

# Fisheries, the inverted food pyramid

---

**Jeppe Kolding<sup>1,2</sup>, Alida Bundy<sup>3</sup>, Paul A.M. van Zwieten<sup>4</sup>, and Michael J. Plank<sup>5,6</sup>**

<sup>1</sup> Department of Biology,  
University of Bergen,  
High Technology Center,  
PO Box 7800, N-5020, Bergen Norway  
Email: [jeppe.kolding@uib.no](mailto:jeppe.kolding@uib.no)

<sup>2</sup> Hjort Centre for Marine Ecosystem Dynamics,  
5817 Bergen, Norway.

<sup>3</sup> Fisheries and Oceans Canada,  
Bedford Institute of Oceanography,  
PO Box 1006, Dartmouth, NS B2Y 4A2, Canada.  
Email: [alida.bundy@dfo-mpo.gc.ca](mailto:alida.bundy@dfo-mpo.gc.ca)

<sup>4</sup> Aquaculture and Fisheries Group  
Wageningen University  
PO Box 338, 6700AH Wageningen  
Email: [paul.vanzwieten@wur.nl](mailto:paul.vanzwieten@wur.nl)

<sup>5</sup> School of Mathematics and Statistics,  
University of Canterbury,  
Christchurch 8140, New Zealand.  
Email [michael.plank@canterbury.ac.nz](mailto:michael.plank@canterbury.ac.nz)

<sup>6</sup> Te Pūnaha Matatini, a New Zealand Centre of Research Excellence.

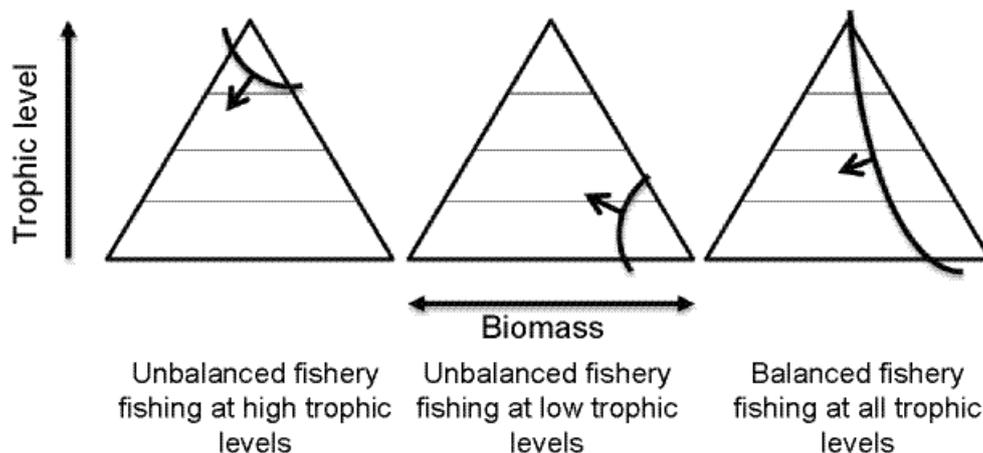
## **Abstract**

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 to 2007, show that human exploitation across trophic levels is highly unbalanced and skewed towards low productive species at high trophic levels, which are around two trophic levels higher than the animal protein we get from farming. Overall exploitation levels from low trophic species were less than 15% of production, and only 18% of the total number of exploited groups and species were harvested above 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 utilisation 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 trophic levels, ie balanced harvesting, has the potential to significantly increase overall catches from global marine fisheries.

**Key words:** Ecosystem approach to fisheries, Balanced harvesting, Exploitation rate, Food security, Ecopath

## Introduction

Half of the world's primary production is marine (Field et al., 1998), yet we harvest very little of this food energy when it is converted via the marine food web 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), around 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 (EBFM, 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, species, stocks and sizes in order to minimise ecosystem impacts and increase potential yield.



**Figure 1.** Different fishing patterns on a fish community, illustrated as a Lindeman trophic pyramid with fish predators at the top and phytoplankton 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 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) ( Fig. 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. (2012; 2011) 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.

Balanced harvesting has been theoretically explored in a number of recent size-based modelling papers ([Law et al., 2013](#); [2012](#); [2014](#); [Jacobsen et al., 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 Zwieter, 2011](#); [Kolding and Zwieter, 2014](#); [Kolding et al., 2015a](#); [2015b](#)) 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 balanced harvesting. 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 operationalise 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 standardised 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 ([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 utilising marine production across trophic levels and sizes from these ecosystems, and that particular configurations of exploitation will not be consistent with balanced harvesting. 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**

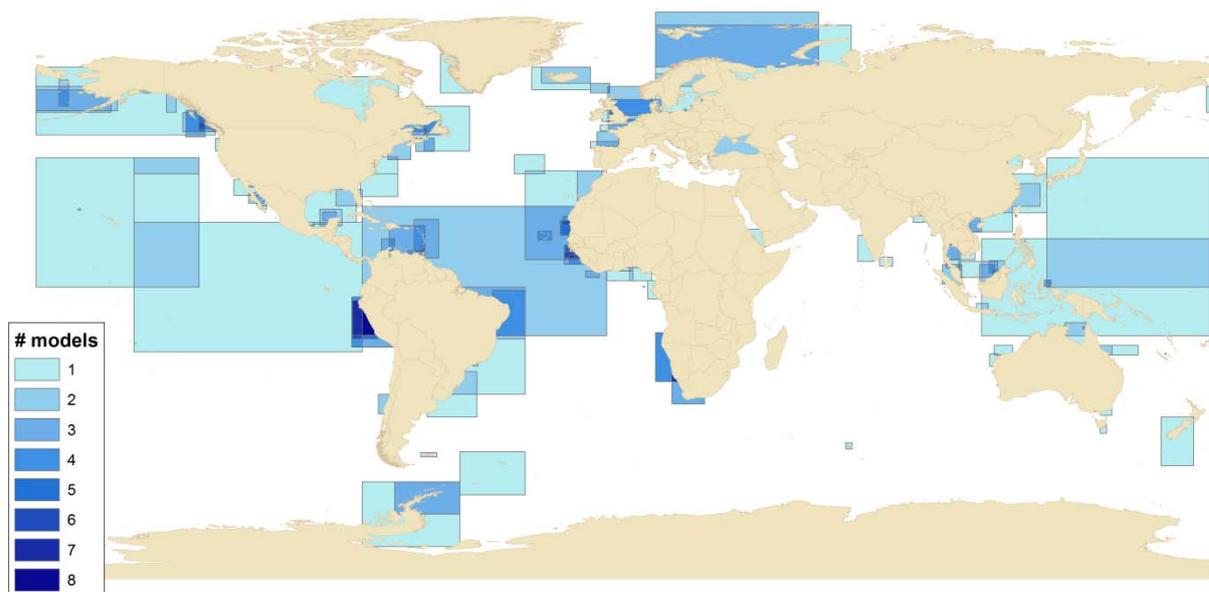
### *Balanced harvest*

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, in order to assess whether balanced harvesting occurs, estimates of yield and production are required across all species in the exploited ecosystem, ideally by trophic level or size. Such estimates are readily available in a standardised format from Ecopath models ([Christensen and Pauly, 1992](#)) by species or functional groups and trophic level. 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 ( $\text{ton} \cdot \text{yr}^{-1}$ ) and  $B_i$  = Biomass (ton)), total annual catch (yield,  $Y_i = F_i \cdot B_i$ , where  $F_i$  = Fishing mortality ( $\text{yr}^{-1}$ ), the production to biomass ratio ( $P_i/B_i$  = total mortality  $Z_i$  ( $\text{yr}^{-1}$ ))). Using the data from these models, catches versus 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 general 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, food web properties and the impacts of fishing on ecosystems (Christensen and Pauly, 1992; Christensen and Walters, 2004; Walters et al., 1997; 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 ( $M_2$  and  $F$ ), accumulation of biomass ( $BA$ ) and net migration ( $E_i$ ). 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 standardised portrait of an ecosystem and its fisheries, from which estimates of production, fisheries exploitation, trophic level of functional groups, trophic flows and other food-web properties can be derived.



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

230 published Ecopath models from all over the world, covering around 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 trophic level 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 greater than zero and less than 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 (Fig. 2, Table 1, **Supplementary online material**), with a total number of functional species groups of 3665 of which 1889 (52%) were fished, which we defined as a catch fraction bigger than 0.1% of production.

**Table 1.** 110 Ecopath models split into 5 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

The models were categorised into 5 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 1). 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 trophic level (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 fishes (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 trophic level. 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 generalisation that all the individual species groups in the models can be condensed and summarised into generic TL groups at the meta-level.

#### *Global Meta-Analysis*

Functional groups from all models were ordered into 0.1 interval trophic level 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 trophic level bin included. The ratio of catch to production is the exploitation rate,  $E = Y/P$ , so

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

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 less than 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 both 0 and 1, as well as differences between ecosystem types, a separate slopes analysis was carried out through an analysis of covariance with  $\log_{10}(\text{yield})$  on  $\log_{10}(\text{production})$ , ecosystem type and their interaction as explanatory factors with ecosystem type as co-variate. Significance of difference from slope=1 was carried out with  $\log_{10}(\text{production})$  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  $\log_{10}(\text{production})$  as a random effect was also used. As the  $y$ -intercept ( $\log_{10}(\text{yield})$ ) at  $x=\text{zero}$  ( $\log_{10}(\text{production})$ ) has no meaning unless the fishery is perfectly balanced, the  $y$ -intercepts were centred at a production level of 1000  $\text{kg}/\text{km}^2/\text{yr}$ , which is equivalent to a trophic level of around 4.5. At the centred intercept  $\log(Y)=\log(E)$ . The results are tabulated and also presented graphically in **Supplementary online 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 trophic balance index (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 (that is, their exploitation rate,  $E$ ) at each of these levels. The evenness of exploitation (TBI) is given by the coefficient of variation of  $Y/P$ , i.e.  $\text{TBI} = \text{sd}(Y_i/P_i) / \text{mean}(Y_i/P_i)$  where  $Y_i$  and  $P_i$  are respectively the total catch and total production of the  $i^{\text{th}}$  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,  $\text{TBI}=0$ ; the maximum value of TBI for  $N = 5$  groups is 2.24. Models that did not contain groups at trophic level 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 trophic level, and for only those functional groups that were fished with an exploitation rate  $E=Y/P > 0.001$  at each trophic level.

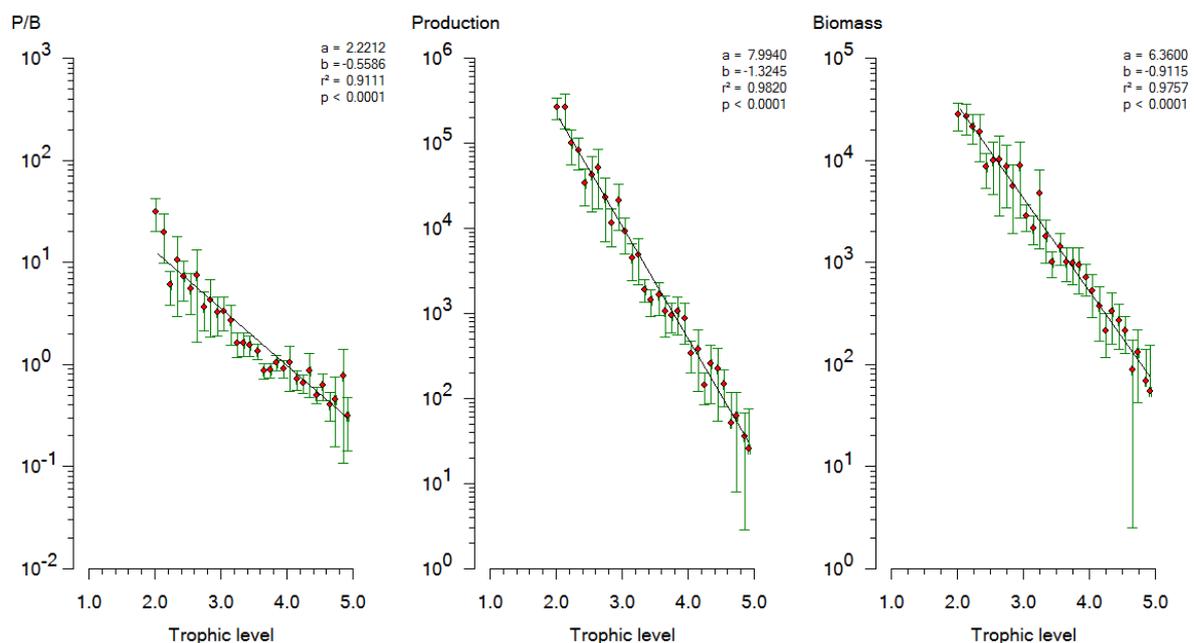
As the TBI provides a single measure of the evenness of exploitation across the whole ecosystem ( $\text{TL}=2+$ ), we can explore whether it is related to other ecosystem or fisheries attributes or to broader natural or economic drivers. For the former, we explored the relationship between TBI and ecosystem 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 standardised 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/](http://www.seaaroundus.org/lme/) 27 April 2015). Several papers have suggested that there is a strong link between primary production (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. Lastly, we used the UNDP Human Development Index (<http://hdr.undp.org/en/countries/profiles>) as a measure of the broader social and economic 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 online material**.

## Results

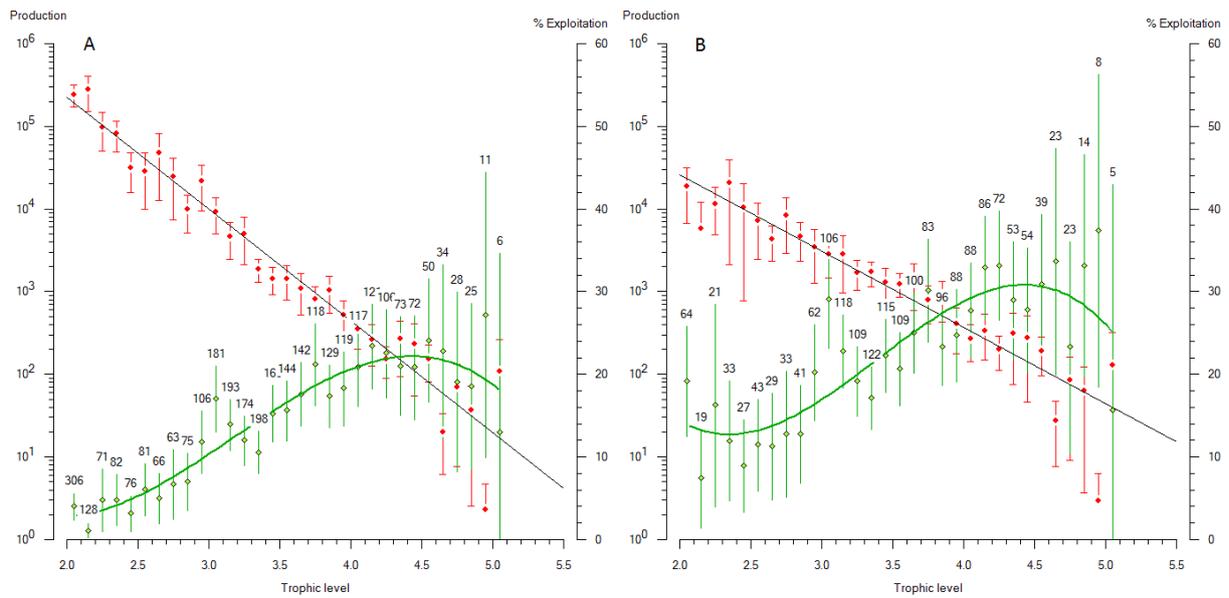
### Global Meta-Analysis

Overall, there is a strong decrease in total production with increasing TL (Fig. 3), with about 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)).

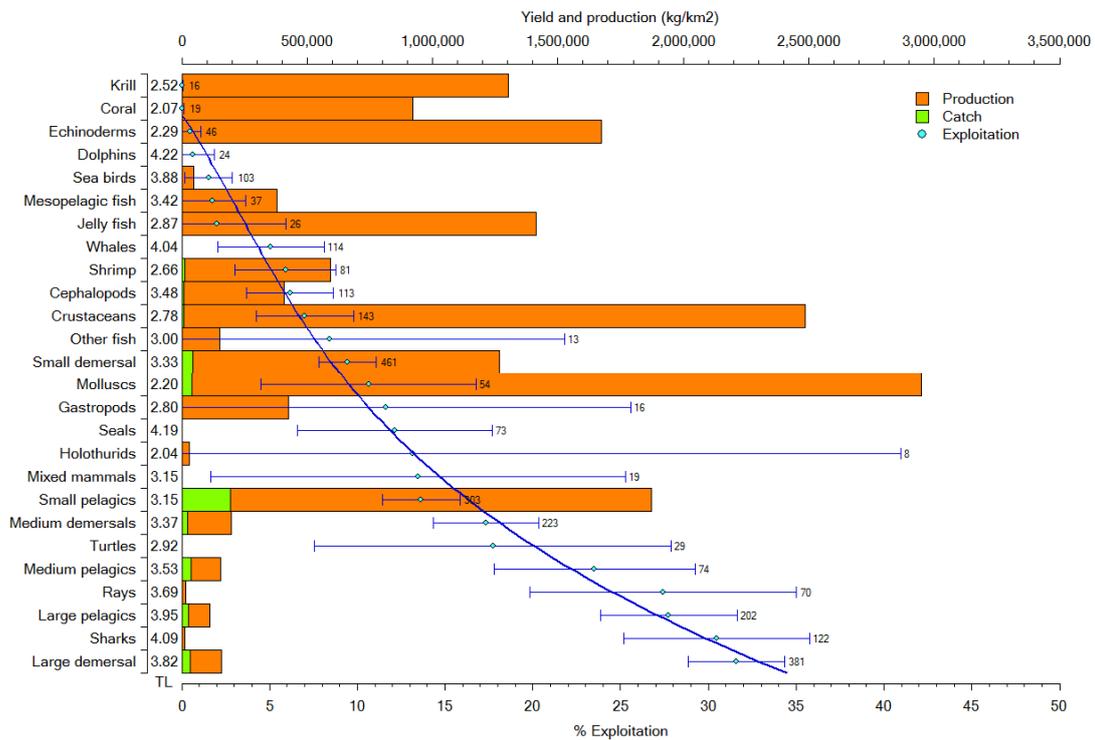


**Figure 3.** Overall relationships between production to biomass ratio (P/B, year<sup>-1</sup>), production (kg·km<sup>-2</sup>·year<sup>-1</sup>) and biomass (kg·km<sup>-2</sup>) with mean trophic level in 0.1 intervals of all functional species groups (except TL < 2) in 110 Ecopath models. Error bars are 95% confidence intervals.

Figure 4a shows the global overall fishing pattern, expressed as average exploitation rate (E) per 0.1 trophic level intervals in comparison with the total average production (kg/km<sup>2</sup>/yr<sup>-1</sup>). There is a marked peak of around 20-25% exploitation at trophic levels 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 (Fig. 4b). In this case the mean exploitation pressure rises by about 10% on average, but the overall pattern of higher exploitation on high trophic levels than on low trophic levels does not change much, though the slope of the total production per unit area line is less steep.



**Figure 4.** A: Left axis: Total (average) production per unit area ( $\text{kg}\cdot\text{km}^2\cdot\text{year}^{-1}$ ) against trophic level (TL) in 110 Ecopath models (Fig. 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).



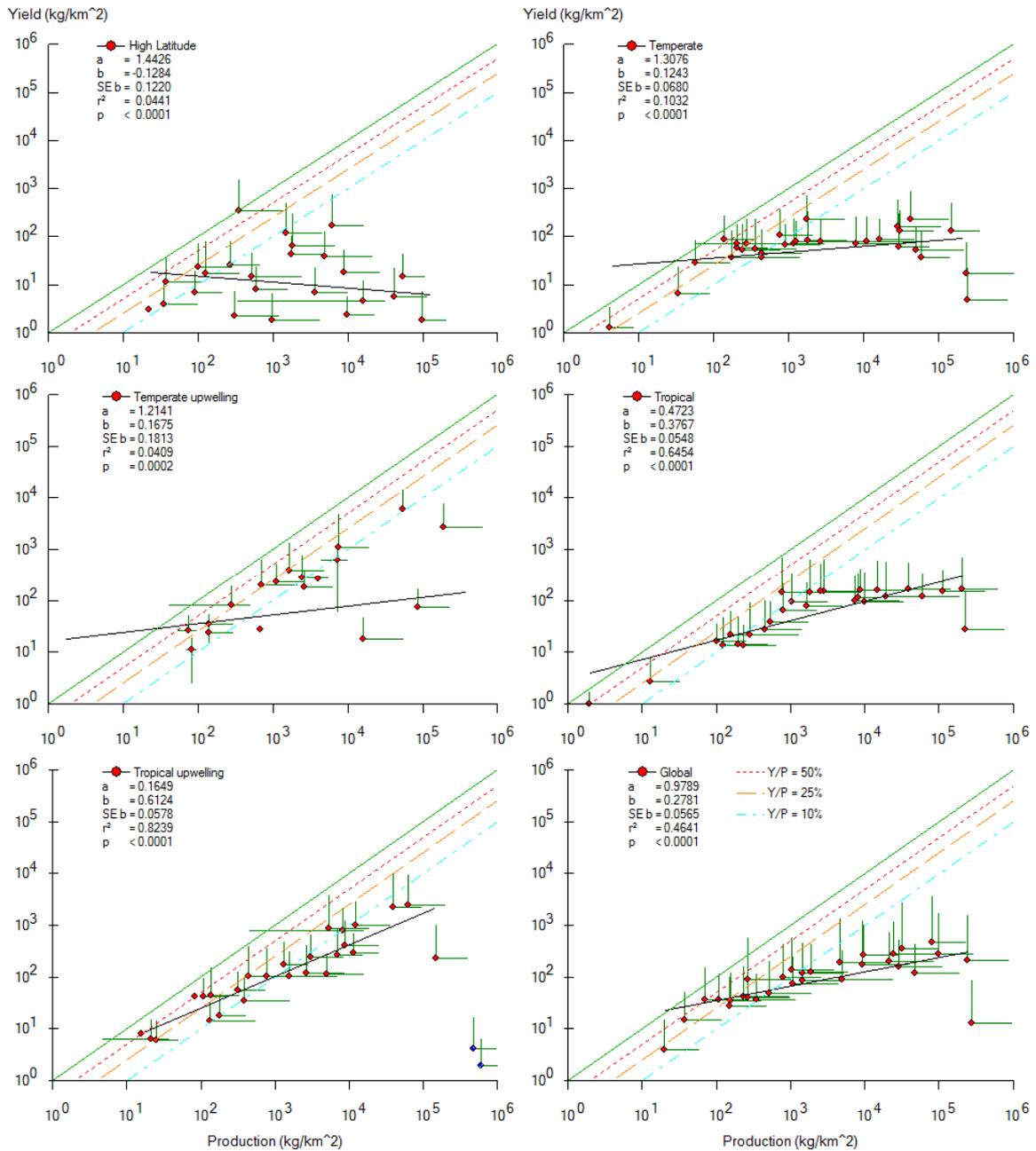
**Figure 5.** Total mean production (orange bars) and total mean yield (green bars) in  $\text{kg}\cdot\text{km}^{-2}$  of major functional species groups (top axis) and overall mean exploitation rates (line) with 95% confidence intervals and number of functional groups in each category (bottom axis). X-axis is ordered by exploitation rate. TL = mean trophic level.

The general pattern can also be illustrated by using main taxonomic groups instead of TL-groups (Fig. 5). Small pelagics (e.g. sardines, herrings, and mackerels) constitute around 50%

of the total catches in all models combined, but the mean exploitation rate is only about 15% of their total production. Large demersal and pelagic fish (e.g. gadoids, groupers, and tunas), elasmobranchs and turtles (Fig. 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 to be broad geographical differences in exploitation patterns (Fig. 6). High latitude (Arctic and Antarctic) and temperate (primarily North Atlantic and North Pacific, Fig. 1) fisheries are the least balanced in terms of production. In fact, the slopes of the linear catch regressions on trophic levels 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 trophic levels (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 Figs 4 and 5. The results of the non-linear regressions are given in Table 2 and Fig. 7. While the linear components (trends) are in accordance with the least square regressions in Fig. 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 around 8000 kg/km<sup>2</sup>.

When only the exploited components of the ecosystems are included in the analysis (Table 2, bottom), the slopes become uniformly more positive (steeper), and the intercept larger (thus closer to the 1:1 line), indicating a higher average fishing pressure, as in Fig. 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.



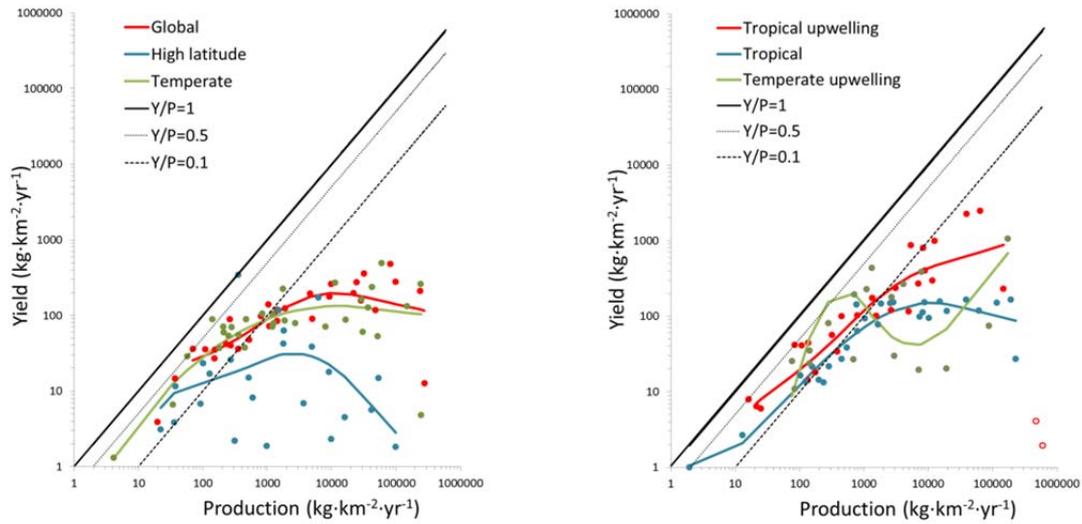
**Figure 6.** Average fishing pattern in five main ecosystem types across the world since 1970, and the total global average, expressed as  $\log_{10}$  yield ( $\text{kg} \cdot \text{km}^2 \cdot \text{year}^{-1}$ ) versus  $\log_{10}$  production (same units). Each point is the mean of functional groups in 0.1 TL intervals (Fig. 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.

Table 2. Results of the regression analysis of  $\log_{10}(\text{yield})$  over  $\log_{10}(\text{production})$  globally and on five different ecosystem types using a general additive model (GAM). Each observation represents the mean of functional groups in trophic level in 0.1 lower trophic level intervals between 2 and 5.1. p values gives tests of slopes on the 1:1 line of  $\log_{10}(\text{catch})$  over  $\log_{10}(\text{production})$ . 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).

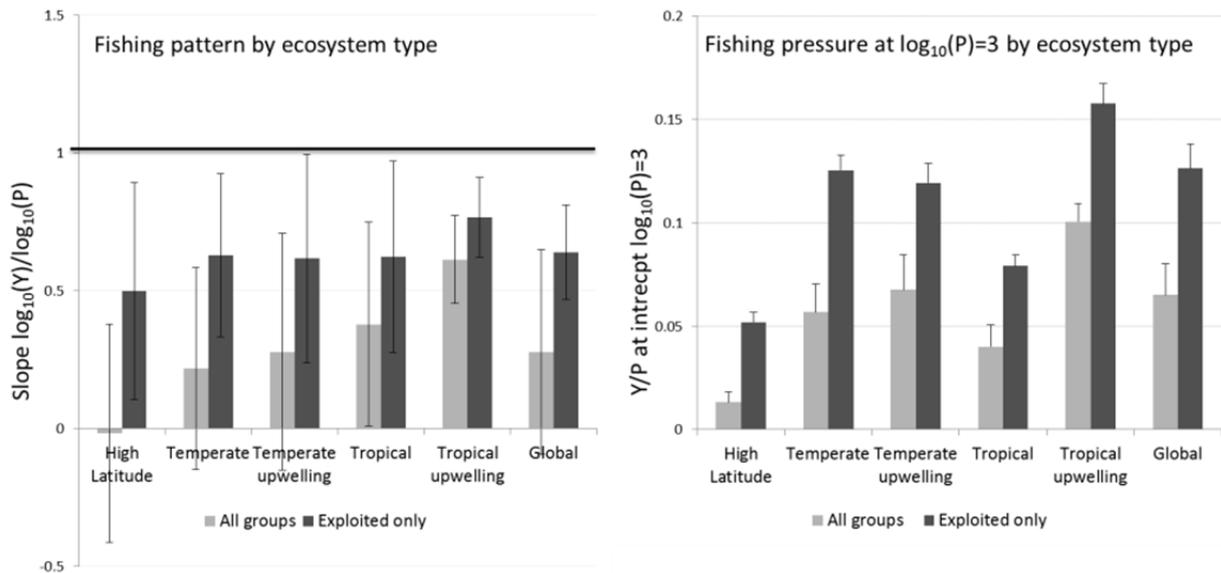
All groups	Linear component					Non-linear component : Spline				
	Nobs	Intercept	Pr> t	Slope	Pr> t	DF	Smoothing parameter	GCV	SumSq	Pr>ChiSq
<b>Global</b>	30	0.98	<0.01	0.28	<0.001	3.00	0.990	0.07	1.97	<0.001
<b>High Latitude</b>	24	1.17	<0.001	-0.02	<0.001	1.00	0.997	0.41	1.63	<0.05
<b>Temperate</b>	31	1.10	<0.001	0.22	<0.001	3.00	0.990	0.14	2.85	<0.001
<b>Temperate upwelling</b>	17	0.99	<0.05	0.28	<0.001	3.00	0.891	0.32	1.75	<0.05
<b>Tropical</b>	28	0.47	<0.001	0.38	<0.001	3.00	0.984	0.04	2.39	<0.001
<b>Tropical upwelling</b>	26	0.17	Ns	0.61	<0.001	3.00	0.980	0.10	10.06	<0.05
<b>Exploited groups only (<math>E &gt; 0.001</math>)</b>										
<b>Global</b>	30	0.18	ns	0.64	<0.001	3.00	0.990	0.07	0.27	ns
<b>High Latitude</b>	23	0.22	ns	0.50	<0.01	0.14	0.331	0.33	0.09	ns
<b>Temperate</b>	31	0.21	ns	0.63	<0.001	3.00	0.988	0.09	0.86	<0.01
<b>Temperate upwelling</b>	17	0.23	ns	0.62	<0.05	2.00	0.097	0.27	0.11	ns
<b>Tropical</b>	28	0.03	ns	0.62	<0.001	3.00	0.982	0.07	0.76	<0.01
<b>Tropical upwelling</b>	26	-0.10	ns	0.77	<0.001	3.00	0.981	0.06	0.14	ns

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

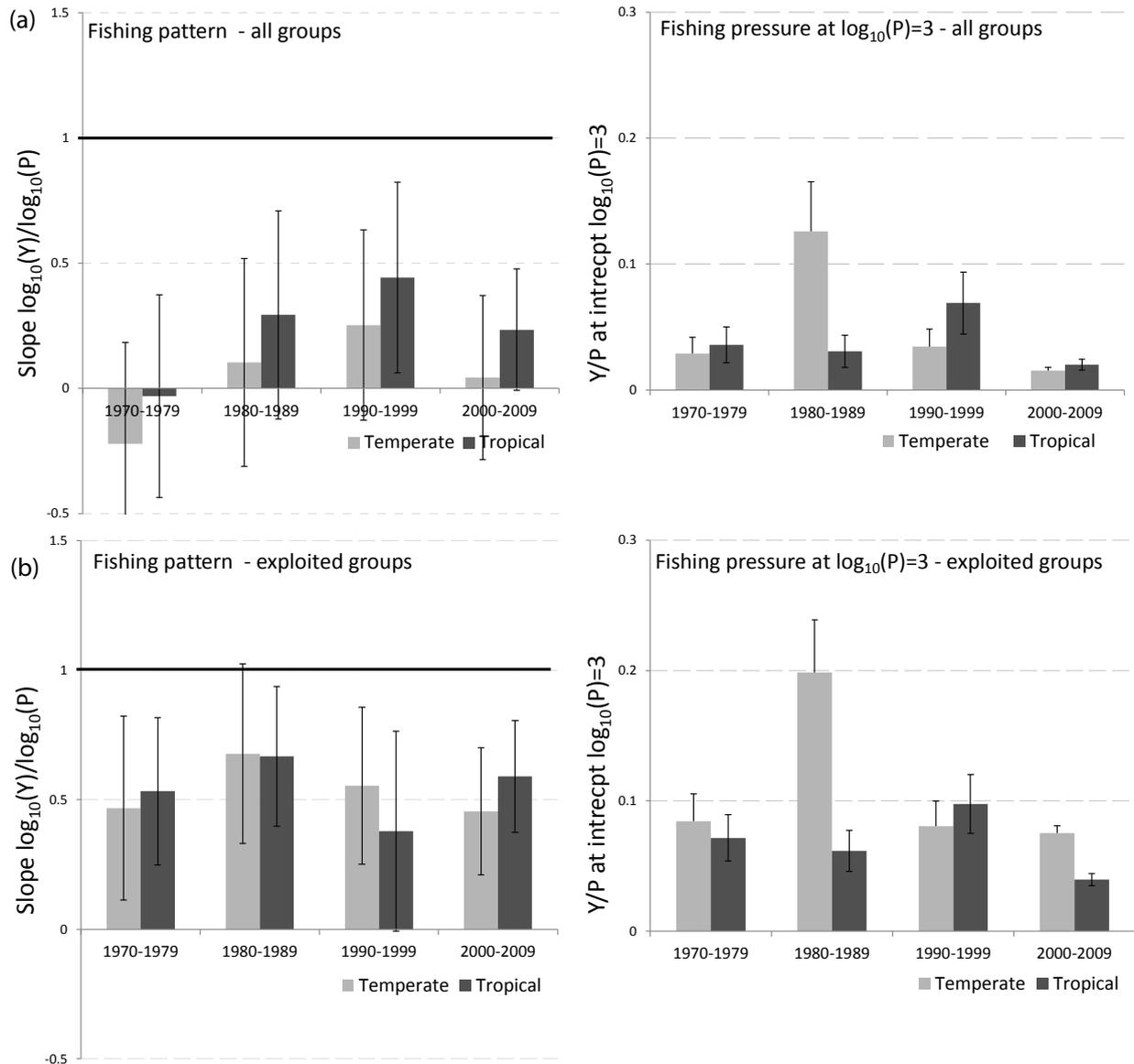
The y-intercepts are centred at a production level of  $1000 \text{ kg/km}^2/\text{yr}$ , which is equivalent to a trophic level of around 4.5, where exploitation rates generally peak (Fig. 4). Considering first the case where all functional groups are included, tropical upwelling fisheries are the most heavily exploited (mean E around 10% for exploited groups at  $P=1000 \text{ kg}\cdot\text{yr}^{-1}$ ), 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.



**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 trophic levels. 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 online material).



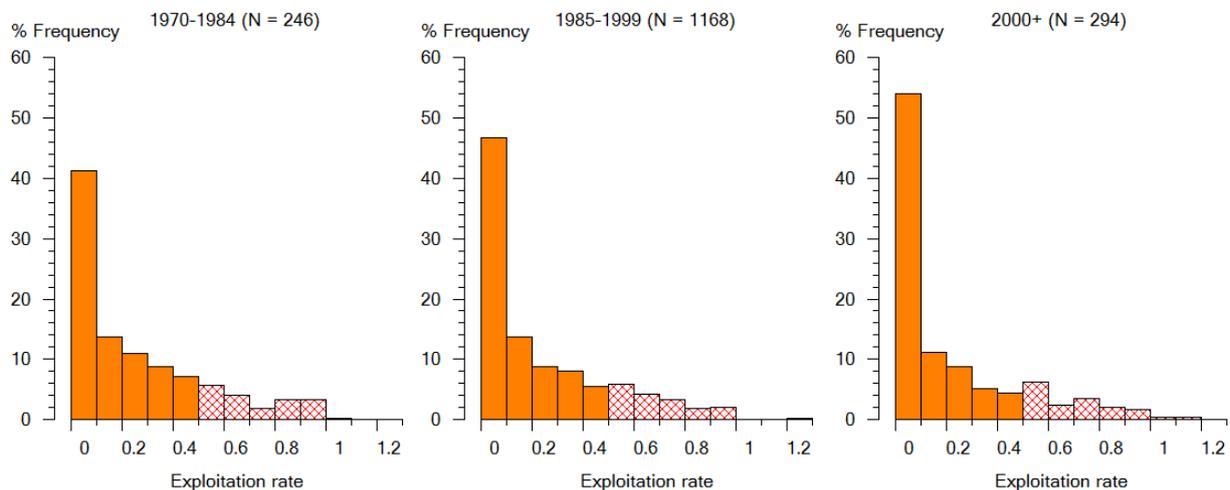
**Figure 8.** Left panel: Fishing pattern. Values of the slope of the regression of  $\log_{10}(Y)$  over  $\log_{10}(P)$  for the five ecosystem types. Error bars ( $\pm 1.96 \cdot SE$ ) indicate significance of the difference between the slope = 1 (balanced) and slope = 0. Black horizontal line represents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



**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 ( $\pm 1.96 \times SE$ ) 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  $\log_{10}(P)=3$  ( $=1 \text{ ton} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$ ), for which groups exploitation is generally highest.

The general tendency of the world's fisheries has been to gradually expand the number of targets and fish lower in the trophic food web (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 TBI analysis below). 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 to the 40% upper reference exploitation limit suggested by Pikitch et al. (2012). Figure 10 shows that the proportion of groups with less than 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 3 decades.

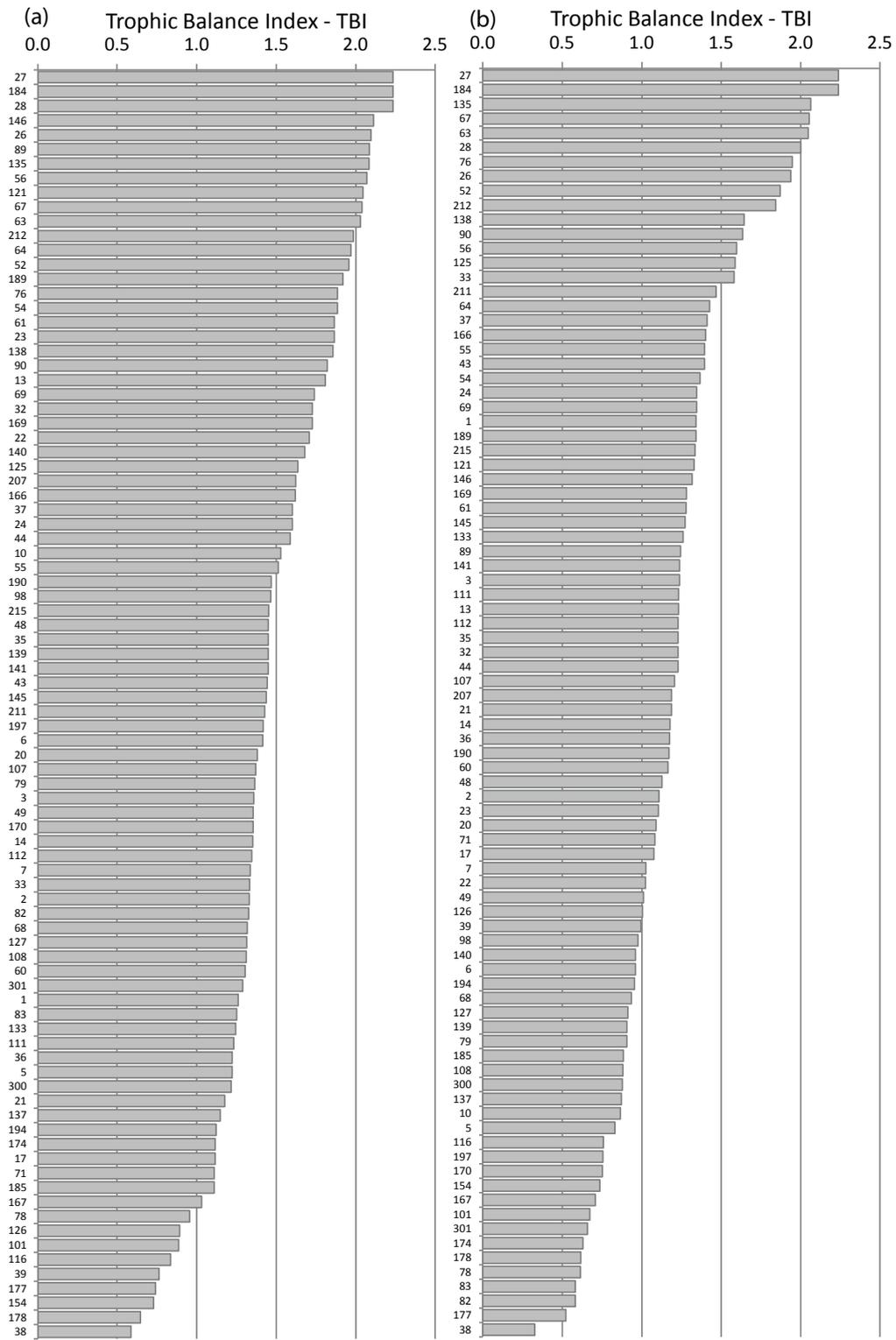


**Figure 10.** Frequency distribution of all fished functional groups ( $F/Z > 0.001$ ) by 15 year intervals since 1970 in relation to their fishing pressure (exploitation ratio). Relative proportion of overfished groups ( $F/Z > 0.4$ ) are indicated by hatched bars and have decreased slightly from 18% to 16% over the period. N is total number of exploited groups in each time period.

### *Trophic Balance Index.*

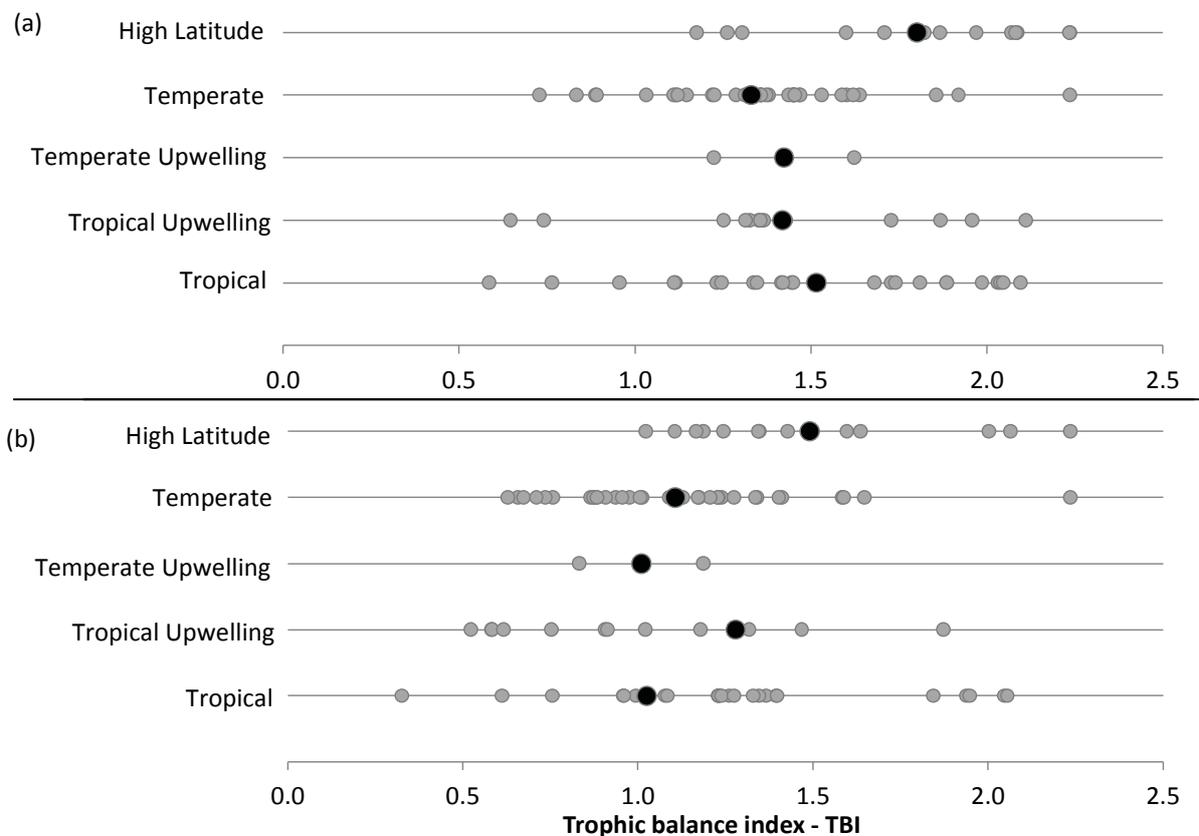
The TBI provides a single measure of balanced exploitation for each ecosystem: the exploitation rate  $E$  is exactly the same for all trophic levels when  $TBI=0$ . Observed values ranged from the maximum of 2.24 for 3 models to a low of 0.59. Thus no individual ecosystem had perfectly balanced exploitation rates (Fig. 11a). The same pattern is seen 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 (Fig. 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 trophic levels, and the number of exploited functional groups included at each trophic level bin.

In the ecosystems at the top of Figure 11, where TBI was at, or close to, maximum, only one trophic level was exploited, usually trophic level 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 trophic levels. When all functional groups were considered, 9 ecosystems had a TBI lower than 1, of which 5 were tropical ecosystems and 4 were temperate ecosystems. When only exploited functional groups were considered, 29 ecosystems had a TBI lower than 1, composed of 13 tropical (7 upwelling) and 16 temperate (1 upwelling) systems.



**Figure 11.** Trophic Balance Index 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 online material**.

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 a wide spread of TBI values (Fig. 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. Students 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.



**Figure 12.** Trophic Balance Index (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 ( $E > 0.001$ ).

TBI and total catch rates had a significant negative relationship across all models ( $\log_{10}(\text{yield})$   $\text{kg}/\text{km}^2/\text{yr}$ ),  $r^2 = 0.38$ ,  $p<0.001$  (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 time period, Large Marine Ecosystem (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)

Table 3. Results of linear regressions ( $r^2$ ) of TBI with exploitation ( $E = Y/P$ ) and  $\text{Log}_{10}(\text{catch}/\text{area})$  by ecosystem type. \*\* < 0.01, \*\*\* < 0.001. Tropical and temperate regressions were negative or non-significant for temperate and all functional groups (FG), high latitude were non-significant.

	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

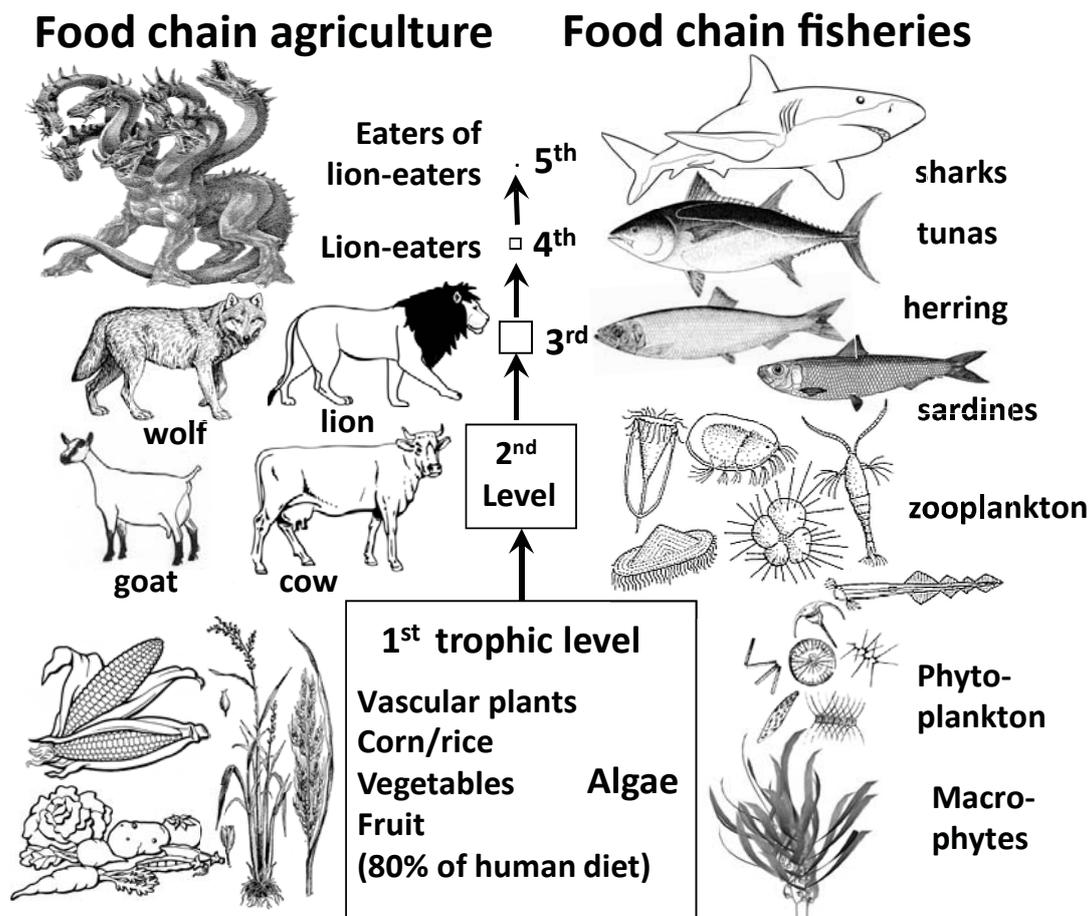
## Discussion

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 (Fig. 2, Table 1, **Supplementary online material**). All models were based on the same standardised 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 (Fig. 4) shows a marked peak at trophic levels 4-5, and very light exploitation (< 10%) at TL 2-3, indicating that fisheries removals are disproportionately taken from the high trophic level species (Fig. 5). While nearly all high trophic level groups have traditionally been exploited all over the world for centuries, some of the low trophic level groups, such as jellyfish and echinoderms, have little acceptance as human food. Still, several highly productive low trophic level groups such as small demersal fish, crustaceans, cephalopods and molluscs are regularly consumed by humans and, on average, are lightly exploited (Fig. 5). The average TL at which humans feed is around 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 around 99% of the corresponding energy being lost in transfer inefficiency if we follow the general 10% transfer rule (Fig. 3B). This may explain why only around 2% of the global 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 utilised or overexploited (FAO, 2014).

The aquatic food chain, however, is fundamentally 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  $\mu\text{m}$  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 (Fig. 13), which again cascade into higher trophic levels. Land-based food chains are thus generally shorter because of much larger organisms at TL 1-3, and thereby much more efficient in 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 trophic levels 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 trophic levels 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 fish is correct, it is even more noteworthy considering that the captures of these species has also increased 4-fold over the past 50 years from around 5 million ton to 20 million ton (Smith et al., 2011). Similar long-term changes with a decrease in large high trophic level species and a cascading increase in low trophic levels, 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).



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

While several high level trophic groups are heavily exploited (Fig. 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 trophic levels. 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 5 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 around 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 less than 10% of the annual production (Fig. 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 world's 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 (Fig. 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 to be well within safe margins (Fig. 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 trophic levels. The general concern that we are fishing too many small fish, thus endangering the sustenance of higher trophic levels (Pikitch et al., 2012; Smith et al., 2011) seems not supported by the present analysis since higher trophic levels, which have the lowest abundance and production (Fig. 3), are the most heavily exploited. Our results indicate that there is potential to increase exploitation at low trophic levels if we want to balance extraction across the ecosystem. In practice this would be operationalised at the species and stock level, excluding any low trophic level 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: (1) The novel logarithmic  $Y/P$  plots (Fig. 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 (2) the Trophic Balance Index (Bundy et al., 2005), which gives the coefficient of variation of fishing pressure across exploited trophic levels. 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 across ecosystem-specific trophic levels 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 trophic levels 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 temperate ecosystems are the least balanced, whereas fisheries in upwelling and tropical ecosystems appear more balanced across all trophic levels. This indicates that these fisheries exploit a wider variety of the available production more equally (Fig. 8a). When only exploited groups are considered, this picture is less clear, but still confirmed that tropical fisheries exploit a broader range of trophic levels 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 (Fig. 7), which makes sense as they are traditionally focused on highly productive, low trophic level 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 balanced harvesting 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 (Fig. 12): exploitation patterns are very uneven and skewed towards the higher trophic levels, 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. Further investigation is required to determine whether TBI decreased because of increased exploitation across lower trophic levels as a response to the collapse of larger, higher trophic level 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 primary production, 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 primary production is metabolized when reaching TLs 4-5. At the global level, the fishing pattern is strongly skewed towards high TLs; it is possible that 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; 2015b), 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 (Garcia et al., 2015a; Burgess et al., 2015, Charles et al., 2015), 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; 2015b). 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 online material**

The following supplementary material is available at ICESJMS online: SOM Table 1, A full list of the 110 Ecopath models used in this study, and the Model ID, model name in repository, associated ecosystems, countries, ecosystem types, Large Marine Ecosystem classification and number, stock status, primary productivity level and FAO Zone. SOM Table 2, list of Model ID and the corresponding literature reference for each model.

### **Acknowledgements**

We are grateful to Jeroen Steenbeek for extracting the Ecopath data from the model repository and for preparing figure 2, and to Villy Christensen for permission to use these models. We also sincerely thank Richard Law for inspiration and following this work since its inception. Lastly, we thank the four anonymous reviewers and the editor for their constructive comments and suggestions to previous versions of the manuscript.

### **References**

- Alverson, D. L., and Pereyra, W. T. 1969. Demersal Fish Explorations in the Northeastern Pacific Ocean — An Evaluation of Exploratory Fishing Methods and Analytical Approaches to Stock Size and Yield Forecasts. *Journal of the Fisheries Research Board of Canada*, 26: 1985-2001.
- Béné, C., Barange, M., Subasinghe, R., Pinstруп-Andersen, P., Merino, G., Hemre, G.-I., and Williams, M. 2015. Feeding 9 billion by 2050 – Putting fish back on the menu. *Food Security*, 7: 261-274.
- Beveridge, M. C. M., Thilsted, S. H., Phillips, M. J., Metian, M., Troell, M., and Hall, S. J. 2013. Meeting the food and nutrition needs of the poor: the role of fish and the opportunities and challenges emerging from the rise of aquaculture. *Journal of Fish Biology*, 83: 1067-1084.
- Bonhommeau, S., Dubroca, L., Le Pape, O., Barde, J., Kaplan, D. M., Chassot, E., and Nieblas, A.-E. 2013. Eating up the world's food web and the human trophic level. *Proceedings of the National Academy of Sciences*, 110: 20617-20620.
- Boudreau, P. R., and Dickie, L. M. 1992. Biomass spectra of aquatic ecosystems in relation to fisheries yield. *Canadian Journal of Fisheries and Aquatic Science*, 49: 1528-1538.
- Branch, T. A., Jensen, O. P., Ricard, D., Ye, Y., and Hilborn, R. A. Y. 2011. Contrasting Global Trends in Marine Fishery Status Obtained from Catches and from Stock Assessments. *Conservation Biology*, 25: 777-786.
- Bundy, A., Coll, M., Shannon, L. J., and Shin, Y.-J. 2012. Global assessments of the status of marine exploited ecosystems and their management : what more is needed ? *Current Opinion in Environmental Sustainability*, 4: 292-299.
- Bundy, A., Fanning, P., and Zwanenburg, K. C. T. 2005. Balancing exploitation and conservation of the eastern Scotian Shelf ecosystem: application of a 4D ecosystem exploitation index. *ICES Journal of Marine Science*, 62: 503-510.

- Burgess, M. G., Diekert, F. K., Jacobsen, N. S., Andersen, K. H., and Gaines, S. D. 2015. Remaining questions in the case for balanced harvesting. *Fish and Fisheries*, 10.1111/faf.12123.
- Caddy, J. F., and Sharp, G. D. 1986. An ecological framework for marine fishery investigations. *FAO Fisheries Technical Paper*: 283, 152 pp, FAO, Rome, Italy.
- CBD 1992. Convention on Biological Diversity, Rio de Janeiro, Brazil. <http://www.cbd.int/rio/>, <http://www.cbd.int/rio/> Access, 17 February, 2015.
- Charles, A., Garcia, S.M. and Rice, J. 1015. Balanced harvesting in fisheries: economic considerations. *ICES Journal of Marine Sciences*. Online September 10, 2015, doi: 10.1093/icesjms/fsv161
- Chassot, E., Bonhommeau, S., Dulvy, N. K., Mélin, F., Watson, R., Gascuel, D., and Le Pape, O. 2010. Global marine primary production constrains fisheries catches. *Ecology Letters*, 13: 495-505.
- Christensen, V., Coll, M., Piroddi, C., Steenbeek, J., Buszowski, J., and Pauly, D. 2014. A century of fish biomass decline in the ocean. *Marine Ecology Progress Series*, 512: 155-166.
- Christensen, V., and Pauly, D. 1992. ECOPATH II — a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling*, 61: 169-185.
- Christensen, V., and Walters, C. J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling*, 172: 109-139.
- Costello, C., Ovando, D., Hilborn, R., Gaines, S. D., Deschenes, O., and Lester, S. E. 2012. Status and solutions for the world's unassessed fisheries. *Science*, 338: 517-520.
- Daan, N., Gislason, H., G. Pope, J., and C. Rice, J. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES Journal of Marine Science*, 62: 177-188.
- Daan, N., Gislason, H., Pope, J. G., and Rice, J. C. 2011. Apocalypse in world fisheries? The reports of their death are greatly exaggerated. *ICES Journal of Marine Science: Journal du Conseil*, 68: 1375-1378.
- Duarte, C. M., Holmer, M., Olsen, Y., Soto, D., Marbà, N., Guiu, J., Black, K., et al. 2009. Will the Oceans Help Feed Humanity? *BioScience*, 59: 967-976.
- FAO 2006. The State of World Aquaculture. Food and Agriculture Organisation of the United Nations, Rome, [www.fao.org/docrep/009/a0874e/a0874e00.html](http://www.fao.org/docrep/009/a0874e/a0874e00.html)
- FAO 2014. The State of World Fisheries and Aquaculture. Opportunities and Challenges. Food and Agriculture Organisation of the United Nations, Rome, <http://www.fao.org/3/a-i3720e/index.html>.
- Field, C. B., Behrenfeld, M. J., Randerson, J. T., and Falkowski, P. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, 281: 237-240.
- Froese, R., Zeller, D., Kleisner, K., and Pauly, D. 2012. What catch data can tell us about the status of global fisheries. *Marine Biology*, 159: 1283-1292.
- Froese, R., Zeller, D., Kleisner, K., and Pauly, D. 2013. Worrying trends in global stock status continue unabated: a response to a comment by R.M. Cook on “What catch data can tell us about the status of global fisheries”. *Marine Biology*, 160: 2531-2533.
- Garcia, S. M., Kolding, J., Rice, J., Rochet, M.-J., Zhou, S., Arimoto, T., Beyer, J., et al. 2011. Selective Fishing and Balanced Harvest in Relation to Fisheries and Ecosystem Sustainability. Report of a scientific workshop organized by the IUCN-CEM Fisheries Expert Group (FEG) and the European Bureau for Conservation and Development (EBCD) in Nagoya (Japan), 14-16 October 2010., iv + 33pp pp, Gland, Switzerland and Brussels, Belgium.

- Garcia, S. M., Kolding, J., Rice, J., Rochet, M.-J., Zhou, S., Arimoto, T., Beyer, J. E., et al. 2012. Reconsidering the Consequences of Selective Fisheries. *Science*, 335: 1045-1047.
- Garcia, S. M., Rice, J., and Charles, T. 2015a. Balanced Harvesting: A bridge linking the norms of fisheries management and conservation of biodiversity. *ICES Journal of Marine Science*, this volume.
- Garcia, S. M., Zerbi, A., Aliaume, C., Do Chi, T., and Lasserre, G. 2003. The ecosystem approach to fisheries. Issues, terminology, principles, institutional foundations, implementation and outlook., *FAO Fisheries Technical Paper*: 443, 71 pp, Rome.
- Garcia, S. M. E., Bianchi, G., Charles, A., Kolding, J., Rice, J., Rochet, M.-J., Zhou, S., et al. 2015b. Balanced Harvest in the Real World. Scientific, Policy and Operational Issues in an Ecosystem Approach to Fisheries. Report of an international scientific workshop of the IUCN Fisheries Expert Group (IUCN/CEM/FEG) organized in close cooperation with the Food and Agriculture Organization of the United Nations (FAO). p. 94. Gland (Switzerland), Brussels (Belgium) and Rome (Italy): IUCN, EBCD, FAO, Rome.
- Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., et al. 2008. A Global Map of Human Impact on Marine Ecosystems. *Science*, 319: 948-952.
- HLPE 2014. Sustainable fisheries and aquaculture for food security and nutrition. A report by the High Level Panel of Experts on Food Security and Nutrition of the Committee on World Food Security. FAO, Rome, <http://www.fao.org/cfs/cfs-home/downloads/en/> Access, 14 April, 2015.
- IUCN 2013. Latest review of science reveals ocean in critical state. International Union for Conservation of Nature, <http://www.iucn.org/?13784/Latest-review-of-science-reveals-ocean-in-critical-state> Access, 14 April, 2015.
- Jacobsen, N. S., Gislason, H., and Andersen, K. H. 2014. The consequences of balanced harvesting of fish communities. *Proceedings of the Royal Society B: Biological Sciences*, 281: 2013- 2701.
- Jennings, S., and Collingridge, K. 2015. Predicting Consumer Biomass, Size-Structure, Production, Catch Potential, Responses to Fishing and Associated Uncertainties in the World's Marine Ecosystems. *PLoS ONE*, 10: e0133794.
- Jennings, S., Oliveira, J. A. A. D. E., and Warr, K. J. 2007. Measurement of body size and abundance in tests of macroecological and food web theory. *Journal of Animal Ecology*, 76: 72-82.
- Jennings, S., Pinnegar, J. K., Polunin, N. V. C., and Boon, T. W. 2001. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, 70: 934-944.
- Jul-Larsen, E., Kolding, J., Overå, R., Raakjær Nielsen, J., and Zwieten, P. A. M. v. 2003. Management, co-management or no-management? Major dilemmas in southern African freshwater fisheries. Part 1: Synthesis. *FAO Fisheries Technical Paper*: 426/1, 127 pp, Rome.
- Kawarazuka, N., and Béné, C. 2011. The potential role of small fish species in improving micronutrient deficiencies in developing countries: building evidence. *Public Health and Nutrition*, 14: 1927-1938.
- Kerr, S. R., and Dickie, L. M. 2001. *The Biomass Spectrum. A predator-prey theory of aquatic production*, Columbia University Press, New York. 320 pp. 0-231-08459-5.
- Kleisner, K., and Pauly, D. 2011. Stock-catch status plots of fisheries for Regional Seas. The state of biodiversity and fisheries in Regional Seas. *Fish Centre Res Rep*, 19: 37-40.
- Kolding, J., Béné, C and Bavinck, M. 2014. Ch. 22 Small-scale fisheries - importance, vulnerability, and deficient knowledge. pp 317-331 In S. Garcia, J. Rice and A.

- Charles (eds). Governance for Marine Fisheries and Biodiversity Conservation. Interaction and coevolution. Wiley-Blackwell. DOI: 10.1002/9781118392607.ch22
- Kolding, J., Jacobsen, N. S., Andersen, K. H., and van Zwieten, P. A. M. 2015a. Maximizing fisheries yields while maintaining community structure. *Canadian Journal of Aquatic Sciences*, Published on the web 21 September 2015, 10.1139/cjfas-2015-0098.
- Kolding, J., Law, R., Plank, M., and Zwieten, P. A. M. v. 2015b. The optimal fishing pattern. *In Freshwater Fisheries Ecology*, p. 920. Ed. by J. F. Craig. Wiley Blackwell. ISBN: 978-1-118-39442-7.
- Kolding, J., and Zwieten, P. A. M. v. 2011. The tragedy of our legacy: how do global management discourses affect small scale fisheries in the South? *Forum for Development Studies*, 38: 267 - 297.
- Kolding, J., and Zwieten, P. A. M. v. 2014. Sustainable fishing of inland waters. *Journal of Limnology*, 73: 132 - 148.
- Kozlovsky, D. G. 1968. A critical evaluation of the trophic level concept. 1. Ecological efficiencies. *Ecology & Society*, 49: 48-60.
- Law, R., Kolding, J., and Plank, M. J. 2013. Squaring the circle: reconciling fishing and conservation of aquatic ecosystems. *Fish and Fisheries*, 10.1111/faf.12056.
- Law, R., Plank, M. J., and Kolding, J. 2012. On balanced exploitation of marine ecosystems: results from dynamic size spectra. *ICES Journal of Marine Science: Journal du Conseil*, 69: 602-614.
- Law, R., Plank, M. J., and Kolding, J. 2014. Balanced exploitation and coexistence of interacting, size-structured, fish species. *Fish and Fisheries*, 10.1111/faf.12098.
- Murawski, S.A. 2007. Ten myths concerning ecosystem approaches to marine resource management. *Marine Policy* 31: 681-690.
- Patrick, W. S., and Link, J. S. 2015. Myths that Continue to Impede Progress in Ecosystem-Based Fisheries Management. *Fisheries*, 40: 155-160.
- Patterson, K. 1992. Fisheries for small pelagic species: an empirical approach to management targets. *Reviews in Fish Biology and Fisheries*, 2: 321-338.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F., Jr. 1998. Fishing down marine food webs. *Science*, 279: 860-863.
- Pauly, D., and Palomares, M. L. 2005. Fishing down marine food web: it is far more pervasive than we thought. *Bulletin of Marine Science*, 762: 197 - 211.
- Pauly, D., Watson, R., and Alder, J. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 360: 5-12.
- Pikitch, E., Boersma, P. D., Boyd, I. L., Conover, D. O., Cury, P., Essington, T., Heppell, S. S., et al. 2012. Little Fish, Big Impact: Managing a Crucial Link in Ocean Food Webs., Lenfest Ocean Program, 108 pp, Washington DC.
- Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., et al. 2004. Ecosystem-Based Fishery Management. *Science*, 305: 346-347.
- Plagányi, É. E. 2007. Models for an ecosystem approach to fisheries. *FAO Fisheries Technical Paper: 477*, 108 pp, Rome.
- Reid, D., Graham, N., Suuronen, P., He, P., and Pol, M. 2016. Implementing balanced harvesting—practical challenges and other implications. *ICES Journal of Marine Science*, this issue.
- Ricard, D., Minto, C., Jensen, O. P., and Baum, J. K. 2012. Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. *Fish and Fisheries*, 13: 380-398.
- Rice, J., and Gislason, H. 1996. Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. *ICES Journal of Marine Science*, 53: 1214-1225.

- Romanuk, T. N., Hayward, A., and Hutchings, J. A. 2011. Trophic level scales positively with body size in fishes. *Global Ecology and Biogeography*, 20: 231-240.
- Sethi, S. A., Branch, T. A., and Watson, R. 2010. Global fishery development patterns are driven by profit but not trophic level. *Proceedings of the National Academy of Sciences*, 107: 12163-12167.
- Sheldon, R. W., Prakash, A., and Sutcliffe, W. H., Jr. 1972. The Size Distribution of Particles in the Ocean. *Limnology and Oceanography*, 17: 327-340.
- Smith, A. D., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-Montes, H., et al. 2011. Impacts of fishing low-trophic level species on marine ecosystems. *Science*, 333: 1147-1150.
- Swingle, H.S. 1950. Relationships and dynamics of balanced and unbalanced fish populations. Alabama Polytechnical Institute, Bulletin No. 274, 45 pp.
- Tsikliras, A. C., and Polymeros, K. 2014. Fish market prices drive overfishing of the 'big ones'. *PeerJ*, 10.7717/peerj.638.
- UNCLOS 1982. United Nations Convention on the Law of the Sea (UNCLOS) of 10 December 1982.  
[http://www.un.org/depts/los/convention\\_agreements/convention\\_overview\\_convention.htm](http://www.un.org/depts/los/convention_agreements/convention_overview_convention.htm) Access, 17 February, 2015.
- Walters, C., Christensen, V., and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries*, 7: 139-172.
- Ware, D. M., and Thomson, R. E. 2005. Bottom-Up Ecosystem Trophic Dynamics Determine Fish Production in the Northeast Pacific. *Science*, 308: 1280-1284.
- Watson, R. A., Cheung, W. W. L., Anticamara, J. A., Sumaila, R. U., Zeller, D., and Pauly, D. 2012. Global marine yield halved as fishing intensity redoubles. *Fish and Fisheries*, 10.1111/j.1467-2979.2012.00483.x.
- Worm, B., and Branch, T. A. 2012. The future of fish. *Trends in Ecology & Evolution*, 27: 594-599.
- Zhou, S., Smith, A. D. M., and Knudsen, E. E. 2014. Ending overfishing while catching more fish. *Fish and Fisheries*, 10.1111/faf.12077: n/a-n/a.
- Zhou, S., Smith, A. D. M., Punt, A. E., Richardson, A. J., Gibbs, M., Fulton, E. A., Pascoe, S., et al. 2010. Ecosystem-based fisheries management requires a change to the selective fishing philosophy. *Proceedings of the National Academy of Sciences*, 107: 9485-9489.

**Appendix 1.** 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 standard deviations of the means.

Groups	# Groups	# 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
Sea birds	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
<b>Total</b>	<b>3655</b>	<b>1889</b>	<b>3.04</b>	<b>1.01</b>	<b>11.82</b>	<b>59.6</b>	<b>22</b>	<b>86.12</b>	<b>0.65</b>	<b>0.33</b>