Ecological Modelling 514 (2026) 111495

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Balancing fishing effort along the tropical tuna abundance-size spectrum

Alex Tidd *, Mariana Travassos Tolotti, Patrice Guillotreau, Nicolas Barrier, Laurent Dagorn

MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Sète, France

ARTICLE INFO

Keywords:
Sustainability
Balanced harvest
Tunas
Indian ocean
Fishing fleets
Fleet-based management

ABSTRACT

The ecosystem approach to fisheries is widely recognised as a key management goal, yet its definition and implementation remain debated. Most fisheries management relies on single-species strategies with technical measures to reduce bycatch. However, selective removals disrupt species composition, affecting ecosystem dynamics and resilience. We present a proof-of-concept model based on balanced harvesting that allocates fishing pressure proportionally across three tuna stocks—yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*), and bigeye tuna (*Thunnus obesus*)—in the Indian Ocean according to their size-biomass ratios. The model optimises fishing effort by gear using a predefined objective function based on length-based population dynamics, ensuring a balanced harvest while maintaining each tuna species' biomass within its maximum sustainable yield (B_{MSY}) limit. By assigning fishing mortality (F-multiplier) to each fleet, the model aims to maintain, within the bounds of B_{MSY} for each stock, the ecosystem structure (based on size-abundance relationships) over a 20-year simulation. Results indicate significant reductions in fishing mortality across gears relative to 2020 levels. While some gears, such as purse seine free-school, show increased catches and revenues (146%), others, like purse seine log-school, experience declines (-22%). Overall, fishing at B_{MSY} improves total revenues and catches by 51% and 34%, respectively, compared to 2020. This work demonstrates that it is possible to maintain each tuna stock within B_{MSY} bounds by managing fishing fleets while preserving ecosystem structure, a significant goal of the ecosystem approach to fisheries.

1. Introduction

Fisheries management must often deal with conflicting objectives, including social, biological, and economic considerations. Policymakers must identify the fundamental objectives and incorporate them into management plans. Conservation goals are achieved by setting biological targets and limit reference points, for example, thresholds for stock biomass and yields that guide management actions and indicate when the fishery is approaching unacceptable levels of risk (Sainsbury, 2008). These reference points are part of harvesting strategies that rely on indicators from monitoring data or stock status models to prevent overfishing and ensure sustainable yields and recruitment (Peterman, 2004).

Policy advice is typically provided on a stock-by-stock basis, although this approach can be complex in mixed fisheries where fleets simultaneously catch multiple species of varying sizes. An alternative ecosystem-based strategy is offered by the 'balanced harvest' paradigm (see Caddy and Sharp, 1986; Hall, 1996; Hall et al., 2000; Bundy et al., 2005; Branch et al., 2010; Garcia et al., 2012), which proposes that aligning fishing pressure with natural population size structure and productivity can reduce ecological disruption while maintaining ecosystem functioning. Rather than aiming to manage every species at B_{MSY} (the spawning biomass required to achieve maximum sustainable yield) while minimising bycatch and inspired by this paradigm, an alternative strategy could involve providing fleet-based management advice. This approach would focus on analysing the technical interactions among fishing fleets targeting the same species at varying ages or lengths, thereby helping preserve ecosystem structure. Since fleets exhibit varying selectivity and influence fishing mortality by fish size/age, this approach could offer a more tailored and effective management option, e.g., setting a total allowable catch (TAC) by gear for each species (Vinter et al., 2004), taking into account their respective selectivity. This can be achieved by assigning F-multiplier to each fleet (i) to reach specific biological targets for each stock and (ii) to maintain the structure of the ecosystem, i.e., a stable relationship between biomass and individual size that is consistent with size-spectrum theory. Accordingly, this study aims to develop a straightforward length-based

* Corresponding author at. MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Sète, France.
E-mail address: alex.tidd@ird.fr (A. Tidd).

https://doi.org/10.1016/j.ecolmodel.2026.111495
Received 9 July 2025; Received in revised form 12 January 2026; Accepted 12 January 2026
Available online 22 January 2026

population dynamics model for three tropical tuna species, yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*), and bigeye tuna (*Thunnus obesus*) in the Indian Ocean, optimising the F-distribution by gear to achieve B_{MSY} management objectives simultaneously for the three species.

Intensive harvesting affects species composition and size structure, thereby reducing productivity, weakening ecosystem resilience, and increasing long-term socioeconomic risks (Pauly et al., 1998; Garcia and Rosenberg, 2010). These effects are often exacerbated by external factors, including climate variability, market fluctuations, and global demand (Miller et al., 2018; Weatherdon et al., 2016). Furthermore, the selectivity of fishing gears, particularly in mixed fisheries, can disproportionately remove different size classes of fish communities, with implications for recruitment and trophic stability (Blanchard et al., 2012; Barange et al., 2014). Rather than concentrating fishing pressure on a few highly targeted species or size classes, balanced harvest seeks to maintain ecosystem structure and function by aligning fishing mortality with natural production across the size spectrum. Rather than concentrating fishing pressure on a few highly targeted species or size classes, balanced harvest seeks to maintain ecosystem structure and function by aligning fishing mortality with natural production across the size spectrum. While full implementation of balanced harvesting remains conceptually and operationally challenging, its principles offer a useful heuristic for designing management strategies that are both ecologically and economically sustainable. In this study, we explore whether balanced patterns of exploitation can emerge from gear-specific effort optimisation under constraints that preserve plausible size structures, without explicitly imposing balanced harvest as a model assumption. Classical yield-per-recruit (YPR) approaches optimise overall fishing mortality relative to cohort growth, but they do not address how it is distributed across size classes or gears. Because our objective is to evaluate gear-specific, size-selective patterns that simultaneously maintain biomass near B_{MSY} for three species, we use a size-spectrum framework that complements rather than replaces traditional YPR-based methods.

Indian Ocean tuna fisheries harvest pelagic fish of various sizes, encompassing five main species groups: tropical, neritic and temperate tuna, billfish and sharks. Tropical and neritic tuna represent the largest fished biomass, totalling 51 % and 32 % of all IOTC catches, respectively. Tropical tuna includes yellowfin, bigeye and skipjack. In contrast, neritic tuna includes bullet (*Auxis rochei*), frigate (*Auxis thazard*) and longtail tuna (*Thunnus tonggol*), kawakawa (*Euthynnus affinis*), narrow-barred Spanish mackerel (*Scomberomorus commerson*) and Indo-Pacific king mackerel (*Scomberomorus guttatus*). Here, we develop a model that balances harvesting across the three tropical tuna stocks. Our approach requires age-structured stock assessment outputs, which are currently only available for yellowfin, bigeye, and skipjack (IOTC...2024...SC27...R[E], 2024). Most neritic tuna species are also assessed, but only using biomass-aggregated models (e.g., catch-only methods); therefore, population estimates by age and size are unavailable.

We focus on developing an optimisation process that incorporates a predefined objective function into collective length-based population-dynamics models. We use a Genetic Algorithm (GA), i.e. a stochastic search algorithm influenced by biological evolution and natural selection. This approach offers an alternative to traditional solution methods for multimodal, complex, highly nonlinear problems, using a derivative-free algorithm (Holland, 1975). The objective of the search routine is for the GA to select the fittest individual from a population of randomly generated solutions (individuals) and to minimise (or maximise) this value. From this set of solutions, another population is bred under the principle of 'survival of the fittest', originating from the Darwinian theory of natural selection. Typically, the fittest individuals dominate the weakest in models that replicate the biological mechanisms of reproduction, evolution, crossover, selection, and mutation. This optimisation process will estimate balanced fishing pressure across all length groups for all fishing fleets, relative to the base-year fishing mortalities by fleet, as provided in the input files to the stock assessment for 2020 (IOTC, 2021) (the initial year). The optimisation process will be constrained to ensure that the stocks reach the target estimated biomass bounds at their maximum sustainable yield (B_{MSY}) by the end of a 19-year projection, consistent with IOTC rebuilding projections for yellowfin tuna (IOTC, 2023) .[1] Given the overfishing and overfished status of yellowfin tuna prior to 2024 (IOTC, 2021), we aim to determine the optimal level of exploitation that conserves all three tuna stocks while also accounting for revenue levels for each fleet segment.

It is important to note that the model framework is not intended to replace or replicate a complete stock assessment. Instead, it functions as an equilibrium, scenario-based tool that uses existing B_{MSY} reference points as fixed inputs and explores how alternative allocations of fishing pressure across gears influence long-term equilibrium outcomes under balanced-harvesting principles, contrasting gear-specific exploitation patterns with current species-specific harvest strategies. Therefore, it is hoped that this analysis provides a complementary perspective aligned with ongoing discussions on implementing the ecosystem approach to fisheries in the Indian Ocean.

2. Methods

This study applies a deterministic, length-based equilibrium model for scenario exploration, not for conducting a full stock assessment. Key biological reference points (e.g., B_{MSY}, steepness, maturity) are taken directly from IOTC assessments and kept fixed. The model evaluates how alternative gear- and size-specific fishing mortalities would influence equilibrium biomass and size structure under balanced-harvest principles, providing a complementary perspective to current species-specific harvest strategies. The model is explicitly equilibrium-based and, therefore, does not simulate transient dynamics, environmental variability, or annual stock fluctuations.

2.1. Data

The Indian Ocean Tuna Commission (IOTC, https://iotc.org/) routinely performs single-species assessments for yellowfin, bigeye, and skipjack using Stock Synthesis (SS3) (Methot and Wetzel, 2013), which provides the basic framework for our study. The basis of the IOTC SS3 stock assessment is an age-based model structured across multiple areas, with seasonality represented by a quarterly time step, and combined genders. For this study, the IOTC Secretariat provided stock numbers by length, catch by gear by length, and maturity ogives by length, aggregated by species, year, and length.

2.2. The operating model (OM)

The biological operating models (OMs) used in this study comprise three simple length-structured population-dynamics models of the Indian Ocean skipjack, yellowfin, and bigeye tuna stocks. Mortality and annual recruitment of juvenile fish govern the stock's dynamics. Both fishing and natural mortality cause stock numbers to decline each year as the class ages. The fish population is divided into discrete length classes (cohorts) ranging from 18 to 150 cm in 4-cm increments. Natural and fishing mortality due to fishing gear are applied separately to each length class. The survivors from each length class contribute to the growth of the subsequent length class. Therefore, survivors in each length class are equal to the total mortality subtracted from the population length class. The growth rate influences how individuals within the population grow; here, we use the Brody growth rate K (rate of

[1] Interestingly, the stock status has been re-assessed in 2024 and is no longer considered overfished or subject to overfishing; the probability of finding YFT in the green quadrant now exceeds 88% (IOTC, 2024).

growth towards the asymptote) and apply it to the survivors at length $N_{l,\ t}$. It assumes a constant growth rate applied to the entire population without accounting for size-specific differences. Incorporating size-specific growth differences would require more complex models, additional data inputs and assumptions.

The model is iterated over multiple time steps to simulate the dynamics of each tuna stock. Skipjack rarely exceed 100 cm in length, with most of the population distributed below 62 cm. However, to enable a consistent comparison across species within the length-based framework, we extended the length bins up to 150 cm to match the observed length range of yellowfin and bigeye. Zeros were included for skipjack catch and population numbers beyond 100 cm, ensuring that the regression and optimisation procedures could be applied uniformly across species. Simulations were conducted using R software by projecting the estimates of stock numbers at length (l), $N_{l,\ t}$ from the baseline year 2020 for 19 years (time t) based on the standard length-structured population equation:

$$N_{l,\ t} = R_{l,\ t} + N_{l-1,t-1}e^{-Z_{l-1,t-1}} \tag{1}$$

with Z the total mortality, which is the sum of $F_{l,\ t}$ and natural mortality $M_{l,\ t}$ and $R_{l,\ t}$ the number of recruits entering length class l.

Although Eq. (1) is a discrete recurrence relation, we do not simulate somatic growth transitions between length classes, as is done in age-structured or size-spectrum models. Instead, we treat length classes as independent population compartments, in which abundance changes over time due to mortality, recruitment and gear-specific mortality. This compartmental structure is consistent with other length-based simulation frameworks that prioritise practical implementation over population structure tracking (Froese et al., 2018; Haddon, 2011). Abundance in each length class l at time t is derived from individuals surviving from the immediately smaller length class (l–1) at time t–1, after accounting for total mortality. This approach enables us to examine how different gear types, each with its own selectivity and fishing mortality, influence the length distribution and stock dynamics over time. While this simplifies the underlying length-dependent growth process, it improves the tractability of simulating fishing effects under balanced-harvest scenarios. To approximate somatic production at length $P_{l,\ t}$, we use a simple proxy based on:

$$N_{l,\ t} = N_{l,\ t} - P_{l,\ t} + P_{l-1,\ t} \text{ where } P_{l,\ t} = K * N_{l,t} \tag{2}$$

This productivity proxy does not model physical growth between length bins, but rather serves as a biomass indicator of potential production (Law et al., 2012; Hall et al., 2006). This approach enables us to examine how different fishing gears, through their selectivity and intensity, alter the stock's length structure and productivity over time. The modelling framework is not intended as a formal stock assessment. Instead, it is a scenario-based simulation that explores the implications of balanced harvesting across length classes, utilising empirically informed life-history parameters and gear-specific selectivity.

At each time step, the Spawning Stock Biomass (SSB) is calculated as follows from the length-weight relationship for each species estimated (see Table 1 for coefficients a and b in Chassot et al. (2016)):

$$W_{l,} = al^b \tag{3}$$

$$SSB_t = \sum N_{l,t}W_lO_l \tag{4}$$

Where W_l the fish weight at the mid-length class l in kilogrammes, and O_l is the proportion of mature fish at length l and time t, as provided by IOTC.

The stock-recruitment relationship is assumed to be of the Beverton and Holt type (Beverton and Holt, 1957), which implies that there is an asymptotic maximum in recruitment:

$$R_t = \frac{(4hR_0SSB_{t-1})}{(S_0(1-h) + SSB_{t-1}(5h-1))} \tag{5}$$

R_0 represents the unfished virgin recruitment numbers at length, an equivalent approximation to age 0 for each species-specific length range. S_0 is the unfished virgin SSB (taken from IOTC stock assessment reports), and h is the steepness of the stock-recruitment curve. SSB is calculated as the numbers at length using species-specific maturity ogives (see eqn (4)). The total recruitment R_t is thus derived from SSB (eqn (5)). This recruitment is not dynamically allocated across length classes; instead, it is allocated across length classes using a fixed recruitment-at-length vector that yields $R_{l,\ t}$ (eqn (1)). We use a normal distribution (bell-shaped) selectivity function to represent the probability of recruits falling into each length class, and we adjust the mean and standard deviation by species.

Catch numbers at length by gear, $C_{l,g,t}$ are related to the fishing mortality at length through the Baranov catch equation (Baranov 1918). The model accounts for the simultaneous processes of fishing and natural mortality over the modelled time step:

$$C_{l,g,t} = N_{l,t}\frac{F_{l,g,t}}{Z_{l,t}}\left(1 - e^{-Z_{l,t}}\right) \tag{6}$$

Where F is the total fishing mortality at length, the catch equation can be estimated via non-linear optimisation to calculate F-at-length for a given catch number-at-length. Having catch numbers at length for each gear (g) (Table 2 for gear information and description) for the base year 2020, we can estimate F-at-length for each species and gear combination. $F_{l,g,t}$. Total mortality Z is the sum of F and natural mortality M, estimated

Table 2
Gear definitions and descriptions.

ID	Gear (g)	Description
1	LL – Longline	Uses a main line with thousands of baited hooks to catch large, high-value tuna like bigeye and yellowfin in deep water.
2	PSLS – FAD/log associated Purse Seine	Encircles tuna aggregations around man-made Fish Aggregating Devices (FADs), resulting in mixed-species, multi-size catches that include juveniles.
3	LINE – Handline	A broad category that includes handline and trolling line gear that use baited or lured hooks to selectively catch surface-schooling tuna.
4	BB – Baitboat	Pole-and-line vessels use live bait to attract and capture tuna schooling at the surface.
5	OTH	Unspecified fishing methods that can include trawl, lift net, and beach seine.
6	PSFS – un-associated Purse Seine	Targets visible, free-swimming schools of tuna at the surface, generally catching larger, mature skipjack and yellowfin.
7	GILL – Gillnet	Uses vertical panels of netting that entangle fish by their gills.

Table 1
Shows the parameters used in the OM for each tuna species.

Species (s)	M	R_0	S_0	h	a	b	K	B_{MSY} min	B_{MSY} max
yft	0.66	132,958	3323,090	0.8	2.46E-05	2.9667	0.88*	1146,000	1885,000
bet	0.29	66,070	1847,000	0.8	2.22E-05	3.01211	$0.31^{\pm}$	332,000	694,000
skj	0.80	217,549	2065,019	0.8	4.97E-06	3.39292	0.8^{π}	369,187	678,936

Values of K^* (*Dortel et al., 2013*), π (*Tandog-Edralin et al., 1990*) *taken from Fishbase, and* $\pm$ (*Fu et al., 2023*). S_0, R_0 and B_{MSY} from the stock assessment reports.

approximate annual averages applied across all length groups. The equation is:

$$Z_{l,t} = F_{l,g,t} + M_{l,t} \tag{7}$$

We assume that the length composition for each gear represents its underlying selectivity pattern, so the gear-specific *F*-at-length curve is obtained directly from its empirical length-frequency distribution. The F-multiplier (Fmult – see below Section 2.3) is then used to uniformly rescale this curve, modifying the overall fishing mortality exerted by that gear without altering its relative selectivity across lengths. Thus, the optimisation adjusts only the magnitude of fishing mortality per gear, while holding the selectivity pattern fixed.

2.3. The genetic algorithm (GA)

The genetic algorithm (GA) provides an efficient method for optimising fleet-specific exploitation patterns. Its role is not to estimate biological parameters or stock status, which are instead taken directly from existing IOTC assessments. Instead, it searches over alternative combinations of gear-specific fishing effort multipliers to identify patterns of exploitation that satisfy predefined constraints: maintaining each stock within its biomass-at-MSY bounds while preserving the ecosystem's size-abundance structure. Because the model operates at equilibrium with fixed biological reference points, the GA's role is to optimise the distribution of fishing pressure across gears, rather than to infer population dynamics. This use of optimisation aligns with other scenario-based fisheries analyses, in which effort distributions are evaluated relatively to fixed biological limits. Further, fleet viability is explicitly found by estimating fleet-specific catches and revenues under the optimised effort pattern, allowing us to assess whether balanced harvesting produces biologically and economically sustainable outcomes for each fleet.

The Genetic Algorithm uses a probabilistic search process, starting with an initial population of potential solutions (sets of Fmult, as in eqn's (8,9)) represented as genetic strings (a single set of proposed fishing effort multipliers). Each solution has an objective value that serves as a fitness measure (a performance metric used to rank solutions), allowing the fittest individuals (ones that satisfy the objective function and constraints) to outcompete weaker ones and drive the search toward optimal solutions. The fittest individuals are selected to produce offspring for the next generation. In each generation, selected individuals undergo crossover with a predetermined mutation rate (a random change in Fmult to maintain diversity), yielding a new population with improved fitness. Here, a crossover probability of 0.8 was used to promote the mixing of favourable traits, and a mutation probability of 0.05 was used to maintain population diversity and explore new areas of the solution space, which are the recommended settings for evolutionary optimisation (Holland and Schnier, 2006). Less fit individuals are gradually removed, ensuring that only the best solutions propagate. Thus, the procedure identifies a set of variables that optimise the fitness of each individual and the population as a whole. The optimisation was run for up to 1000 generations, or terminated earlier if convergence was reached, defined as no further improvement in the objective function value over 200 (runs) successive generations. This stopping criterion ensured a stable solution while maintaining computational efficiency.

We optimise the fishing mortality rates (*F* from Eqn (6) based on the 2020 catch numbers by gear) using the Fmult Eqn (8,9) for each gear (*g*, $G =$ number of gears) type (Table 2) to achieve within the range of $\mathrm{B_{MSY}}$ of all three species. Fleet-specific F-multipliers are encoded as a vector that makes up an individual *i*, candidate fishing strategy in the genetic algorithm (e.g., the initial population is 300 fishing strategy combinations of Fmult during the optimisation search, Eqn (8)):

$$\begin{gathered} Gene_i = [Fmult_1,\ Fmult_2,\ Fmult_3\cdots\cdots,\ Fmult,\ G] \\ constrained\ by: \\ 0.3 <= Fmult,\ g <= 1.0\ for\ all\ g = 1\cdots,G \\ Gene_{300} = [0.25,\ 0.56,\ 0.91\cdots] \end{gathered} \tag{8}$$

The total biomass of each species at length $B_{s,l}$, is then used to calculate the spawning biomass via Eqn (3), which links Eqn (9) and 10 (below).

$$B_s = \sum_{l=1}^{L} B_{s,l} \times exp\left(- \sum_{g=1}^{G} F_{s,l,g}\mathrm{Fmult}_g \right) \tag{9}$$

The optimisation occurs between the stock assessed $\mathrm{B_{MSY}}$ range ($\mathrm{B_{MSY\,min}}$) and ($\mathrm{B_{MSY\,max}}$) Eqn (10). The objective function (Eqn (10)) includes constraints to ensure that the spawning biomass (*SSB*) for each species (*s, S* = number of species) remains within the specified maximum (max) and minimum (min) $\mathrm{B_{MSY}}$ estimates, ensuring ($\mathrm{B}_{\mathrm{MSY}\,min} \le B \le \mathrm{B}_{\mathrm{MSY}\,max}$) and that the regression coefficient between total stock numbers and length, in log-scale, is negative ($\log(N) = \beta_1 \log(l)$, $\beta_1 < 0$), to maintain the structure of spreading fishing pressure across the three species while maximising R^2 of the linear regression, ensuring the best fit possible in this minimisation. Specifically, a negative slope in this log–log relationship is expected under natural or moderately exploited conditions, consistent with ecological theory and size-spectrum models (Andersen and Beyer, 2006; Law et al., 2012). In balanced and unbalanced systems, the abundance of individuals typically declines with body size (i.e., larger individuals are rarer), producing a negative linear relationship in log-log space. In this deterministic simulation, a flat or positive slope indicates a distortion of the size structure driven by the model's fishing pattern, specifically the disproportionate removal of smaller size classes. By constraining the slope of the linear regression to be negative and maximising the R^2 value of the regression model, we favour solutions that spread fishing effort across length classes in an ecologically consistent way, without over-targeting large or small individuals.

$$\begin{aligned} Objective\ (Fitness) = & \left(\mathrm{Penalty_{biomass}} = \sum_{s=1}^{S} \lambda_s \max\left(0, \mathrm{B}_{\mathrm{MSY}\,min,s} - B_s\right)^2 \right. \\ & \left. + \max\left(0, B_s - \mathrm{B}_{\mathrm{MSY}\,max,s}\right)^2 \right) \\ & + \left(\mathrm{Penalty_{slope}} = max\ (0,\ \beta_1) \times C \right) - R^2) \end{aligned} \tag{10}$$

If certain conditions are violated (e.g., if the resulting biomass falls below a certain threshold or the regression slope of the stock numbers versus length becomes positive), a penalty term (λ_s *or C*) is added to the objective function, thereby reducing the fitness of feasible solutions, a process known as removal criteria (selection). No absolute fitness threshold was imposed; instead, individuals were ranked based on relative fitness, and selection favoured those with improved objective-function values. The genetic algorithm was terminated when either (i) no further improvement in the best fitness score was observed over successive generations (convergence criterion) or (ii) a maximum of 1000 generations was reached. In practice, convergence was typically achieved well before the maximum generation limit, indicating a stable solution and that further iterations would not improve the outcome.

Furthermore, we conduct a sensitivity analysis by incrementally adjusting the bounds (the search area of Fmult), which helps to understand how the optimal solutions change with slight variations in the bounds. This analysis provides insights into the model's stability and reveals the robustness and resilience of the optimal solutions. By varying the bounds, we can reduce the risk of overfitting the model to a narrow range of conditions, thereby promoting general solutions that can handle uncertainties. Optimising for the final year (year 20) is beneficial because the main objective is to achieve a specific biomass target by a particular end date. This approach simplifies optimisation by focusing on a single target rather than multiple yearly targets. The process accounts for years of cumulative fishing mortality, potentially leading to more sustainable long-term management. See Fig. 1 for a conceptual overview of the methods.

Following the optimisation, potential revenue was estimated by combining the resulting catch predictions with economic data, specifically by multiplying catch weight by mean price per tonne for each gear type (Macfadyen et al., 2019).

2.4. Sensitivity and uncertainty analysis

Next, we test our results by implementing a stable solution and re-running the model (out of the optimisation) 100 times with a coefficient of variation (CV) of 15 % around a) growth and natural mortality, b) natural mortality, and c) growth to characterise the uncertainty around the estimates of the results. This sensitivity analysis was conducted within the same equilibrium framework used for optimisation to ensure internal consistency with the biological reference points derived from recent IOTC base-case assessments. Testing uncertainties outside this framework, such as alternative steepness values or dynamic recruitment variability, would yield different stock–recruit relationships and, consequently, different reference points, effectively creating a new operating model that is not comparable to the optimisation outputs. Because the goal of this study is not to re-estimate reference points but to explore relative exploitation patterns under fixed biological benchmarks, sensitivity tests were restricted to biological parameters (growth and natural mortality) that vary without altering those benchmarks. We therefore imposed stochastic variation (CV = 15 %) on growth and natural mortality. We re-ran the equilibrium model to evaluate the robustness of predicted SSB trajectories and fleet-specific outcomes while maintaining consistency with the optimisation constraints.

3. Results

3.1. Biomass and catch trajectories

The 19-year simulation under the optimised fishing strategy led to divergent biomass trajectories for the three tuna species (Fig. 2). Yellowfin tuna biomass recovered to target levels, skipjack tuna remained stable, and bigeye tuna initially declined before returning to its minimum B_{MSY} benchmark by the end of the simulation. This rebuilding phase initially reduced catches in year one. As biomass recovered, total annual catch increased by 34 % across the fishery by the end of the projection period compared to baseline levels. Concurrently, the population's size structure shifted towards a more balanced state (Fig. 3). Gear-specific selectivity strongly shaped length-specific abundance patterns, especially at large sizes.

3.2. Fishing strategy and economics

The optimisation produced a set of gear-specific fishing effort multipliers (F-multipliers) required to achieve the biomass targets (Fig. 4). These multipliers varied substantially, ranging from 0.7 to 1.0, indicating where effort needed to be reduced or could be maintained. The economic impact of these presents the projected pay-offs or gains for all fleets fishing at the target biomass levels, showing an overall increase in yields (34 %) and revenues (54 %) (revenues not shown in Table 3). The distribution of benefits was gear-specific: longline, handline, and purse seine free-school fleets saw the most significant gains, while purse seine log-set and artisanal gears saw reductions of 22 % and 46 %, respectively (Table 3).

3.3. Size spectrum

The best strategy after the 19-year optimisation successfully established a negative linear relationship between log(numbers) and log (length), characteristic of a size-structured population that retains a coherent negative size-spectrum slope (Fig. 3). The slope of this relationship was approximately −4. Some curvature in the largest size classes reflects the inherent selectivity patterns of the different gears, with some gears preferentially targeting larger individuals.

3.4. Sensitivity and uncertainty analysis

The optimisation was run across different bounds for the effort multipliers. Results were stable across most bounds, though for more restrictive bounds (0.8 and 0.9–1.0) (Fig. 5), yellowfin tuna did not consistently reach B_{MSY}. The requirement for the line fleet to reduce effort most significantly was a consistent feature across all sensitivity runs, confirming its key role in rebuilding the yellowfin stock from its degraded level assessed before 2024. With greater flexibility in F-

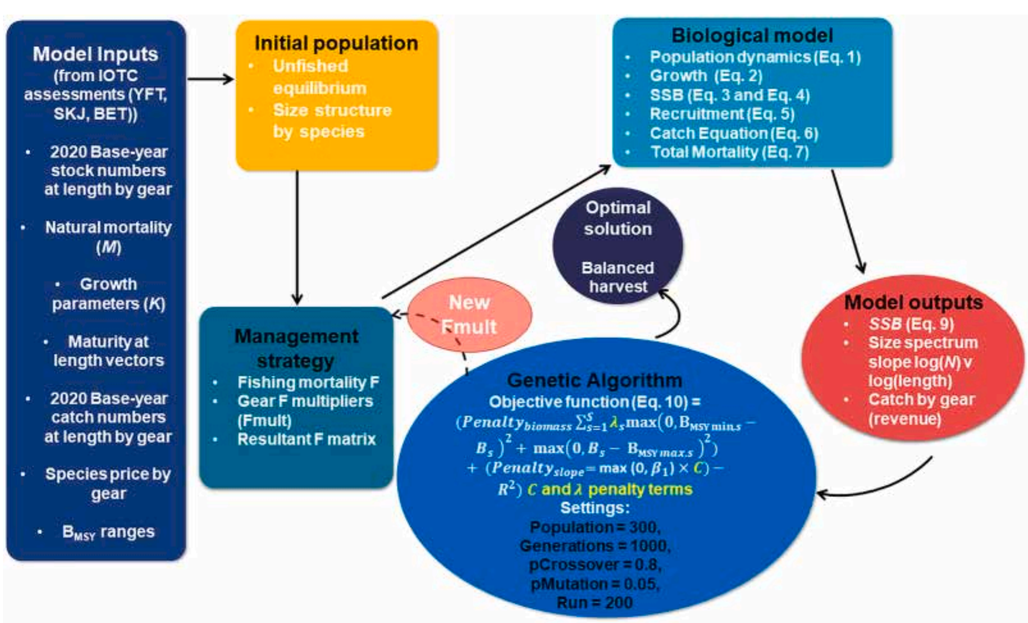

Fig. 1. Conceptual framework of the study methods.

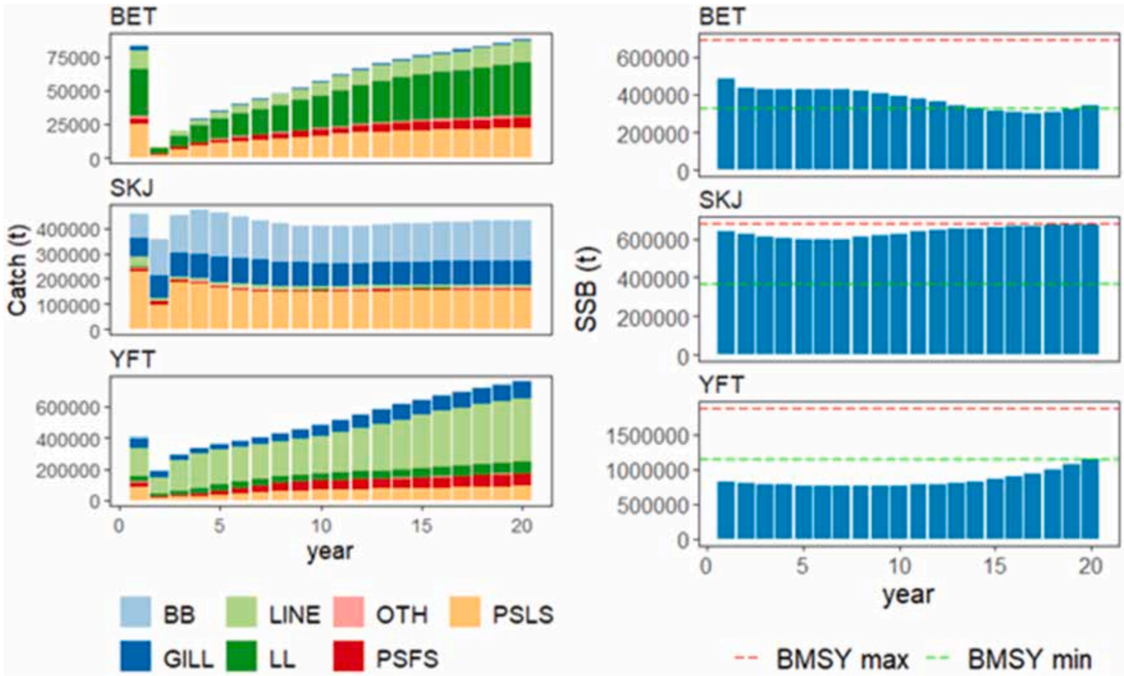

Fig. 2. Resulting catches by gear for 0.7–1.0 bounds (left) and (right) the spawning stock biomass (YFT = yellowfin, SKJ = skipjack and BET = bigeye).

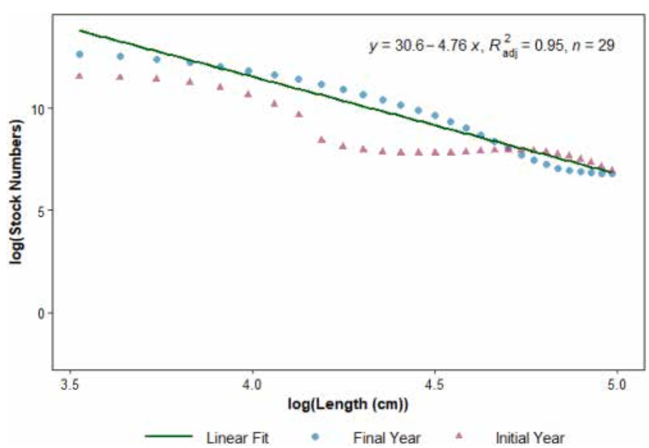

Fig. 3. Purple dots indicate the logarithm of the total stock numbers in 2020 (initial year) versus the logarithm of length. The blue dots indicate the logarithm of the total stock numbers after the 20-year (final year) simulation (with 0.7–1.0 effort bounds) with a green regression line – note the extreme values of minimal and maximum length removed, showing the main distribution range of the stock numbers that are exploited by all gears.

multipliers, the model focused on reductions in effort on fleets that most efficiently promoted biomass rebuilding. A sensitivity analysis of growth and natural mortality parameters indicated that absolute *SSB* projections vary substantially, particularly for yellowfin tuna over longer time horizons. (Fig. 6). Yellowfin tuna exhibited the widest uncertainty bands in its spawning stock biomass (*SSB*) trajectory, especially by year 20, reflecting its sensitivity to biological assumptions. However, across all sensitivity runs, the direction of stock response, the relative performance of fleets, and the requirement to reallocate fishing mortality away from juvenile-selective gears remained consistent. The relative effects of reallocating fishing mortality across gears are robust to plausible biological uncertainty. Because recruitment variability and alternative steepness values would fundamentally alter the underlying reference points and thus lie outside the equilibrium framework, they were excluded from this sensitivity analysis.

4. Discussion

This study addresses a key gap by applying a size-spectrum optimisation model to implement balanced harvest in a multi-species tuna fishery. While balanced harvest is well-theorised (Zhou et al., 2019; Jacobsen et al., 2014; Hall et al., 2006) and Genetic Algorithms are established in fisheries (Holland and Schnier, 2006), their combined application to achieve simultaneous multi-species B_{MSY} targets and a balanced size spectrum is novel. By design, this framework is tractable but does not account for transient dynamics, such as recruitment variability or environmental forcing. Instead, it uses fixed B_{MSY} values from IOTC assessments to ensure management relevance while isolating the effects of redistributing fishing mortality across fleets. Consequently, our results should be viewed as a demonstration of potential under average conditions. Real-life factors, such as poor recruitment years or fluctuations in fishing effort, could alter these outcomes. The logical next step is to test these strategies within a stochastic Management Strategy Evaluation (MSE) to assess their robustness for proper operational use (Punt et al., 2016).

The optimised exploitation pattern demonstrates that balanced fishing across gears and length classes can restore tropical tuna populations to B_{MSY} levels while maintaining a coherent size structure. The negative log(N)–length (~ -4) slopes observed across stocks correspond closely to predictions from size-spectrum theory (Andersen and Pedersen, 2010; Zhou et al., 2019; Law et al., 2012), indicating that the optimised F vector preserves the characteristic decline in abundance with size that is central to ecosystem functioning.

Traditional management of multispecies tuna fisheries relies on single-species catch limits, which ignore the realities of mixed-fishery operations. In practice, fleets operating with different gear selectivities simultaneously capture species, creating selectivity-driven trade-offs in which rebuilding one stock can hinder another (Link, 2010) or create unintended effects on non-target species (Tolotti et al., 2023). Our framework partially addresses these issues by reallocating fishing mortality across gears rather than setting independent catch limits. This shifts the objective from maximising total catch to maintaining stock biomass within sustainable bounds and preserving the population's size structure (Garcia et al., 2012; Zhou et al., 2019). By doing so, it offers a

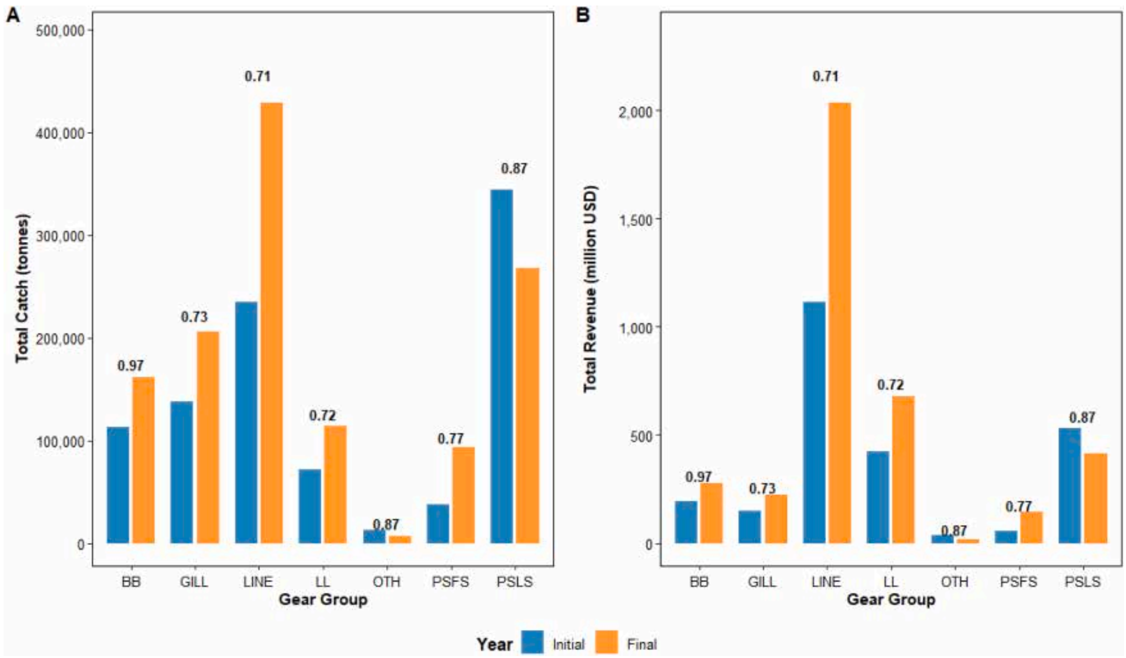

Fig. 4. Comparison of catch (A) and revenue (B) totals in tonnes and $, respectively, from 2020 (year 1) to year 20, the final year of the optimisation. The figures above the bars in simulation year 20 represent the F-Mult applied to year 1 fishing mortality at length estimates.

Table 3
Final year approximate estimates of catch and revenue, and the % change from 2020.

species	gear	catch (t)	revenue ($)	change (%)	Total change by gear (%)
BET	BB	562	958,474	10	
SKJ	BB	158,235	269,632,280	39	
YFT	BB	2294	3909,046	−553	43
BET	GILL	1090	1179,890	−188	
SKJ	GILL	94,819	102,594,053	21	
YFT	GILL	110,306	119,350,670	46	50
BET	LINE	15,982	75,864,425	12	
SKJ	LINE	14,346	68,100,164	−162	
YFT	LINE	398,394	1891,175,891	54	82
BET	LL	39,651	234,536,925	13	
SKJ	LL	476	2815,786	−212	
YFT	LL	74,387	439,997,076	53	61
BET	OTH	1445	3968,925	−63	
SKJ	OTH	2793	7669,931	−203	
YFT	OTH	2815	7729,723	21	−46
BET	PSFS	7301	11,323,971	47	
SKJ	PSFS	6842	10,612,679	−3	
YFT	PSFS	78,758	122,153,345	66	146
BET	PSLS	22,406	34,751,842	−12	
SKJ	PSLS	153,803	238,548,464	−51	
YFT	PSLS	91,393	141,750,341	5	−22

*Estimated revenues by gear type obtained from first dock sale average prices; see Macfadyen et al. (2019).

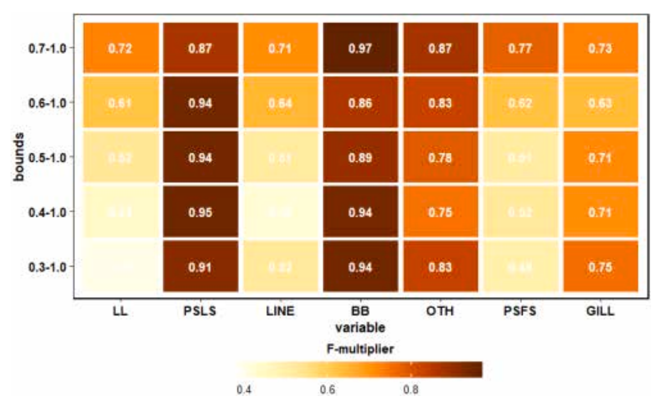

Fig. 5. Sensitivity analysis resulting from the GA optimisation at different ranges of F-multiplier bounds after 20 years (Fishing mortality reductions).

practical pathway to ecosystem-based management where catch quotas fixed by species are insufficient.

A key feature of the optimisation is the front-loaded cost of rebuilding: reductions in fishing mortality initially reduce catches, particularly in fleets interacting heavily with juvenile yellowfin and bigeye. However, as *F* stabilises at sustainable levels, biomass increases and long-term yields improve. These trends highlight how balanced exploitation can maintain B_{MSY} targets while allowing future catch gains, particularly in gears that harvest larger individuals. In contrast, gears focused on smaller size classes, such as purse-seine log-sets, experience persistent reductions, reflecting their disproportionate impact on early life stages. This reinforces known multispecies trade-offs: skipjack may achieve biomass above B_{MSY}, yet opportunities to harvest this surplus are constrained by the need to protect juvenile YFT and BET, a classic challenge in mixed fisheries.

The gear-specific outcomes underscore important socio-economic implications. While line and purse-seine free-school fleets gain substantially in both catches and revenues, artisanal fleets (e.g., other unspecified gears) and purse-seine log-sets face reductions of 46 % and 22 %, respectively. These findings suggest that, although the biological optimisation is coherent, equitable implementation will require transitional mechanisms or differentiated reference points to avoid the disproportionate burdens on small-scale fisheries identified by Pelage et al. (2021). This highlights a classic yet necessary management trade-off: short-term economic costs for long-term biological and economic sustainability. The 19-year projection shows that this initial investment is rewarded, with total catches and revenues ultimately increasing by 34 % and 54 % respectively, by the end of the simulation. While some specific gears, such as purse seine free-school, show increased catches and revenues (146 %), others, like purse seine log-school, experience declines (−22 %). This underscores that the balanced harvest strategy is not a short-term fix but a restructuring plan,

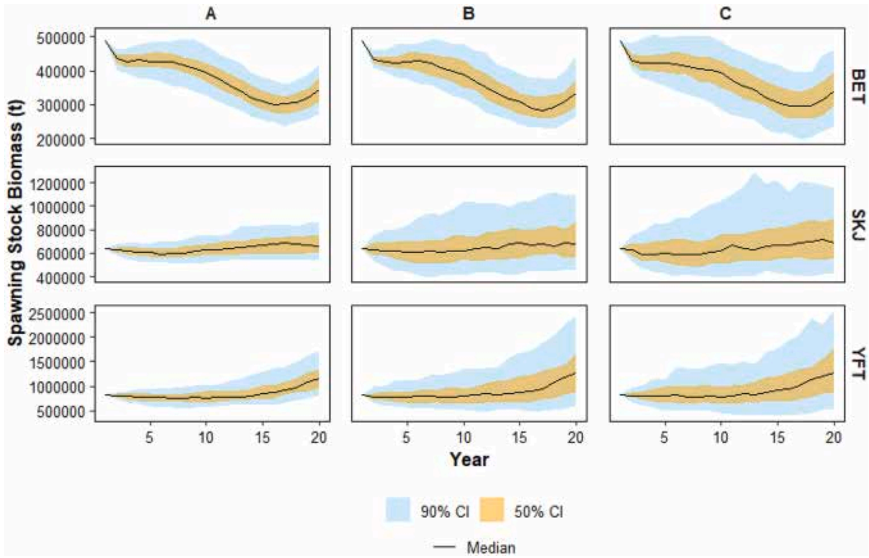

Fig. 6. Shows 100 iterations incorporating uncertainties in mortality *M* and growth *K*, based on the 0.7 - 1.0 bounds results. A) 15 % CV around growth, B) 15 % CV around natural mortality, and C) 15 % CV around growth and natural mortality.

where short-term sacrifices in certain gear types lead to a more profitable and resilient fishery for the majority of participants in the long run.

The model also highlights how multispecies constraints can produce nonlinear or counterintuitive outcomes. While skipjack often exceeds B_{MSY}, BET biomass dips below its starting level before recovering, largely due to mixed-fishery interactions and juvenile bycatch. Penalising poor performance in YFT and BET during optimisation was necessary to keep all three stocks above their B_{MSY} thresholds. This outcome mirrors earlier theoretical work (e.g., Andersen and Pedersen, 2010; Law et al., 2012), showing that although small and mid-sized fish are the most productive size classes, they are also the most vulnerable to fishing because removing them disproportionately reduces future recruitment and biomass production.

Overall, these results show that an exploitation pattern across fleets that preserves the expected size-spectrum relationship between abundance and body size improves long-term fishery performance, but requires short-term reductions in fishing mortality and catches for some fleets during the rebuilding phase. This approach complements existing species-based TACs by retaining fixed biomass and yield targets, while achieving them through gear-specific redistribution of fishing mortality. Explicitly accounting for mixed-fishery interactions and gear selectivity reduces the risk that effort directed at one fleet undermines stock rebuilding in others, thereby improving resilience in multispecies tuna fisheries.

Taken together, these findings suggest that balanced, fleet-specific exploitation patterns can operate as a practical complement to existing harvest strategies in the Indian Ocean, providing a transparent way to explore trade-offs across species, gears, and size classes. Although simplified and equilibrium-based, the framework highlights where current selectivity patterns undermine rebuilding objectives and where modest reallocation of fishing pressure could yield ecological and economic gains. Importantly, the approach highlights the structural constraints of mixed tuna fisheries, particularly the dependence of skipjack exploitation on juvenile yellowfin and bigeye mortality, constraints that are not always apparent in single-species assessments. By explicitly accounting for gear- and size-specific interactions, the model reveals the limits of decades of single-stock MSY management and points toward integrated, size-aware, ecosystem-consistent policies that complement conventional TACs.

5. Conclusion

This study provides proof of concept for applying a balanced harvest framework to the Indian Ocean tropical tuna fisheries. The results demonstrate that initial reductions in fishing mortality, particularly for fleets targeting larger individuals, are a necessary trade-off condition for rebuilding depleted stocks and achieving higher long-term yields and revenues. By adopting a fleet-based perspective, the approach highlights technical interactions among gears, differences in size selectivity, and their collective ability to meet specific biomass-by-species targets while promoting a more even size structure within the ecosystem.

The principal limitation of the framework is its equilibrium structure, which does not explicitly include recruitment variability or environmental forcing. As such, it is not intended to replace full stock assessments. Instead, by using fixed B_{MSY} reference points from current IOTC assessments, the approach remains anchored to established management benchmarks while providing a complementary tool for exploring gear-specific exploitation patterns and long-term rebuilding trajectories under a balanced-harvest perspective.

The findings offer practical insights for managers considering output-based measures—such as effort limits, TACs, or fleet-specific *F*-controls to mitigate overfishing risks, strengthen ecosystem resilience, and secure the long-term contribution of tunas to regional food systems. Extending this framework to achieve a more complete representation of balanced harvests would require including neritic tunas and other ecologically linked species (e.g., billfishes, sharks), but these data are currently unavailable. This gap underscores the wider systemic challenge: fisheries management remains centred on target species, and a genuine ecosystem-based approach that reflects ecosystem structure is still emerging. The work presented here supports the case for progressing toward that paradigm shift.

Ethics

Additionally, the research does not involve human participants or animals.

CRediT authorship contribution statement

Alex Tidd: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Mariana Travassos Tolotti: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Patrice Guillotreau:** Writing – review & editing, Writing – original draft. **Nicolas Barrier:** Writing – review & editing, Writing – original draft, Resources, Formal analysis. **Laurent Dagorn:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no competing financial or non-financial interests that could have influenced the work reported in this paper.

Acknowledgements

The authors thank the International Seafood Sustainability Foundation (ISSF) for its involvement in the overall project. They are also grateful to all individuals and national institutes of the Indian Ocean Tuna Commission (IOTC) involved in collecting, managing, and curating the data made available by the IOTC Secretariat for this study. The authors acknowledge the Celimer project for providing high-performance computing and storage capacities. The authors thank the editor and the anonymous reviewers for their detailed and constructive feedback. Their comments greatly strengthened the methodological clarity, interpretation, and positioning of the study. We are also grateful to Lola De Cubber for her careful proofreading and insightful suggestions, which helped improve the clarity of this manuscript.

Funding: The research presented here has been funded by the French interprofessional body for the fishing sector, France Filière Pêche (FFP), through the MANFAD project. Grant agreement number PH/2019/24.

Data availability

The data supporting this study's findings are available from the IOTC upon reasonable request.

References

Andersen, K.H., Pedersen, M., 2010. Damped trophic cascades driven by fishing in marine ecosystems. Proc. Roy. Soc. Lond. B 277, 795–802. https://doi.org/10.1098/rspb.2009.1512.

Andersen, K.H., Beyer, J.E., 2006. Asymptotic size determines species abundance in the marine size spectrum. Am. Nat 168 (1), 54–61. https://doi.org/10.1086/504849.

Barange, M., Merino, G., Blanchard, J.L., Scholtens, J., Harle, J., Allison, E.H., et al., 2014. Impacts of climate change on marine ecosystem production in societies dependent on fisheries. Nat Clim Chang 4 (3), 211–216. https://doi.org/10.1038/nclimate2119.

Baranov, F.I., 1918. K voprosu o biologicheskikh osnovaniyakh rylmogo khozyaistva. [On the question of the biological basis of fisheries.]. Nauchn. Issled. Ikhtiologicheskii Inst. Izv 1, 81–128.

Beverton, R.J.H., Holt, S.J., 1957. On the dynamics of exploited fish populations. Fishery Investigations Series IIXIX. Ministry of Agriculture, Fisheries and Food, London, pp. 1–533.

Blanchard, J.L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J.I., Holt, J., Dulvy, N.K., Barange, M., 2012. Potential consequences of climate change for primary production and fish production in large marine ecosystems. Philos. Trans. R. Soc. B 367, 2979–2989. https://doi.org/10.1098/rstb.2012.0231.

Branch, T.A., et al., 2010. The trophic fingerprint of marine fisheries. Nature 468, 431–435. https://doi.org/10.1038/nature09528.

Bundy, A., Fanning, P., Zwanenburg, K.C.T., 2005. Balancing exploitation and conservation of the eastern Scotian Shelf ecosystem: application of a 4D ecosystem exploitation index. ICES J. Mar. Sci. 65, 503–510. https://doi.org/10.1016/j.icesjms.2004.12.008.

Caddy, J.F., Sharp, G.D., 1986. An ecological framework for marine fishery investigations. FAO Fisheries Technical Paper 283. https://www.fao.org/4/t0019e/T0019E00.htm.

Chassot, E., Assan, C., Esparon, J., Tirant, A., Delgado, D., Molina, A., Dewals, P., Augustin, E., Bodin, N., 2016. Length-weight relationships for tropical tunas caught with purse seine in the Indian Ocean: update and lessons learned. IOTC-2016-WPDCS12-INF05. https://horizon.documentation.ird.fr/exl-doc/pleins_textes/divers17-01/010067418.pdf.

Dortel, E., Massiot-Granier, F., Rivot, E., Million, J., Hallier, J.P., Morize, E., Munaron, J. M., Bousquet, N., Chassot, E., 2013. Accounting for age uncertainty in growth modelling, the case study of yellowfin tuna (*Thunnus albacares*) of the Indian Ocean. PLoS ONE 8 (4), e60886. https://doi.org/10.1371/journal.pone.0060886.

Froese, R., Demirel, N., Coro, G., Kleisner, K.M., Winker, H., 2018. Estimating stock status from length frequency distributions. ICES J. Mar. Sci. 75 (6), 2004–2015. https://doi.org/10.1093/icesjms/fsy078.

Fu, D., DeBruyn, P., Fiorellato, F., Nelson, L., Pierre, L., Fernandez Diaz, C., Chassot, E., 2023. Assessing the impact of growth on estimates of fishing mortality—An illustration with Indian Ocean bigeye tuna. Reg. Stud. Mar. Sci. 62, 102981. https://doi.org/10.1016/j.rsma.2023.102981.

Garcia, S.M., Rosenberg, A.A., 2010. Food security and marine capture fisheries: characteristics, trends, drivers and future perspectives." philosophical transactions of the Royal Society of London. B Biol. Sci. 365, 1554. https://doi.org/10.1098/rstb.2010.0171.

Garcia, S.M., Kolding, J., Rice, J., Rochet, M.J., Zhou, S., Arimoto, T., Smith, A.D.M., 2012. Reconsidering the consequences of selective fisheries. Science 335 (6072), 1045–1047. https://doi.org/10.1126/science.1214594.

Haddon, M., 2011. Modelling and Quantitative Methods in Fisheries, 2nd Edition. CRC Press. https://www.taylorfrancis.com/books/mono/10.1201/9781439894170/modelling-quantitative-methods-fisheries-malcolm-haddon.

Hall, M.A., 1996. On bycatches. Rev, Fish Biol, Fish. 6, 319–352. https://doi.org/10.1007/BF00122585.

Hall, M.A., Alverson, D.L., Metuzals, K., 2000. Bycatch: problems and solutions. In: Sheppard, C.R.C. (Ed.), Seas At the Millennium: An environmental evaluation. Vol. III: Global Issues and Processes. Pergamon Press and Elsevier Science, Amsterdam and Oxford, pp. 204–219. https://doi.org/10.1016/s0025-326x(00)00111-9. Reprinted in *Marine Pollution Bulletin* **41**(1-6).

Hall, S.J., Collie, J.S., Duplisea, D.E., Jennings, S., Bravington, M., Link, J., 2006. A length-based multispecies model for evaluating community responses to fishing. Can. J. Fish. Aquat. Sci. 63 (6), 1344–1359. https://doi.org/10.1139/f06-039.

Holland, J.H., 1975. Adaptation in Natural and Artificial Systems. MIT Press, USA. (2nd Ed. https://doi.org/10.1145/1216504.1216510. University of Michigan Press1992.

Holland, D., Schnier, K.E., 2006. Individual habitat quotas for fisheries. J Env. Econ Manage 51 (1), 72–92. https://doi.org/10.1016/j.jeem.2005.04.005. https://iotc.org/sites/default/files/documents/2024/06/IOTC-2023-SC26-R_Rev1E.pdf.

IOTC–2021–WPTT23–12, 2021. Preliminary Indian Ocean yellowfin tuna stock assessment 1950-2020 (Stock Synthesis). https://iotc.org/sites/default/files/documents/2021/10/IOTC-2021-WPTT23-12.pdf.

IOTC-2024-SC27-ES04_YFT. Report of the 27th Session of the Scientific Committee of the IOTC, 2–6 December 2024,. Cape Town, South Africa (2024). https://iotc.org/sites/default/files/documents/2024/11/IOTC-2024-SC27-ES04_YFTE.pdf.

IOTC–SC26 2023. Report of the 26th Session of the IOTC Scientific Committee. Online, 4 –8 December 2023. IOTC–2023–SC26–R[E]: 207 pp (2023).

Jacobsen, N.S., Gislason, H., Andersen, K.H., 2014. The consequences of balanced harvesting of fish communities. Proc. R. Soc. B: Biol. Sci. 281 (1775), 20132701. https://doi.org/10.1098/rspb.2013.2701.

Law, R., Plank, M.J., Kolding, J., 2012. On balanced exploitation of marine ecosystems: results from dynamic size spectra. ICES J. Mar. Sci. 69, 602–614. https://doi.org/10.1093/icesjms/fss031.

Link, J., 2010. Ecosystem-based Fisheries management: Confronting Tradeoffs. Cambridge University Press. https://doi.org/10.1017/cbo9780511667091.

Macfadyen, G., Huntington, T., Defaux, V., Llewellin, P., James, P., 2019. Netting billions: a global valuation of tuna (an update). Report Produced By Poseidon Aquatic Resources Management Ltd. https://www.pewtrusts.org/-/media/assets/2020/10/poseidon_tunavalue_technicaldocuments_merged_final.pdf.

Methot, R.D., Wetzel, C.R., 2013. Stock Synthesis: a biological and statistical framework for fish stock assessment and fishery management. Fish, Res 142, 86–99. https://doi.org/10.1016/j.fishres.2012.10.012.

Miller, D.D., Ota, Y., Sumaila, U.R., Cisneros-Montemayor, A.M., Cheung, W.W.L., 2018. Adaptation strategies to climate change in marine systems. Glob, Change Biol 24, e1–e14. https://doi.org/10.1111/gcb.13829.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F.Jr, 1998. Fishing down marine food webs. Science 279, 860–863. https://doi.org/10.1126/science.279.5352.860.

Pelage, L., Bertrand, A., Ferreira, B.P., Lucena-Frédou, F., Justino, A.K.S., Frédou, T., 2021. Balanced harvest as a potential management strategy for tropical small-scale fisheries. ICES J. Mar. Sci. 78, 2547–2561. https://doi.org/10.1093/icesjms/fsab136.

Peterman, R.M., 2004. Possible solutions to some challenges facing fisheries scientists and managers. ICES J. Mar. Sci. 61, 1331–1343. https://doi.org/10.1016/j.icesjms.2004.08.017.

Punt, A.E., Butterworth, D.S., de Moor, C.L., De Oliveira, J.A.A., Haddon, M., 2016. Management Strategy evaluation: best practices. Fish Fish 17, 303–334. https://doi.org/10.1111/faf.12104.

Sainsbury, K.J. Best practice reference points for Australian Fisheries. Australian Fisheries Management Authority, Canberra, Australia, 156 pp (2008). https://www.agriculture.gov.au/sites/default/files/sitecollectiondocuments/fisheries/environment/bycatch/best-practice-references-keith-sainsbury.pdf#:~:text=Reference%20points%20are%20the%20operational,or%20triggers%20to%20initiate%20specific.

Tandog-Edralin, D.D., Cortez-Zaragoza, E.C., Dalzell, P., Pauly, D., 1990. Some aspects of the biology and population dynamics of skipjack (*Katsuwonus pelamis*) in Philippine waters. Asian Mar. Biol. 7, 15–29. https://doi.org/10.1515/9789882200265-007.

Tolotti, M., Guillotreau, P., Forget, F., Capello, M., Dagorn, L., 2023. Unintended effects of single-species fisheries management. Environ. Dev. Sustain. 25 (9), 9227–9250. https://doi.org/10.1007/s10668-022-02432-1.

Vinter, M., Reeves, S., Patterson, K., 2004. From single-species advice to mixed-species management: taking the next step. ICES J. Mar. Sci. 61, 1398–1409. https://doi.org/10.1016/j.icesjms.2004.08.018.

Weatherdon, L.V., Magnan, A.K., Rogers, A.D., Sumaila, U.R., Cheung, W.W.L., 2016. Observed and projected impacts of climate change on marine fisheries, aquaculture, coastal tourism, and human health: an update. Front, Mar, Sci 3, 48. https://doi.org/10.3389/fmars.2016.00048.

Zhou, S., Kolding, J., Garcia, S.M., et al., 2019. Balanced harvest: concept, policies, evidence, and management implications. Rev Fish Biol Fish. 29, 711–733. https://doi.org/10.1007/s11160-019-09568.