REVIEW

The role of small pelagic fish in diverse ecosystems: knowledge gleaned from food-web models

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ABSTRACT: Small pelagic fish (SPF) are important forage species and a target of major fisheries within diverse ecosystems. SPF are a critical link between plankton and higher trophic levels. Understanding the network of dependencies among species and fisheries supported by SPF is required for effective resource management and assessment of risks posed by environmental and anthropogenic stressors. Food-web models represent a synthesis of knowledge of these dependencies and are a platform for evaluating the consequences of change in SPF productivity. From Ecopath food-web models archived within EcoBase (www.ecobase.ecopath.org) and from peer-reviewed literature, we compiled physiological parameters, biomasses, diets, and fishery catch rates that define SPF characteristics. From 199 models, metrics characterizing demand on ecosystem production, contribution to predators and fisheries, and sensitivities to changes in SPF were calculated. Across all models, globally, SPF represented 43% of total fish production and were supported by 8% of total primary production (14% in open ocean and 10% in upwelling models). In turn, SPF represented 18% of total fish and invertebrate catch (53% in upwelling models). From a services perspective, considering all direct and indirect trophic pathways, SPF were major contributors to predators and fisheries. On average, SPF supported 22% of seabird production, 15% of mammal production, and 34% of total fisheries catch. Support to upper trophic levels was greater in upwelling models (33% of seabird, 41% of mammal, and 62% of fishery production). These analyses show the importance of accounting for direct and indirect support by SPF to predators and fisheries when making management decisions.

KEY WORDS: Forage fish · Mesopelagic fish · Food-web · Ecosystem services · EcoBase · Ecopath · ECOTRAN

1. INTRODUCTION

Small pelagic fish (SPF) such as anchovy, sardine, and herring are a major resource for both predators and fisheries and can act as an important ecosystem-structuring agent among diverse ecosystems, from polar to tropical and from oligotrophic open ocean to eutrophic upwelling systems. They are the target spe-

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cies in many of the world's largest fisheries (Tam et al. 2008, Van Voorhees 2012, Pikitch et al. 2014, Watari et al. 2019), and they can act as important structuring agents in pelagic ecosystems. SPF are major prey species for higher trophic level (TL) fish, seabirds, and marine mammals (Cury et al. 2011, Ruzicka et al. 2013, Ouled-Cheikh et al. 2022) and are commonly referred to as 'forage fish' in recognition of this role. They can themselves be a major consumer of phytoplankton and zooplankton production (Cury et al. 2000, Smith et al. 2011). They serve as a critical energy transfer node in pelagic food-webs, linking lower and upper TLs (Bakun et al. 2010), and they can exert control in limiting both lower and upper TL production (Rice 1995).

The ecological role and importance of SPF can vary between ecosystem types. In oligotrophic oceanic systems, small mesopelagic species (e.g. Myctophidae) are not only important forage for predatory fish but also play an important role in global carbon cycles as a carbon pump to sub-surface waters via their diel migration behavior (Davison et al. 2013). In highly productive upwelling ecosystems, the mid-TLs are often occupied by very few SPF species (Cury et al. 2000). In such 'wasp-waist' food-webs, where energy flow through mid-TLs is channeled through a small number of species, SPF have enhanced influence on the large-scale dynamics of the ecosystem. Well-documented changes in SPF dynamics have been coincident with large-scale and persistent changes in ecosystem structure (e.g. Anderson & Piatt 1999, Roux et al. 2013)

SPF share common behavioral and physiological characteristics distinct from other consumer groups that define their own sensitivities to local conditions. They are short-lived, grow rapidly, tend to form schooling aggregations, and can respond more rapidly to environmental change than longer-lived species (Peck et al. 2021, Baez et al. 2022b). They are sensitive to climate variability (Alheit & Hagen 1997, Chavez et al. 2003, Alheit & Niquen 2004) and to changes in competition for plankton resources, such as during jellyfish blooms, with negative consequences to higher TLs and fisheries (Robinson et al. 2014, Chiaverano et al. 2018, Baez et al. 2022a).

The purpose of this study is to evaluate the ecological role of SPF in diverse ecosystem types. We first aim to quantify the importance of SPF in terms of the demands they place upon lower TL production and in terms of their contribution as a resource to support higher trophic consumer and fishery production. We next aim to quantify the role of SPF as an ecosystem structuring agent in pelagic ecosystems in terms of their importance as a link between lower and higher TLs. Identification of critical trophic links and knowledge of how the dynamics of these groups propagate through the ecosystem is critical to the development of effective management strategies to maintain resilient ecosystems and to better understand the consequences of potential management actions. The development of ecosystem models and model analysis tools is critical to this task, particularly in the context of increasing demand for fishery resources and changing environmental conditions.

Our approach is to analyze the characteristics of SPF and quantify the effects they have on other consumer groups through a suite of metrics derived from food-web models representing diverse ecosystems around the globe. From publicly available Ecopath food-web models (www.ecopath.org; Christensen & Walters 2004) archived within the EcoBase repository of food-web models (www.ecobase.ecopath.org; Colléter et al. 2015) and additional models from the literature, we compiled metrics summarizing SPF physiological characteristics, trophic position, productivity, contribution to fisheries, rates and sources mortality, direct and indirect demands placed upon food-web resources, direct and indirect contributions to higher TL production, and the sensitivities of different food-web components to changes in SPF abundance. For each of these metrics, we identify how the ecological role of SPF differs among major ecosystem types (eastern boundary upwelling, continental shelf, open ocean, bay/fjord/lagoon, estuary, and coral reef) and across latitudes. We include additional analyses to consider key SPF groups individually and to compare 4 major eastern boundary current upwelling systems (the Humboldt, Benguela, California, and Canary Current ecosystems).

2. METHODS

We analyzed 199 food-web models to compare the roles of SPF in terms of their functional trophic relationships to other living groups within diverse ecosystem types and latitude zones (Table 1). Table 2 defines 27 metrics characterizing SPF within each model analyzed within this study. Each metric and its derivation is detailed below, and the statistical analysis of these metrics is described in Section 2.4.

2.1. Selection of food-web models

Ecopath (www.ecopath.org) is a publicly available and popular modeling platform for the construction

Table 1. Sample size of analyzed models and models that include small pelagic fish (SPF) by ecosystem type and latitude zone

	Total models	Unique ecosystems	Models with SPF
Ecosystem type			
Upwelling	27	10	27
Continental shelf	97	65	89
Open ocean	23	16	15
Bay/fjord/lagoon	33	28	22
Estuary	8	7	6
Coral reef	11	10	5
Total	199	136	164
Upwelling system			
Humboldt Current	8	3	8
Benguela Current	11	2	11
California Current	3	2	3
Canary Current	5	3	5
Total	27	10	27
Latitude zone			
Polar	13	10	10
Temperate	112	74	96
Tropical	74	53	58
Total	199	137	164

and analysis of food-web models (Christensen & Walters 2004). Ecopath calculates rates of biomass transfer between each taxonomic group or functional group defined in the model given their diets, intrinsic (weight-specific) production rates, production efficiencies, catch rates within defined fisheries, and biomass densities. Data required for each parameter are typically assembled from a wide variety of sources that may span months to decades of observation. Ecopath models, therefore, represent a broad synthesis of abundance, diet, physiology, and fishery knowledge.

We primarily relied upon Ecopath food-web models available in the EcoBase model repository (www. ecobase.ecopath.org). EcoBase is an open-access repository of 205 published Ecopath model parameter sets and metadata available for download (Colléter et al. 2015). We developed a script within Matlab (www. matworks.com) to query, parse parameters, and further analyze models from EcoBase. EcoBase was accessed in September 2022. Of 205 marine food-web models, 181 models were successfully processed through all steps to confirmation of mass-balance. EcoBase models were excluded if they represented freshwater or beach ecosystems (6), could not be verified to be in mass balance (12), or there remained undiagnosed processing errors by our script (6). We added an additional 18 models not yet included in the

EcoBase repository for a total of 199 models analyzed in this study. Model name, citation, ecosystem type, and latitude information are provided in Table S1 in the Supplement at www.int-res.com/articles/suppl/m741p007_supp.xlsx (see Table S29 for a list of excluded models). Model locations are shown in Fig. 1.

2.2. Ecosystem type classifications

Models were classified by ecosystem type and by latitude zone: polar (>60°), temperate (24°−60°), and tropical (0°−24°). We used EcoBase metadata ecosystem type assignments as guidance, but inspected and then re-classified each model into 6 types based on geographic location, domain area, and community composition: eastern boundary current upwelling, continental shelf, open ocean, bay/fjord/lagoon, estuary, or coral reef. Upwelling models were further sub-divided into 4 large marine ecosystems: (1) Humboldt Current, (2) California Current, (3) Benguela Current, and (4) Canary Current. Model counts within each ecosystem type and latitude zone are given in Table 1.

2.3. Functional group definitions

There were >3800 unique functional groups defined among the 199 analyzed models. Our analyses required the development of a common set of definitions for all functional groups. SPF were restricted to planktivorous, schooling species. When resolved by the models, 9 separate SPF sub-groups were considered: (1) anchovy (Engraulidae); (2) sardine, (3) herring, (4) menhaden, and (5) sprat (Clupeidae); (6) smelt (Osmeridae); (7) shad (Alosidae); (8) bonga shad (Dorosomatide); and (9) surface-associated flyingfish (Exocoetidae), saury (Scomberesocidae), and halfbeaks (Hemiramphidae). The classifications of ambiguously named groups, such as 'small pelagics' and 'fish planktivorous', were evaluated individually based on taxonomic details provided by published model descriptions. Hybrid groups that included both SPF and non-SPF were classed as non-SPF pelagic fish. Counts of models with aggregated SPF and resolved SPF groups are provided in Table 1. We also analyzed the role of small mesopelagic fish but we did not pool them with other SPF species, which are predominately epipelagic. All other groups in each model were assigned to a major lower TL producer class (primary producers, zooplankton, benthic inver-

Table 2. A brief description of each metric evaluated in this analysis. SPF: small pelagic fish

Metric	Definition	Units
Physiological rate and trophic position metrics		
P/B	Production rate to biomass ratio	yr^{-1}
P/Q	Production efficiency: production to consumption ratio	Ratio
TL	Trophic level: number of trophic steps preceding consumption of prey by SPF, referenced from primary producers or detritus at TL = 1 and weighted by the contribution of each prey type to the SPF diet	—
OI	Omnivory index: TL variance of prey types in an SPF group's diet, weighted by the contribution of each prey type to the diet	—
Biomass, production, and catch metrics		
B/B_{fishes}	SPF biomass to total fish biomass ratio	%
$P/P_{PrimProd}$	SPF production to total primary production ratio	Ratio
P/P_{fishes}	SPF production to total fish production ratio	%
C	Catch: rate that an SPF group is caught by a fishery. C = retained landings + discarded biomass	$t\ km^{-2}\ yr^{-1}$
C/C_{total}	Ratio of an SPF group's catch to total catch of all fish + invertebrate groups	%
C_{scaled}	Catch rate of SPF scaled by the geographic area of the model	$t\ yr^{-1}$
Mortality metrics		
$M2$	Predation mortality rate: total rate that an SPF group is eaten by all consumer groups (biomass yr^{-1}), divided by the SPF group's biomass	yr^{-1}
F	Fishing mortality rate: total rate that an SPF group is caught by a fleet (biomass yr^{-1}), divided by the SPF group's biomass	yr^{-1}
$M2_{fishes}$	Mortality rate due to predation by all fishes	yr^{-1}
$M2_{seabirds}$	Mortality rate due to predation by all seabirds	yr^{-1}
$M2_{mammals}$	Mortality rate due to predation by all mammals	yr^{-1}
Metrics of group demands upon (footprint) and contributions to (reach) the food-web		
$f_{PrimProd}$	Gross footprint on primary production: fraction of total primary production that contributes to the production of an SPF group, via all direct and indirect trophic pathways. The gross footprint includes the costs of metabolism and feces losses at each trophic step but excludes senescence losses	%
θ_{fishes}	Reach of SPF group to fishes: fraction of all fish production that is supported by an SPF group via all direct and indirect trophic pathways	%
$\theta_{seabirds}$	Reach to all seabird production	%
$\theta_{mammals}$	Reach to all mammal production	%
$\theta_{fisheries}$	Reach to all fishery production	%
$\theta_{landed\ groups}$	Reach to all fishery-targeted groups	%
Food-web sensitivity metrics		
$\Delta P_{pelagic\ fishes}$	Scenario response of pelagic fishes: relative change in production of all non-SPF pelagic fishes following a forced 20% reduction in SPF biomass	% Change
$\Delta P_{demersal\ fishes}$	Scenario response of all demersal fishes	% Change
$\Delta P_{seabirds}$	Scenario response of all seabirds	% Change
$\Delta P_{mammals}$	Scenario response of all mammals	% Change
$\Delta P_{landed\ groups}$	Scenario response of all fishery-targeted groups	% Change
$\Delta P_{fisheries}$	Scenario response of all fisheries	% Change
tMTI	Total mixed trophic impact: net bottom-up and top-down impact that a change in an SPF group's biomass will have on all other groups. Expressed as a percentile ranking compared to the impacts caused by change to each group in the model	Percentile rank

tebrates) or to a major higher TL consumer class (squid, non-SPF pelagic fish, demersal fish, seabirds, marine mammals, fisheries) (see Tables S27 & S28 for functional group definitions).

All metrics, with the exception of tMTI (see Section 2.5.5), were derived from individual food-web models at their original level of taxonomic resolution. Metrics from individual functional groups were binned into SPF and SPF sub-groups via summation (biomass, catch, production rates, footprint, reach,

and food-web modification-scenario response metrics) or as production-weighted means (TL, omnivory index [OI], physiological rate, and mortality metrics). Production rates were calculated from the product of the biomass and production/biomass ratio as provided by each model. When present, multi-stanza groups were aggregated in the same manner (e.g. juvenile and adult sardines were aggregated into a single sardine group and this aggregated sub-group also contributes to the larger, aggregated SPF group).
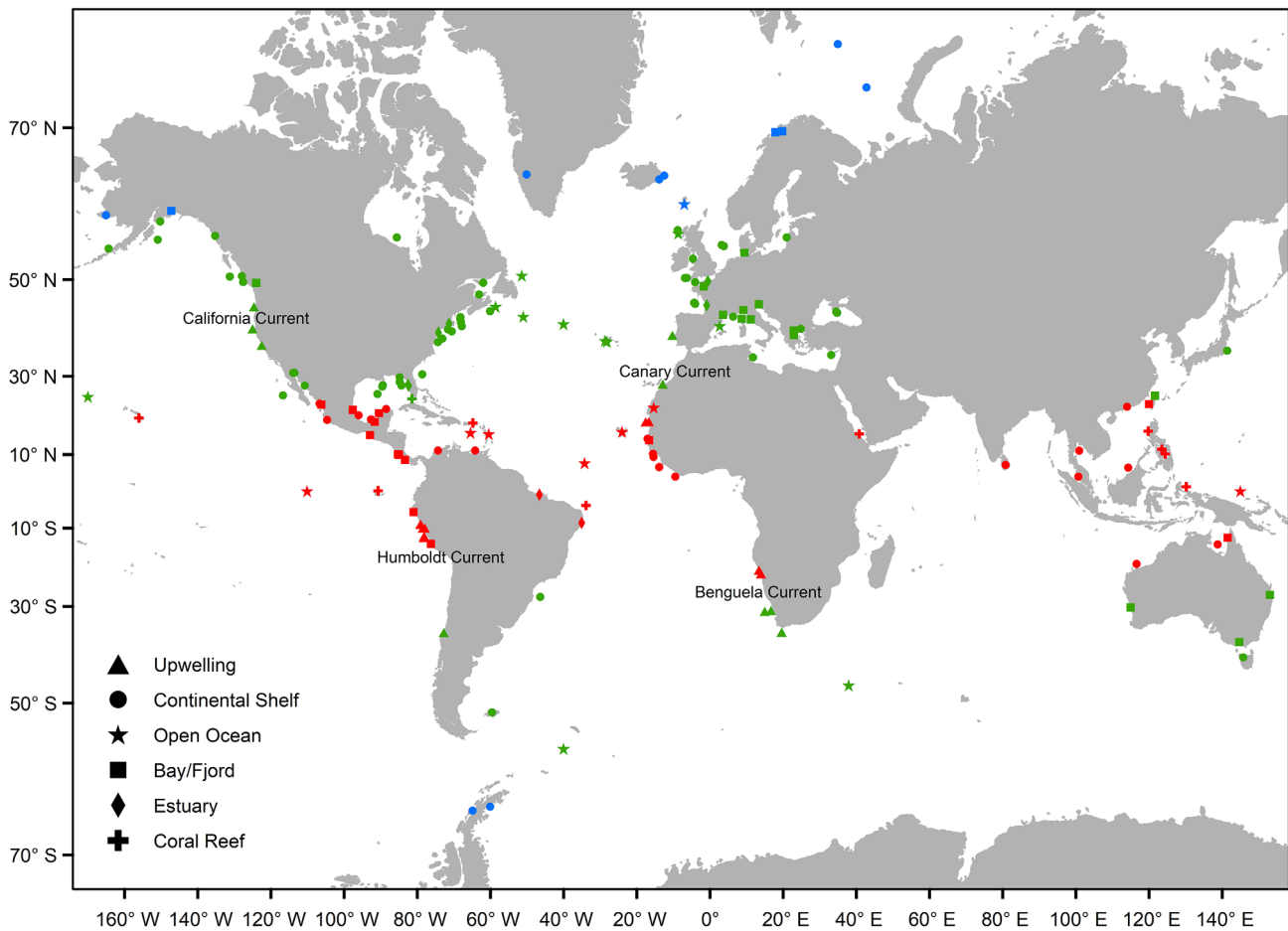
Fig. 1. Locations and ecosystem types of 199 analyzed Ecopath food-web models. Blue: polar models; green: temperate models; red: tropical models

2.4. Statistical analyses

Because taxonomic resolution varies widely between models, our statistical analyses consider SPF as an aggregated functional group, giving the greatest possible global coverage among ecosystem types and latitude zones. The distribution of SPF parameters, derived metrics, and sensitivity analyses were compared across ecosystem types and latitudes using generalized linear mixed effect models (GLMMs). GLMMs are used to describe the relation between a response variable Y (i.e. food-web metrics) and one or more independent or interacting fixed-effect terms. GLMMs also account for random-effects terms that are additional sources of variability in the food-web metric beyond error due to random sampling (Zuur et al. 2013). Ecosystem type (categorical) and latitude (continuous) are fixed-effect terms. Individual food-webs (i.e. specific ecosystems) are treated as a random effect, controlling for the fact that each ecosystem may be represented by multiple food-web models.

The main GLMM model structure was $Y \sim 1 + \text{eco-system type} + \text{latitude} + (1|\text{individual food web})$. A second GLMM analysis was conducted to focus on the differences between individual upwelling ecosystems: $Y \sim 1 + \text{upwelling system} + (1|\text{individual food web})$.

Most food-web metrics were normally distributed, following square root or log transformation, and were modeled with the 'fitglme' function of Matlab (www.mathworks.com) using the default identity link function. The reach contribution of SPF to landed groups targeted by fisheries ($\theta_{\text{landed groups}}$; see Section 2.5.4) best matched a zero-inflated beta distribution and was modeled with the 'glmmTMB' function in R (Brooks et al. 2017). Mortality rates due to predation by seabirds and mammals (see Section 2.5.3) followed Tweedie distributions and were modeled using the 'glmmPQL' function within the 'MASS' package in R (Venables & Ripley 2002). Significance of differences of most metrics among ecosystem types and among latitude zones, i.e. those modeled with the 'fitglme' and

'glmmPQL' functions, were determined at the α = 0.05 level using *t*-statistics. Significant differences of θ$_{\text{landed groups}}$, modeled with the 'glmmTMB' function, were determined at the α = 0.05 level using *z*-statistics.

2.5. Definition and derivation of food-web metrics

2.5.1. Trophic level and omnivory index

We surveyed SPF diets in terms of trophic level (TL) and omnivory index (OI), which are both dimensionless. TL represents a group's position in the food web as the number of trophic steps that biomass and energy pass through before being consumed by the group. TLs were calculated by Ecopath (Christensen et al. 2005) as the biomass-weighted mean of the TL of each prey type consumed by the group, referenced to TL = 1 for primary producers and detritus. The OI is the variance of the TL of all prey items consumed by a consumer group, weighted by the contribution of each prey type to the consumer's diet. OI was calculated as in Ecopath (Christensen et al. 2005). OI = 0 indicates that the group eats only one prey type, and a large OI means that the group has a varied diet and feeds across several TLs. OI is robust against differences in taxonomic resolution among the food-web models.

2.5.2. Production, biomass, and catch

We surveyed SPF productivity in terms of intrinsic rates of production (P/B), production efficiencies (P/Q), standing stock biomass, rates of biomass production, and rates of fishery catch. P/B is a group's defined intrinsic rate of production relative to biomass (yr^{-1}), and P/Q is the dimensionless ratio of a group's production rate relative to its consumption rate. To minimize variability among models due to differences in area of geographic coverage and differences in ecosystem primary production, we considered SPF production relative to total primary production (P/P_{PrimProd}) and relative to total fish production (P/P_{fishes}). We considered SPF biomass relative to total fish biomass (B/B_{fishes}) and fishery catch rates relative to total catch rates of all fish and invertebrates (C/C_{total}).

2.5.3. Natural mortality and fishery mortality

We surveyed the natural mortality ($M2$; yr^{-1}) and fishing mortality rates (F; yr^{-1}) of all models, and we

resolved the main drivers of predation mortality ($M2_{\text{fishes}}$, $M2_{\text{seabirds}}$, and $M2_{\text{mammals}}$). The consumption matrix Q_{gc} describes the predation pressure on each producer, g, (rows) in terms of biomass consumed per period of time by each consumer, c, (columns) and is calculated via Ecopath or Rpath algorithms (Christensen & Walters 2004, Lucey et al. 2020):

$$Q_{gc} = D_{gc} \cdot q_{\cdot c} \qquad (1)$$

where D_{gc} is the diet matrix defining the fraction of each prey type g in the diet of each consumer c, and $q_{\cdot c}$ is a horizontal vector defining the consumption rate of each consumer. The mortality rates of an SPF group g were calculated from the elements of Q_{gc}, summing down rows corresponding to specific consumer or fishery groups c and dividing by the standing stock biomass of the SPF group (equations represent element-wise operations unless noted by bracket notation [], in Eqs. 3 & 7). We assumed $F = 0$ among models that did not include a fishing fleet (n = 8).

2.5.4. Demands upon and contributions to the food-web (footprint and reach)

The demands upon and contributions to other groups in the food-web by SPF are expressed with footprint (f) and reach ($θ$) metrics, respectively. We calculated the footprints of SPF and other major consumer classes upon primary producers and the reach of these groups to predatory fish, seabirds, marine mammals, and fisheries.

The importance of SPF as energy transfer nodes was evaluated within the ECOTRAN framework (Steele & Ruzicka 2011). ECOTRAN is a modeling platform that can be used to describe trophic interactions between multiple species and fishing fleets, the recycling of detritus and nutrients, and the exchange of material between sub-regions and depth strata via sinking, physical flux, and migration (Ruzicka et al. 2016). ECOTRAN models can be run as time-dynamic simulations; however, in the context of this study, physical fluxes and migration are not considered, and all metrics and simulations were evaluated as steady-state expressions of the food-web. ECOTRAN is based on the transformation of a food-web expressed as a matrix of predation pressures upon each producer g by each consumer c (Q_{gc}) into a donor-driven trophic matrix (A_{cg}) describing the fraction of production flowing from each producer g (columns) to each consumer c (rows) (Steele 2009, Steele & Ruzicka 2011):

$$A_{cg} = \frac{Q_{gc}}{\sum_c (D_{gc} \cdot q_{\cdot c})} \qquad (2)$$

where term $\sum_c (D_{gc} \cdot q_{\cdot c})$ is the total predation pressure upon group g. Each element of A_{cg} represents a proportion of total biomass input to a producer group and has a value between 0 and 1. Expression of the food-web as trophic matrix A_{cg} is convenient for quantifying the role of any functional group in terms of its energy demand on lower TLs and its contribution to higher TLs. (The ECOTRAN platform code base used for this review is archived at https://github.com/JimRuzicka-NOAA/SmallPelagicFish_EwEreview).

The footprint of consumer c upon producer g (e.g. SPF as consumer c and phytoplankton as producer g) is calculated as the fraction of g production that supports the production of c via all direct and indirect trophic pathways:

$$f_{c\cdot} = \left[\left[diag(1/te_{\cdot g})\right] - [A_{cg}]\right]^{-1} \cdot [d_{g\cdot}] \qquad (3)$$

The footprint of a specific consumer c on producer g is vector element $f_{c\cdot}$. Term $te_{\cdot g}$ is a horizontal vector of transfer efficiencies for each producer g to the next TL that accounts for losses to metabolism, feces production, and senescence. The footprint is calculated for all consumers by driving the food-web with the external input of 1 unit of the individual producer group g of interest. Term $d_{g\cdot}$ is the vertical food-web driver vector with all elements = 0 except $d_{g\cdot} = 1$ for the producer group of interest. To prevent double counting the contribution of group g to group c, feedback loops and detritus recycling pathways within the trophic matrix are deactivated. Detritus uptake is set to zero (except flow between detritus pools). Elements of vector $f_{c\cdot}$ are recalculated for each group c consecutively with predation upon group c set to zero. Losses due to metabolic costs and feces production at each trophic step are included in the footprint calculations by setting all transfer efficiencies $te_{\cdot g} = 1$ except for the terminal detritus group, which is defined as 0.1. Senescence losses do not contribute to group c production or to the footprint of c upon producer g, but are directed to detritus pools in A_{cg}. This calculation of the gross footprint is analogous to the primary production required (PPR) calculated by Ecopath (Christensen et al. 2005, Essington 2006) when g is a primary producer. As descriptive shorthand in the text, the footprint of SPF on primary production is given as $f_{\mathrm{SPF,PrimProd}}$.

The reach of SPF group g is the fraction of any consumer group c production that is supported by the SPF group. From Ruzicka et al. (2012), the reach of g is calculated by iteratively multiplying the contribution of g to the diets of each consumer through diet matrix D_{gc}. Matrix T_{gc} represents the fraction of biomass passing through each trophic linkage in the food-web that originated with g. T_{gc} is estimated through iteration as:

$$T_{gc} = \theta_{c\cdot} \cdot D_{gc} \qquad (4)$$

Vertical reach vector $\theta_{c\cdot}$ is the fractional contribution of g to the diet of each consumer. $\theta_{c\cdot}$ is initialized as $\theta_{c\cdot} = D_{g\cdot}'$, the vertical transpose of row g in the diet matrix. In each iteration of Eq. (4), T_{gc} represents the contribution of g to the diet of each consumer through direct and indirect trophic pathways up to length $l =$ iteration count. The total contribution of g to each consumer is recalculated after each iteration by summing T_{gc} down all rows:

$$\theta_{c\cdot} = (\Sigma_g T_{gc})' \qquad (5)$$

The reach of g (e.g. SPF) to any specific consumer c is then element c in the final reach vector $\theta_{c\cdot}$. Before calculating the reach, the diet composition of each consumer ($D_{\cdot c}$) was renormalized to sum to 1 after setting all cannibalism elements $D_{cc} = 0$, and the contribution of g to itself was set to $\theta_{g\cdot} = 1$ in each iteration. We performed a maximum of $l = 1000$ iterations with progression halted once no element of θ differed by more than 0.0001 from the previous iteration. As descriptive shorthand in the text, the reach of an SPF group to a specific consumer group is given as $\theta_{\mathrm{SPF,consumer}}$.

2.5.5. Sensitivity analyses (abundance scenarios and mixed trophic impact)

The effects of changes in SPF abundance on all other elements of each food-web were investigated using the methodology developed by Steele (2009). A set of forced changes to food-web structure represents a 'scenario'. Energy flow through SPF was modified by reducing the availability of SPF to predators by an arbitrary but standardized 20% within each trophic matrix A_{cg} (SPF rows in A_{cg} were reduced by 20%). Surplus prey production no longer consumed by the reduced SPF group was distributed proportionally among all other consumers so that total predation pressure on each group remained unchanged. The production rates of all functional groups were calculated for the unmodified base model and the

modified sensitivity model using Eq. (3). Resulting changes to functional group productivities represent the consequences of a linear reapportioning of available prey among consumers (Collie et al. 2009). Sensitivities of each major consumer class c (SPF, mesopelagic fish, non-SPF pelagic fish, demersal fish, seabirds, mammals, fisheries) were calculated as the change in production relative to the base model:

$$\Delta P_c = (P_{c\,base} - P_{c\,modified})/P_{c\,base} \quad (6)$$

The sensitivity of other groups in the food-web to changes in SPF abundance was also evaluated with mixed trophic impact indices (MTI). MTI is a dimensionless metric that quantifies the net direct and indirect impact that a hypothetical change in biomass of impactor group g would have on every other model group c. MTI was calculated as described by Ulanowicz & Puccia (1990):

$$\mathrm{MTI}_{gc} = \left[[I] - [(D_{gc}) - (A_{cg})]\right]^{-1} - [I] \quad (7)$$

where I is the identity matrix, and flow to detritus pools c in trophic matrix A_{cg} is set to 0. The overall sensitivity of the food-web to changes in each model group was summarized as the total MTI (tMTI) (Pranovi et al. 2003, Coll et al. 2007). The tMTI of a group is the sum of all its impacts weighted by the inverse of the biomass of each impacted group. To compare SPF groups across different food-web models, we used the percentile rank of SPF tMTI among the tMTI of all other living groups in each model. Aggregations of SPF, seabirds, mammals, and fleets into pooled functional group classes were made prior to the calculation of MTI by adding appropriate elements of the consumption matrix and deriving the new diet and trophic matrices from the aggregated Q_{gc}.

3. RESULTS

3.1. TL and OI

Across all models, the global median TL of SPF is 3.10 (TL interquartile range [IQR]$_{1,3}$ = 2.88–3.30; Table S2). For context, SPF feed at a lower TL than do other pelagic fish, squid, demersal fish, seabirds, or mammals (Fig. 2a). SPF TLs differ significantly among ecosystem types (t_{157} = 2.66, p < 0.01) and are lowest in upwelling and reef system models (Table 3). TLs also differ significantly by latitude (t_{157} = 5.68, p < 0.01), with the lowest TLs in tropical systems

(Table S4; additional detailed results are included in Tables S2–S26).

The OIs are similar for SPF (median OI = 0.14, IQR$_{1,3}$ = 0.06–0.27), squid, other pelagic fish, seabirds, and mammals, but they feed across a narrower range of TLs than do demersal fishes (Fig. 2b). The OIs of SPF do not differ significantly among ecosystem types, though OI trends higher in coral reef models and lower in the open ocean (Table 3). OIs do differ significantly by latitude (t_{157} = −5.30, p < 0.01; Table S4).

3.2. Physiology

SPF have higher P/B rates than other fish, seabirds, and mammals (median P/B = 1.50, IQR$_{1,3}$ = 1.07–2.11, n = 164), but SPF rates are only half that of cephalopods (Fig. 2c). P/B rates differ significantly among ecosystem types (t_{157} = 2.46, p = 0.02) and latitude zones (t_{157} = −6.20, p < 0.01), being highest in coral reef and tropical models and lowest in upwelling and polar models (Table 3, Table S4).

Growth efficiencies (i.e. P/Q) are similar to those of other fish groups (median P/Q = 0.16, IQR$_{1,3}$ = 0.11–0.23) but are substantially lower than those of cephalopods and much higher than those of warm-blooded seabirds and mammals (Fig. 2d). While P/Q do not differ significantly among latitude zones, they do differ among ecosystem types (t_{157} = 3.03, p < 0.01) and are highest in continental shelf and estuary models and lowest in upwelling models (Table 3).

3.3. Biomass, production, and fishery catch

Across all models, SPF represent 35% of the median total fish biomass (B/B_{fishes} IQR$_{1,3}$ = 20–47%). This is comparable to demersal fishes but nearly twice the biomass of non-SPF pelagic fishes (Fig. 3a). The SPF proportion of total fish biomass is highest in upwelling models (Fig. 4a) and differs significantly among ecosystem types (t_{157} = −2.84, p = 0.01; Table 3). The SPF biomass contribution to total fish biomass does not differ significantly across latitudes (Table S4). In terms of production, SPF are as productive as all other non-SPF pelagic and demersal fish combined, whether scaled relative to total primary production or to total fish production. Across all models, the global median SPF production is 0.2% the scale of total primary production ($P/P_{PrimProd}$ IQR$_{1,3}$ = 0.1–0.6%) and represents 43% of total fish production (P/P_{fishes} IQR$_{1,3}$ = 24–64%; Fig. 3b,d). SPF production rates relative to total fish production are not significantly re-
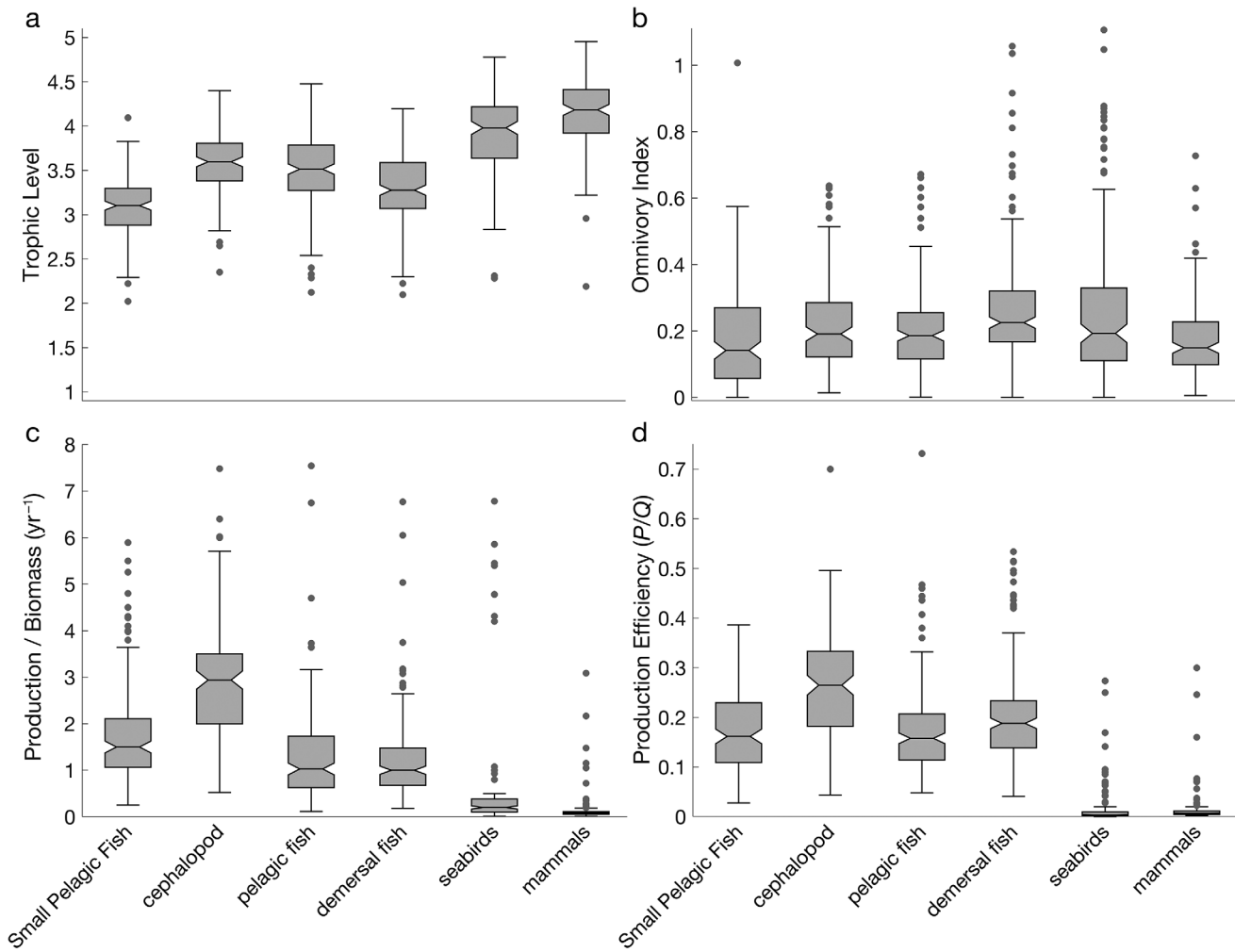
Fig. 2. Global distribution of small pelagic fish metrics from food-web models by consumer class. (a) Trophic level, (b) omnivory index, (c) production to biomass ratio, (d) production to consumption ratio (P/Q). In each boxplot, the notch and center bar represent the median, the shaded area represents the interquartile range (IQR) between the 1st and 3rd quartiles, whiskers represent highest and lowest observations within 150% of the IQR, and dots represent outliers outside the IQR

lated to latitude but did differ significantly among ecosystem types $(t_{157} = -3.16$, p < 0.01; Fig. 4d, Table 3). The highest median production rates relative to total fish production are in shelf and upwelling models and lowest in estuary and coral reef models.

The proportion of SPF in the total catch of fish and invertebrates across all models, globally, is comparable to that of non-SPF pelagic fishes, and the median proportion of SPF in the total catch is only slightly lower than that of demersal fish (median $C/C_{total} = 18\%$, $IQR_{1,3} = 2-48\%$; Fig. 3c). The relative contribution of SPF to total catch is significantly different among ecosystem types $(t_{157} = -2.71$, p = 0.01), with the greatest contribution in upwelling systems (median $C/C_{total} = 53\%$, $IQR_{1,3} = 8-75\%$; Fig. 4c, Table 3). Actual catch rates SPF are markedly higher in upwelling models (median $C = 1.7$ t km^{-2} yr^{-1},

$IQR_{1,3} = 0.3-5.6$ t km^{-2} yr^{-1}; Table 3), with 6 outliers ranging from 14 to 90 t km^{-2} yr^{-1} all representing the Humboldt Current system in Chile and Peru.

3.4. Mortality rates

Across all models, $M2$ in the pooled SPF group is about 14 times greater than F: median $M2 = 1.01$ yr^{-1} $(IQR_{1,3} = 0.62-1.38$ yr^{-1}, n = 164) versus $F = 0.07$ yr^{-1} $(IQR_{1,3} < 0.01-0.21$ yr^{-1}; Table S8). The median predation mortality on SPF is twice that suffered by non-SPF pelagic fish and demersal fish but half that suffered by squid. The major contributors to predation mortality are piscivorous fish, which impose much higher mortality than does fishing (median $M2_{fish} = 0.73$ yr^{-1}, $IQR_{1,3} = 0.41-1.11$ yr^{-1}; Table S8). The

Table 3. Distributions of food-web metrics for small pelagic fishes (SPF) within different ecosystem types. See Table 2 for definitions of each metric. Values shown are the 50th percentile and the 25th–75th percentiles. Significance determined by generalized linear mixed effect analysis: NS, p > 0.05; *p < 0.05; **p < 0.01; ***p < 0.001. Total catch C and geographically scaled catch C_{scaled} omit models with currencies other than tons live weight: shelf n = 83, bay/fjord n = 21, estuary n = 5

	Upwelling (n = 27)	Shelf (n = 89)	Ocean (n = 15)	Bay/fjord (n = 22)	Estuary (n = 6)	Coral reef (n = 5)	Sig.
TL	2.90	3.12	3.22	3.10	2.95	2.74	**
	2.60–3.20	2.98–3.35	3.05–3.28	2.78–3.17	2.82–3.22	2.65–3.02	
OI	0.18	0.12	0.09	0.13	0.22	0.28	NS
	0.13–0.27	0.03–0.27	0.03–0.20	0.08–0.27	0.09–0.31	0.16–0.44	
P/B	1.34	1.51	1.43	1.51	2.17	3.00	*
(yr^{-1})	1.24–1.65	0.97–2.11	0.88–2.81	0.87–1.86	1.99–3.41	1.97–4.05	
P/Q	0.10	0.20	0.16	0.12	0.21	0.14	**
	0.10–0.14	0.14–0.26	0.10–0.22	0.07–0.20	0.16–0.25	0.10–0.18	
B/B_{fishes}	40.31	32.99	26.20	28.97	13.29	19.65	**
(%)	35.7–59.3	21.1–48.9	7.30–47.3	16.5–39.7	6.7–23.2	8.75–28.5	
$P/P_{PrimProd}$	0.27	0.18	0.30	0.18	0.12	0.35	NS
(%)	0.17–0.88	0.08–0.54	0.04–0.72	0.11–0.35	0.03–0.22	0.26–0.66	
P/P_{fishes}	45.94	43.85	38.10	39.09	25.21	26.98	**
(%)	37.0–67.8	26.8–66.1	4.25–65.0	18.4–53.8	11.9–40.5	18.4–35.1	
C/C_{total}	53.41	25.22	6.94	8.86	7.26	16.52	**
(%)	8.47–75.0	3.91–48.2	0.09–13.0	<0.01–43.3	2.14–17.6	4.45–22.0	
C	1.70	0.25	0.03	0.25	0.10	0.50	***
(t km^{-2} yr^{-1})	0.31–5.57	0.04–0.95	<0.01–0.13	<0.01–1.52	0.02–0.52	0.30–2.67	
C_{scaled}	282 509	29 725	15 975	127	28	18 290	–
(t yr^{-1})	16 038–914 776	3672–161 146	9–72 232	<0.01–1753	20–1119	2214–27 786	

combined predation mortality due to seabirds and marine mammals is less than that of the rate of F (median $M2_{seabirds}$ = 0.01 yr^{-1}, IQR$_{1,3}$ < 0.01–0.04 yr^{-1}; $M2_{mammals}$ = 0.02 yr^{-1}, IQR$_{1,3}$ < 0.01–0.07 yr^{-1}; Table S8). Predation mortality by fishes differs significantly by latitude (t_{157} = −6.66, p < 0.01; Table S10) and between ecosystem types (t_{157} = 2.28, p = 0.02), and $M2_{fishes}$ was highest in the estuary and coral reef models (Table 4). Mammal-driven mortality also differs significantly by latitude (t_{157} = 4.26, p < 0.01; Table S10) and between ecosystem types (t_{157} = 2.52, p = 0.01) and is greatest in open ocean ($M2_{mammals}$ = 0.03 yr^{-1}, IQR$_{1,3}$ = <0.01–0.15 yr^{-1}) and continental shelf models ($M2_{mammals}$ = 0.03 yr^{-1}, IQR$_{1,3}$ = <0.01–0.01 yr^{-1}; Table 4). Seabird-driven predation mortality does not differ significantly among ecosystem types or by latitude (Table 4, Table S10).

Across all models, the F on SPF was comparable to F on non-SPF pelagic and demersal fish groups (median F = 0.07 yr^{-1}, IQR$_{1,3}$ = <0.01–0.21 yr^{-1}, n = 164; Table S8). However, the median global F rate is not a good indicator of fishing pressure in specific ecosystems. F on SPF differs significantly among ecosystem types (t_{157} = −2.31, p = 0.02) and by latitude (t_{157} = −2.05, p = 0.04). Fishing pressure is highest in coral reef (F = 0.16 yr^{-1}, IQR$_{1,3}$ = 0.09–0.75 yr^{-1}) and upwelling models (F = 0.11 yr^{-1}, IQR$_{1,3}$ = 0.03–0.17 yr^{-1})

and lowest in the open ocean and polar ecosystems (F < 0.01 yr^{-1}, IQR$_{1,3}$ = <0.01–0.01 yr^{-1}; Table 4, Table S10).

3.5. Demands upon and contributions to the food-web (footprint and reach)

The demands that SPF impose upon the ecosystem can be expressed with footprint metrics, the proportion of a lower TL group's production that supports SPF production via all direct and indirect trophic pathways. The global median SPF footprint on total net primary production is 8.4% ($f_{PrimProd}$ IQR$_{1,3}$ = 3.3–19%; Fig. 5a). This is comparable to the high-end estimates of the demands that non-SPF pelagic fish (12%) and demersal fish place on the ecosystem (13%; Table S14). The SPF footprint on phytoplankton does not differ significantly among ecosystem types or by latitude but tends to be higher in open ocean models (Fig. 5c, Table S15).

The contribution of SPF to the ecosystem is expressed by reach metrics, the proportion of a consumer group's production that is supported by SPF via all direct and indirect trophic pathways. The global median contribution of SPF to other fish is θ_{fishes} = 4.7% (IQR$_{1,3}$ = 1.9–8.2%), to seabird produc-
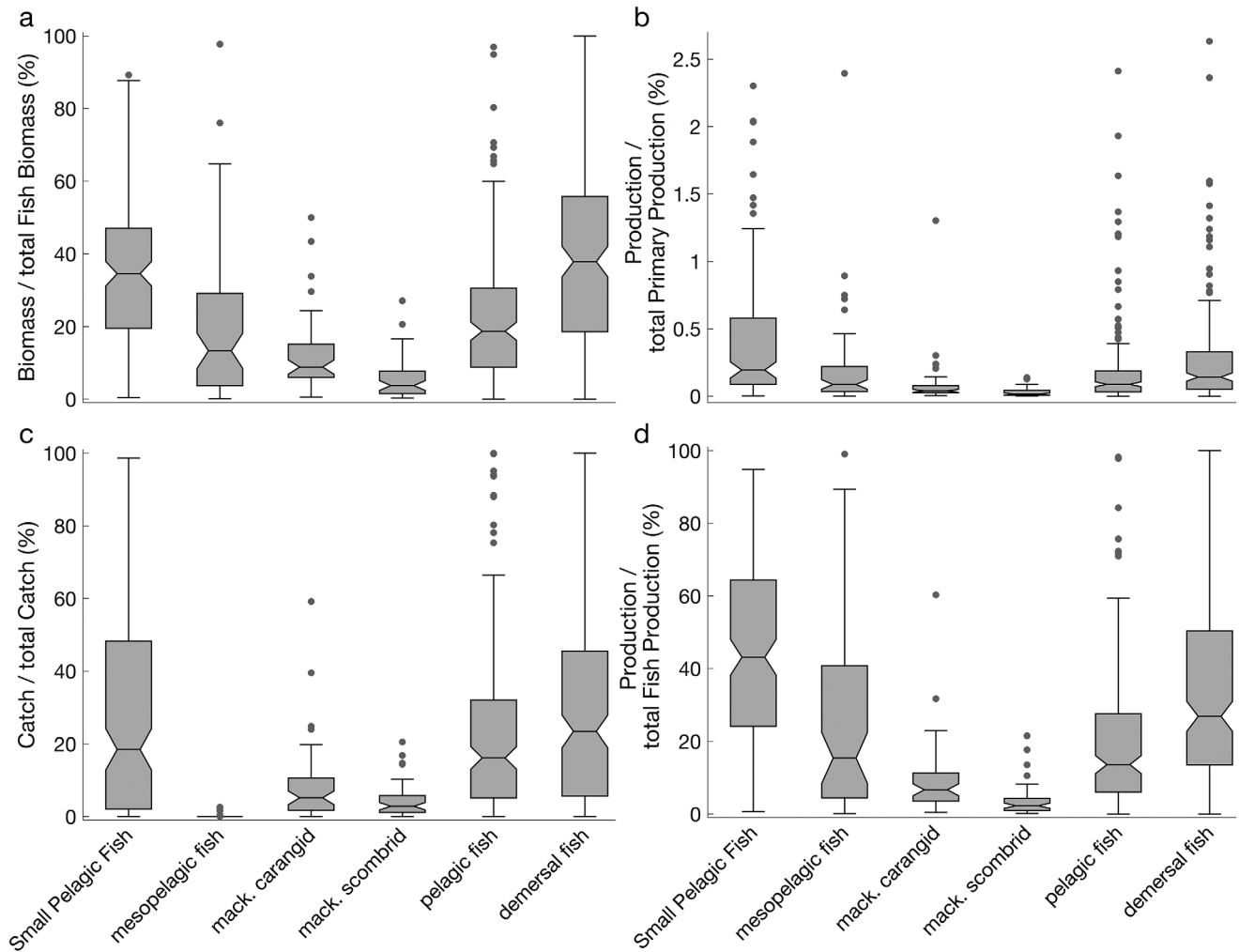
Fig. 3. Global distribution of metrics of biomass, production, and fishery catch for small pelagic fish (SPF), mesopelagic fishes, small carangid mackerels, small scombrid mackerels, non-SPF pelagic fishes, and demersal fishes. (a) Group biomass to total fish biomass ratio; (b) group production to primary production ratio, (c) group catch in fisheries to total fish and invertebrate catch, (d) group production to total fish production. Boxplot parameters as in Fig. 2

tion is $\theta_{seabirds} = 22\%$ (IQR$_{1,3}$ = 0.2−48%), and to mammal production is $\theta_{mammals} = 15\%$ (IQR$_{1,3}$ = 1.2−41%; Fig. 5b). These contributions to higher TLs are much higher than those of cephalopods or other fish (Fig. 5b, Table S14). SPF reach to other fish was slightly higher in continental shelf and upwelling models but did not differ significantly between ecosystem types. Reach to seabirds and mammals were both significantly higher in upwelling models ($\theta_{seabirds} = 33\%$, IQR$_{1,3}$ = 24−80%, $t_{157} = -2.08$, p = 0.04; $\theta_{mammals} = 41\%$, IQR$_{1,3}$ = 35−55%, $t_{157} = -4.84$, p < 0.01; Fig. 5d, Table S15).

Across all models, the reach contribution of SPF to fisheries is greater than their contribution to other consumer groups (global median $\theta_{fisheries} = 34\%$, IQR$_{1,3}$ = 12−59%; Fig. 5b, Table S14). The SPF contribution to fisheries is greater than either demersal fish or non-SPF pelagic fish, but less than all non-SPF

fish combined (Table S14). The global median SPF contribution to fisheries is nearly 10 times greater than that of squid. SPF reach to fisheries differs significantly among ecosystem types ($t_{157} = -2.88$, p < 0.01) but not among latitude zones. SPF reach to fisheries is greatest in upwelling models (upwelling median $\theta_{fisheries} = 62\%$, IQR$_{1,3}$ = 25−80%; Fig. 5d). Across all models, the contribution of SPF to the landed groups targeted by fisheries is much lower than the SPF contribution to fleets themselves (global median $\theta_{landed\ groups} = 1.8\%$, IQR$_{1,3}$ = 0.46−6.3%; Table S14) and is comparable to the SPF reach to fishes in general. SPF reach to groups targeted by fisheries differs significantly by ecosystem type ($z_{153} = -1.98$, p = 0.05), and the median is slightly higher in upwelling systems (upwelling median $\theta_{landed\ groups} = 4.0\%$, IQR$_{1,3}$ = 2.0−18%; Table S15).
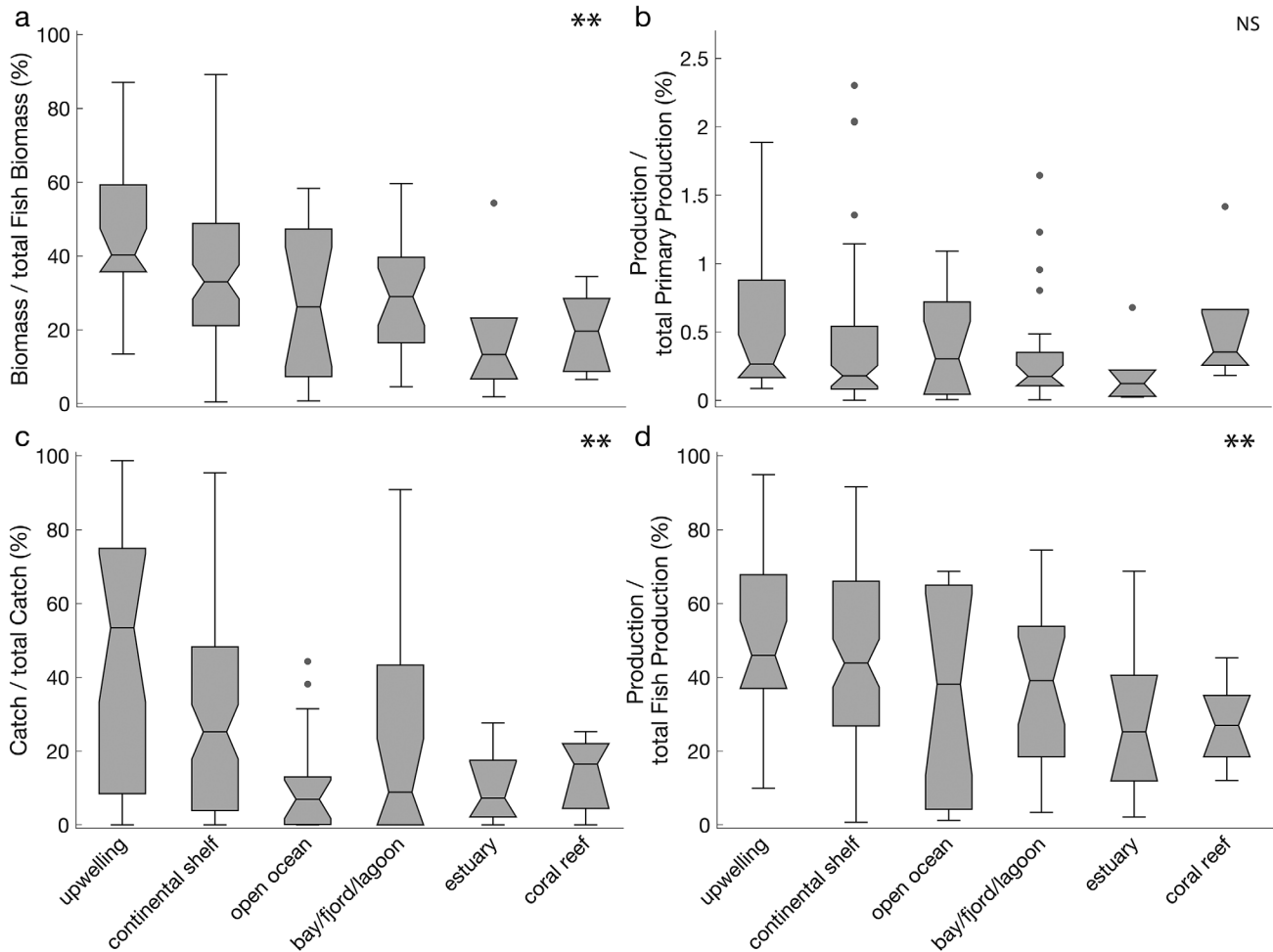
Fig. 4. Distribution of metrics of biomass, production, and fishery catch for small pelagic fish by ecosystem type. (a) Group biomass to total fish biomass ratio, (b) group production to primary production ratio, (c) group catch in fisheries to total fish and invertebrate catch, (d) group production to total fish production. Boxplot parameters as in Fig. 2. Significant differences between ecosystem types determined by generalized linear mixed effect analysis: NS, p > 0.05; *p < 0.05; **p < 0.01; ***p < 0.001

3.6. Comparison of major upwelling systems

Table 5 provides the distributions of SPF metrics among the 4 major eastern boundary current upwelling ecosystems. SPF in the Humboldt Current are parameterized with higher median P/B rates than other upwelling systems, but the California Current models have the highest growth efficiencies (P/Q). SPF in the Humboldt Current represent a significantly higher proportion of the total fish biomass (median B/B_{fishes} = 69%, t_{23} = 2.77, p = 0.01), are significantly more productive than other upwelling systems relative to total fish production (median P/P_{fishes} = 80%, t_{23} = 2.87, p = 0.01), and represent a significantly higher proportion of the total catch (median C/C_{total} = 84%, t_{23} = 2.46, p = 0.02). F also differs significantly among the 4 upwelling systems and is highest in the Humboldt Current (F = 0.36 yr^{-1}, t_{23} =

3.29, p < 0.01). In the Humboldt Current, the median F rate is nearly one-third the predation mortality rate ($M2$ = 1.29 yr^{-1}; Table S11).

SPF footprints on primary production do not differ significantly among upwelling systems but tend to be higher among Humboldt Current models (median f_{PrimProd} = 23%). The median contribution of SPF to higher TL consumers, the reach (θ), is substantially higher in the Humboldt Current. Among Humboldt Current models, 13% of total fish production, 90% of seabird production, 69% of marine mammal production, and 90% of fishery production is supported by SPF. By comparison, the median SPF contributions to fisheries in the other 3 upwelling ecosystems range from $\theta_{\text{fisheries}}$ = 25% in the California Current to 62% in the Benguela Current, contributions to seabird production range from θ_{seabirds} = 10% in the Canary Current to 32% in the Benguela. SPF contributions

Table 4. Distributions of mortality rates for small pelagic fishes within different ecosystem types. See Table 2 for definitions of each metric. Values shown are the 50th percentile and the $25^{th}-75^{th}$ percentiles. Significance determined by generalized linear mixed effect analysis: NS, $p > 0.05$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

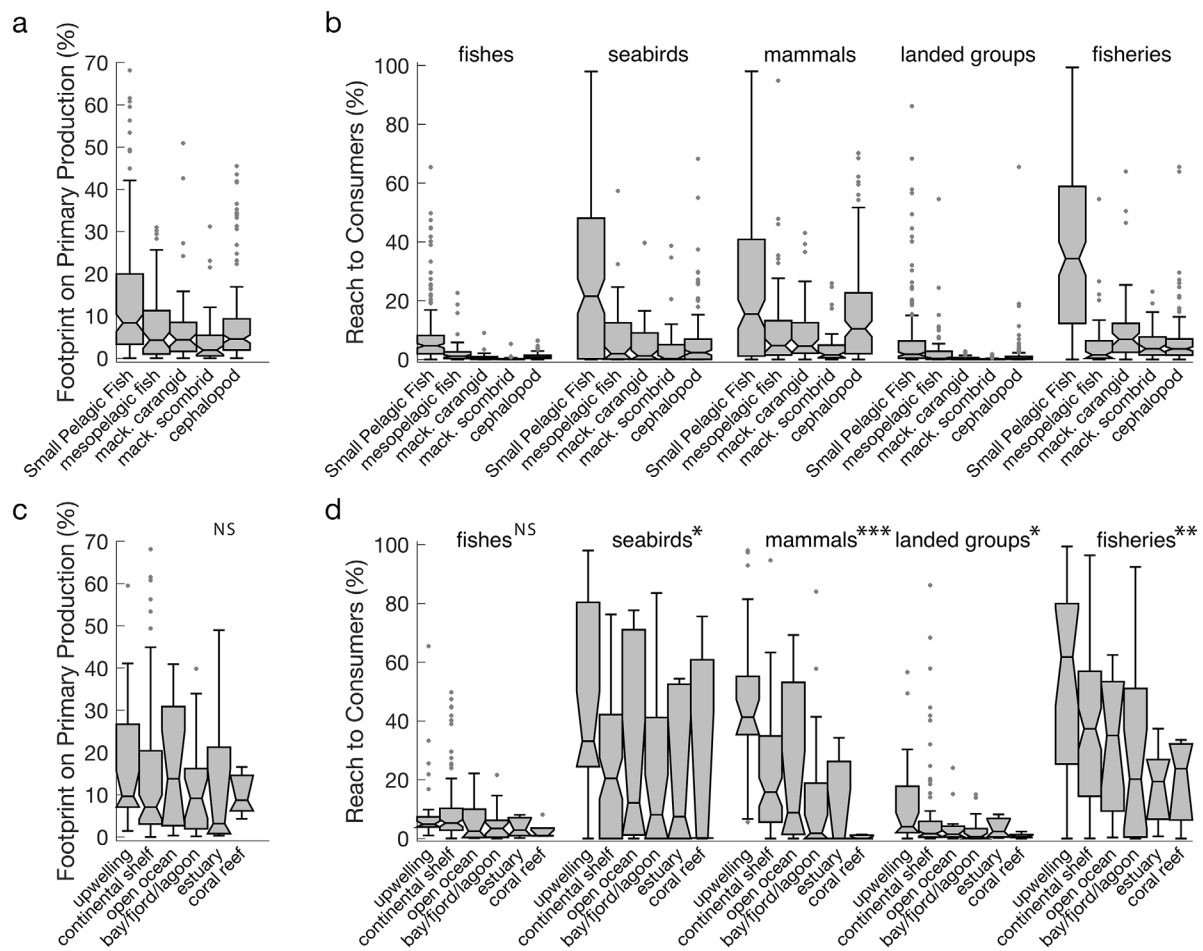|	Upwelling (n = 27)	Shelf (n = 89)	Ocean (n = 15)	Bay/fjord (n = 22)	Estuary (n = 6)	Coral reef (n = 5)	Sig.
$M2$	1.01	0.92	1.04	0.78	1.18	1.41	*
(yr^{-1})	0.64−1.21	0.65−1.39	0.75−1.81	0.36−1.30	1.02−1.74	1.16−2.21	
F	0.11	0.08	0.01	0.06	0.05	0.16	*
(yr^{-1})	0.03−0.17	0.01−0.26	<0.01−0.01	<0.01−0.28	<0.01−0.21	0.09−0.75	
$M2_{fishes}$	0.79	0.62	0.65	0.57	1.07	1.20	*
(yr^{-1})	0.50−0.95	0.36−1.10	0.35−1.20	0.35−1.03	0.95−1.74	0.82−1.72	
$M2_{seabirds}$	0.03	0.01	0.03	0.01	0.02	0.02	NS
(yr^{-1})	0.01−0.09	<0.01−0.03	<0.01−0.04	<0.01−0.06	<0.01−0.10	0.01−0.10	
$M2_{mammals}$	0.02	0.03	0.03	<0.01	<0.01	0	*
(yr^{-1})	0.01−0.07	<0.01−0.09	<0.01−0.15	<0.01−0.02	<0.01−0.03	−	

Fig. 5. Group demands on primary production (footprint) and contributions to higher trophic level consumers (reach). (a) Footprint of small pelagic fish (SPF), mesopelagic fishes, small carangid mackerels, small scombrid mackerels, and cephalopods on primary production. (b) Reach of SPF, mesopelagic fishes, small carangid mackerels, small scombrid mackerels, and cephalopods to all fishes, seabirds, mammals, landed groups targeted by fisheries, and fisheries production. (c) Footprint of SPF on primary production in different ecosystem types (upwelling, continental shelf, open ocean, bay/fjord/lagoon, estuary, and coral reef). (d) Reach of SPF to all fishes, seabirds, mammals, landed groups targeted by fisheries, and fisheries production in different ecosystem types. Boxplot parameters as in Fig. 2. Significant differences between ecosystem types determined by generalized linear mixed effect analysis in (c) and (d): NS, $p > 0.05$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

Table 5. Comparison of food-web metrics for small pelagic fishes (SPF) among 4 major eastern boundary current upwelling zones. See Table 2 for definitions of each metric. Values shown are the 50th percentile and the 25th–75th percentiles. Significance determined by generalized linear mixed effect analysis: NS, p > 0.05; *p < 0.05; **p < 0.01; ***p < 0.001

	Humboldt (n = 8)	Benguela (n = 11)	California (n = 3)	Canary (n = 5)	Sig.
P/B (yr^{-1})	1.93 1.76–2.21	1.28 1.24–1.34	1.09 1.02–1.36	1.30 1.05–1.32	**
P/Q	0.13 0.10–0.15	0.10 0.10–0.10	0.23 0.18–0.25	0.14 0.10–0.14	***
B/B_{fishes} (%)	68.9 58.7–78.7	37.0 35.7–39.3	26.2 21.0–38.2	42.6 33.0–50.2	*
P/P_{fishes} (%)	79.5 65.1–89.5	39.1 35.3–43.3	48.3 35.4–67.6	49.0 39.5–56.4	*
C/C_{total} (%)	83.6 76.8–88.9	53.4 <0.01–60.2	9.56 2.39–22.4	28.1 18.2–52.5	*
F (yr^{-1})	0.36 0.19–0.50	0.05 <0.01–0.11	0.03 0.01–0.06	0.14 0.11–0.15	***
$f_{PrimProd}$ (%)	22.81 13.0–39.2	8.61 6.71–27.2	9.65 6.16–14.6	7.14 6.14–10.8	NS
$\theta_{seabirds}$ (%)	89.5 85.6–93.3	31.6 29.2–57.1	23.7 5.93–55.2	9.77 8.66–22.8	NS
$\theta_{mammals}$ (%)	69.1 44.1–95.1	41.4 20.0–47.0	35.8 13.9–51.4	37.5 19.3–38.4	NS
$\theta_{fisheries}$ (%)	90.3 83.3–95.1	61.7 12.3–69.1	25.0 20.4–29.3	35.9 23.2–56.9	**

to marine mammal production range from median $\theta_{mammals} = 36\%$ in the California Current to 41 % in the Benguela Current. However, only the reach to fisheries differs significantly between the upwelling systems ($t_{23} = 3.10$, p = 0.01).

3.7. Differences among SPF types

Table 6 summarizes the metrics of biomass, catch, and reach contributions to the ecosystem of 9 major SPF groups. Sardine, herring, and anchovy have the greatest representation among all models analyzed. The most productive groups relative to total fish production are smelt (median $P/P_{fishes} = 23\%$), anchovy (19 %), sardine (14 %), and menhaden (14 %). In terms of contribution to higher TLs, the greatest support to seabirds is from smelt ($\theta_{seabirds} = 18\%$), anchovy (9.3 %), bonga shad (7.8 %), and menhaden (6.6 %). The greatest support to marine mammals is from smelt ($\theta_{mammals} = 18\%$), sardine (6.3 %), and anchovy (5.7 %).

The most heavily harvested groups relative to total fish catch are menhaden (median $C/C_{total} = 33\%$), bonga shad (20 %), sardine (11 %), and herring (5.1 %). F rates are highest for bonga shad ($F = 0.20$ yr^{-1}), menhaden (0.17 yr^{-1}), and sardine (0.14 yr^{-1}). The most

important groups supporting fisheries via direct and indirect trophic pathways are menhaden ($\theta_{fisheries} = 36\%$), bonga shad (22 %), and sardine (17 %), matching the groups with the highest harvest and fishery mortality rates. Anchovy and herring support 10 and 8.1 % of the total fishery catch, respectively.

Small mesopelagic fishes, small carangid mackerels, and small scombrid mackerels are also well-represented among food-web models but are considered separately from the pooled SPF group. These 3 groups feed at slightly higher TLs than most other SPF groups (median TL = 3.4, 3.5, and 3.6, respectively; Table S6). Mesopelagic fish production relative to total fish production is on average, globally lower than that of the SPF group as a whole ($P/P_{fishes} = 15\%$; Fig. 3d) but comparable to the median production rates of anchovy (19 %) and sardine (14 %), individually. The relative production rates of small carangid ($P/P_{fishes} = 6.7\%$) and scombrid mackerels (2.3 %) are also lower than those of most SPF groups (Fig. 3d). Mesopelagic fish contribute very little to the total catch (Fig. 3c), and the reach contribution of mesopelagics to fishery production is much lower than the contribution of most other SPF groups ($\theta_{fisheries} = 1.6\%$; Fig. 5b). Small mackerels also contribute less to support fishery production than most other individual SPF groups ($\theta_{fisheries} = 6.9$ and 3.7 % for carangids and scombrids, respectively; Fig. 5b, Table S18).

Table 7 identifies the top 3 individual SPF groups in each ecosystem type in terms of their footprint demands on primary production and their reach contribution to fishery production. Anchovy, sardine, and herring are among the most important groups in terms of both footprint and reach in most ecosystem types. Carangid mackerels also appear among the 3 most important groups in several ecosystem types. Mesopelagic fishes, smelts, and carangid mackerels are the most important groups in open ocean models in terms of their resource demands and in terms of their contribution to fishery production. Mesopelagic fishes have a moderately larger footprint on primary production in coastal bay/fjord/lagoon models than in oceanic models, though this is estimated from only 2 bay/fjord/lagoon models.

Table 6. Comparison of food-web metrics among specific types of Small pelagic fishes (SPF) across all models, globally. See Table 2 for definitions of each metric. Values shown are the 50th percentile and the 25th–75th percentiles

	Sardine (n = 56)	Herring (n = 52)	Anchovy (n = 50)	Smelt (n = 27)	Sprat (n = 11)	Menhaden (n = 9)	Bonga shad (n = 9)	Shad (n = 8)	Flyingfish (n = 14)
P/B (yr^{-1})	1.29 0.95–1.65	1.03 0.74–1.42	1.80 1.40–2.49	1.43 0.89–1.78	1.21 1.05–1.31	1.55 1.18–2.25	0.87 0.86–1.22	0.60 0.43–1.22	2.28 1.24–2.81
P/Q	0.11 0.10–0.16	0.15 0.11–0.21	0.15 0.10–0.22	0.22 0.16–0.29	0.14 0.12–0.24	0.12 0.08–0.22	0.06 0.06–0.10	0.21 0.14–0.22	0.16 0.11–0.23
B/B_{fishes} (%)	9.37 4.04–23.3	10.38 2.99–16.9	10.51 4.82–26.7	10.34 3.59–27.0	3.69 3.06–4.37	9.44 4.45–15.8	7.86 6.28–16.6	1.31 0.59–2.65	2.00 0.72–3.20
P/P_{fishes} (%)	14.44 4.09–24.9	8.55 3.69–18.2	19.03 8.39–33.3	25.11 6.47–47.8	5.53 4.15–7.74	13.99 6.14–20.8	6.90 3.63–21.2	1.67 0.66–2.47	1.95 0.99–4.06
C/C_{total} (%)	11.40 1.65–24.6	5.07 0.66–16.8	2.93 <0.01–22.5	0.05 <0.01–1.80	1.35 1.16–2.82	33.49 1.46–37.1	19.54 16.0–29.8	0.39 0.09–1.78	0.19 0.00–1.48
F (yr^{-1})	0.14 0.03–0.42	0.06 <0.01–0.21	0.08 <0.01–0.30	<0.01 0–<0.01	0.08 0.02–0.16	0.17 0.08–0.59	0.20 0.10–0.31	0.06 0.01–0.15	0.01 <0.01–0.03
$f_{PrimProd}$ (%)	3.70 0.68–7.83	3.07 1.04–6.77	5.75 1.62–9.68	5.79 0.88–13.2	1.02 0.52–3.38	2.41 0.89–3.31	1.13 0.57–3.10	0.44 0.10–1.10	0.44 0.23–1.00
$\theta_{seabirds}$ (%)	5.70 3.74–25.9	2.48 0.13–3.77	9.26 1.38–20.8	17.63 5.24–44.3	3.43 0.60–10.4	6.61 1.50–13.0	7.80 6.66–9.66	1.31 0.31–2.01	0.16 <0.01–2.91
$\theta_{mammals}$ (%)	6.29 2.28–17.5	3.87 0.42–8.11	5.71 0.74–31.3	13.32 1.73–29.5	3.95 1.41–6.96	1.27 0.00–6.58	1.88 1.39–6.48	0.26 0.12–1.25	0.26 0.00–1.51
$\theta_{fisheries}$ (%)	16.51 7.26–29.5	8.05 2.28–22.6	10.21 1.58–33.4	5.93 0.95–21.3	2.95 2.17–4.85	35.81 3.75–40.0	21.90 16.9–34.5	0.47 0.16–1.75	1.13 0.36–5.86

Table 7. Identification of the 3 most important small pelagic fish groups in each ecosystem type in terms of their demands on primary production and their contribution to fishery production via all direct and indirect trophic pathways. Mesopelagic fishes, small carangid mackerels, and small scombrid mackerels are included in the rankings. See Table 2 for definitions of each metric. Values shown are medians of all models in each ecosystem type

	Upwelling		Continental shelf		Open ocean		Bay/fjord/lagoon		Estuary		Coral reef	
$f_{PrimProd}$ (%)	Anchovy	4.0	Anchovy	7.6	Mack. Carangid	50.9	Mesopelagic	16.3	Anchovy	6.5	Mack. Carangid	11.0
	Sardine	3.9	Sardine	4.5	Smelt	18.8	Herring	8.6	Mack. Carangid	3.7	Anchovy	8.7
	Herring	3.1	Herring	3.1	Mesopelagic	12.5	Mack. Carangid	8.3	Sardine	2.3	Sardine	3.5
$\theta_{fisheries}$ (%)	Anchovy	30.5	Menhaden	37.3	Mack. Carangid	50.5	Herring	74.4	Sardine	16.3	Sardine	17.4
	Sardine	16.5	Bonga shad	21.9	Smelt	33.0	Bonga shad	17.2	Mack. Scombrid	6.5	Mack. Scombrid	16.1
	Mack. Carangid	7.2	Sardine	17.6	Mesopelagic	10.6	Sardine	13.7	Anchovy	5.3	Mack. Carangid	13.8

3.8. Sensitivity analysis

The effects of a 20% reduction of SPF biomass on other consumer groups are shown in Fig. 6a. The effects were usually smaller than the 20% forced reduction of SPF. The net effect on predators and fisheries was generally negative. Seabirds, mammals, and fisheries declined in most ecosystem types. Pelagic fishes, demersal fishes, and fishery-targeted landed groups potentially include both competitors and predators of SPF and generally increased when the availability of SPF was reduced. These fish groups and fisheries were most sensitive in upwelling models.

While the SPF reduction scenarios highlight the bottom-up effects on higher TL consumers when the availability of SPF as a trophic link between lower and upper TLs is altered, the MTI analysis considers the role of SPF as both a predator and as prey. Fig. 6b shows the percentile rank of the total MTI (tMTI) of SPF on all living groups in the food-web in relation to the tMTI ranking of all other living groups in each model. In general, SPF are among the most influential groups in most ecosystem types, with median tMTI rankings within the upper 75th percentile in upwelling, continental shelf, and coral reef models and within the upper 66th percentile in open ocean and bay/fjord/lagoon systems. In estuary models, however, SPF were below the median in terms of net effects on food-web groups. Also shown are the tMTI rankings of mesopelagic fishes and small mackerels. These latter groups show a lot more variability between ecosystem types than SPF but generally have lower tMTI rankings. However, mesopelagic fishes in open ocean models have comparable tMTI rankings to SPF.
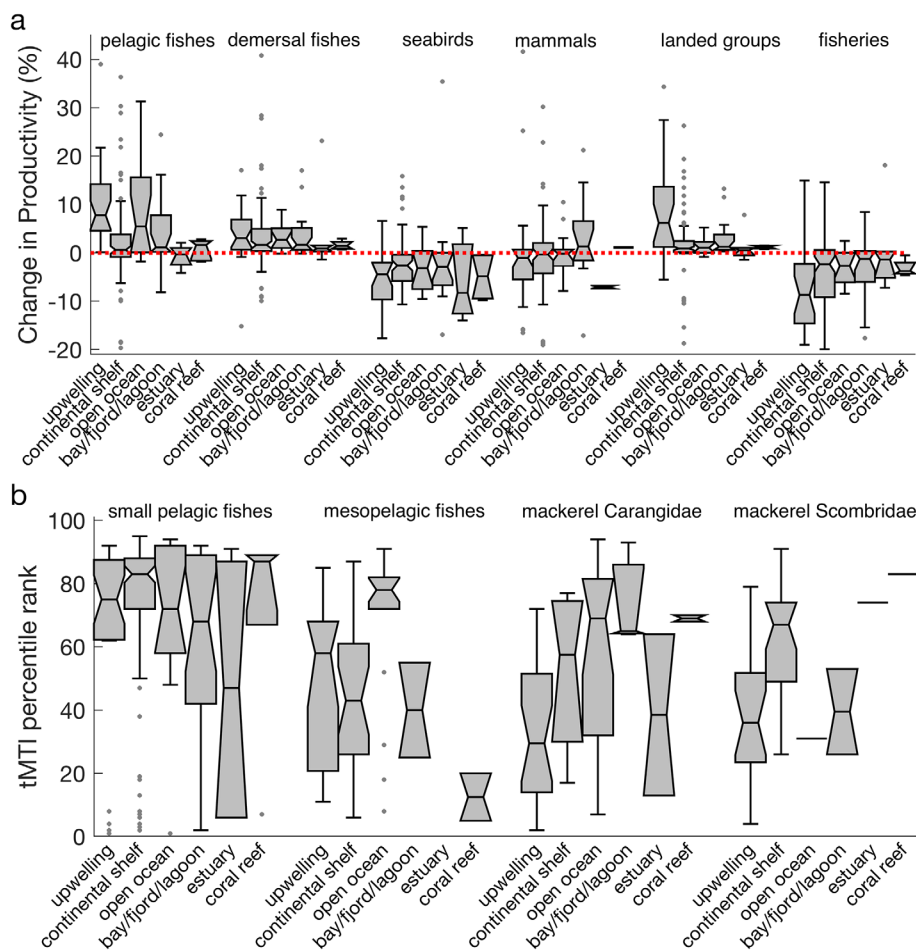

Fig. 6. (a) Effects of a 20% reduction in small pelagic fish (SPF) biomass upon the productivity of major consumer classes (squid, non-SPF pelagic fish, demersal fish, seabirds, marine mammals, and fisheries. Results presented as percent change in production relative to an unaltered model. Results are arranged by ecosystem type (upwelling, continental shelf, open ocean, bay/fjord/lagoon, estuary, and coral reef). (b) Distributions of the percentile ranking of total mixed trophic impact (tMTI) of SPF on living groups in each ecosystem model by ecosystem type. Boxplot parameters as in Fig. 2

4. DISCUSSION

4.1. Approach of this review and analysis

The purpose of this study was to evaluate the role of SPF as a resource to predators and fisheries and as an ecosystem-structuring agent among diverse ecosystems. Our approach was to take advantage of the large body of peer-reviewed Ecopath food-web models (Christensen & Walters 2004) to derive a suite of metrics that characterize SPF in terms of their trophic position, productivity, the demands they place on lower TL resources, the contributions they provide to higher TL consumers, and the sensitivity of different living groups to variability in SPF abundance and biomass.

Our analyses were restricted to metrics that could be derived from mass-balanced Ecopath food-webs rather than from time-dynamic, environmentally driven ecosystem simulations such as those produced by Ecosim and Ecospace (e.g. Coll et al. 2006), Atlantis (e.g. Kaplan et al. 2019), or OSMOSE (e.g. Travers et al. 2006). We did this because of the large number and high ecosystem diversity represented by existing Ecopath models, the relative uniformity of the parameterization structure allowed for rapid analyses across models, and so that our analyses focused on the implications of food-web structure rather than time-dependent variability in environmental conditions. Metrics and sensitivity analyses derived from steady-state food-webs as presented here are informative of the trophic relationships and energy flow patterns averaged across seasons and years, but they cannot capture the non-linear dynamics of interacting functional groups with differing response rates to changing conditions. We considered evidence of consistent differences in SPF characteristics among ecosystem types to be informative of the range of ecological roles that SPF can take within ecosystems subject to different physical drivers and environmental conditions.

We were not selective of the models analyzed and made no attempt to evaluate the quality of any model. Models within the EcoBase archive were only rejected if there were persistent reading errors by our analysis code or if the food-web model was not in thermodynamic balance (i.e. predation demands exceeded production for any group). Additional peer-reviewed models were added to the analysis based on the authors' knowledge of work done within regions of their personal expertise. We did not limit the coverage of any ecosystem to a specific era or climate condition (e.g. Pacific models representing either El Niño or La Niña conditions). We considered all such models to be valid representations of that ecosystem at different points in time. Comparison of models by ecosystem type was limited by model availability, and ecosystem types were not necessarily evenly represented. Coverage of Indian Ocean ecosystems was particularly poor, while coverage of the Humboldt and Benguela Current ecosystems was particularly good. Our statistical analyses used GLMMs to control for the fact that individual ecosystems may be represented by multiple food-web models. Finally, we did not explicitly include the pelagic juvenile stages of fish species as a major consumer class. Juveniles of non-SPF species are known to be both important planktivores and prey; for example, juvenile hake in the Southern Benguela (Shannon et al. 2003) and juvenile mackerel in the Canary Current (Garrido et al. 2015).

4.2. The importance of SPF as a consumer group

SPF are a very productive mid-TL group. They have high intrinsic production rates (Fig. 2c) and, given the resources, their biomasses can grow faster than the other major fish groupings defined in this study. Across all models analyzed, SPF were about as productive as all other pelagic and demersal fish combined (Fig. 3d). However, SPF production efficiency was not higher than other fish (P/Q; Fig. 2d), and high SPF production rates place high demands on ecosystem resources. As an average across ecosystem models, we estimate that SPF used 8% of the total primary production ($f_{PrimProd}$; Fig. 5a). SPF demands are slightly higher in open ocean models, where SPF used 14% of the primary production on average and mesopelagic fishes used 13% (Fig. 5a). In upwelling models, we estimate that SPF required 10% of the total primary production on average (Fig. 5c). Jarre-Teichmann & Christensen (1998) used a standard Ecopath algorithm to estimate the PPR to support anchovy and sardine production within the same 4 major upwelling ecosystems as studied here. Their estimated range of 10—25% agrees with our upwelling footprint estimates of 7—23% (Table S17). High estimates of the PPR to support coastal fisheries of all targeted species (24—35%) led Pauly & Christensen (1995) to suggest that there is little unused plankton production that could be exploited to expand production of the world's major fisheries.

4.3. The importance of SPF as a producer group

Reach metrics (θ) calculated in our analysis show that SPF are major contributors to higher TL con-

sumer and fishery production (Fig. 5d). Our work follows the analysis of 72 globally distributed food-web models by Pikitch et al. (2014) to estimate the contributions of forage fish and euphausiids to support the production of predators and fisheries. They characterized the importance of SPF to predators in terms of diet composition and found that SPF represented at least 10% of the diets in nearly half of all predator groups in their model set. The highest direct predatory dependence on SPF was in upwelling models (if euphausiids are excluded), and seabirds were particularly dependent on SPF. In our analysis, the importance of SPF to seabirds, mammals, and fisheries was also highest in upwelling models (Fig. 5d) and comparable to contributions of all other pelagic and demersal fishes combined. A study of covariance between observed seabird breeding success and SPF abundance confirmed the high dependence of seabird populations on SPF abundance in real-world ecosystems (Cury et al. 2011).

Pikitch et al. (2014) presented support service metrics analogous to the reach metrics calculated here, though they only accounted for direct trophic linkages from SPF to fisheries and predatory fish targeted by fisheries. They estimated that SPF support to fisheries accounts for 20% of the monetary value of the global catch of fish. Our reach estimates show that SPF directly and indirectly supports, on average across all models, 34% of the global catch. This is about twice the fraction of total catch that is composed of SPF ($C/C_{total} = 18\%$; Fig. 3c). Pikitch et al. (2014) did not provide rates of total catch in terms of weight to allow for a direct comparison of their monetary value-based support service estimate to our biomass-based rach estimate. However, they did observe that the value of the fisheries supported by SPF, but not composed of SPF, was also about twice the value of the SPF catch, indicating the importance of accounting for the indirect role that SPF play in supporting fisheries when making management trade-off decisions.

4.4. SPF as an ecosystem-structuring agent

Upwelling ecosystems stand out in our analyses because in these systems SPF are shown to be an important energy-transfer node. The SPF play the largest role as consumers of lower trophic production and as producers supporting predators and fisheries in upwelling systems. This is especially true in the Humboldt Current (Table 5), which produces more fish per unit area than any other region in the world's oceans (Chavez et al. 2008).

Marine food-webs are structured with high species diversity at the bottom and top TLs, but in upwelling ecosystems, the middle TLs are occupied by a small number of planktivorous SPF. This food-web configuration is termed a 'wasp-waist' structure (Bakun 1996). In a wasp-waist food-web, SPF groups have been hypothesized to play a pivotal role in ecosystems (e.g. Travers-Trolet et al. 2014), exerting strong bottom-up resource limits on the production of top TLs and strong top-down predation pressure limiting the biomass of bottom TLs (Cury et al. 2000). The implication of wasp-waist trophic control is that changes in SPF abundance would affect multiple TLs across the pelagic food-web. A reduction in SPF abundance would lead to a reduction in predator production and an increase in production among the mid-TL competitors of SPF. The mid-TL groups that take advantage of reduced competition do not themselves necessarily constitute an efficient alternate energy transfer pathway to higher TLs (e.g. jellyfish and mesopelagic fish) and increased detritus production and benthic food-web production may result (Shannon et al. 2009).

Our sensitivity analysis of steady-state food-webs shows which groups would benefit and which suffer from a reduction in SPF abundance. The especially large footprint and reach metrics and the strong effects that SPF have on seabirds, marine mammals, and fisheries in our sensitivity analysis on upwelling models are consistent with a wasp-waist structured food-web with strong bottom-up control by SF on predator populations. We also see that demersal fish production increases when SPF are reduced, but we did not distinguish whether this is due to increased detritus production and increased benthic food-web production or to lower competition for plankton among those demersal species that include plankton in their diets. At least in upwelling systems such as the Benguela, this has been shown to be the former (e.g. Shannon et al. 2009).

The form of the static food-web scenarios conducted here only simulates the effects of a reapportioning of available prey among consumers (i.e. no prey switching by predators) and is not able to evaluate the importance of top-down control by SPF on plankton. This is another necessary condition of a true wasp-waist system. However, the tMTI analysis does consider the net effects of both bottom-up processes, where SPF as prey limit predator production and top-down processes, where SPF as a predator limit plankton production. We see that SPF do have a relatively high impact on the food-web compared to other groups (Fig. 6b), but their impact in upwelling systems is not noticeably high compared to other eco-

system types. Other studies have cast into doubt the importance of wasp-waist control in specific ecosystems. In the northern California Current, a high degree of omnivory and the importance of euphausiids in the diets of consumers at multiple TLs creates pathways of bottom-up control that bypass the limitations of the narrow waist of SPF at mid-TLs (Miller et al. 2010). High taxonomic but low species diversity at mid-TLs can provide alternate trophic pathways between lower and upper TLs in upwelling systems (Fréon et al. 2009). Fréon et al. (2009) found a high degree of variability in the amount of lower TL production consumed by SPF and the amount of production that SPF, in turn, transfer to higher TLs. Wasp-waist control is a dynamic process, and evidence of top-down control on prey is dependent on the time-period and SPF abundance when the ecosystem is evaluated (Coll et al. 2008). Whether or not wasp-waist control is an accurate description of the tropho-dynamics of upwelling ecosystems, this survey of food-web models and that of Pikitch et al. (2014) show the important role that SPF can play as an energy transfer node across multiple ecosystem types.

Mesopelagic fish are also a mid-trophic SPF group, though we considered them separately in our analyses. Although previous modeling studies do show mesopelagics as having notable impacts on competitor and predator groups (e.g. Smith et al. 2011), we did not find mesopelagic fish to be as important an energy transfer node as other SPF groups. Though they place a large demand on primary production in open ocean models and bay/fjord/lagoon models (Table S19) they do not in turn contribute as much as other SPF species to predators or fisheries. Only in their support of marine mammals in the open ocean do they match the importance of other SPF groups. However, the biomass and trophic role of mesopelagic fish are poorly quantified in most ecosystems. These results may reflect our limited knowledge of mesopelagic fish biomass and trophic ecology when these models were constructed. Mesopelagic fish do have an additional important ecological role. Their daily vertical migration from the epipelagic in the daytime to the mesopelagic at night makes this group of SPF an important pathway for transferring plankton production and carbon from the surface to deep waters (Davison et al. 2013, Anderson et al. 2019).

4.5. Implications and next steps

The management of a single species considers the physiological limits of its productivity, its demogra-

phy, and how it is likely to respond to a realistic range of environmental conditions. Instead, an ecosystem-based fishery management (EBFM) approach 'takes major ecosystem components and services — both structural and functional — into account in managing fisheries' (Garcia et al. 2003, Lidström & Johnson 2020). EBFM is potentially more accurate because it considers the competitive and predator—prey interactions between multiple species within a changing environment that limit species' growth, thus ensuring the integrity of the ecosystem and consequently the sustainability of the target single species. EBFM is also a more versatile approach than single-species management because it allows consideration of the cost and benefit trade-offs of management policies. In ecosystems where SPF occupy a critical position for energy transfer within the food-web, or are themselves both a targeted fishery and the forage-base supporting other targeted fisheries, development of EBFM tools and protocols 'seems especially warranted' (Pikitch et al. 2014).

Though we did see some evidence of SPF playing a central wasp-waist ecosystem-structuring role in the upwelling models analyzed here, this role was not particularly stronger in upwelling models than in other models we examined. However, we did find that SPF do act as important energy transfer nodes linking lower and upper TLs and that this was particularly evident in upwelling systems and also true in continental shelf and open ocean systems. SPF appear to have a lesser structuring role in bay/fjord/lagoon, estuary, and coral reef systems, as evidenced by smaller footprint demand and reach contribution metrics and smaller impact on other consumer groups in food-web sensitivity analyses. These findings support those of Essington & Munch (2014), who concluded that trade-offs between fisheries that target SPF versus those that target predatory fish that prey on SPF are highly variable and depend on the balance between bottom-up control of SPF in food-webs and top-down control exerted through predation pressure. Our results may also reflect the lack of knowledge of early life stages of SPF and of coastal areas, where those early stages congregate.

SPF are traded internationally but global supply and price are volatile because biomasses of individual stocks depend on regionally highly variable climatic conditions (FAO 2022). Ecosystem-structuring processes are dynamic, and a next logical step following this analysis would be to conduct analyses with these same models within a time-dynamic framework. Nevertheless, even without temporally dynamic comparative modeling, this study underlines a central and

often overlooked aspect of EBFM; namely, that the complex inter-relations between SPF and their predators have variable and complex implications for simultaneous management of multiple fisheries and conservation, and that indicators such as reach and footprint as examined in this study and as found to vary with ecosystem type can be a useful tool in focusing management considerations per ecosystem type. For example, in the case of upwelling and coral reef systems, reach and footprint patterns highlight productivity-linked changes (climate change) and seabird forage as key management considerations, whereas in the open ocean processes that might influence mesopelagic fish warrant stronger focus, and in bay/fjord and coral reef systems, marine mammal—SPF interactions seem less important. Even a non-dynamic food-web model, informed by robust trophic ecology studies and multi-species ocean survey data, can serve as valuable tools for EBFM, highlighting the interactions between SPF and other species and revealing potential trade-offs between multi-species management goals and conservation objectives across diverse ecosystems. We believe this review highlights the need to continue research on network indicators, such as reach and footprint, for the management of exploited ecosystems, particularly within the context of climate change.

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