

Modelling the effects of fishing on the biomass of the world's oceans from 1950 to 2006

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Supplement. Further information on the EcoTroph model

DESCRIPTION OF THE ECOTROPH MODEL

Note: The EcoTroph model is described in detail in Gascuel et al. (2009), which can be downloaded from www.fisheries.ubc.ca/node/366.

EcoTroph models a continuous transfer of biomass from low to high trophic levels (TLs) based on 3 fundamental properties of ecosystems: biomass, production and kinetics. We used a discrete approximation to the continuous form so that we could apply it to real ecosystems. For all TLs ≥ 2 , the trophic spectrum was divided into discrete intervals of width $\Delta\tau = 0.1$, with the value of biomass or production in the interval equal to the area under the curve bounded by the interval. The biomass and production of primary producers were assumed to occur at TL = 1.0.

In order to estimate ecosystem biomass by TLs, we start by calculating the production and kinetics by TL (see below). This can be done for the unexploited state or for a year or decade of interest. We then apply EcoTroph's main equation, which gives the biomass as a function of production and kinetics as:

$$B_{\tau} = P_{\tau} / K_{\tau} \quad (\text{S1})$$

where K_{τ} is the speed of the trophic flow measuring how fast biomass is transferred to higher trophic levels in the food web (in TL yr⁻¹).

Calculating production by TL

EcoTroph assumes that production flows continuously from primary producers to herbivores and predators and declines predictably between TL from natural energy losses due to digestion, respiration, excretion, partial consumption, etc.

This rate of decline is called the transfer efficiency (TE). It is calculated as the proportion of production remaining after a transfer of one TL, that is, $TE = P(\tau + 1)/P(\tau)$, which can also be defined as the exponential rate of decline $\mu_\tau = -\log(TE)$. If the ecosystem is exploited, production declines at a faster rate between the trophic levels targeted by fisheries. The fishing mortality F_τ and its corresponding exponential rate of decline (the fishing loss rate ϕ_τ) are:

$$F_\tau = Y_\tau / B_\tau \quad (S2a)$$

$$\phi_\tau = Y_\tau / P_\tau \quad (S2b)$$

where Y_τ is the fisheries catch at τ . Note that this implies that catches are directly related to fishing mortality, such that smaller catches are only possible under a reduced fishing mortality, and vice versa.

An approach based on the single-species statistical catch analysis by Pope (1972) is used to estimate production under the unexploited state when catch data by TL are available.

If we assume that the catch of a TL interval is removed from the production at exactly half of the TL interval, then the production at τ is:

$$P_{\tau+\Delta\tau} = P_\tau \times \exp(-\mu_\tau \Delta\tau) - Y_\tau \times \exp(-\mu_\tau \times 0.5\Delta\tau) \quad (S3)$$

where P_τ is the production of the TL just before $\tau + \Delta\tau$, Y_τ is the capture removed at exactly half of the trophic level interval and $\exp(-\mu_\tau \Delta\tau)$ accounts for natural energy losses in $\Delta\tau$.

The production trophic spectrum can thus be solved starting with primary production at $P(\tau=1)$, removing catch as needed at each half TL interval and accounting for natural losses as set by the parameter μ . To derive the production by TL in the unexploited state, we simply set catches to be zero, such that:

$$P_{\tau+\Delta\tau} = P_\tau \times \exp(-\mu_\tau \Delta\tau) \quad (S4)$$

Once P_τ is derived from Eq. 3, the fishing loss rate ϕ_τ can be calculated for each τ as:

$$\phi_\tau = (1/\Delta\tau) \times \log(P_\tau/P_{\tau+\Delta\tau}) - \mu_\tau \quad (S5)$$

Calculating kinetics by TL

The kinetics K_τ are obtained from an empirical model that predicts K_τ as a function of sea surface temperature H ($^\circ\text{C}$) and TL. This model was parameterized by Gascuel et al. (2008) based on the P/B values (equivalent to the kinetics in EcoTroph) of 1718 groups from 55 published Ecopath models (Christensen & Pauly 1992), and it explains 54% of the observed variance in kinetics. This model is assumed to correspond to the unexploited state of the system and is described in the following equation:

$$K_{\tau,\text{unexpl}} = 20.19 \times \tau^{-3.26} \times \exp(0.041H) \quad (S6)$$

where τ is the trophic level and H is the sea surface temperature in °C.

When the ecosystem is exploited, the kinetics of the targeted TL increase because production is being removed from that TL at a faster rate. When catch or fishing mortality is known, the unexploited kinetics are adjusted to account for fishing mortality as

$$K_{\tau} = K_{\tau, \text{unexpl}} + F_{\tau} \quad (S7)$$

where $K_{\tau, \text{unexpl}}$ refers to the kinetics in the unexploited state (from Eq. 6) and F_{τ} is the fishing mortality at τ .

The kinetics must be solved iteratively because the biomass at τ is required to calculate F_{τ} (see Eq. 2a). However, Eq. (7) can be re-arranged as $K_{\tau} = K_{\tau, \text{unexpl}} + \phi_{\tau} K_{\tau}$, because $F_{\tau} = \phi_{\tau} K_{\tau}$ (see Eqs. 2a and 2b), and this version of the equation has the analytical solution $K_{\tau} = K_{\tau, \text{unexpl}} / (1 - \phi_{\tau})$ for $\phi_{\tau} < 1$. Note that this is an update from the original formulation of the model presented in Gascuel et al. (2009).

CATCH TROPHIC SPECTRUM AND SMOOTHING

To be incorporated in EcoTroph, the species-specific catch data of each cell for each year were transformed into an approximation of a continuous catch trophic spectrum over the TL interval 2.0 to 5.0.

We assumed that the variation in TL of the individuals of a species is positively related to the species' mean TL. In other words, as mean TL increases for a species, there is greater variation in the TL of the individuals in the population due, for example, to diet shifts in ontogeny (as an illustration, compare zooplankton and sharks). We modelled the distribution of TLs of individuals within a species as log-normal with a standard deviation S defined as $S_{\tau} = \text{smooth} \times \log(\tau - 0.05)$. The constant 'smooth' represents the strength of the smoothing as TL increases and τ is the mean TL (centered at $\Delta\tau / 2$).

An approximation to a continuous distribution of catch over TL for a cell was obtained by first standardizing the log-normal distribution of the individuals of a species over TL. The contribution of each TL interval to the total area under the curve of the distribution was then multiplied by the catch of the species in that cell and year. Lastly, the ecosystem catch for each TL interval was obtained by summing over all of the species-specific catch records that occurred in the interval, which resulted in a catch trophic spectrum for a given cell in a given year.

SCENARIOS OF ECOSYSTEM RESPONSE TO FISHING

EcoTroph assumes by default that declines in catches are a result of reduced fishing mortality, which is not realistic in many instances (Mullon et al. 2005). To compensate for this behavior, 3 scenarios of ecosystem response to fishing were applied to the default biomass predictions of the model. The biomass predictions were modified if a signal of overexploitation was detected in a cell for a given decade. The signal was based on trends in catches over time.

We tested for overexploitation over TL intervals of 0.5, starting at interval TL = 2.0–2.4, and summed catches over each interval. The following 3 criteria needed to be met for a given TL interval to be considered overexploited in a decade:

- (1) Decline in catch: a decline in catch must have occurred from the previous decade.
- (2) Exploitation level: the cell must be fully accessed; that is, for at least one decade in the 1950–2006 period, the observed catch must reduce ecosystem biomass by at least 10% of the cell’s biomass at maximum sustainable yield (B_{MSY}). This allowed us to filter out cells that are only marginally exploited by fisheries and where overexploitation is unlikely to have occurred even if a decline in catch is observed. Maximum sustainable yield was assumed to occur at 50% of the unexploited biomass of the ecosystem (a conservative estimate).
- (3) Relative catch: the catch previously recorded in the cell must be at least 20% of the maximum recorded catch in the cell for 1950–2006 or the decline must occur past the decade where the maximum catch was recorded. This prevents small fluctuations in catch level (especially in early decades) from generating an overexploitation signal.

Furthermore, under Scenario 2, biomass is allowed to recover as a function of TL if overexploitation stops. If the catch increased in a given TL interval that was previously overexploited, we assumed that overexploitation had stopped in that interval. The biomass was allowed to recover from that of the previous (overexploited) decade to that predicted by EcoTroph (i.e. from Scenario 1) as a function of TL. Recovery R to equilibrium biomass was a declining linear relationship of TL, with full recovery at TL=2 ($R(2)=1$) and no recovery at TL=5 ($R(5)=0$), as defined in the relationship $R(\tau) = -0.33\tau + 1.67$ (where $0 \leq R \leq 1$).

Table 2 in the main text includes the equations used to calculate biomass under all 3 scenarios, given the default biomass predictions of EcoTroph (i.e. Scenario 1).

TRANSFER EFFICIENCY

The transfer efficiency parameter (TE) controls how efficiently energy is transferred between TLs. The default value, 10%, means that 90% of the production is lost over a transfer of one TL. A single value was used for all ecosystems as we deemed it outside of the scope of this study to build a worldwide model of ecosystem TE based on the point estimates available from Ecopath models (Christensen & Pauly 1992; see also an approach proposed in Pauly & Palomares 2005 and further explored in Appendix II of Gascuel et al. 2009).

In order to verify the sensitivity of our biomass predictions to TE , EcoTroph was run with values of TE between 5% and 15%, which represent a realistic range of TE expected for the world’s marine ecosystems (Pauly & Christensen 1995). Because it was impractical to run the sensitivity analyses at a global scale, we used instead a set of $0.5 \times 0.5^\circ$ cells belonging to 3 Large Marine Ecosystems representative of different ecosystem types: the North Sea (heavily exploited temperate system), the Gulf of Mexico (tropical system) and the Guinea Current (upwelling system). In the results presented below, we used the decade 1970 as an example.

The predictions of total ecosystem biomass of EcoTroph were very sensitive to the value of TE , as shown in Table S1. As TE increases, total biomass predicted between TLs 2 and 5 increased rapidly and the change was even greater for predators. In contrast, cells generally responded similarly to changes in TE ; that is, although the absolute value of biomass is quite sensitive to even small changes in TE , the relative spatial trends describing the cells most impacted by fishing were very robust to this parameter. Note that this statement does not hold for systems so heavily fished that observed catches are greater than the available production. Fig. S1 shows for a range of TE values the decline of total biomass for each cell in terms of its percentile. A 5th percentile indicates that the cell is within the top 5% highest biomass declines observed in that ecosystem. In both the Gulf of Mexico and the Guinea Current, there was almost no change in

the percentile to which each cell belonged as a function of TE . In the North Sea, however, where catches are often higher than observed production, the percentile of cells changed in some instances by as much as 40% as TE increased from 0.05 to 0.15. This phenomenon occurs because the TE also affects the proportion of unexploited ecosystem production occurring in higher TLs (not shown here): as TE increases, the proportion of ecosystem biomass occurring in high TLs also increases. Therefore, if catches are so high that P_t goes to 0 for a wide range of high TLs, the relative biomass decline observed is greater under high TE s.

In summary, the absolute biomass values predicted by EcoTroph were very sensitive to TE , but in the majority of cases, different ecosystems (i.e. cells) responded similarly to changes in TE . Catches were rarely high enough to drive production to zero and so, in general, the relative spatial trends of biomass decline between cells are robust to the TE parameter, under the assumption that TE is approximately the same in all ecosystems.

VALIDATION OF THE USE OF PRIMARY PRODUCTION FOR THE YEAR 1998

We used a model of global primary production by Sarmiento et al. (unpubl. data) for the period 1950–2004 to verify that the spatial trends in primary production (PP) for the year 1998 were representative of the period 1950–2004. We used the following method:

1. Calculate mean PP and standard deviation over 1950–2004 for each cell i : PP_i and SD_i .
2. For each year y , calculate the overall proportion of cells PP_y that are within 1 SD_i of their mean cell PP_i .
3. Calculate mean of PP_y over 1950–2004 and compare with PP_{1998} .

This approach allowed us to verify that the spatial variation in PP for 1998 was typical of that seen over 1950–2004. For 1998, the proportion of cells within 1 SD of their mean cell PP_i was 0.740, which was slightly above the mean PP_y of 0.724 (Fig. S2). We thus concluded that the spatial trends of PP for 1998 were representative of other years in 1950–2004.

LITERATURE CITED

- Christensen V, Pauly P (1992) The ECOPATH II – a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol Model* 61:169–185
- Gascuel D, Morissette L, Palomares MLD, Christensen V (2008) Trophic flow kinetics in marine ecosystems: Toward a theoretical approach to ecosystem functioning. *Ecol Modell* 217:33–47
- Gascuel D, Tremblay-Boyer L, Pauly D (2009) EcoTroph (ET): a trophic level based software for assessing the impacts of fishing on aquatic ecosystems. Fisheries Centre Research Report 17(1). University of British Columbia, Vancouver
- Mullon C, Freon P, Cury P (2005) The dynamics of collapse in world fisheries. *Fish Fish* 6:111–120
- Pauly D, Christensen V (1995) Primary production required to sustain global fisheries. *Nature* 374:255–257
- Pauly D, Palomares MLD (2005) Fishing down marine food webs: it is far more pervasive than we thought. *Bull Mar Sci* 76:197–211
- Pope J (1972) An investigation into the accuracy of virtual population analysis. *ICNAF Res Bull* 9:65–74

Table S1. Relative change in the 1970s total and predator biomass predicted by EcoTroph for 3 representative Large Marine Ecosystems (LMEs) as a function of the transfer efficiency parameter TE . Biomass was normalized to the biomass predicted under $TE = 0.10$, which is the value used for the main analysis of this report.

LME	Subset	TE				
		0.05	0.075	0.10	0.125	0.15
Gulf of Mexico	Total	0.292	0.593	1.000	1.521	2.167
	Predator	0.059	0.328	1.000	2.169	3.951
North Sea	Total	0.356	0.644	1.000	1.448	2.010
	Predator	0.055	0.320	1.000	2.728	6.505
Guinea Current	Total	0.326	0.614	1.000	1.500	2.132
	Predator	0.071	0.344	1.000	2.239	4.28

Fig. S1. Spatial trends in the response of individual cells within 3 representative Large Marine Ecosystems (LMEs) to changes in the transfer efficiency parameter TE . The LMEs represented are the Gulf of Mexico (top), the North Sea (middle) and the Guinea Current (bottom), and the decade chosen was the 1970s. The values of TE used in the model are 0.05, 0.075, 0.1, 0.125 and 0.15 (from left to right). Spatial trends are represented in terms of the percentile to which each cell beyond (each circle on the map stand for one $0.5 \times 0.5^\circ$ cell). A cell belonging to the 5th percentile is amongst the 5% most impacted of the LMEs, where impact is defined as a decline in fished biomass. A rough outline of the coasts is included for clarity as a dark blue line

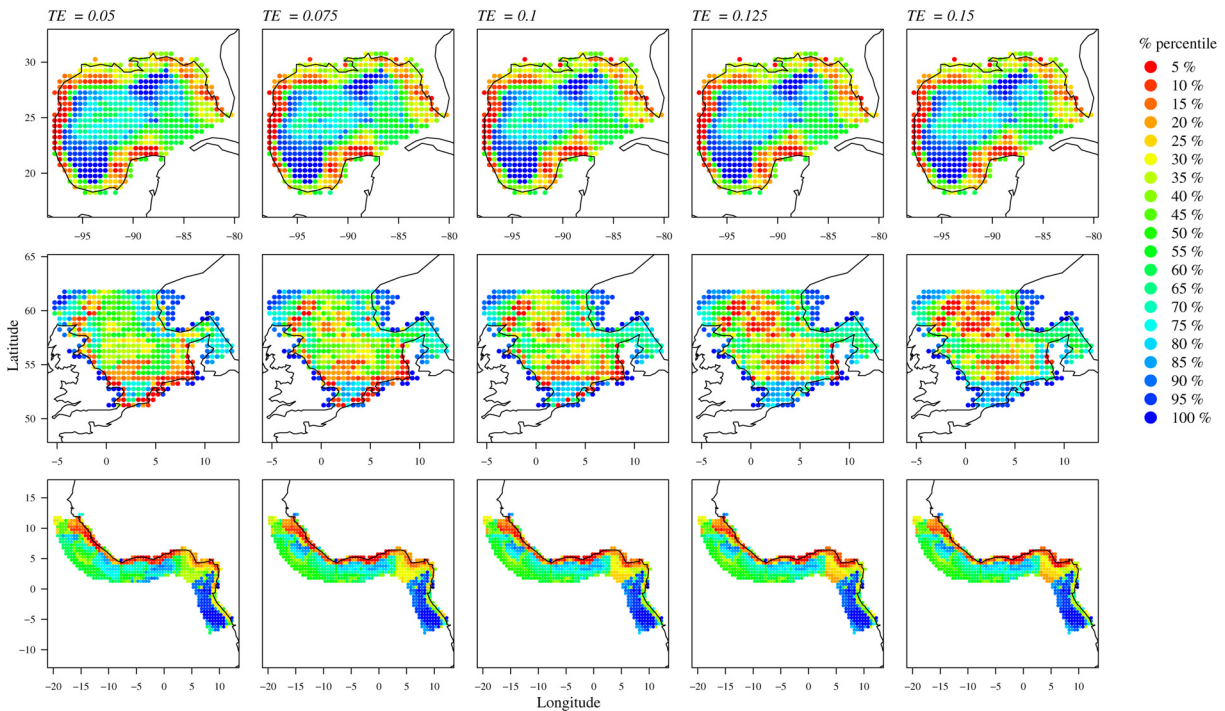


Fig. S2. Frequency count of the proportion of cells by year that are within 1 standard deviation of their mean cell primary production (PP) for each year in the time period 1950–2004

Mean % of cells within 1 SD of mean PP 1950–2004 = 0.724
% of cells within 1 SD in 1998 = 0.740

