3.35 | 0.7230 | 0.91 | 4.56 | 0.85 | 0.0000 | 0.83 |
| 14 | Other crustaceans | 2.55 | 4.5150 | 8.00 | 30.00 | 0.66 | 0.0022 | 0.25 |
| 15 | Cephalopoda | 3.28 | 0.2720 | 7.50 | 25.00 | 0.97 | 0.0000 | 0.59 |
| 16 | Zooplankton | 2.01 | 4.4000 | 85.00 | 306.00 | 0.30 | | 0.01 |
| 17 | Phytoplankton | 1.00 | 26.5838 | 114.87 | | 0.45 | | |
| 18 | Detritus | 1.00 | 28.5000 | | | 0.03 | | |

Note: Bold text indicates model estimation.

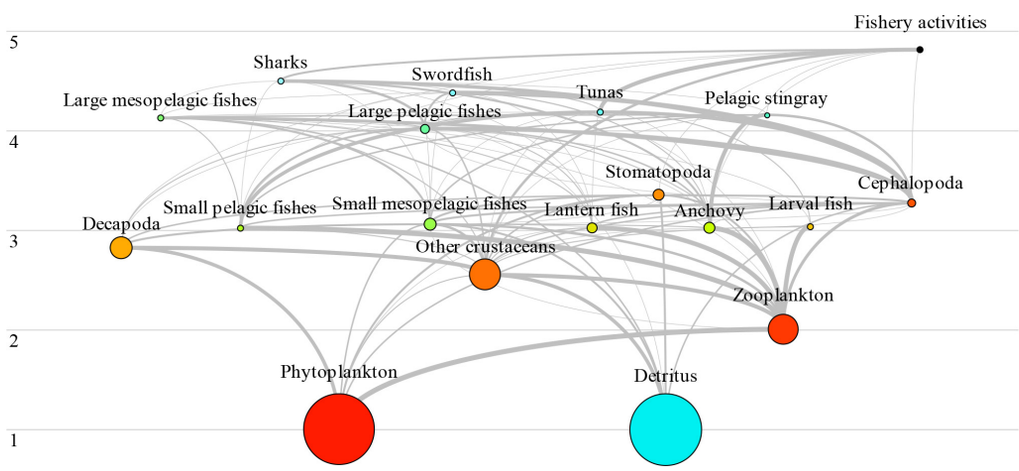


**Figure 2 Food web of the Western and Central Pacific Ocean ecosystem**

Tunas ranked third in both metrics, with a keystone index of 0.0058 (Figure 3). Two additional groups—small mesopelagic fish (0.0571) and Cephalopoda (0.0321) —also displayed positive keystone index values, indicating strong regulatory roles within the WCPO pelagic ecosystem.

### Transfer efficiency (TE) and mixed trophic impact analysis

Energy flow within the WCPO ecosystem was distributed across four discrete trophic levels (Table 3). The overall TE of the system was 12.60%. Efficiency from primary producers (12.63%) slightly exceeded that from detritus (12.05%). The highest TE was observed in the transfer from trophic levels III to IV (16.92%), while lower efficiencies were recorded in the transitions from level II to III (8.24%) and from level IV to higher trophic levels (14.36%).

Mixed trophic impact analysis revealed the net influence of both direct and indirect interactions among all functional groups (Figure 4). Tunas, a key fishery target, exerted the strongest positive impact on fishing fleets among all groups. As active predators, tunas had a distinct negative effect on larval fish and were strongly positively impacted by their primary prey (small pelagic fish). Phytoplankton, as the primary producers in the system, exerted positive effects on the majority of functional groups. Similarly, zooplankton, as ubiquitous small-sized prey, displayed broadly positive impacts consistent with their central role in energy transfer. Overall, most functional groups exerted pronounced positive effects on their predators and negative effects on their prey, as observed for small pelagic fish, decapods, and cephalopods. Certain functional groups also showed negative interactions due to diet overlap (e.g., Decapoda vs. other crustaceans, lantern fish vs. Cephalopoda).

### General ecosystem indices

Ecopath models characterize ecosystem properties using a suite of diagnostic indices that reflect system size, stability, maturity, and trophic dynamics. The TST of the WCPO ecosystem in 2023 was estimated at 6 912.24 t/km$^2$/year. Flows into the detritus pool contributed 33.06% (2 285.42 t/km$^2$/year), while total exports accounted for 32.18% (2 224.65 t//km$^2$/year). The estimated NPP was 3 053.68 t/km$^2$/year, substantially exceeding total system respiration,

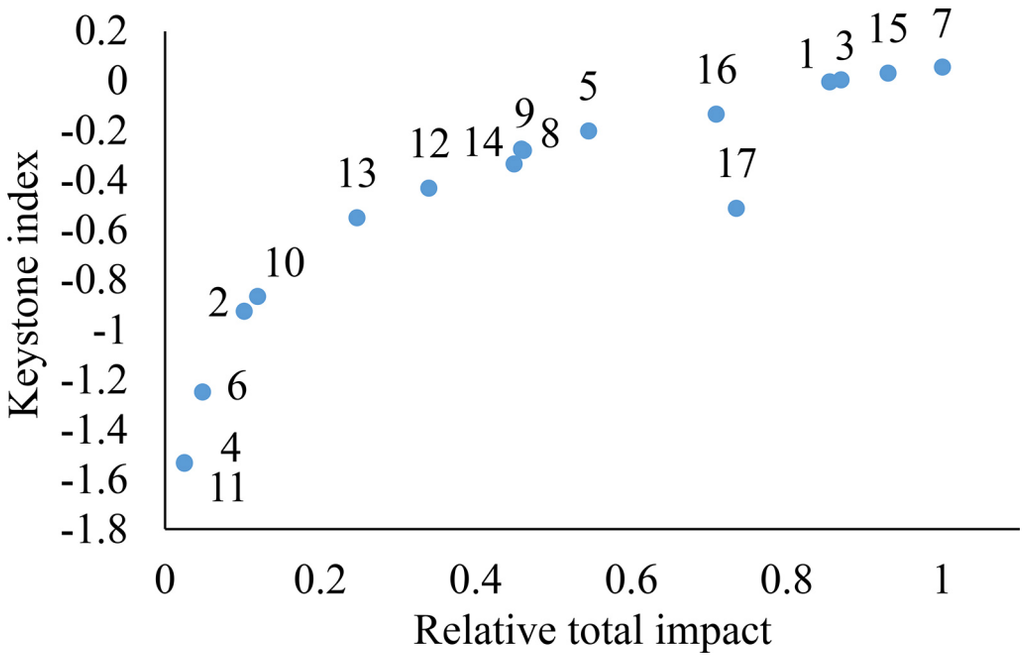


**Figure 3 Keystone index and relative total impact of functional groups in the Western and Central Pacific Ocean ecosystem**

Functional group numbers represented by digits correspond to those in Table 2.

**Table 3 Transfer efficiency across trophic levels in the Western and Central Pacific Ocean ecosystem**

| Source | Trophic level | | | Proportion of total system flow | Transfer efficiency (%) |
|---|---|---|---|---|---|
| | II% | III% | IV% | | |
| Producer | 7.87 | 17.03 | 15.01 | 0.66 | 12.63 |
| Detritus | 16.49 | 15.72 | 6.75 | 0.34 | 12.05 |
| All flows | 8.24 | 16.92 | 14.36 | | 12.60 |

resulting in the TPP/TR ratio greater than 1. The SOI was 0.27. Nutrient flow in the WCPO ecosystem was predominantly derived from food chains rooted in phytoplankton, which accounted for 66% of the total energy input. The remaining 34% originated from POM detritus (Table 4).

### Model quality evaluation and parameter sensitivity analysis

The pedigree index of the 2023 WCPO Ecopath model was 0.84, indicating relatively high overall data quality (Table 4). Sensitivity analysis indicated that the value ranges of key ecosystem indices widened as the uncertainty in model input parameters increased (Figure 5). However, the variation in output indices remained smaller than the imposed uncertainty on inputs. For example, the maximum range of uncertainty for each input parameter was 40%, while the ranges of changes in output indices were significantly less than 40%. Changes in biomass and P/B values affected all five model-derived indices (TST, TP, NPP, TPP/TR ratio, and TPP/TB ratio), with P/B exerting a greater overall influence than biomass. Variation in Q/B ratios had a substantial impact on TPP/TR but minimal impact on other indicators.

As the resampling range of input parameters increased, a larger proportion of simulations failed to meet model balance conditions. In general, the variation ranges for biomass, P/B, and Q/B closely reflected the original uncertainty bounds of the input data. Broader CIs for input parameters were associated with a decline in the proportion of successfully balanced models and an increase in the CV of the output indices. For example, the proportion of successful biomass simulations ranged from 12.00% to 51.50%, while for Q/B, the success rate ranged from 22.30% to 83.70%.

## DISCUSSION

### Trophic level structure and TE

An Ecopath model integrating empirical field data was developed to elucidate trophic architecture and trophodynamics within the WCPO ecosystem in 2023. Relative to earlier assessments (Allain et al., 2007), the trophic positions of apex predators, including sharks, swordfish, tunas, and pelagic stingrays, were markedly lower. Overall, the WCPO ecosystem exhibited a narrow trophic range, with functionally similar groups occupying closely aligned positions.

EE estimates for most functional groups were consistent with historical baselines, with notably higher values among small-bodied prey taxa, consistent with patterns previously reported for this region (Allain et al., 2007; Choy et al., 2016). A distinct increase in shark EE was observed compared with previous studies (Booth et al., 2020; Howell et al., 2013), likely driven by intensified fishing pressure. As incidental catch with minimal commercial value, sharks contributed energy primarily through by-catch removal during commercial fishing and subsequent trophic redistribution (Kindong et al., 2022).

The lowest TE occurred between trophic levels II and III, a pattern likely attributable to depleted biomass among small-sized prey occupying level II. Overexploitation of these intermediate consumers may have disrupted energy transmission across the mid-trophic domain, reducing overall TE below the canonical 10% threshold proposed by Lindeman

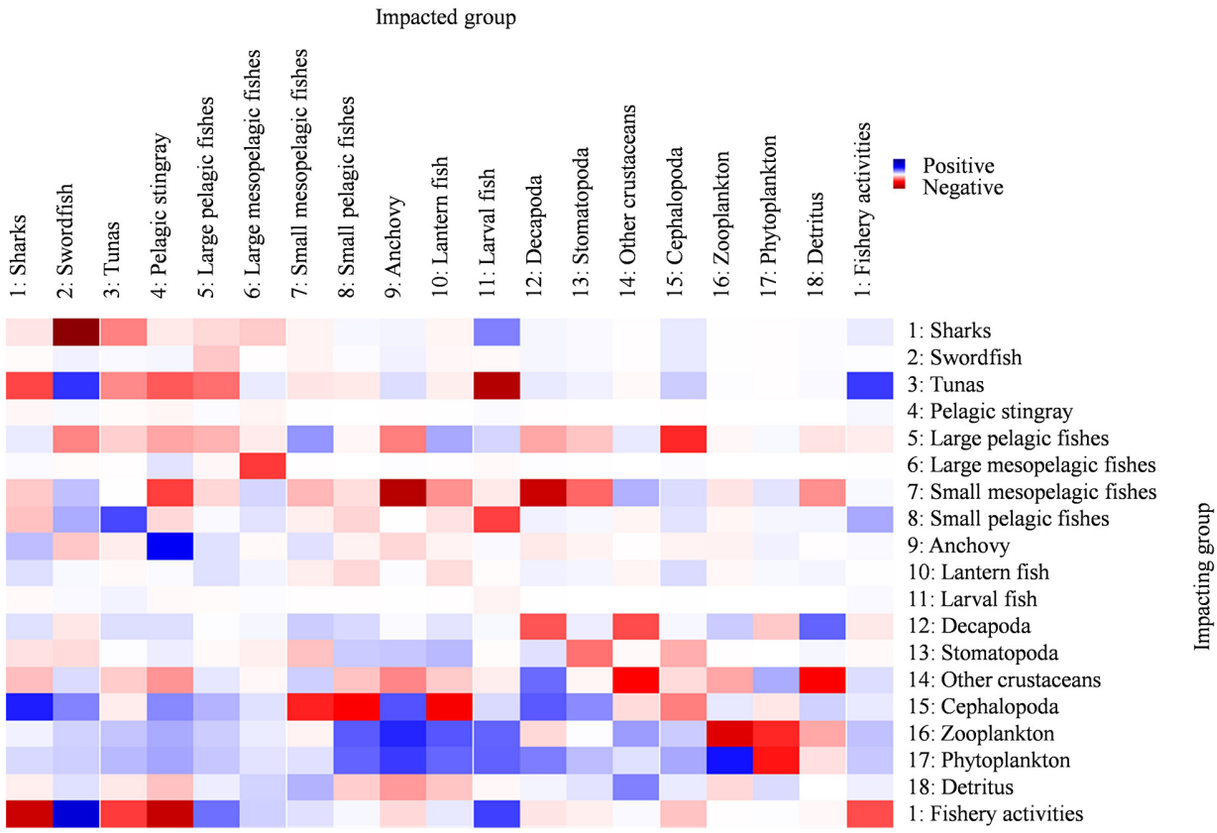


**Figure 4 Mixed trophic impacts among functional groups in the Western and Central Pacific Ocean ecosystem**

**Table 4 General ecosystem parameters of the Western and Central Pacific Ocean model**

| Parameter | Value | Unit |
|---|---|---|
| Sum of all consumption | 1 573.14 | t km$^2$/year |
| Sum of all exports | 2 224.65 | t km$^2$/year |
| Sum of all respiratory flows | 829.03 | t km$^2$/year |
| Sum of all flows into detritus | 2 285.42 | t/km$^2$/year |
| Total system throughput | 6 912.24 | t/km$^2$/year |
| Sum of all production | 3 483.17 | t/km$^2$/year |
| Calculated total net primary production | 3 053.68 | t/km$^2$·year/$^1$ |
| Total primary production/total respiration | 3.68 | |
| Net system production | 2 224.65 | t/km$^2$/year |
| Total primary production/total biomass | 73.43 | |
| Total biomass (excluding detritus) | 41.59 | t/km$^2$ |
| Total catch | 0.01 | t/km$^2$/year |
| System Omnivory Index | 0.27 | |
| Ecopath pedigree | 0.84 | |
| Proportion of total flow originating from phytoplankton | 0.66 | |
| Proportion of total flow originating from detritus | 0.34 | |
| Finn's cycling index | 0.48 | |
| Finn's mean path length | 2.26 | |

(1942). Despite this, the total system TE reached 12.60%, marginally exceeding Lindeman's benchmark. This elevated efficiency likely resulted from comparatively high EE values across multiple groups.

### Role of tunas in the WCPO ecosystem

As apex predators with high biomass, tuna species play a critical role in maintaining trophic structure and regulating prey dynamics in the WCPO ecosystem. These species support both regional food security and biodiversity conservation through their dual ecological and economic significance (Griffiths et al., 2019). According to recent stock assessment by the WCPFC, the principal tuna species in the WCPO remain within biologically sustainable limits, with no indication of overfishing or depletion (WCPFC, 2024). The estimated EE value for tunas was 0.45, representing a decline relative to earlier assessments (Allain et al., 2007; Howell et al., 2013). More than 70% of tuna production was extracted through fisheries, with natural predation accounting for only a minor fraction, indicating reduced energy retention within the

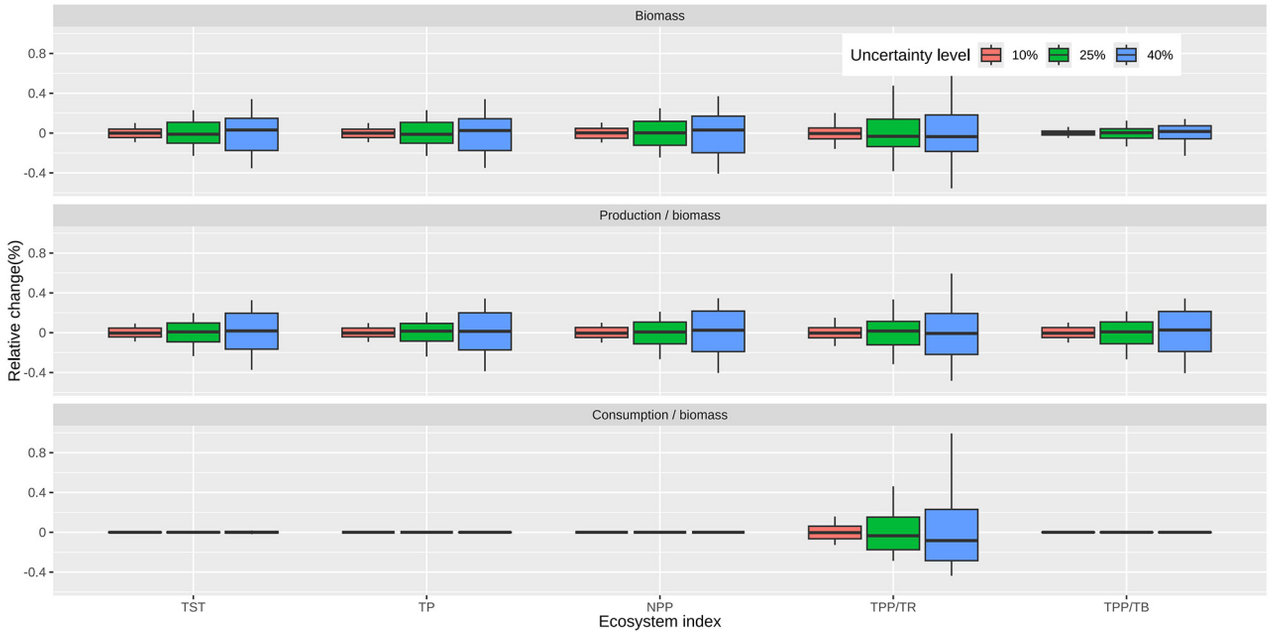


**Figure 5 Analysis of parameter uncertainty in the Ecopath model for the Western and Central Pacific Ocean**

ecosystem via trophic pathways. Both the keystone index and relative total impact metrics identified tunas as keystone species of the WCPO trophic network, exerting strong regulatory effects on the biomass distribution of multiple functional groups (Olson et al., 2016). Shifts in tuna abundance can alter predatory-prey dynamics and cascade through lower trophic levels, thereby modifying ecosystem structure and stability (Lin et al., 2023). Despite current stock sustainability, precautionary management is essential to mitigate long-term risks associated with elevated harvest and environmental perturbations. Climate-driven variability in tuna abundance, distribution, and ecosystem stability also warrant careful consideration. Notably, previous studies have shown that bigeye tuna abundance is reduced during strong El Niño events relative to other climatic phases (Lin et al., 2023). Such reductions may impair the functional role of tuna within the pelagic food web, interact with ongoing fishing pressure, and contribute to broader alterations in ecosystem structural integrity.

MTI analysis was used to quantify direct and indirect effects among functional groups (Taghavimotlagh et al., 2021), revealing a food web dominated by top-down control. Tunas exerted strong positive influence on the fishing fleet due to their relatively high exploitation rates, underscoring their economic importance to regional fisheries (Olson et al., 2016; WCPFC, 2024). Positive MTI values were also observed between tunas and swordfish, likely reflecting shared predator interactions with sharks (Fujinami et al., 2018). Given the opportunistic feeding behavior of sharks, when one fish species is subjected to increased predation pressure, the other benefits from a reduced probability of being preyed upon (Fujinami et al., 2018; Preti et al., 2012).

### General ecosystem indices

The WCPO ecosystem encompasses an expansive spatial domain and exhibits a relatively simplified food web structure. Notably, the TST in 2023 substantially exceeded estimates from 2002 (Godinot & Allain, 2003), indicating considerable expansion in ecosystem scale over the past two decades. Hallmarks of mature ecosystems include high biodiversity, complex trophic interactions, efficient energy utilization, and enhanced resilience to perturbation (Christensen et al., 2005; Odum, 1969). NSP, defined as the difference between TPP and TR, approaches zero in equilibrium systems (Christensen et al., 2005). Similarly, a TPP/TR ratio near unity signals efficient assimilation of production into respiration with minimal surplus accumulation (Odum, 1969). The 2023 TPP/TR ratio of 3.68 aligned with values reported for oligotrophic open-ocean systems (Jiang et al., 2010; Watari et al., 2019), potentially reflecting the influence of high biomass apex predators such as tunas. These indicators also indicated that this ecosystem is currently disturbed to a low extent and lead to a relatively stable system compare with other studies (Godinot & Allain, 2003; Lin et al., 2013).

The OI results revealed low trophic generalism among most functional groups, indicative of dietary specialization. Tunas primarily consumed small pelagic fish and cephalopods (Ohshimo et al., 2018). Within the WCPO ecosystem, functional groups with lower OI included both higher and lower trophic level fishes. Apex predators such as sharks, swordfish, and tunas had a relatively high concentration of prey compositions, resulting in low OI values (Kubodera et al., 2007; Trujillo-Olvera et al., 2018). Lower trophic groups including anchovy, lantern fish, and larval fish relied predominantly on zooplankton. In contrast, functional groups such as cephalopods and stomatopods displayed broader dietary ranges and correspondingly higher OI values (Katugin et al., 2014; Watanabe et al., 2004). The prevalence of specialized feeding strategies contributed to reduced trophic complexity and a simplified food web architecture. Consequently, the SOI of the ecosystem was relatively low (0.27), comparable to other WCPO offshore systems (Jiang et al., 2010; Lin et al., 2013). However, it should be noted that the low SOI in most offshore ecosystems may be partly caused by ecosystem degradation due to fishing pressure and environmental change (Heymans et al., 2016), while the low SOI in open ocean ecosystems was probably due to the specialized diet of pelagic species. Nevertheless, long-term ecosystem-based monitoring in the WCPO still requires greater attention from RFMOs including WCPFC.

### Evaluation of overall model uncertainty

Sensitivity analysis of the static ecosystem model was conducted using a Monte Carlo resampling framework to evaluate the influence of input uncertainty on model outputs. The analysis showed that the overall output values of the model change less than the range of input parameter changes, indicating that the ecosystem is relatively stable. Changes in biomass and the P/B ratio of functional groups influenced all five output indicators, while uncertainty in P/B exerted a stronger effect on model outputs than uncertainty in biomass or the Q/B ratio. This pattern differs from several previous assessments (Susini & Todd, 2021; Wang et al., 2025) and highlights the importance of improving parameter accuracy to enhance overall model performance. Biomass estimates for most functional groups were derived from field survey data, which contributed to enhanced model reliability. In contrast, most P/B values were derived through indirect estimation rather than direct measurement, introducing cumulative uncertainty (Lin et al., 2013). Uncertainty in P/B for functional groups occupying critical trophic positions, including apex predators and primary producers, can propagate through trophic transfers and influence energy flow across multiple trophic levels. For instance, variability in the P/B ratio for tunas may alter energy pathways throughout the entire pelagic food web (Allain et al., 2007; Ohshimo et al., 2018). Beyond parameter sensitivity analysis, future analyses will focus on quantifying the sensitivity of input parameters variations across different functional groups on model outputs to identify sensitive groups prone to uncertainty of model projection.

Comparisons with previous ecosystem studies provided contextual insight into the relative scale, stability, and trophic structure represented in the WCPO model (Allain et al., 2007; Godinot & Allain, 2003). However, differences in spatial coverage, functional group definitions, and data sources among studies limit direct comparability. Such contrasts should therefore be interpreted as indicative rather than definitive and used primarily to inform ecosystem-based management perspectives (Lira et al., 2018; Morissette, 2007).

The trawl gear used in this survey consisted of a 40 mm stretched cod-end mesh and relatively large mesh at the trawl mouth, limiting effective sampling of small-bodied, non-commercial, low-trophic-level species. As a result, biomass estimates for certain functional groups, such as anchovy, likely underestimated true abundance, contributing to elevated EE values and emphasizing the importance of model-based biomass adjustment. Improving baseline data quality for forage fish and other small-bodied functional groups remains a priority for further model refinement (Coll et al., 2013).

Generally, the Ecopath model allows for the representation of species across different life stages using a multi-stanza structure, assuming comparable mortality rates and diet composition within each stage (Christensen et al., 2005). Implementing this approach requires detailed biological information for each life stage, which remains limited for many high-seas species. Consequently, all larval fish were aggregated into a single functional group based on shared body size, vertical distribution, and feeding behavior (Christensen et al., 2005). This simplification may introduce additional uncertainty into the model projections. As biological data for pelagic species continue to expand, future models may incorporate more refined functional group definitions. Further investigation of interactions among multiple sources of uncertainty will also be necessary to evaluate their combined effects on representation of ecosystem processes (Heymans et al., 2016).

## COMPETING INTERESTS

The authors declare that they have no competing interests.

## AUTHORS' CONTRIBUTIONS

G. C.: Writing - original draft, Visualization, Investigation, Formal analysis, Data curation. W. W.: Visualization, Investigation, Data curation. R.R. Z.: Investigation. B.L. L.: Resources, Data curation. S.Q. W.: Resources, Data curation. X.J. D.: Supervision, Methodology, Conceptualization. D.Y. H.: Writing - review & editing, Supervision, Methodology, Conceptualization. All authors read and approved the final version of the manuscript.

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