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Fisheries, the inverted food pyramid

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A global assessment of fishing patterns and fishing pressure from 110 different Ecopath models, representing marine ecosystems throughout the world and covering the period 1970–2007, show that human exploitation across trophic levels (*TLs*) is highly unbalanced and skewed towards low productive species at high *TLs*, which are around two *TLs* higher than the animal protein we get from terrestrial farming. Overall, exploitation levels from low trophic species were $<$15% of production, and only 18% of the total number of exploited groups and species were harvested $>$40% of their production. Generally, well-managed fisheries from temperate ecosystems were more selectively harvested at higher exploitation rates than tropical and upwelling (tropical and temperate) fisheries, resulting in potentially larger long-term changes to the ecosystem structure and functioning. The results indicate a very inefficient utilization of the food energy value of marine production. Rebuilding overfished components of the ecosystem and changing focus to balancing exploitation across a wider range of *TLs*, i.e. balanced harvesting, has the potential to significantly increase overall catches from global marine fisheries.

Keywords: balanced harvesting, ecopath, ecosystem approach to fisheries, exploitation rate, food security.

Introduction

Half of the world's primary production (PP) is marine (Field *et al.*, 1998), yet we harvest very little of this food energy when it is converted via the marine foodweb into fish and invertebrates useful to humans. Still, our fisheries are widely considered to be in a poor state with little room for expansion. According to the FAO statistics (FAO, 2014), ~90% of the fished stocks are either fully exploited (61%) or beyond sustainable limits (29%), and thus their potential to meet the future demand of essential micronutrients and protein for the growing human population has been questioned (HLPE, 2014; Béné *et al.*, 2015). Heavy exploitation has also led to substantial structural changes in the fished stocks and ecosystems (Pauly *et al.*, 2005; Halpern *et al.*, 2008; Christensen *et al.*, 2014) raising concerns about the status of the aquatic resources globally (Bundy *et al.*, 2012; Watson *et al.*, 2012; IUCN, 2013). For fisheries governance and management, the overarching challenge is to meet the international conventions (UNCLOS, 1982; CBD, 1992) of maintaining stocks at their most productive levels, while minimizing the impacts of extraction (Kolding *et al.*, 2015a; Garcia *et al.*, 2015a). The Ecosystem Approach to Fisheries (EAF; Garcia *et al.*, 2003) and Ecosystem-Based Fisheries Management (Pikitch *et al.*, 2004) have been proposed as holistic frameworks to deal with these objectives, and have since become one of the most important goals in fisheries management in many jurisdictions. Operationalization of the EAF, however, has proven to be difficult, in part due to misconceptions about its scope and lack of understanding how to implement it (Murawski 2007), though there has been some success in some regions (Patrick and Link, 2015). In this paper, we explore the concept of Balanced Harvesting as a means to make EAF actionable, providing advice on how fishing pressure could be distributed across trophic levels (*TLs*), species, stocks, and sizes to minimize ecosystem impacts and increase potential yield.

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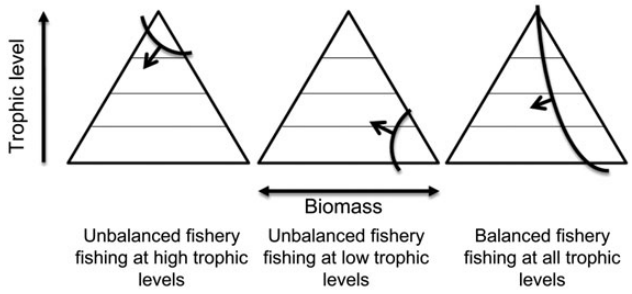

Figure 1. Different fishing patterns on a fish community illustrated as a Lindeman trophic pyramid with fish predators at the top and phytoplankon and detritus eaters at the bottom. The width of the triangle represents relative biomass on a logarithmic scale. Black curves represent selective removals, arrows the direction of increased fishing pressure. By fishing proportionally at all trophic levels and sizes, the pyramid stays internally intact. Reproduced with permission from Kolding and van Zwieten (2011), Forum for Development Studies.

Ecosystem structure and functioning can be graphically represented by the classical Lindeman trophic pyramid, and one suggestion to preserve its shape is the idea of harvesting a slice of the pyramid proportional to the abundance at its different levels (Jul-Larsen *et al.*, 2003; Bundy *et al.*, 2005) (Figure 1). Although the concept of balanced harvesting (BH) has been suggested in several papers since the 1950s (e.g. Swingle, 1950; Caddy and Sharp, 1986; Bundy *et al.*, 2005; Zhou *et al.*, 2010), a precise definition was first proposed by Garcia *et al.* (2011, 2012) as an approach to fishing that "distributes a moderate fishing mortality across the widest possible range of species, stocks, and sizes in an ecosystem, in proportion to their natural productivity, so that the relative size and species composition is maintained". While the operational definition of 'productivity' varies somewhat among studies (Law *et al.*, 2014; Burgess *et al.*, 2015), the rationale of BH is that all sizes and species are harvested at similar rates as they are produced.

BH has been theoretically explored in many recent size-based modelling papers (Jacobsen *et al.*, 2014; Law *et al.*, 2012, 2013, 2014), suggesting that matching exploitation rate with productivity as a function of species and body sizes preserves the ecosystem structure closer to its original state, and provides higher potential yields, than when exploitation is targeting large fish only. These characteristics have been explored and supported empirically in less selective small-scale inland African fisheries (Kolding and van Zwieten, 2011; Kolding and van Zwieten, 2014; Kolding *et al.*, 2015a,b) and a temperate shelf ecosystem (Bundy *et al.*, 2005). However, a broader, more comprehensive investigation into the distribution of fisheries exploitation patterns across stocks and species in different ecosystems in relation to BH has not been attempted. The aim of this paper is to analyse and describe empirically observed fisheries harvesting patterns at the global, regional, and ecosystem scale with respect to BH. We do not attempt to discuss economic, regulatory, or technical constraints on the observed fishing patterns as these will depend on cultural, social, and economic choices discussed elsewhere (Charles *et al.* 2015; Reid *et al.* 2016). We aim to provide a framework from which a discussion on how to design and operationalize EAF ecologically can be further developed. The data are derived from a global set of Ecopath models, which encompass descriptions of a wide range of marine ecosystems, temporal coverage of the past five decades and from which standardized values of catches, production, and mortality terms can be extracted. We use two approaches to explore these data: (i) a meta-analysis where metrics are combined across models at the global and regional levels and (ii) the trophic balance index (TBI; Bundy *et al.*, 2005), which examines variability in fishing patterns at the ecosystem scale. We then relate these results to the global and regional results.

We hypothesize that there will be general spatial and chronological differences in overall patterns in utilizing marine production across *TL*s and sizes from these ecosystems, and that particular configurations of exploitation will not be consistent with BH. We then explore whether these results can be attributed to the broader social and economic context across the globe and by ecosystem type. We will also use the results to present a general framework of how to measure, represent, and evaluate the overall fishing pattern and pressure in exploited multispecies ecosystems in relation to BH.

Methods

Balanced harvest

Balanced harvest is a strategy that distributes fishing in proportion to production (Garcia *et al.*, 2012), at the trophic, species, stock, or size levels in the ecosystem. Thus, to assess whether BH occurs, estimates of yield and production are required across all species in the exploited ecosystem, ideally by *TL* or size. Such estimates are readily available in a standardized format from Ecopath models (Christensen and Pauly, 1992) by species or functional groups and *TL*. Ecopath (see below) provides estimates of total annual production for each entity *i*, which depending on the Ecopath model may be a specific life stage of a species, the aggregate population of a given species, or a functional group ($P_i = P/B_i \cdot B_i$, where $P_i =$ production (ton yr^{-1}) and $B_i =$ Biomass (ton)), total annual catch (yield, $Y_i = F_i \cdot B_i$, where $F_i =$ Fishing mortality (yr^{-1}), the production to biomass ratio ($P_i/B_i =$ total mortality Z_i (yr^{-1}))). Using the data from these models, catches vs. production can be compared over the whole ecosystem. It also follows from the above definitions of Y, P, and P/B that the ratio Y/P is equivalent to F/Z, i.e. the fraction of deaths caused by fishing, also conventionally called the exploitation rate E (Patterson, 1992). As a rule of thumb in fisheries, F/Z should not exceed 0.5 [which means that $F =$ natural mortality (M) (Alverson and Pereyra, 1969]. However, Patterson (1992) and Pikitch *et al.* (2012) proposed that the exploitation rate should not exceed 0.4, particularly on forage fish, for harvest to be sustainable. This is the upper level of exploitation rate that was used in this analysis.

Ecopath with Ecosim

Ecopath with Ecosim (EwE) is a modelling framework widely used to describe and explore trophic interactions, foodweb properties and the impacts of fishing on ecosystems (Christensen and Pauly, 1992; Walters *et al.*, 1997; Christensen and Walters, 2004; Plagányi, 2007). Here we use only the Ecopath component of the EwE framework, and we use mostly input parameters. Ecopath models provide a "snapshot" of an ecosystem, accounting for the biomass of each functional group of species, their diet composition, production per unit of biomass or turnover rate (P/B), consumption per unit of biomass (Q/B), mortality from predation and fishing ($M2$ and F), accumulation of biomass (BA), and net migration (Ei). The principle behind this ecosystem modelling approach is that, for the time period of the model, biomass and energy flows in an ecosystem are calibrated so that no more is used than can be accounted for. Ecopath provides a standardized portrait of an ecosystem and its fisheries, from which estimates of production,

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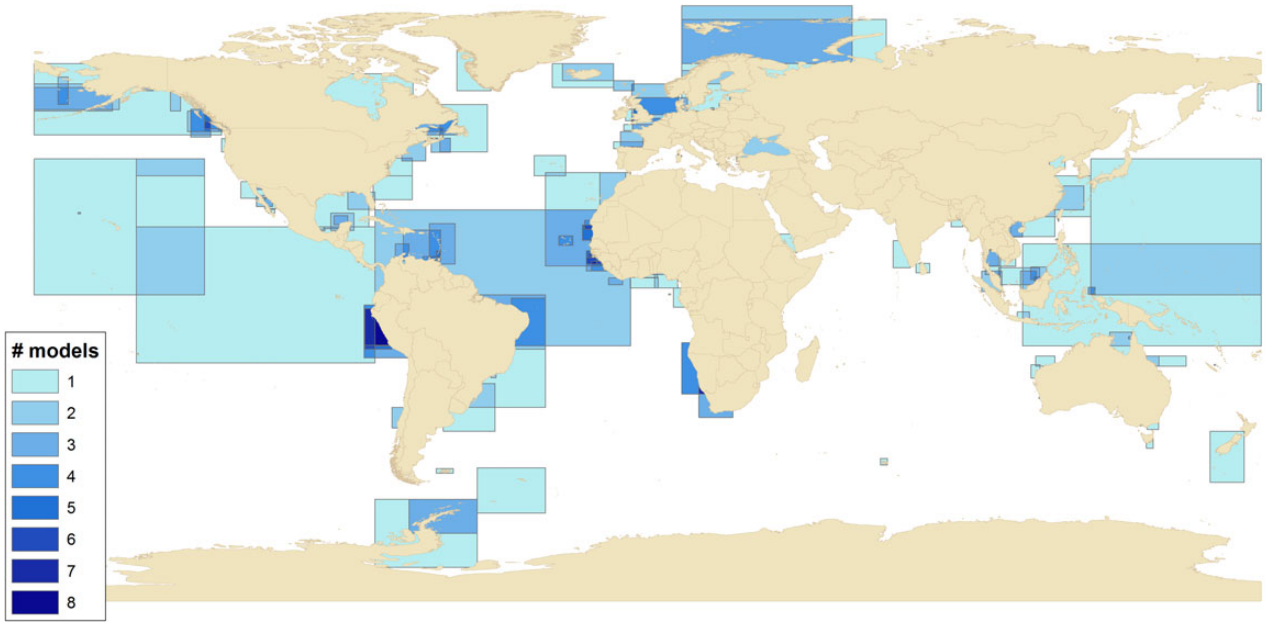

Figure 2. Geographical distribution of the 110 Ecopath models used in the analysis.

fisheries exploitation, *TL* of functional groups, trophic flows, and other foodweb properties can be derived.

Two hundred and thirty published Ecopath models from all over the world, covering ~40% of the world's ocean surface (Christensen *et al.*, 2014), were used as the starting point for this meta-analysis of the fishing patterns by *TL* globally and regionally by ecosystem. In addition to the criteria used by Christensen *et al.* (2014) to select these models, we added the following criteria to ensure that the models were appropriate for this analysis. Models were only included if: (i) they represented time periods since 1970, (ii) one or more functional groups experienced fishing mortality, (iii) most functional group biomasses were entered as input to the model as opposed to calculated by the model, ensuring that the model is well grounded in data, (iv) they were applied to exploited natural ecosystems (i.e. aquaculture-based models were excluded), and (v) ecotrophic efficiency (*EE*, the fraction of the production that is used in the system) was >0 and <1 (meaning that each functional group was constrained to use only the production that was available). This reduced the number of models from 230 to 110 (Figure 2, Table 1; Supplementary material), with a total number of functional species groups of 3665 of which 1889 (52%) were fished, which we defined as a catch fraction $>0.1\%$ of production.

The models were categorized into five main ecosystem types: high latitude, temperate, temperate upwelling, tropical and tropical upwelling (Table 1). The functional groups of all 110 models were classified into 36 main taxonomic groups (Appendix). Of the fished groups, 89% were fish, crustaceans, cephalopods, and elasmobranchs, while the remaining 11% were marine mammals, invertebrates, and seaweed.

Ecopath models are composed of user defined functional groups, ranging from primary producers (e.g. phytoplankton, macrophytes) to top predators (e.g. sharks, orcas), and can comprise a life stage of a species (e.g. juveniles), a single species, or an assemblage of related species or taxa. The number of functional groups per model ranged from 8 to 88 (mean = 30 ± 17 SD; median = 27). The mean *TL* of each functional group is estimated by Ecopath from the input consumption matrix, and was used here as the primary basis to describe ecosystem structure across the wide geographical range of models. Since there is a positive correlation between TL and size in fish (Jennings *et al.*, 2001, 2007; Romanuk *et al.*, 2011), TL can also be used as a rough proxy for organism size. This is further substantiated by examining the relationship between P/B, production, and biomass with *TL*. Previous studies have shown strong log-linear relationships between these metrics and size (Sheldon *et al.*, 1972; Boudreau and Dickie, 1992; Kerr and Dickie, 2001) and similar strong relationships exist in the Ecopath models with TL (Figure 3). The strong log-linear relation between production and TL also supports the generalization that all the individual species groups in the models can be condensed and summarized into generic TL groups at the meta-level.

Table 1. One hundred and ten Ecopath models split into five main ecosystem types and grouped by 10-year time periods.

Type	1970–1979	1980–1989	1990–1999	2000–2009	Total
High latitude	2	3	7	1	13
Temperate	4	7	25	4	40
Temperate upwelling		1	2	1	4
Tropical	7	6	15	5	33
Tropical upwelling	2	5	8	5	20
Total	15	22	57	16	110

Global meta-analysis

Functional groups from all models were ordered into 0.1 interval *TL* bins (by lower interval limits), and the fishing pattern and pressure over the whole ecosystem graphically illustrated as the log average catches plotted against log average production per unit area for each functional group or *TL* bin included. The ratio of catch to production is the exploitation rate, $E = Y/P$, so

$$\log(Y) = \log(P) + \log(E).$$

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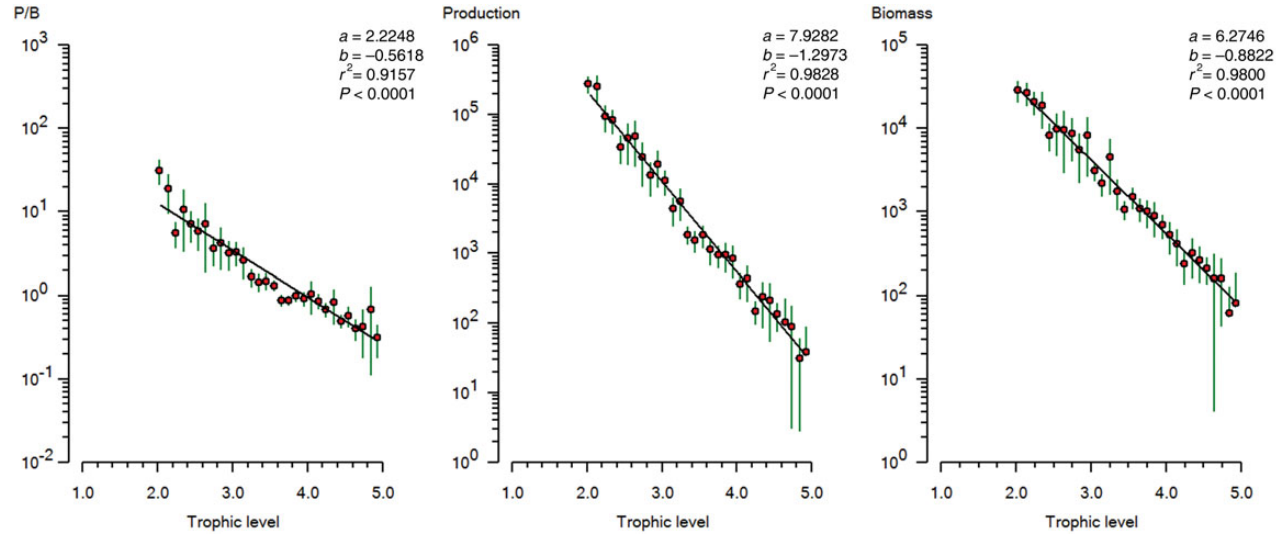

Figure 3. Overall relationships between production to biomass ratio (P/B, year^{-1}), production (kg km^{-2} yr^{-1}), and biomass (kg km^{-2}) with mean *TL* in 0.1 intervals of all functional species groups (except $TL < 2$) in 110 Ecopath models. Error bars are 95% confidence intervals. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

If all functional groups have the same exploitation rate E, then a linear regression of $\log(Y)$ against $\log(P)$,

$$\log(Y) = a\log(P) + b,$$

would have a slope of $a = 1$ and an intercept of $b = \log(E)$. Deviations from a slope of 1 indicate systematic differences in exploitation rate among functional groups. In particular, slopes <1 indicate that groups with low P are being exploited harder than groups with high P. The further the slope is away from 1, the more uneven the exploitation rate.

The intercept b of the linear regression represents the log average exploitation rate $\log(E)$. The closer the points lie to the $y = x$ line, where catch = production ($E = 1$), the higher the fishing pressure. The smaller the deviation around the slope, the more consistent is the exploitation pattern. Thus the $\log(Y)$ vs. $\log(P)$ plot gives a united comprehensive picture of both fishing pattern (how we fish) and fishing pressure (how much we fish) on the whole ecosystem.

To test differences of slopes from 0 and 1, as well as differences between ecosystem types, a separate slopes analysis was carried out through an analysis of covariance with $\log_{10}$(yield) on $\log_{10}$(production), ecosystem type and their interaction as explanatory factors with ecosystem type as co-variate. Significance of difference from slope = 1 was carried out with $\log_{10}$(production) as an offset. All linear regressions appeared to have approximately dome-shaped residuals (very low or very high TL groups were less exploited than in between): to further explore these, a generalized additive mixed model using the same three parameters as fixed effect, and a spline through $\log_{10}$(production) as a random effect was also used. As the y-intercept ($\log_{10}$(yield)) at x = zero ($\log_{10}$(production)) has no meaning unless the fishery is perfectly balanced, the y-intercepts were centred at a production level of 1000 kg km^{-2} yr^{-1}, which is equivalent to a *TL* of ~4.5. At the centred intercept $\log(Y) = \log(E)$.The results are tabulated and also presented graphically in Supplementary material. All statistical models were implemented using SAS/STAT® software Version 8 of the SAS system for Windows using the GLIMMIX and GAM procedures.

Trophic balance index

The TBI (Bundy *et al.*, 2005), one component of an Ecosystem Exploitation Index, measures the evenness (pattern) of exploitation across functional group levels such as TLs, species, stocks, or size groups by comparing the ratio of yield to production (i.e. their exploitation rate, E) at each of these levels. The evenness of exploitation is given by the coefficient of variation of Y/P, i.e. TBI = sd(Y_i/P_i)/mean(Y_i/P_i) where Y_i and P_i are, respectively, the total catch and total production of the ith TL group. To enable comparisons across ecosystems, we standardized the number of groups in each model to $N = 5$: TL 2.0–2.49, TL 2.5–2.99, TL 3.0–3.49, TL 3.5–3.99, TL 4.0+. When the exploitation rate Y_i/P_i is the same across all these groups, TBI = 0; the maximum value of TBI for $N = 5$ groups is 2.24. Models that did not contain groups at $TL = 4$ or higher were excluded from the analysis. This reduced the total number of models to 88 for estimating TBI. As above, the analyses were carried out for all functional groups at each *TL*, and for only those functional groups that were fished with an exploitation rate $E = Y/P > 0.001$ at each *TL*.

As the TBI provides a single measure of the evenness of exploitation across the whole ecosystem ($TL = 2+$), we can explore whether it is related to other ecosystem or fisheries attributes or to broader natural or economic drivers. For the former, we explored the relationship between TBI and ecosystem type (see Table 1), exploitation (Y/P and catch/area for each ecosystem model), and ecosystem status. For the latter, in the absence of a standardized measure of ecosystem status for each ecosystem, we used the proportion of stocks that were either overexploited, or collapsed at the large marine ecosystem (LME) scale for each model (Kleisner and Pauly (2011), data downloaded from www.seaaroundus.org/lme/ 27 April 2015). Several papers have suggested that there is a strong link between PP and fisheries production (e.g. Ware and Thomson, 2005; Chassot *et al.*, 2010), so we explored whether there was a link between TBI and PP, that is whether fisheries located in highly productive areas of the world are exploited more or less in balance than less productive areas. Finally, we used the UNDP Human Development Index (http://hdr.undp.org/en/countries/profiles) as a measure of the broader social and economic

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context of countries associated with each ecosystem, to test whether the pattern of exploitation of marine ecosystem was related to social and economic status. These data are provided in Supplementary material.

Results

Global meta-analysis

Overall, there is a strong decrease in total production with increasing TL (Figure 3), with ~95% loss of energy between each integer level. This is slightly higher than expected from the general "10% rule" of trophic transfer efficiency in ecosystems (the so-called Lindeman efficiency, Kozlovsky, 1968).

Figure 4a shows the global overall fishing pattern, expressed as average exploitation rate (E) per 0.1 *TL* intervals compared with the total average production (kg km^{-2} yr^{-1}). There is a marked peak of ~20–25% exploitation at *TL*s 4–5, and light exploitation (<10%) at TL 2–3. This analysis assumes that all species or groups (above TL = 2) are potentially exploitable and therefore includes all functional groups in all ecosystems. However, it is perhaps more relevant to compare the fishing pattern when only the actually exploited functional groups are included (Figure 4b). In this case the mean exploitation pressure rises by ~10% on average, but the overall pattern of higher exploitation on high *TL*s than on low *TL*s does not change much, though the slope of the total production per unit area line is less steep.

The general pattern can also be illustrated by using main taxonomic groups instead of TL-groups (Figure 5). Small pelagics (e.g. sardines, herrings, and mackerels) constitute ~50% of the total catches in all models combined, but the mean exploitation rate is only ~15% of their total production. Large demersal and pelagic fish (e.g. gadoids, groupers, and tunas), elasmobranchs and turtles (Figure 5) are sustaining the highest exploitation rates of up to 30–35% of production. The 95% confidence limits of gastropods and sea cucumbers (holothurids) are the widest, showing that these groups have a wide range of exploitation and are under very heavy exploitation in some ecosystems (typical examples are abalone and bêche-de-mer fisheries). Overall, it can be concluded that these results confirm consumer preference for large slow-growing fish, as well as selected high value species (Sethi *et al.*, 2010). Thus, the global fishing pattern is not proportional to production, and therefore is not in balance (*sensu* Garcia *et al.*, 2012).

Next we increased the resolution to main geographical fishing areas (Table 1), and explored the fishing pressure and pattern from a balanced harvest point of view, using all functional groups greater than TL = 2 in 0.1 intervals. If all the fished groups have the same exploitation rate, they should be on a straight line with a slope = 1, and with the intercept = log(F/Z) representing the average fishing pressure. Interestingly, there appear broad geographical differences in exploitation patterns (Figure 6). High latitude (Arctic and Antarctic) and temperate (primarily North Atlantic and North Pacific, Figure 1) fisheries are the least balanced in terms of production. In fact, the slopes of the linear catch regressions on *TL*s of these two types are nearly flat and not significantly different from zero ($p > 0.05$), while tropical fisheries appear the most balanced with slopes closer to 1, and a more consistent exploitation pattern across *TL*s (small deviation around the slope). For all fisheries, however, the least productive components (towards the origo) are the most heavily exploited relative to production (closer to the 1:1 line) in accordance with the global picture in Figures 4 and 5. The results of the non-linear regressions are given in Table 2 and Figure 7. While the linear components (trends) are in accordance with the least square regressions in Figure 6, the non-linear components are all significant due to the dome-shaped or more complex distribution of the residuals. These distributions generally indicate lower exploitation at annual production levels beyond ~8000 kg km^{-2}.

When only the exploited components of the ecosystems are included in the analysis (Table 2, bottom), the slopes become

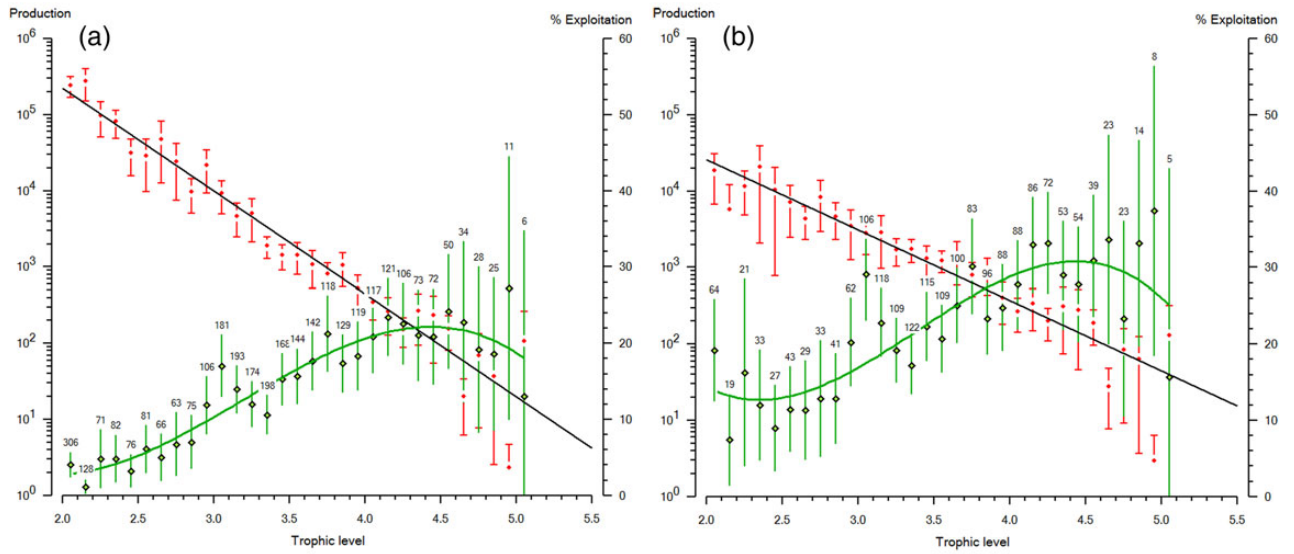

Figure 4. (a) Left axis: Total (average) production per unit area (kg km^{-2} yr^{-1}) against *TL* in 110 Ecopath models (Figure 2) across the world since 1970. All functional groups included. (b) Same as A but only with exploited functional groups ($E > 0.001$) included. Right axes: The global fishing pattern and pressure expressed as average exploitation rate ($E = Y/P = F/Z$) against *TL* in 0.1 intervals. Error bars represent the 95% confidence limits and small numbers = sample size (number functional groups in each TL interval). This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

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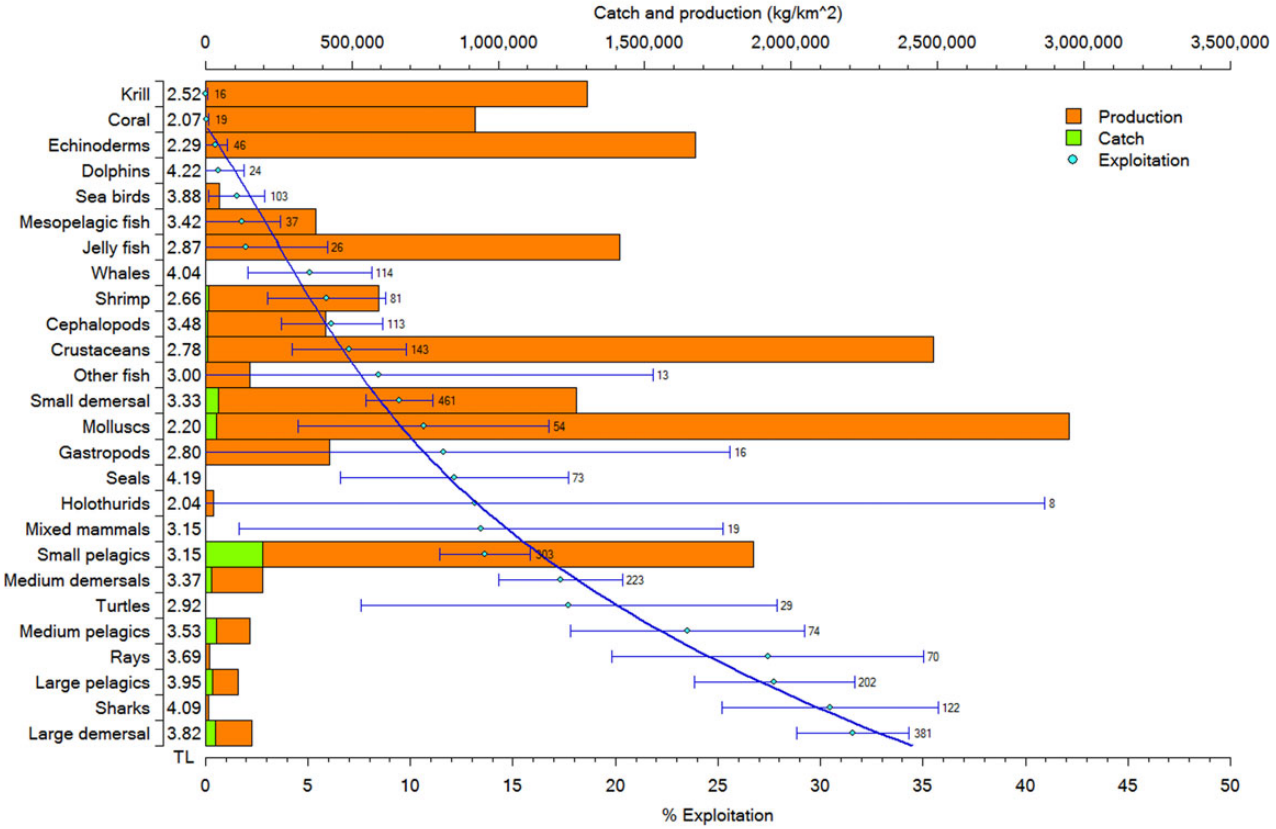

Figure 5. Total mean production (orange bars) and total mean yield (green bars) in kg km^{-2} of major functional species groups (top axis) and overall mean exploitation rates (line) with 95% confidence intervals and number of functional groups in each category (bottom axis). *X*-axis is ordered by exploitation rate. TL = mean trophic level. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

uniformly more positive (steeper), and the intercept larger (thus closer to the 1:1 line), indicating a higher average fishing pressure, as in Figure 4b. The trends also become more linear, except for temperate and tropical fisheries. However, all slopes are still significantly different from 1, indicating that even among the exploited groups the fisheries are still uneven in their exploitation rate across the targeted species. Tropical upwelling systems are the most balanced, high-latitude systems the least, while the temperate upwelling, temperate and tropical systems have very similar slopes.

The results of Figures 6, 7 and Table 2, and the difference between different ecosystems can also be summarized as in Figure 8, where the linear components of the general additive model are compared for all functional groups, and for exploited functional groups ($E > 0.001$).

The *y*-intercepts are centred at a production level of 1000 kg km^{-2} yr^{-1}, which is equivalent to a *TL* of ~4.5, where exploitation rates generally peak (Figure 4). Considering first the case where all functional groups are included, tropical upwelling fisheries are the most heavily exploited (mean $E \sim 10\%$ for exploited groups at $p = 1000$ kg yr^{-1}), but also one of the most evenly exploited (slope is closest to one). Exploitation rates in temperate fisheries are slightly higher than tropical fisheries, and are less balanced. High-latitude systems have the lowest exploitation rates and are least balanced. When only the exploited groups are considered, a slightly different interpretation of the balance of fisheries exploitation emerges: as noted above, there is little effective difference between slopes in temperate, temperate upwelling, and tropical systems, although as above, tropical upwelling systems are the most balanced with the highest exploitation rates and high-latitude systems are still the least balanced.

The general tendency of the world's fisheries has been to gradually expand the number of targets and fish lower in the trophic foodweb (Pauly *et al.*, 1998; Pauly and Palomares, 2005), so it would be interesting to examine these trends more closely in the available Ecopath models. This analysis comes with the caveat that the models included are not all from the same areas in the different time periods, and therefore direct comparisons are not possible (but see the Trophic Balance Index section). Figure 9 shows the temporal changes in fishing patterns by decade since 1970 for fisheries in temperate ($N = 40$) and tropical ($N = 33$) ecosystems, respectively. For temperate fisheries, the results indicate an increase in slope until 1990 followed by a decrease (left panel), indicating a more selective and less balanced pattern, concomitant with a decrease in exploitation level since 1980 (intercept, right panel). For tropical fisheries, there is no clear pattern in variation of either fishing pattern or fishing pressure over time. We also examined the proportion of exploited functional groups globally at different exploitation rates over 15-year intervals, and compared this with the 40% upper reference exploitation limit suggested by Pikitch *et al.* (2012). Figure 10 shows that the proportion of groups with <10% exploitation increased from 41 to 54% since 1960, while the proportion of overexploited groups decreased slightly from 18 to 16%. Figures 9 and 10 indicate that the global fishing pressure has not increased over the last three decades.

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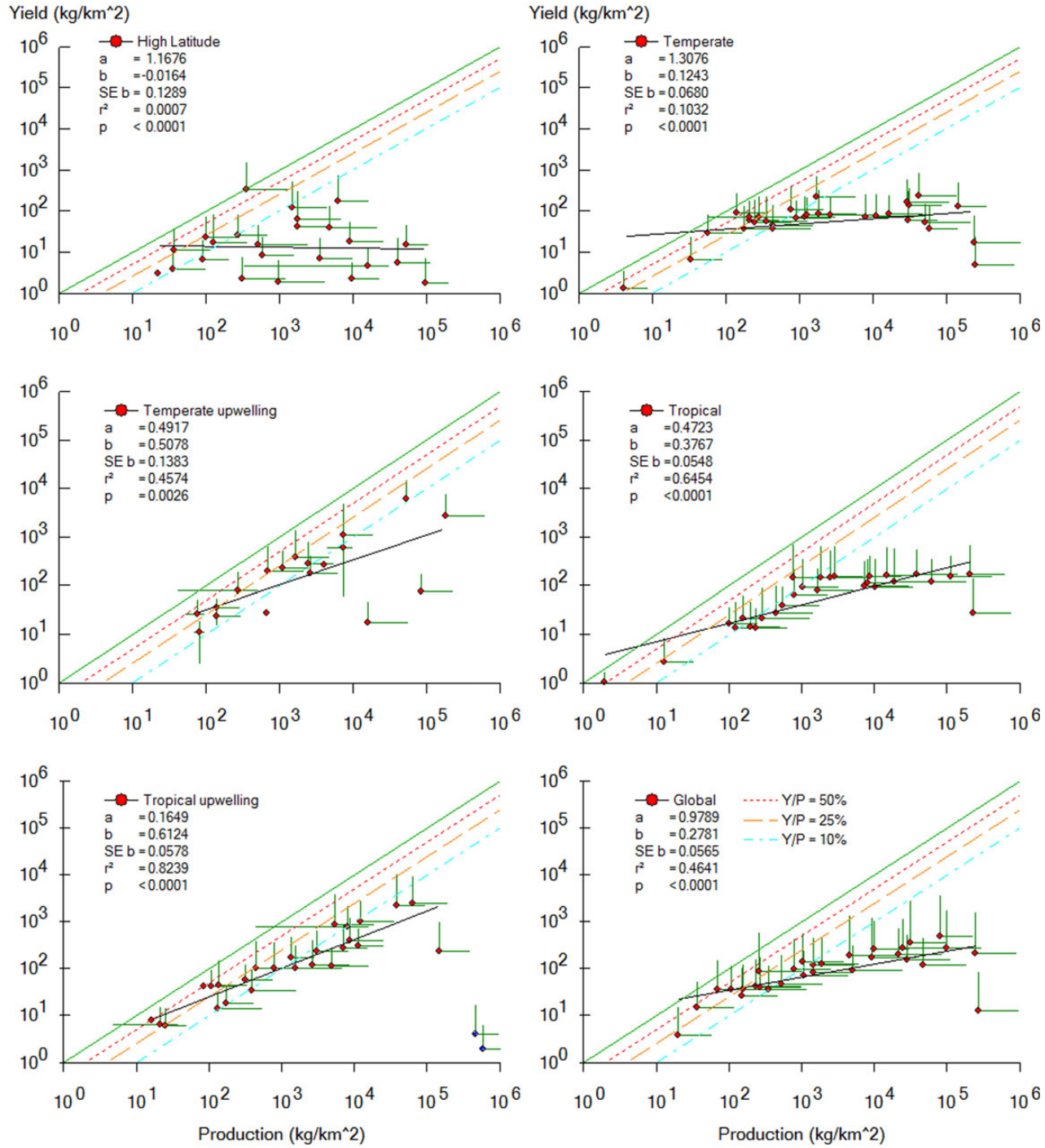

Figure 6. Average fishing pattern in five main ecosystem types across the world since 1970, and the total global average, expressed as $\log_{10}$ yield (kg km^{-2} yr^{-1}) vs. $\log_{10}$ production (same units). Each point is the mean of functional groups in 0.1 *TL* intervals (Figure 3) between TL 2 and TL 5, green error bars are standard deviations. The more the slope deviates from the 1:1 line (green) between yield and production, the more "unbalanced" (*sensu* Garcia *et al.*, 2012) the fishery is. Fishing pressure or exploitation rate (E) is inversely correlated with orthogonal distance from the 1:1 line where yield = production. Exploitation rates equivalent to 10, 25, and 50% are given as parallel lines. *p*-values give the test of slopes $\neq 1$. All slopes are significantly different from 1, but High latitude, Temperate, and Temperate upwelling are not significantly different from zero. Two outliers consisting of benthos and gastropods (blue circles) have been omitted from the trend in Tropical upwelling. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Trophic balance index

The TBI provides a single measure of balanced exploitation for each ecosystem: the exploitation rate E is exactly the same for all *TL*s when TBI = 0. Observed values ranged from the maximum of 2.24 for 3 models to a low of 0.59. Thus no individual ecosystem had perfectly balanced exploitation rates (Figure 11a). The same pattern is seen

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Table 2. Results of the regression analysis of log10(yield) over log10(production) globally and on five different ecosystem types using a GAM.

		Linear component				Non-linear component: spline				
All groups	**Nobs**	**Intercept**	**Pr > |t|**	**Slope**	**Pr > |t|**	**d.f.**	**Smooting parameter**	**GCV**	**SumSq**	**Pr > ChiSq**
Global	30	0.98	<0.01	0.28	<0.001	3.00	0.990	0.07	1.97	<0.001
High latitude	24	1.17	<0.001	−0.02	<0.001	1.00	0.997	0.41	1.63	<0.05
Temperate	31	1.10	<0.001	0.22	<0.001	3.00	0.990	0.14	2.85	<0.001
Temperate upwelling	17	0.99	<0.05	0.28	<0.001	3.00	0.891	0.32	1.75	<0.05
Tropical	28	0.47	<0.001	0.38	<0.001	3.00	0.984	0.04	2.39	<0.001
Tropical upwelling	26	0.17	n.s.	0.61	<0.001	3.00	0.980	0.10	10.06	<0.05
Exploited groups only (E > 0.001)										
Global	30	0.18	n.s.	0.64	<0.001	3.00	0.990	0.07	0.27	n.s.
High latitude	23	0.22	n.s.	0.50	<0.01	0.14	0.331	0.33	0.09	n.s.
Temperate	31	0.21	n.s.	0.63	<0.001	3.00	0.988	0.09	0.86	<0.01
Temperate upwelling	17	0.23	n.s.	0.62	<0.05	2.00	0.097	0.27	0.11	n.s.
Tropical	28	0.03	n.s.	0.62	<0.001	3.00	0.982	0.07	0.76	<0.01
Tropical upwelling	26	−0.10	n.s.	0.77	<0.001	3.00	0.981	0.06	0.14	n.s.

Each observation represents the mean of functional groups in *TL* in 0.1 lower *TL* intervals between 2 and 5.1. *p* values give tests of slopes on the 1:1 line of log10(catch) over log10(production). Regressions are over all trophic groups (top) and exploited groups only (E > 0.001) (bottom). GCV, generalized cross-validation (method in choosing the smoothing parameter of the spline).

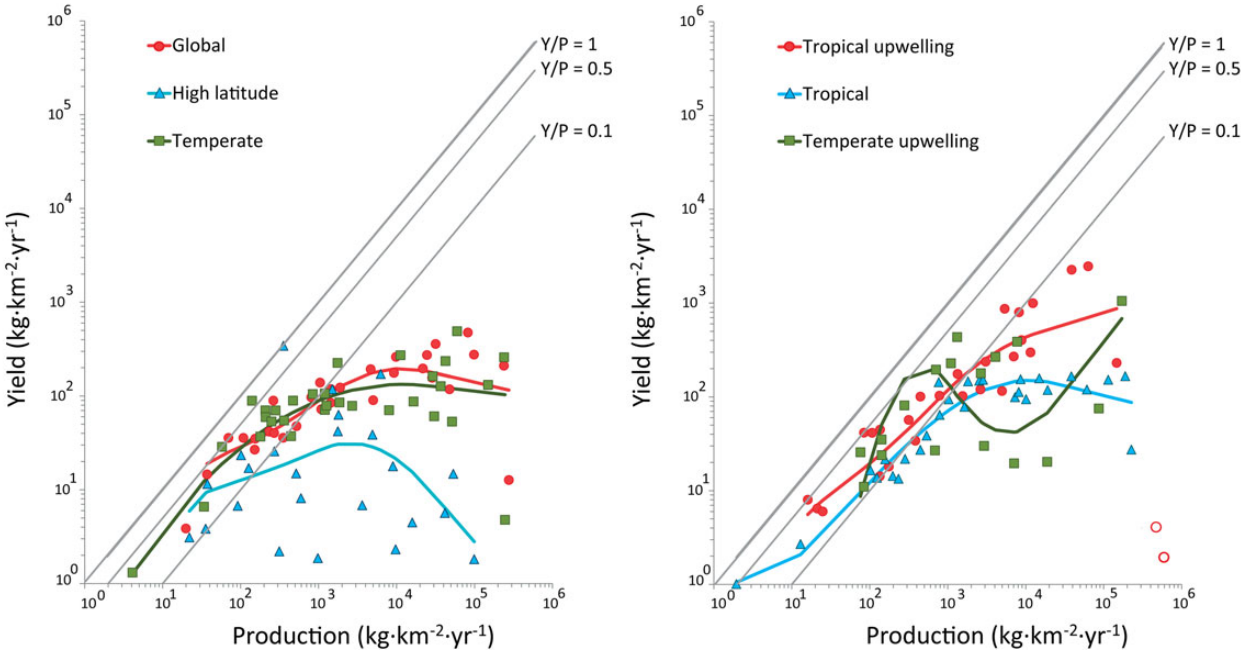

Figure 7. A summary of the fishing pattern and fishing pressure globally and across five different ecosystem types using a mixed effects model with a spline as random effect to show the general non-linear and non-balanced harvest patterns across *TL*s. High latitude and temperate fisheries, left panel, and temperate upwelling, right panel, are least balanced, and tropical and tropical upwelling fisheries, right panel, the most balanced. Each point is the mean of all functional groups in 0.1 TL intervals between TL 2 and TL 5. Open circles are groups of gastropods and benthic organisms and are not taken into account. All non-linear patterns are significantly different from the linear component. In the regression all data points (averages per trophic bin of 0.1) are weighted for the number observations over which the average is taken (see Supplementary material). This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

when only exploited functional groups with E > 0.001 are included in each TL, although there are some differences in the rank order of the ecosystems (Figure 11b), and the values of TBI were generally lower in accordance with the steepening of the slopes (Table 2). Differences between the two results are also due to the variation in exploitation within *TL*s, and the number of exploited functional groups included at each *TL* bin.

In the ecosystems at the top of Figure 11, where TBI was at, or close to, maximum, only one *TL* was exploited, usually *TL* 4+, and the models were either of high-latitude systems or from oceanic systems. Models at the bottom of Figure 11, with lower TBIs, were more evenly exploited across all *TL*s. When all functional groups were considered, 9 ecosystems had a TBI <1, of which 5 were tropical ecosystems and 4 were temperate ecosystems. When only exploited functional groups were considered, 29 ecosystems had a TBI <1, composed of 13 tropical (7 upwelling) and 16 temperate (1 upwelling) systems.

When examined by ecosystem type (Table 1) the lowest TBI values occurred in the tropical systems, and the highest in the high-latitude and temperate systems, but for each ecosystem type, there is

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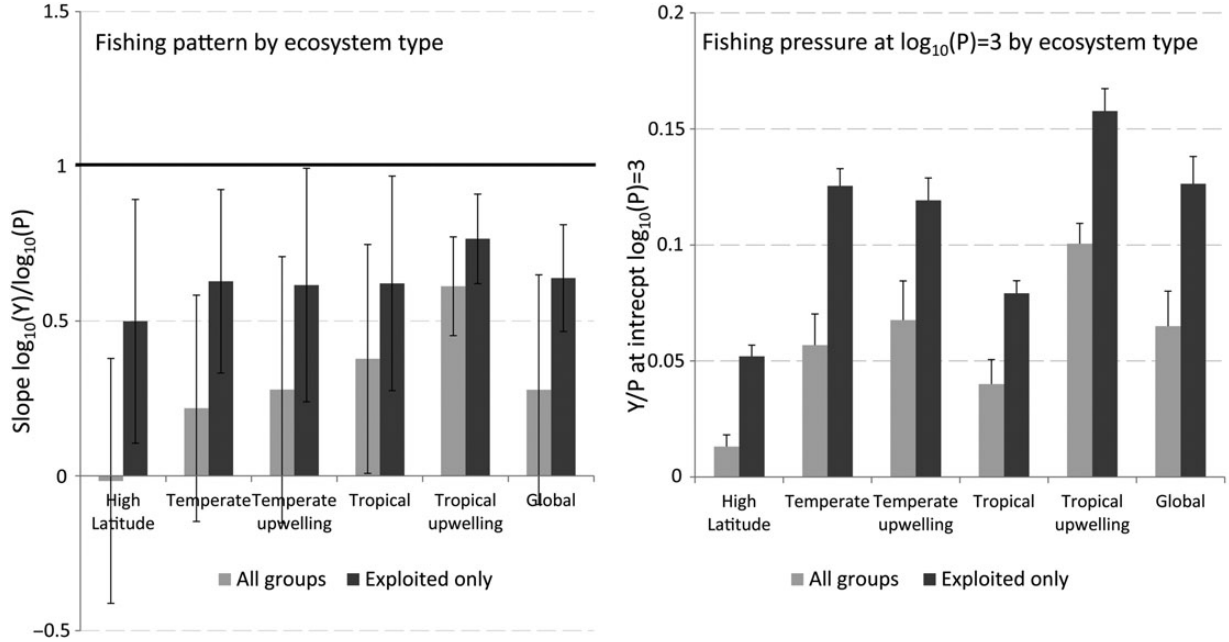

Figure 8. Left panel: Fishing pattern. Values of the slope of the of the regression of $\log_{10}(Y)$ over $\log_{10}(P)$ for the five ecosystem types. Error bars ($\pm$ 1.96SE) indicate significance of the difference between the slope = 1 (balanced) and slope = 0. Black horizontal line represents slope = 1. Right panel: Fishing pressure. Exploitation rate (Y/P) per ecosystem type calculated from the intercept of the regression of $\log_{10}(Y)$ over $\log_{10}(P)$ centered on $\log_{10}(P) = 3$ (=1 ton km^{-2} yr^{-1}), for which groups exploitation is generally highest (Figure 4). Values are shown for models including all groups by *TL* bins of 0.1 and exploited groups only.

a wide spread of TBI values (Figure 12). However, statistically, the means of these distributions are different [ANOVA: $F = 3.605$, $p < 0.01$ (all groups); $F = 3.425$, $p < 0.05$(exploited groups)], indicating some relationship between the balance of exploitation in an ecosystem and the type of ecosystem. Student's *t*-test showed a significant difference between mean TBI of fisheries exploiting high latitude and temperate ecosystems [$p < 0.001$ (all groups); $p < 0.01$ (exploited groups)] and between fisheries exploiting high latitude and tropical upwelling ecosystems [$p < 0.01$ (all groups); $p < 0.01$ (exploited groups)]: in each case, mean TBI is higher in the high-latitude systems, where TBI for some high-latitude systems attained maximum possible values, indicating exploitation is completely out of balance with production . A *post hoc* multiple comparison test (Bonferroni corrected) gave the same general pattern. There was no significant difference between tropical and temperate fisheries. These results are largely consistent with the results of the $\log(Y)/\log(P)$ analysis above.

TBI and total catch rates had a significant negative relationship across all models ($\log_{10}$(yield) kg km^{-2} yr^{-1}), $r^2 = 0.38$, $p < 0.001$ (all functional groups) and $r^2 = 0.262$, $p < 0.001$ (exploited groups only); TBI was negatively related to exploitation rate when all functional groups were considered ($r^2 = 0.18$, $p < 0.001$), but there was no significant relationship when only exploited functional groups were used.

When the relationships between TBI and total catch rates or exploitation rates were examined by ecosystem type (exploited groups), there were noisy significant negative relationships between TBI and exploitation rate, and TBI and catch per area in the exploited tropical (including upwelling) ecosystems (Table 3), indicating that in these systems, with greater exploitation, TBI decreased. Relationships were not significant in the temperate systems. There were no significant relationships between TBI and model period, LME stock status (Kleisner and Pauly, 2011), or the Human Development Index, although there is a weak relationship between TBI and primary productivity ($r^2 = 0.086$, $p < 0.05$, not shown) and LME ($r^2 = 0.068$, $p < 0.05$, not shown)

Discussion

In this analysis, we have used a subset of the ecosystem models used by Christensen *et al.* (2014) that encompass a globally representative sample of the world's main marine ecosystems and fisheries over both time and main ecosystem types (Figure 2, Table 1; Supplementary material). All models were based on the same standardized approach and were constructed by independent ecosystem modellers using local datasets and have all been documented (Christensen *et al.*, 2014).

The global overall fishing pattern since 1970 from 110 Ecopath models (Figure 4) shows a marked peak at *TL*s 4–5, and very light exploitation (<10%) at TL 2–3, indicating that fisheries removals are disproportionately taken from the high *TL* species (Figure 5). While nearly all high *TL* groups have traditionally been exploited all over the world for centuries, some of the low *TL* groups, such as jellyfish and echinoderms, have little acceptance as human food. Still, several highly productive low *TL* groups such as small demersal fish, crustaceans, cephalopods, and molluscs are regularly consumed by humans and, on average, are lightly exploited (Figure 5). The average TL at which humans feed is ~2.21 (Bonhommeau *et al.*, 2013), so the marine harvest pattern diverges sharply with human feeding behaviour from land-based sources, where 80% of our diet is from plants (Duarte *et al.*, 2009) at TL = 1. In contrast, we are feeding approximately two TLs higher from the oceans, resulting in ~99% of the corresponding energy being lost in transfer inefficiency if we follow the general 10% transfer rule (Figure 3b). This may explain why only ~2% of the global

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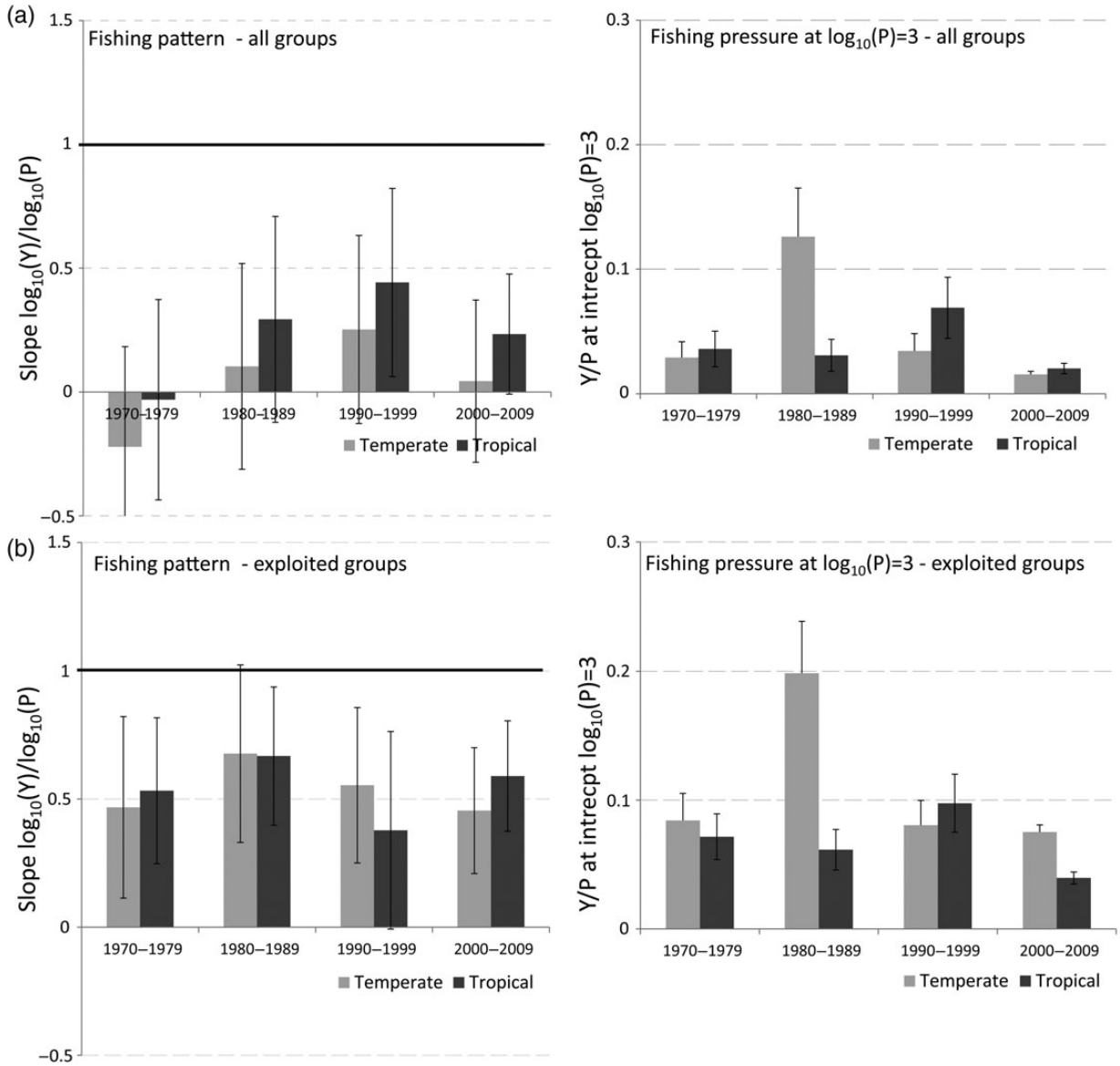

Figure 9. Top 2 panels are all groups in 0.1 TL intervals. Bottom 2 panels are exploited groups ($E > 0.001$) only. Left panels: Fishing pattern. Values of the slope of the regression of $\log_{10}(Y)$ over $\log_{10}(P)$ temperate and tropical systems in 73 Ecopath models spanning four decades. Error bars ($\pm$ 1.96SE) indicate significance of the difference between the slope = 1 (balanced) and slope = 0. Black horizontal line represents slope = 1. Right panels: Fishing pressure. Development in the mean exploitation rate (Y/P) of temperate and tropical systems over four decades. Y/P is calculated from the intercept of the regression of $\log_{10}(Y)$ over $\log_{10}(P)$ centered on $\log_{10}(P) = 3$ (=1 ton km^{-2} yr^{-1}), for which groups exploitation is generally highest.

human food is taken from the oceans (FAO, 2006; Bonhommeau *et al.*, 2013) despite fish being one of the most important sources of animal protein (Béné *et al.*, 2015) and generally believed fully utilized or overexploited (FAO, 2014).

The aquatic food chain, however, is basicly different from land, which must be taken into consideration when comparing human food potential. Most importantly, the overwhelming majority of marine primary producers are micro-algae and cyanobacteria of a few μm in size, in contrast to terrestrial vegetation dominated by large vascular plants. This means that the average size of the herbivorous grazers (*TL* 2) in the two realms differ by several orders of magnitude (Figure 13), which again cascade into higher *TL*s. Land-based food chains are thus generally shorter because of much larger organisms at TL 1–3, and thereby much more efficient at terms of providing food for humans. Still, the global fishing pattern presented here indicates that we potentially could substantially increase food production while rebuilding overfished stocks if we shifted more towards harvesting lower *TL*s and released the pressure at higher level. This conclusion is in line with the general recommendation of Zhou *et al.* (2014) and agrees with the findings of Jennings and Collingridge (2015). The present skewed fishing pattern towards high *TL*s is also in accordance with Christensen *et al.* (2014) who from the same models used here calculated that the abundance of large predatory fish (TL > 3.5) has significantly declined globally over the past 100 years, while the abundance of small fish (*TL* 2–3) has increased. If this increase in small forage

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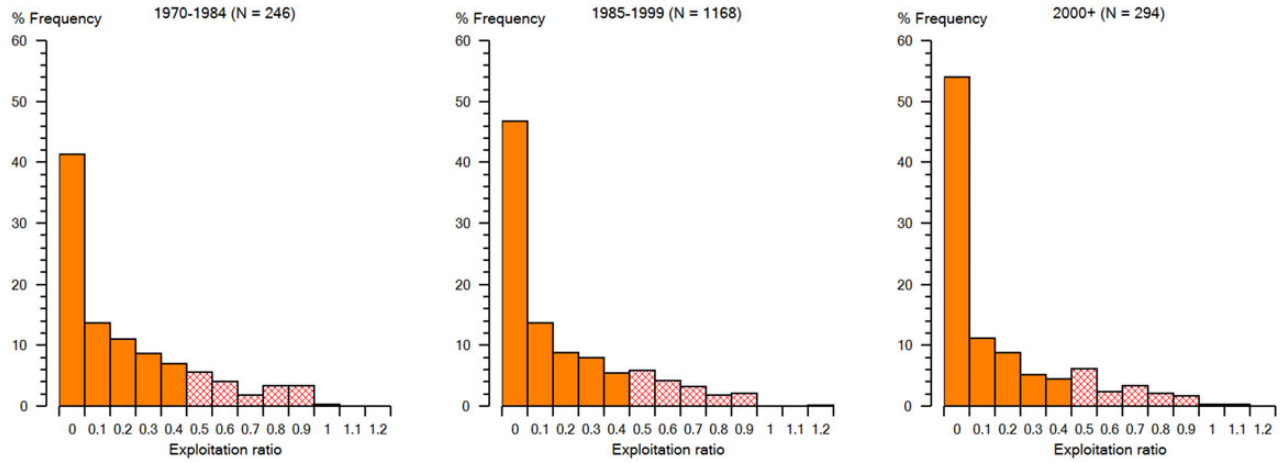

Figure 10. Frequency distribution of all fished functional groups ($F/Z > 0.001$) by 15-year intervals since 1970 in relation to their fishing pressure (exploitation ratio). Relative proportion of overfished groups ($F/Z > 0.4$) is indicated by hatched bars and has decreased slightly from 18 to 16% over the period. *N* is total number of exploited groups in each time period. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

fish is correct, it is even more noteworthy considering that the captures of these species has also increased fourfold over the past 50 years from ~5 to 20 million ton (Smith *et al.*, 2011). Similar long-term changes with a decrease in large high *TL* species and a cascading increase in low *TL*s, as reflected in size distributions have been demonstrated in the heavily fished North Sea (Rice and Gislason, 1996; Daan *et al.*, 2005; Garcia *et al.*, 2012).

While several high level trophic groups are heavily exploited (Figure 5), the overall global fishing pressure (Y/P) at the ecosystem level, where species are aggregated by per 0.1 TL bin is well under 0.4 even for the highest *TL*s. This result is in agreement with Zhou *et al.* (2014), who in their global meta-level analysis found a very light level of marine exploitation on average. Several individual groups or species, however, are overexploited as indicated by the spread in the Y/P plots and Figure 10, although the proportion has apparently not increased over the past five decades. Still, examined from this broader ecosystem perspective and taking into account both exploited and unexploited trophic groups, our results are almost the inverse of the global FAO statistics where 61% of the ~450 assessed stocks were fully exploited and 29% overexploited in 2011 (FAO, 2014). In contrast, the large majority of the exploited functional groups in the present analysis are lightly harvested on average with <10% of the annual production (Figure 10).

Only a small proportion of the world's marine resources are formally assessed (16% of the harvested fish taxa according to Ricard *et al.*, 2012) and most of these stocks are from well-monitored temperate fisheries (Worm and Branch, 2012). For most of the world's fisheries, particularly from tropical and subtropical fisheries, only catch data are available and the regular FAO assessments are mainly based on these (Costello *et al.*, 2012). The reliability of that approach in the absence of additional contextual data is currently under heavy scrutiny (Branch *et al.*, 2011; Daan *et al.*, 2011; Froese *et al.*, 2012, 2013) and it has been questioned how depleted non-assessed stocks actually are in tropical small-scale fisheries (Kolding *et al.*, 2014).

We do not know how many of the stocks included as functional groups in the present set of Ecopath models are also subject to formal stock assessments. However, the direct estimation of fishing pressure in these models, expressed as fishing mortality (F) relative to total mortality (Z), which is equal to yield relative to production (Y/P), is not different from any standard stock assessment method, and is much more robust than assessments based on catch data alone, which contain no information on stock size. If the present set of models, representing species and stocks at the functional group level and covering most of the worlds fished regions, is indeed representative, then the picture that emerges may not be as bleak for the unassessed stocks as otherwise reported (Costello *et al.*, 2012; Worm and Branch, 2012). While tropical fisheries in general do not have higher exploitation rates than temperate fisheries (Figure 8), their exploitation patterns extend over a wider range of trophic groups at higher production levels, so generally lower in the food chain. As well as appearing more balanced in their exploitation pattern when all functional groups are considered from the $\log(Y)/\log(P)$ plots, they also appear well within safe margins (Figures 8 and 9).

Balanced harvesting distributes fishing mortality across groups in proportion to their productivity (Garcia *et al.*, 2012). This suggests that the exploitation rate $E = Y/P$ should not vary too much across species, sizes, or *TL*s. The general concern that we are fishing too many small fish, thus endangering the sustenance of higher *TL*s (Smith *et al.*, 2011; Pikitch *et al.*, 2012) seems not supported by the present analysis since higher *TL*s, which have the lowest abundance and production (Figure 3), are the most heavily exploited. Our results indicate that there is potential to increase exploitation at low *TL*s if we want to balance extraction across the ecosystem. In practice, this would be operationalized at the species and stock level, excluding any low *TL* species or stocks that already have high exploitation rates.

We have tested and illustrated the multispecies fishing pattern and pressure across ecosystems using two different methods: (i) The novel logarithmic Y/P plots (Figures 6 and 7), where slope and deviance from the pattern around the slope indicate the overall balance and the specific deviations from the balance, while the distance from the 1:1 line, expressed globally through a regression model or from individual data points is a measure of pressure (exploitation rate), and (ii) the Trophic Balance Index (Bundy *et al.*, 2005), which gives the coefficient of variation of fishing pressure across exploited *TL*s. The two methods, however, differ in their approach. One is graphical with multiple observations, so it is specifically concerned with changes and patterns detectable within ecosystem components, and their relations along the yield and production axes. In contrast, TBI is a single numeric index that measures the variability of exploitation

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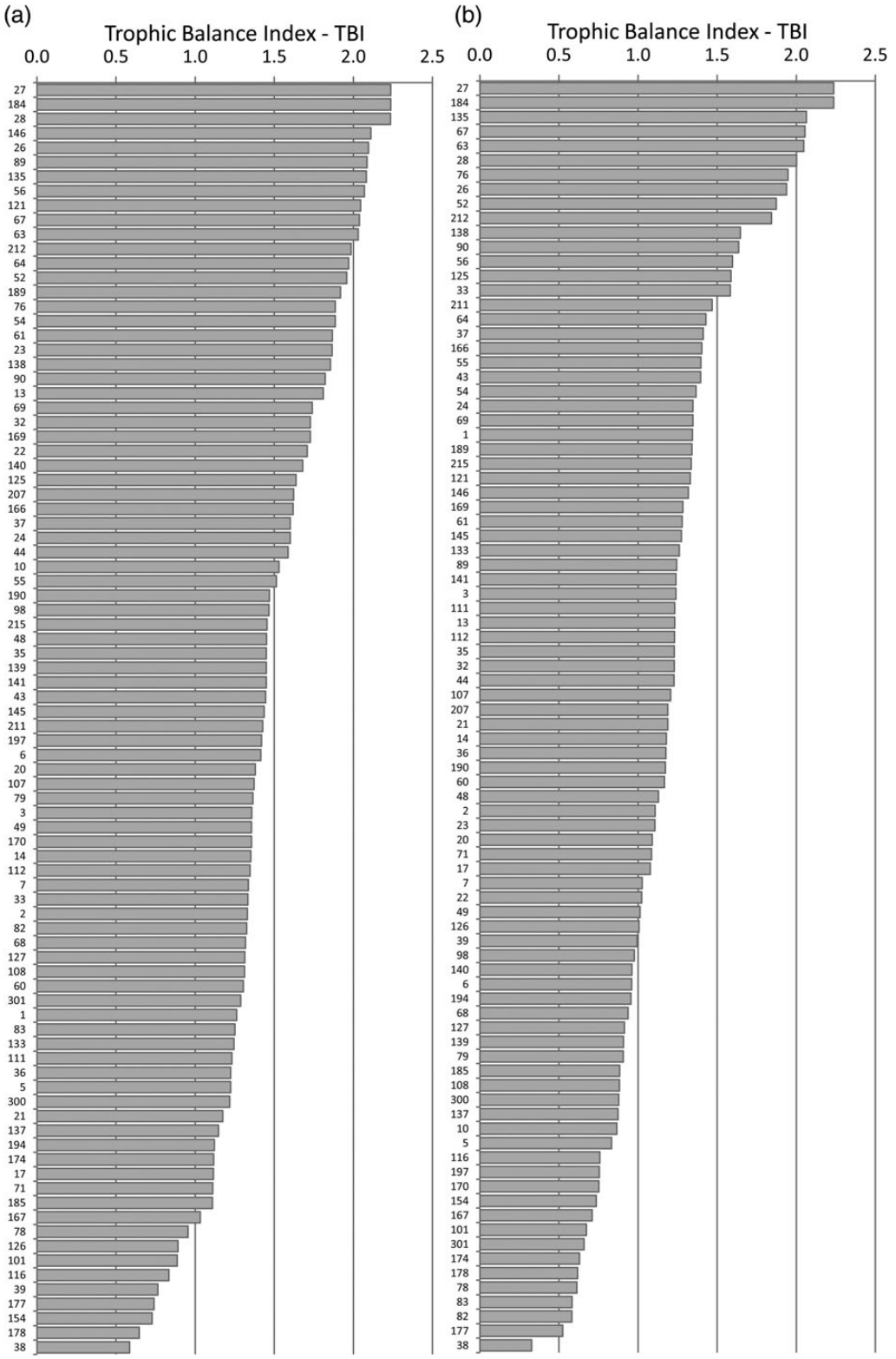

Figure 11. TBI for the subset of 103 modelled, exploited marine ecosystems when (a): all functional groups included. (b) Same as (a) but only including exploited functional groups ($E > 0.001$). Numbers refer to Ecopath models and are provided in Supplementary material.

across ecosystem-specific *TL*s without any assumption of ordering or overall level of exploitation. Still, they complement each other and were largely consistent by equally showing that the world's marine ecosystems are not balanced across *TL*s and functional groups, but clearly subject to highly selective exploitation.

Two sets of analyses were conducted, one using all functional groups and the other only the exploited functional groups within each ecosystem. Regardless of which method was used, from a global perspective, the general tendency emerging when all functional groups were considered is that fisheries in high latitude and

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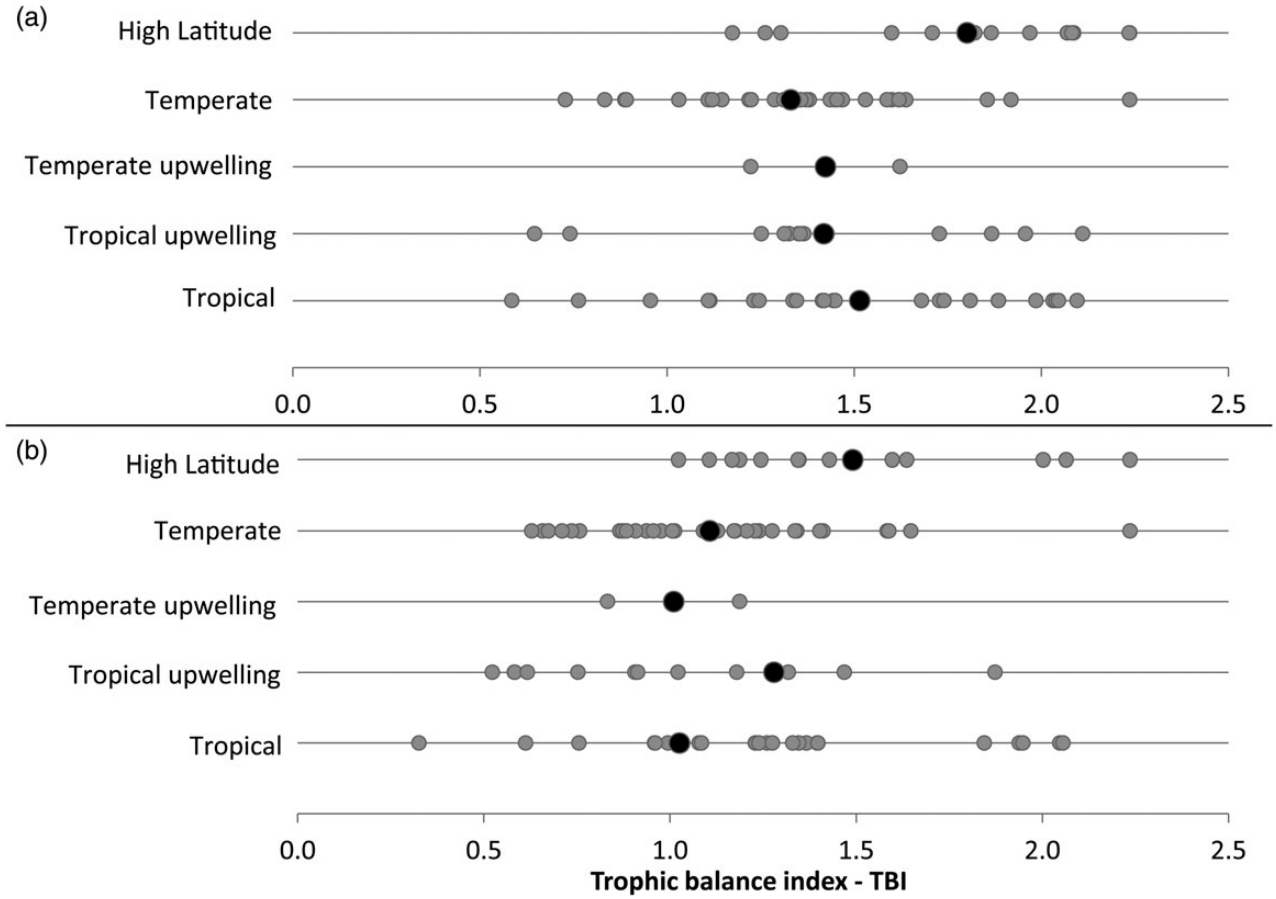

Figure 12. TBI plotted against ecosystem type for the subset of 103 models, where average values are indicated by the black filled circles. (a) All functional groups included. (b) Same as (a) but only including exploited functional groups ($E > 0.001$).

Table 3. Results of linear regressions (r^2) of TBI with exploitation ($E = Y/P$) and $\log_{10}$(catch/area) by ecosystem type.

	TBI and *E*		**TBI and catch/area**	
	All FGs	***E* > 0.001**	**All FGs**	***E* > 0.001**
Tropical (including upwelling)	0.247**	0.216**	0.254**	0.511***
Temperate	0.017	0.166**	0.065	0.146**
High latitude	0.044	0.052	0.068	0.210

Tropical and temperate regressions were negative or non-significant for temperate and all functional groups (FGs), high latitude were non-significant. $^{**}p < 0.01$, $^{***}p < 0.001$.

temperate ecosystems are the least balanced, whereas fisheries in upwelling and tropical ecosystems appear more balanced across all *TL*s. This indicates that these fisheries exploit a wider variety of the available production more equally (Figure 8a). When only exploited groups are considered, this picture is less clear, but still confirmed that tropical fisheries exploit a broader range of *TL*s than temperate fisheries. Therefore, as the overall global fishing pattern plainly shows the world's market preference for large fish at high TLs, and as this preference, to a large extent, is dominated by consumers in Western industrial countries (Sethi *et al.*, 2010; Tsikliras and Polymeros, 2014), a hypothesis was formed that the general fishing pattern would become increasingly balanced when moving from North to South, i.e. from predominantly economically driven fisheries in the developed countries to primarily food-driven fisheries in developing countries, and from high value market species in the temperate shelf fisheries to less valuable industrial species in upwelling systems.

In partial support of this hypothesis, high latitude and temperate fisheries are the least balanced when examining the Y/P plots when all functional groups are considered, while the balance improves when moving into tropical fisheries and upwelling systems. Upwelling fisheries, both temperate and tropical, are the most balanced when all functional groups are considered (Figure 7), which makes sense as they are traditionally focused on highly productive, low *TL* species. However, when only the exploited functional groups were used in the analysis, there was little difference between the different system types (except high latitude), although none were close to balance. A first step towards BH might therefore thus be balancing current exploitation with production of exploited species.

The TBI analysis indicates that across all ecosystems examined there is a wide range of values, mostly at the higher end of the possible range (Figure 12): exploitation patterns are very uneven and skewed towards the higher *TL*s, with no systematic pattern across time or space. The results indicate that there are more tropical (including upwelling) systems at the lower end of TBI values and therefore closer to balance, which is consistent with the results above. On average, fisheries in temperate ecosystems had the lowest TBI when all functional groups were considered. Ecosystems with lower TBI also had higher mean exploitation rates and higher total catches.

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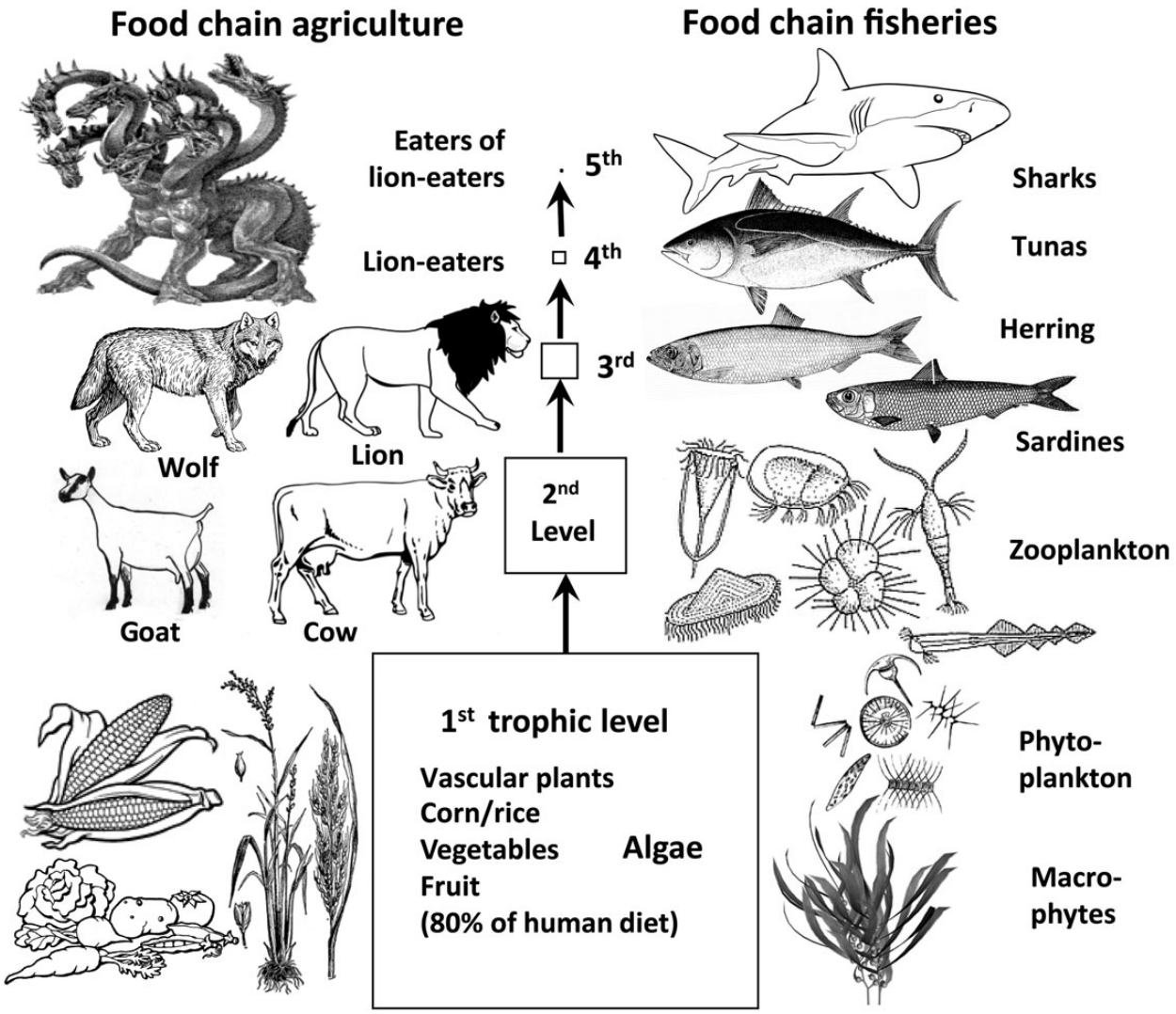

Figure 13. A comparison of the terrestrial agricultural and the aquatic fisheries food chains along *TL*s. The average human *TL* is 2.21 (Bonhommeau *et al.*, 2013), meaning we are ~80% terrestrial vegetarians. In contrast, we are feeding about two TLs higher in most fisheries targeting large fish, resulting in ~99% of the corresponding energy being lost in transfer inefficiency. Modified from Duarte *et al.* (2009).

Further investigation is required to determine whether TBI decreased because of increased exploitation across lower *TL*s as a response to the collapse of larger, higher *TL* species, thus increasing catch, as predicted by our hypothesis. Although we expected that there might be links between the TBI index and other global indices, there were only weak relationships for LME and PP, which are correlated. This lends further support to the indications noted above of differences between ecosystem type and TBI.

In conclusion, the predominant fishing pattern on marine resources is like an inverted food pyramid, which is highly inefficient from an energetic point of view as >99% of the PP is metabolized when reaching TLs 4–5. At the global level, the fishing pattern is strongly skewed towards high TLs; perhaps a more balanced harvest regime would substantially increase yields (Jacobsen *et al.*, 2014; Law *et al.*, 2014; Kolding *et al.*, 2015a); this would require decreasing fishing pressure on and rebuilding and protecting the low productive large predators. If so, this would be a step towards satisfying both our international agreements of extracting the maximum sustainable yield, while maintaining ecosystem structure and functioning (Kolding *et al.*, 2015a; Garcia *et al.*, 2015a,b), and meeting the call for an EAF. However, under the present market preferences for large fish, such a change would have strong economic consequences in some parts of the world (Burgess *et al.*, 2015; Charles *et al.*, 2015; Garcia *et al.*, 2015a), and there would be a need to change human consumption patterns towards small fish instead of large, as is already the case for small-scale fisheries in many Asian and African countries (Kolding *et al.*, 2015a,b). The added bonus, however, would be a much more nutritious diet as small fish are usually eaten whole or beheaded only, and most of the essential micronutrients in fish, such as calcium, iron, zinc, and vitamin A are concentrated in the parts of the fish we normally discard when serving filleted muscle only (Kawarazuka and Béné, 2011; Beveridge *et al.*, 2013; FAO, 2014).

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Appendix

Table A1. The 3655 original functional groups in 110 Ecopath models categorized into 34 main taxonomic groups (sorted with ascending mean *TL*) with corresponding number of groups fished, mean P/B, mean Q/B, and mean *EE* with SD of the means.

Groups	No. of groups	No. of fished	Mean *TL*	SD *TL*	Mean P/B	SD P/B	Mean Q/B	SD Q/B	Mean *EE*	SD *EE*
Detritus	118		1						0.45	0.34
Mangroves	5		1		14.01	29.35			0.16	0.16
Macrophytes	72	2	1.03	0.25	13.81	18.68	0.13	1.1	0.4	0.34
Discards	21	1	1.06	0.28	0.3	1.37	2.86	13.09	0.29	0.35
Phytoplankton	137		1.08	0.33	188.08	214	34.98	238.69	0.61	0.3
Microbial	7		1.86	0.38	211.64	362.28	442.54	719.64	0.63	0.37
Holothurids	8	5	2.04	0.06	1.53	1.83	8.87	8.83	0.69	0.37
Coral	19	2	2.07	0.52	1.87	3.03	33.45	120.94	0.58	0.27
Molluscs	54	26	2.2	0.3	1.93	1.97	11.45	8.76	0.64	0.33
Benthos	279	29	2.24	0.55	8.66	26.03	24.42	54.76	0.73	0.29
Echinoderms	46	11	2.29	0.38	1.03	1.18	4.75	4.41	0.6	0.34
Zooplankton	214	3	2.32	0.41	37.24	58.08	131.11	204.84	0.74	0.27
Krill	16	1	2.52	0.53	4.11	3.92	92.1	183.55	0.8	0.24
Other	29	11	2.55	1.53	3	5.11	12.9	20.01	0.58	0.36
Shrimp	81	52	2.66	0.46	5.57	9.65	30.74	47.91	0.86	0.19
Crustaceans	143	82	2.78	0.38	3.42	7.49	15.7	28.94	0.83	0.21
Gastropods	16	5	2.8	0.5	2.09	0.77	10.49	4.12	0.83	0.2
Jelly fish	26	4	2.87	0.42	15.62	16.04	46.83	51.41	0.43	0.37
Turtles	29	14	2.92	0.58	0.24	0.36	7.9	21.17	0.43	0.32
Other fish	13	6	3	0.71	0.98	1.02	6.19	4.75	0.83	0.25
Mixed mammals	19	8	3.15	1.04	0.07	0.03	23.8	13.72	0.25	0.36
Small pelagics	303	231	3.15	0.48	1.65	1.23	10.28	6.31	0.8	0.23
Small demersal	461	296	3.33	0.54	1.76	3.63	10.52	14.87	0.72	0.28
Medium demersals	223	181	3.37	0.55	0.99	0.95	6.37	5.63	0.78	0.24
Small mammals	3		3.38	0.21	0.32	0.33	103.5	12.62	0.06	0.05
Mesopelagic fish	37	7	3.42	0.44	1.66	1.44	11.88	18.79	0.65	0.33
Cephalopods	113	64	3.48	0.4	2.86	1.79	14.13	16.31	0.81	0.21
Medium pelagics	74	67	3.53	0.54	1.05	0.88	7.56	5.56	0.72	0.27
Rays	70	51	3.69	0.5	0.58	0.82	4.39	3.99	0.52	0.36
Large demersal	381	362	3.82	0.47	0.75	0.56	4.78	3.06	0.71	0.28
Seabirds	103	13	3.88	0.5	1.03	1.97	72.8	54.86	0.2	0.29
Large pelagics	202	177	3.95	0.49	1.17	1.3	8.51	6.87	0.71	0.27
Whales	114	27	4.04	0.56	0.1	0.31	10.22	6.46	0.17	0.28
Sharks	122	108	4.09	0.49	0.51	0.48	4.54	2.84	0.49	0.34
Seals	73	40	4.19	0.43	0.16	0.32	19.34	27.12	0.32	0.34
Dolphins	24	3	4.22	0.43	0.07	0.03	22.18	12.12	0.22	0.32
Total	3655	1889	3.04	1.01	11.82	59.6	22	86.12	0.65	0.33

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