

Novel index for quantification of ecosystem effects of fishing as removal of secondary production

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ABSTRACT: Exploited ecosystems are characterised by exports of secondary production from each fished trophic level that reduce the energy available for upper levels at the ecosystem scale, thus impinging on overall secondary production. Depletion in secondary production is proposed here as a proxy for quantifying the ecosystem effects of fishing. Theoretical analysis of trophic web interactions permits the quantification of the 'loss in production' and provides an ecological basis for defining a new synthetic index (L index) that takes into account both ecosystem properties (primary production and transfer efficiency) and features of fishing activities (trophic level of catches and primary production required). Quantitative meta-analysis of ecological models, representing 51 exploited ecosystems previously classified as overexploited or sustainably exploited, allows the association of a probability of the ecosystem being sustainably fished with each index value. Moreover, by fixing the reference level for this probability, the index provides a basis for estimating the maximum allowable catches. The L index is applied here to several ecosystems worldwide using landings data and ecological models, providing quantification of the disruption of energy flows for ecosystems subjected to different types and levels of fishing pressure. Its application to outputs of calibrated dynamic models enables the evaluation of sustainability of fisheries in past and future scenarios of alternative fisheries management policies. Results highlight the usefulness of this index for quantifying the impacts of fishing and providing directional advice for fisheries management. Thus, the L index may be used to support ecosystem-based management of fisheries.

KEY WORDS: Fishing impacts · Ecosystem functioning · Loss in production · Primary production required · Trophic level · Overfishing · Ecosystem-based fisheries management

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INTRODUCTION

Many fisheries are unsustainable. Overfishing evaluated through historical data (Jackson et al. 2001, Lotze et al. 2006), the decreasing trend of catch per unit (CPUE) effort for predatory fishes (Myers & Worm 2003) and the fishing down food web effect (Pauly et al. 1998a) are evidence of fishing impacts at the global scale. Indirect effects of fishing affect non-target components of the trophic web, from top predators (Springer et al. 2003) to benthic species (Jennings & Kaiser 1998). Fishing impacts propagate along trophic webs through cascading effects (Pace et al. 1999), affecting both the structure and functioning of ecosystems (Murawski 2000) and increasing the need for holistic approaches to fisheries (Pauly et al. 2002). Consequently, an increasing need for ecosys-

tem-based fishery management is being recognised by governmental entities, e.g. the European Community (2002), Canada's Oceans Act (Department of Justice Canada 1996) and the US Commission on Ocean Policy (2004).

The current challenge is to ensure a profitable yield, simultaneously accounting for dramatic changes in population abundances, biodiversity decrease and habitat degradation (Larkin 1996). Within this framework, scientists are searching for robust and quantitative indicators that will prove useful for communicating with stakeholders, monitoring, and assessing and adjusting policies towards defined management objectives (Daan et al. 2005). While several indicators have been proposed to date, very few seem to match all the criteria simultaneously (Rochet & Trenkel 2003).

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In this work, the loss in secondary production due to exploitation is used as a proxy for quantifying the ecosystem impacts of fishing. Its usefulness as an indicator for the ecosystem-based management of fisheries is evaluated through its extensive application.

Production as an indicator in the context of the ecosystem-based management

Using production as an ecosystem indicator is not new. Production integrates a set of fundamental ecological processes and is an indicator of ecosystem functioning (Tilman et al. 1997). Moreover, given the positive linear function between production and biodiversity at a regional scale as well as the bi-directionality of their relationship (Worm & Duffy 2003), a decrease in production might represent a threat to biodiversity and increase the risk of local extinction (Myers & Worm 2005).

Production has also been used in the fishery context to develop ecosystem-based references for fishery management (Bundy et al. 2005). Primary production required to sustain the fishery (PPR) (Pauly & Christensen 1995) enabled quantification of the fishing pressure on ecosystems at a global scale. Tudela et al. (2005) suggested the coupling of PPR over actual primary production (PP) with the mean trophic level of the catch (TL_c) to capture ecosystem effects of fishing.

In this study, theoretical analysis of trophic web interactions allows us to quantify the 'loss in secondary production' due to fishing that results as a function of catches (expressed in terms of PPR), TL_c , PP and transfer efficiency (TE) within the food web. Given the importance of production in determining ecosystem functioning (Tilman et al. 1997), the loss in secondary production due to fishing could be used as a comprehensive measure of alterations caused by exploitation. It could represent a trait summarizing all the effects that fishing might produce at the ecosystem level (sensu Murawski 2000), despite different system alterations produced by the coupling of different direct fishing impacts (Tittensor et al. 2006) and the complexity of ecosystem responses (Worm & Duffy 2003).

Estimation of the loss in secondary production from outputs of models representing well-studied ecosystems *a priori* classified as 'overfished' or 'sustainably fished' (Murawski 2000) enables us to associate a probability of the ecosystem belonging to a sustainably fished situation with each loss value. Applying the L index to different exploitation data, we infer the sustainability of fisheries for various exploited ecosystems worldwide and compare results with published analyses done on the basis of population and community data. Although our application takes advantage of data organized in Ecosim with Ecosim (EwE) food web

models (Christensen & Walters 2004), the L index is independent from EwE. It can be applied to other modelling approaches and landings data, provided that PPR, PP, TE and TL_c can be estimated. Fixing desirable target probabilities, we calculate the maximum sustainable catches (Tudela et al. 2005) that might provide a basis for ecosystem-based management of fisheries. In addition, application of the L index to outputs of dynamic models (Walters et al. 2005) enables us to estimate the sustainability of fisheries over time and to evaluate alternative management options.

Loss in secondary production as a proxy for quantifying effects of fishing

A common feature of exploited ecosystems is the export of a portion of secondary production from each fished trophic level, the type and strength of the impact notwithstanding. Despite the presence of compensatory effects within populations and communities (Walters & Martell 2004), this export at any given trophic level reduces the energy amount available for upper levels at ecosystem scale.

Loss in secondary production due to fisheries export can be derived theoretically by representing any complex food web as an equivalent linear food chain linking production (P_{TL}) at each trophic level (TL) by means of an average TE (Teramoto 1993). TL is here intended as a fractional value and defined as the average TL of prey weighted by their proportion in the diet of the predator (Pauly et al. 1998a, Stergiou & Karpouzi 2002). TE summarizes all the inefficiencies (due to respiration, excretion, and natural mortality) present at each step of the trophic chain and it is obtained as the ratio between the production of 2 adjacent TLs (Lindeman 1942, Pauly & Christensen 1995).

Under the assumptions that the system is in equilibrium and all transfers in the trophic chain are characterized by a single TE, it is possible to estimate P_{TL} given the production of the $TL = 1$ (P_1 , autotrophic production and detritus production by the trophic web) by means of the following equation (Lalli & Parsons 1993):

$$P_{TL} = P_1 \cdot TE^{TL-1} \quad (1)$$

Using Eq. (1) it is possible to estimate the theoretical loss of production at each trophic level caused by harvesting a quantity Y_c at TL_c . As an example, harvesting Y_2 at $TL_c = 2$ results in the following production at each trophic level:

$$\begin{aligned} P_2 &= P_1 \cdot TE \\ P_3 &= (P_1 \cdot TE - Y_2) \cdot TE \\ P_4 &= (P_1 \cdot TE - Y_2) \cdot TE^2 \\ &\dots \end{aligned} \quad (2)$$

$$P_{TL} = (P_1 \cdot TE - Y_2) \cdot TE^{TL-2} = P_1 \cdot TE^{TL-1} - Y_2 \cdot TE^{TL-2}$$

where negative terms represent indirect losses in secondary production at each $TL > 2$. Analogously, harvesting a quantity Y_c at a general TL_c results in a theoretical decrease of production (ΔP) for each TL , that is:

$$\Delta P_{TL} = Y_c \cdot TE^{TL-TL_c} \quad (3)$$

Total decrease in production along all the trophic levels (ΔP_{tot}), due to the fishing at TL_c , can be estimated by summing losses (ΔP_{TL}) from TL_c to the maximum TL of the trophic chain. Since there are small flows subjected to a high number of passages along the trophic chain, flows with very high TL exist, especially if cannibalism and cycling are considered (Baird & Ulanowicz 1989). Therefore, it is mathematically convenient to sum over all possible TL s to infinity. This does not influence the results due to the decreasing contribution of high TL s to ΔP_{tot} . In the continuous domain of TL (τ), estimation of the loss in secondary production would imply the solution of the following integral:

$$\Delta P_{tot} = \int_{TL_c}^{\infty} Y_c \cdot TE^{\tau-TL_c} d\tau \quad (4)$$

Catches can be expressed in terms of PPR (Pauly & Christensen 1995), thus accounting for the different amount of energy required for production at different TL s (from Eq. 1, $Y_c = PPR \cdot TE^{TL_c-1}$). Primary production can be used to normalize primary production required to sustain the fishery ($\%PPR = PPR/P_1$). Thus, the relative loss in production, here called the L index, is estimated by:

$$L = \int_{TL_c}^{\infty} \frac{PPR}{P_1} \cdot TE^{TL_c-1} \cdot TE^{\tau-TL_c} d\tau = -\frac{PPR \cdot TE^{TL_c-1}}{P_1 \cdot \ln TE} \quad (5)$$

where the integral is solved considering that TE is by definition smaller than 1 (Lindeman 1942, Pauly & Christensen 1995).

Losses are simply additive. Therefore, for multitarget fisheries, the total loss in production can be estimated by summing the contribution of each species (i) expressed in Eq. (5) over m caught species (Fig. 1A), as in the following equation:

$$L = -\frac{1}{P_1 \cdot \ln TE} \cdot \sum_i^m (PPR_i \cdot TE^{TL_i-1}) \cong -\frac{PPR \cdot TE^{TL_c-1}}{P_1 \cdot \ln TE} \quad (6)$$

where TL_c is calculated by weighting the TL of the caught species by their proportion in the total catch and reflects the overall strategy of the fishery (Pauly et al. 1998a). For graphic representation and sensitivity analysis, it is convenient to approximate the L index by using total PPR and the TL_c of the multispecies fishery as reported in the right side of Eq. (6), whereas the left-hand side is used to estimate the L index and its reference levels.

The total theoretical decrease in production with respect to the unexploited situation (Eq. 6) represents

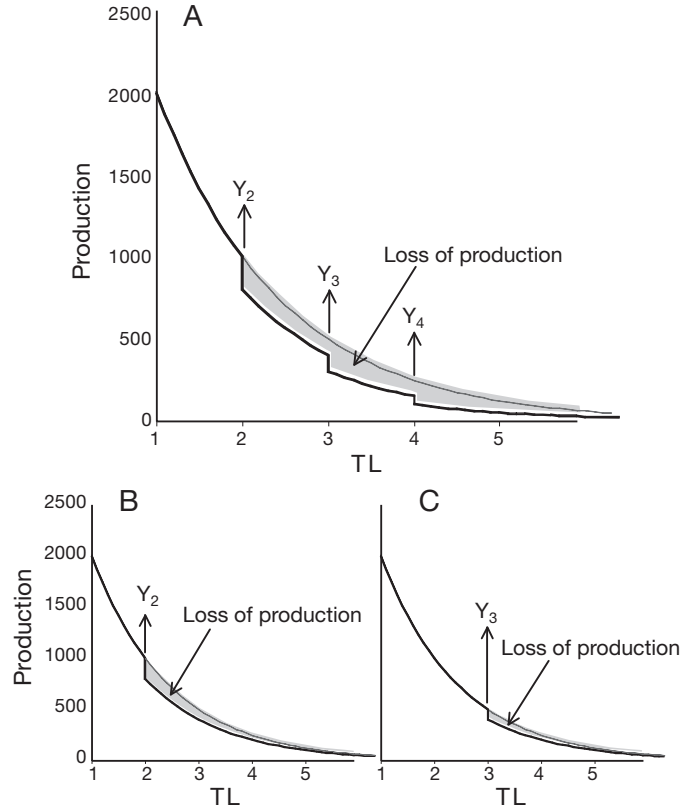


Fig. 1. Theoretical estimates of production at all trophic levels (TL s) when transfer efficiency (TE) is assumed constant for un-fished ecosystems (thin grey line). Theoretical decrease in production at upper TL s is due to appropriation of part of the production at a different TL by the fisheries (thick black line). Catches (Y) taken at different TL s are equivalent in terms of the primary production required to sustain the fishery (PPR). (A) The loss of production (shaded area) for multitarget fisheries (catches at TL 2, 3 and 4). (B, C) Comparing cases for landings coming respectively at TL 2 and 3, the greater loss in the production (shaded areas) for fishing at a lower TL is evident

the ecological costs of fishing at the TL_c . Ecosystems showing equal values of theoretical loss in production, i.e. the same L index value, would be considered equally depleted by fishing exploitation even if subjected to different fishing impacts and regimes.

Eq. (6) states that, for equivalent amount of catches expressed in PPR units, the relative loss in secondary production increases when TL of catches decreases since TE is always <1 . This mathematical result is graphically represented in Fig. 1B,C, where the loss in production in the food web is higher when fishing occurs at lower TL , as well as when catches have the same amount of equivalent PPR . More importantly, this analytical result is in accordance with the negative effects of fishing down the food web that was evaluated at the global scale (Pauly et al. 1998a).

In order to explore the propagation of uncertainty of each of the input variables (PPR , P_1 , TE and TL_c) on the

value of the L index, analytical and numerical sensitivity analyses were carried out, providing evidence of the high influence of TL_c on the L index, of the moderate influence of TE and of relatively low and constant sensitivities of PPR and P_1 (see Appendix 1).

Trophic web models can yield estimates of PPR and P_1 based on the primary producers food chain only (PPR_a and $P_1 = PP$) and also by including detrital production (PPR_b and $P_1 = PP + \text{flows to detritus}$). PPR_b should be preferred for its completeness. However, when using landings data, detrital flows might be difficult to quantify. Therefore, the index was applied using both PPR_a and PPR_b values and their respective normalizing factors for ecosystem models, while only PPR_a and PP were used when applying the L index to landings data.

MATERIALS AND METHODS

Defining an ecosystem-based reference framework for fisheries management. Data regarding %PPR_a and %PPR_b, TL_c and TE were obtained from a set of 91 ecosystem models previously constructed using the EwE software package (Christensen & Walters 2004, www.ecopath.org), and representing ecosystems characterised by different fishing pressures. The ecosystems that were well-studied and had enough information available were evaluated with respect to their fishing pressure and categorised as overfished or sustainably fished ecosystems, based on the criteria proposed by Murawski (2000). According to these criteria, overfished ecosystems involve structural and functional degradation, associated with stock collapses and overall overexploitation of marine resources, whilst in sustainably fished ecosystems, main functioning and structure are preserved. Thus, the ecosystems studied here were given an overexploited status when cumulative fishing impacts manifested at least 1 overexploitation symptom (Murawski 2000). This was done using information obtained from published and unpublished sources, personal communication with experts and modellers of each ecosystem, and findings of previous analyses (Tudela et al. 2005). The available information allowed the classification of 51 models (29 as overexploited and 22 as sustainably exploited; Table 1), while 40 models remained unclassified (Table 2).

A meta-analysis of the 51 classified models was conducted in order to develop a probability measure of sustainability. The L index was estimated for each model using the right side of Eq. (6) and both %PPR_a, %PPR_b, L_1 and L_2 are defined as values of the index estimated for the 29 models of overexploited ecosystems and the 22 sustainably fished ecosystems, respectively. The probability of an ecosystem being sustainably fished (p_{sust}) was defined for any given value of L as:

$$p_{\text{sust}}(L) = \frac{P(L_2 > L)}{P(L_2 > L) + P(L_1 < L)} \quad (7)$$

where $P(L_1 < L)$ is the number of cases within Group 1 that have values of the index lower than a chosen value L. For example, $L_{50\%}$ is the value of L that allows the proportion of overfished models with smaller values of L, $P(L_1 < L)$, to be equal to the proportion of sustainably fished models having greater L values, $P(L_2 > L)$, thus $P(L_1 < L) = P(L_2 > L)$ and $p_{\text{sust}}(L) = 50\%$.

Therefore, for any given value of L, the corresponding p_{sust} is estimated, providing values ranging from 0 to 100%, useful for identifying operational reference points. Fixing any desired reference for sustainability of the fisheries on the basis of risk assumptions, $p_{\text{sust}} = p$, it is possible to back-estimate the corresponding reference value of the index $L = L_p$ that is linked with fishing pressure. In order to consider moderate and low risk of ecosystem overfishing, reference probabilities were set at $p_{\text{sust}} = 75$ and 95% and the associated $L_{75\%}$ and $L_{95\%}$ were used to define an ecosystem-based reference framework for fishery management.

Incorporating uncertainty in the reference framework. Confidence intervals for the identified relationship between L values and p_{sust} were derived through the application of the jackknife resampling method (Crowley 1992) as described in the following steps:

- (1) Randomly extract a subset of k models from the original data set of $n = 51$ models, with $k < n$;
- (2) For the randomly chosen subset, perform analyses using Eq. (7) for estimating p_{sust} values for any L within an appropriate range;
- (3) Repeat the process N times, thus obtaining N independent estimates of p_{sust} for any L.

Resampling was done by extracting a subset of $k = 45$ models guaranteeing approximately 1.8×10^7 different combinations among which $N = 500$ cases were randomly chosen. At the end of the above procedure, N values of p_{sust} were synthetically obtained for any value of L, thus providing estimates of confidence intervals for the relationship between L and p_{sust} .

Applying the loss in secondary production to exploited systems. Suitability of the loss in secondary production for evaluating fishing pressure on ecosystems was assessed by applying the L index to different data: (1) mass-balance models, (2) calibrated dynamic ecosystem models, and (3) landings data sets.

- (1) The L index and p_{sust} were estimated for models not used for defining reference values. Estimated p_{sust} levels provided evaluation of the sustainability of fisheries in the modelled ecosystems ($p_{\text{sust}} < 50\% = \text{overexploited}$; $p_{\text{sust}} > 50\% = \text{sustainably fished}$) and results were evaluated in terms of coherence with partial information available.
- (2) The L index was also estimated using outputs of 4 dynamic ecosystem models (Walters et al. 2005)

Table 1. Ecosystem models previously classified (EO) as sustainably fished or overfished. Models listed by main ecosystem types, grey columns represent values estimated through the L index. EO: exploitation status according to the information available and ecosystem overfishing criteria (Murawski 2000), 1 = ecosystem overfishing; 2 = sustainably fished ecosystem, see first section of 'Materials and methods' for definition; TL_c: trophic level of the catch; TE: transfer efficiency; %PPR_a = % primary production required to sustain the fishery estimated from primary producers relative to primary production; EO_a: ecosystem overfishing; and p_{sust,a}: the probability of the ecosystem being sustainably fished, are estimated with the L index by using %PPR_a; %PPR_b = % primary production required to sustain the fishery estimated from primary producers and detritus relative to primary production and flow to detritus; EO_b and p_{sust,b} are estimated with %PPR_b; Fishery column lists the main fished groups (with % catch, trophic level)

No.	Ecosystem model	EO	TL _c	TE	%PPR _a	EO _a	p _{sust,a} (%)	%PPR _b	EO _b	p _{sust,b} (%)	Fishery	Source
Temperate shelves and seas												
1	Azores archipelago (1997)	2	3.77	10.5	0.31	2	100.00	0.22	2	100.00	Tunas (43.69, 3.82), demersal fishes (20.25, 4.06–4.21)	Guénette & Morato (2001)
2	Cantabric Sea (1994)	1	3.76	38.1	82.35	1	0.00	64.87	1	0.00	Hose mackerel (16.91, 3.83), blue whiting (14.74, 3.84), mackerel (13.62, 3.83), large demersal fishes (10.23, 4.3)	Sánchez & Olaso (2004)
3	Eastern Bering Sea (1950s)	2	3.35	14.3	30.89	1	6.74	27.27	1	6.07	Small flatfish (39.29, 3.2), pelagic fishes (28.57, 3.25), baleen whales (17.86, 3.61), sperm whales (3.57, 4.75)	Trites et al. (1999)
4	Eastern Bering Sea (1980s)	1	3.29	13.2	15.2	1	24.53	14.46	1	25.04	Adult pollock (72.5, 3.28), small flatfish (8, 3.16), pelagic fishes (8, 3.19)	Trites et al. (1999)
5	Faroe Islands (1961)	2	3.85	14.40	14.72	2	66.52	9.97	2	70.71	Cod (29.2, 4.07), haddock (22.9, 3.63), demersal fishes (18.8, 3.66), herring (8.3, 3.39), toothed mammals (2.1, 4.53)	Zeller & Freire (2001)
6	Georgia Strait (1950)	2	3.25	9.5	6.99	2	92.26	5.65	2	87.83	Adult herring (90.82, 3.18)	Pauly et al. (1998b)
7	Icelandic fisheries (1950)	2	3.36	14.20	1.91	2	94.45	1.53	2	95.32	Adult cod (44.6, 3.65), redfish (16.9, 3.11), herring (10.3, 2.9), baleen whales (2.1, 3.2)	Buchary (2001)
8	Lancaster Sound Region (1980s)	2	4.12	8.2	3.29	2	100.00	7.92	2	100.00	Marine mammals (100, 3–4.53)	Mohammed (2001)
9	Newfoundland (1900)	2	3.54	17.30	27.20	1	0.14	27.62	1	0.15	Harp seals (42.86, 4.14), capelin (28.57, 3.27), hooded seals (14.29, 4.72), bivalves (14.29, 2)	Heymans (2003)
10	Newfoundland (1985–1987)	1	3.9	15.5	6.33	2	88.96	7.47	2	78.61	Adult cod (45.8, 4.07), redfish (13.74, 3.52), capelin (9.92, 3.12), adult aplaice (7.63, 3.59)	Bundy et al. (2000)
11	Newfoundland (1995–2000)	1	3.13	14.30	15.11	1	14.27	16.75	1	11.89	Large crabs (29.17, 2.92), capelin (16.67, 3.27), shrimp (16.67, 2.46), harp seals (12.50, 4.14)	Heymans (2003)
12	North Sea (1880)	2	3.77	27.20	0.3	2	95.20	0.33	2	95.87	Herring (38.75, 3.42), plaice (7.5, 3.73), Cod (6.25, 4.38)	Mackinson (2001)
13	North Sea (1963)	1	3.89	16.00	62.64	1	6.41	65.53	1	4.92	Norway pout (20.88, 3.75), sandeel (9.46, 3.67), sprat (9.46, 3.18), saithe (8.48, 4.55), herring (7.67, 3.81)	Fisheries Centre (2007)
14	North Sea (1974)	1	3.89	19.20	61.98	1	0.00	64.85	1	0.00	Norway pout (20.88, 3.75), sandeel (9.46, 3.67), sprat (9.46, 3.18), saithe (8.48, 4.55), herring (7.67, 3.81)	Fisheries Centre (2007)

Table 1. (continued)

No.	Ecosystem model	EO	TL _c	TE	PPR _d	EO _a	P _{sust, a} (%)	PPR _b	EO _b	P _{sust, b} (%)	Fishery	Source
15	North Sea (1981)	1	3.39	11.60	21.83	1–2	35.69	20.28	1–2	41.01	Sandeel (25.89, 3.05), Norway pout (18.08, 3.42), cod (12.72, 3.76), haddock (8.48, 3.5), whiting (8.26, 3.92)	Christensen (1995)
16	Northern British Columbia (1750)	2	3.48	13.30	4.04	2	93.90	5.1	2	84.74	Transient salmon (31.25, 3.13), eulachon (25, 3.04), coho salmon (12.5, 4.12), chinook salmon (12.5, 3.92)	Ainsworth et al. (2002)
17	Northern British Columbia (1900)	2	3.33	13.70	23.26	1	15.15	24.92	1	12.56	Transient salmon (48.15, 3.13), eulachon (14.81, 3.04), Myxetidae (11.11, 3.07), chinook salmon (7.41, 3.92), dogfish (7.41, 3.66)	Ainsworth et al. (2002)
18	Northern British Columbia (1950)	1	3.38	14.30	12.28	1–2	33.37	14.39	1	23.43	Adult herring (33.81, 3.18), transient salmon (28.78, 3.13), adult halibut (7.19, 4.12), coho salmon (4.32, 3.91)	Ainsworth et al. (2002)
19	Northern British Columbia (2000)	1	3.28	14.20	9.77	1–2	38.35	12.42	1	20.97	Transient salmon (29.50, 3.13), adult herring (13.67, 3.18), shrimp (5.76, 2), adult rockfish (5.76, 3.6)	Ainsworth et al. (2002)
20	Northern Gulf of Saint Lawrence (1985–1987)	2	3.57	12	22.94	2–1	53.85	25.25	1–2	45.74	Large cod (51.1, 3.86), redfish (19.71, 3.57), small pelagics (10.22, 3.23), shrimp (7.3, 2.71)	Monrissette et al. (2003)
21	Norwegian and Barents Sea (1950)	2	3.59	10.50	11.66	2	91.99	8.52	2	94.14	Adult cod (41.86, 4.12), adult herring (30.23, 3.08), saithe (9.30, 3.57), haddock (6.98, 3.11)	Dommasnes et al. (2001)
22	Eastern Scotian shelf (1980–1985)	2	3.54	11.00	8.91	2	92.32	59.52	2	86.70	Adult cod (30, 3.77), adult hake (24.12, 3.83), juvenile cod (12.94, 3.53), juvenile hake (7.06, 3.59), haddock (7.06, 3.26), pollock (7.06, 3.77)	Bundy (2005)
23	South Catalan Sea (1994–2000)	1	3.12	12.60	9.45	1–2	44.55	10.6	1	28.71	Sardine (52.99, 2.92), anchovy (17.60, 3), octopuses (4.3, 3.1), hake >25cm (3.93, 4.08)	Coll et al. (2006)
24	Northern-central Adriatic Sea (1990s)	1	3.07	10.0	6.59	2	71.65	15.00	1–2	38.48	Anchovy (20.2, 3), sardine (16.6, 2.92), benthic invertebrates (13.4, 2), crabs (7.3, 2.98), octopus (6.5, 3.29), hake <45 cm. (4.9, 3.96)	Coll et al. (2007)
25	West Greenland coast (1997)	1	3.16	12.10	20.18	1	21.59	15.03	1	20.92	Shrimp (54.72, 2.66), halibut (11.32, 4.12), seals (7.55, 4.32)	Pedersen & Zeller (2001)
Tropical shelves and seas												
26	Bay of Bengal (1984–1986)	1	2.7	9	8.28	1–2	41.06	5.49	2	64.59	Small discarded fishes (29.55, 2.3), medium demersals (28.41, 3.3), small pelagics (10.23, 2.5), shrimp (10.23, 2.21)	Mustafa (2003)

Table 1. (continued)

No.	Ecosystem model	EO	TL _c	TE	PPR _d	EO _a	P _{sust, a} (%)	PPR _b	EO _b	P _{sust, b} (%)	Fishery	Source
27	Brunei Darussalam (1980)	2	3.2	12.9	7.43	2–1	59.74	9.3	2–1	51.00	Pelagic fishes (38.36, 2.97), crustaceans (23.29, 2.83), intermediate & large predators (16.44, 4.18–4.25)	Silvestre et al. (1993)
28	Gulf of Mexico continental shelf (1990s)	1	2.6	9.7	31.65	1	0.00	26.57	1	0.00	Pelagic fishes (46.79, 2.05), demersal fishes (36.07, 3.15–3.82), crustaceans (13.57, 2.5)	Browder (1993)
29	Gulf of Thailand (1963)	2	2.99	5.2	1.76	2	99.21	1.23	2	100.00	Trashfish (23.38, 2.56), mackerel (19.48, 2.96), small pelagics (14.29, 2.9)	Christensen (1998)
30	Gulf of Thailand (1980s)	1	3.14	10.40	16.12	1–2	48.69	14.38	2–1	51.25	Small demersals (58.35, 3.19), small pelagics (16.06, 2.81), medium pelagics (9.85, 3.53), crustaceans (6.32, 2.49)	Christensen (1998)
31	Hong Kong (1990s)	1	2.96	9.1	27.21	1	20.54	21.05	1	19.69	Small pelagics (36.65, 2.94), small demersals (22.45, 2.69–2.92), medium demersals (5.36, 3.3), large demersals (11.14, 2.69–2.92)	Cheung et al. (2002)
32	San Pedro Bay (1994–1995)	2	3.25	9.4	3.06	2	95.17	4.36	2	94.95	Small demersals (28.86, 3.27–3.46), ponyfish (16.02, 3.22), macropifauna (11.46, 2.54), small pelagics (10.08, 2.81), medium demersal fishes (8.43, 3.67)	Campos (2003)
33	South China Deep Sea (1980s)	2	3.46	10.6	9.96	2	77.16	9.38	2	85.52	Intermediate predators (42.11, 3.43),	Pauly & Christensen (1993)
34	Southern Brazil (1990–1994)	1	3.77	6.3	9.77	2	99.06	10.02	2	98.61	Pelagic fishes (41.03, 4.08), weakfish (31, 3.64), sharks (13.17, 3.99), jack mackerel (5.47, 3.18)	Vasconcelos & Gasalla (2001)
35	Southwest coast of India (1994)	1	2.61	13.5	13.2	1	0.00	8.28	1	5.15	Plankton feeders (47.95, 2.11), demersal feeders (21.83, 3.3), medium predators (11.77, 3.21), detritivores (7.47, 2)	Vivekanandan et al. (2003)
36	Southwest coast of India (1995)	1	2.59	13.5	10.67	1	0.00	6.63	1	11.49	Plankton feeders (49.57, 2.11), Demersal feeders (18.86, 3.26), medium predators (12.28, 3.21), detritivores (7.73, 2)	Vivekanandan et al. (2003)
37	Southwest coast of India (1996)	1	2.61	14	11.66	1	0.00	7.26	1	5.69	Plankton feeders (47.95, 2.11), demersal feeders (21.83, 3.26), medium predators (11.77, 3.21), detritivores (7.48, 2)	Vivekanandan et al. (2003)
38	Venezuela north-eastern shelf (1980s)	1	2.80	7.30	20.72	1	25.99	13.33	2–1	60.07	Small pelagics (51.05, 2.58), demersal fishes (15.87, 3.2), benthos (13, 2.21)	Mendoza (1993)
39	Vietnam-China shelf (1980)	2	3.34	7.5	9.73	2	94.79	8.05	2	95.65	Intermediate predators (53.70, 3.45), small demersal fishes (25.31, 3.11), cephalopods (16.05, 3.17)	Pauly & Christensen (1993)

Table 1. (continued)

No. Ecosystem models	EO	TL _c	TE	PPR _a	EO _a	P _{sust, a} (%)	PPR _b	EO _b	P _{sust, b} (%)	Fishery	Source
Coastal areas											
40 Bay of Revellata, Corsica (1998)	2	3.77	18.80	11.91	1	27.49	10.29	1	31.04	Piscivores (27.32, 4.29), medium carnivores (27.32, 4.1), planktivorous fishes (18.04, 3.54), invertebrate feeders (11.85, 3.23–3.27)	Pinnegar (2000)
41 Bolinao reef flat (1991)	1	2.2	10.4	2.75	1	22.88	2.25	1	26.76	Spinefoot (21.10, 2.02), molluscs (17.89, 2), sea cucumbers (12.0, 2), sea urchins (9.94, 2), seaweeds (7.57, 1), parrotfish (7.42, 2)	Aliño et al. (1993)
42 Coast of Western Gulf of Mexico (1990s)	1	3.44	16.2	89.49	1	0.00	65.42	1	0.00	Sharks (15.15, 4.78), mojarras (13.64, 3.04), shrimp (12.12, 2.79), crabs (10.6, 2.5), mackerel (10.6, 3.93)	Arrequín-Sánchez et al. (1993a)
43 Gulf of Lingayen (1990s)	1	3.32	13.5	51.61	1	0.00	32.97	1	5.41	Intermediate predators (28.60, 3.8), Scombrids (20.60, 2.84), demersal fishes (16.16, 3.37), ponyfish (14.39, 3.49)	Pauly & Christensen (1993)
44 Maputo Bay (1980s)	1	2.53	7.6	20.29	1	12.94	14.31	1	18.67	Small pelagics (58.16, 2.14), demersal fishes (20.57, 3.32), benthic invertebrates (19, 2.82)	De Paula et al. (1993)
45 Prince William Sound, Alaska (1994–1996)	2	4.13	14.10	4.46	2	95.72	3.31	2	96.08	Adult salmon (61.87, 4.18), adult herring (29.95, 3.1)	Okey & Pauly (1998)
46 San Miguel Bay (1992–1994)	1	3.00	20.60	14.75	1	0.00	20.77	1	0.00	Sciaenids (22.88, 3.38), Sergestids (16.19, 2.42), pelagics (14.98, 2.96–3.18), Penaeids (11.34, 2.61)	Bundy & Pauly (2001)
Lagoons											
47 Venice lagoon (1988)	2	3.26	7.2	1.2	2	100.00	10.08	2	94.61	Sand smelt (24.39, 3.38), grass goby (24.17, 3.56), macrobenthos omnivorous mixed-feeders (14.35, 2.46), macrobenthos omnivorous predators (9.43, 3.25)	Pranovi et al. (2003)
48 Venice lagoon (1998)	1	2.31	14.5	3.6	1	13.57	18.01	1	0.00	Manila clam (48.8, 2.09–2.46), macrobenthos omnivorous mixed-feeders (26.2, 2.46), macrobenthos, detritivorous (13.9, 2.35)	Pranovi et al. (2003)
Upwelling ecosystems											
49 North Benguela upwelling (1978–1983)	1	2.98	5.9	12.39	2	80.51	8.83	2	88.86	Horse mackerel (41.20, 3.12), anchovy (26.96, 2.44), hake (16.16, 3.42)	Fisheries Centre (2007)
50 Peru upwelling (1953–1959)	2	2.35	3.6	7.99	2	70.09	5.24	2	82.46	Anchoveta (86.13, 2.21), bonito (7.24, 3.37)	Jarre-Teichmann et al. (1991)
51 Peru upwelling (1973–1981)	1	2.67	6.60	7.86	2	64.20	5.25	2	70.52	Anchovy (60.9, 2.44), sardine (24.59, 2.89)	Jarre-Teichmann et al. (1991)

Table 2. Ecosystem models with partial information available on overfishing status classified accordingly with the methodology proposed. Models not classified *a priori* according to EO criteria because only incomplete information was available. EO status and p_{sust} resulting from the application of the L index are reported (grey columns). Abbreviations as in Table 1

No. Ecosystem model	Information	TL _c	TE	PPR _a	EO _a	$p_{\text{sust},a}$ (%)	PPR _b	EO _b	$p_{\text{sust},b}$ (%)	Fishery	Source
Temperate shelves and seas											
52 Atlantic coast of Morocco (1980s)	Highly fished	3.19	10.9	5.54	2	75.70	4.03	2	87.15	Sardine (53.07, 2.92), medium pelagics (27.44, 3.51), cephalopods (7.22, 3.49)	Stanford et al. (2001)
53 Baltic sea (1974)	Highly fished	3.6	25.9	36.33	1	0.00	39.08	1	0.00	Sprat (36.11, 3.45), herring (34.17, 3.46), cod (17.22, 4.19)	Harvey et al. (2003)
54 Bay of Biscay (1970)	Highly fished	3.29	16.3	-	-	-	3.51	2	67.06	Sardine (21.3, 3), anchovy (17.16, 3.14), deepwater fishes (9.47, 3.34), large pelagics (8.87, 3.46), crabs (8.28, 2.72)	Ainsworth et al. (2001)
55 Bay of Biscay (1998)	Highly fished	3.44	16.5	-	-	-	2.98	2	71.08	Anchovy (17.09, 3.16), large pelagics (16.24, 3.52), sardine (9.40, 3), large demersals (8.55, 3.64)	Ainsworth et al. (2001)
56 Central North Pacific ocean (1990–1998)	Top predators fishery	3.92	4.4	12.00	2	100.00	7.00	2	100.00	Skipjack (55.46, 3.85), yellowfin tuna (19.40, 4.12–3.91)	Cox et al. (2000)
57 Chesapeake Bay (1950)	Highly fished; eutrophication problems	2.56	12.5	20.46	1	0.00	13.58	1	0.00	Adult menhaden (46.94, 2.1), adult blue crab (26.15, 3.03)	Walters et al. (2005)
58 Eastern Tropical Pacific ocean (1993–1997)	Top predators fishery	4.69	20.4	9.78	2	77.64	6.29	2	93.74	Large yellowfin tuna (32.69, 4.66), skipjack (24.84, 4.57), small yellowfin tuna (17.15, 4.57), large bigeye (12.97, 5.17)	Olson & Watters (2003)
59 Faroe Islands (1997)	Recovering from high exploitation	3.72	15.40	33.24	1	17.42	22.21	1	22.32	Blue whiting (41.3, 3.55), cod (14.5, 4.09), saithe (8.7, 4.11), haddock (6.5, 3.64), toothed mammals (0.7, 4.67)	Zeller & Freire (2001)
60 Gulf of Maine - Georges Bank (1982)	Highly exploited	3.53	15.6	6.52	2	63.29	3.86	2	74.35	Herring (18.61, 3.36), cod (13.95, 3.99), large demersals (7.56, 3.96), small pelagic feeders (6.98, 3.25), pollock (6.98, 3.87)	Heymans (2001)
61 Icelandic fisheries (1997)	Fished biomass decrease; cod heavily fished	2.85	14.00	-	-	-	2.2	2	67.36	Capelin (63, 2.9), adult cod (9.18, 3.65), redfish (3.4, 3.11)	Mendy & Buchary (2001)
62 Norwegian and Barents Sea (1997)	Medium-high exploitation regime	3.51	3.51	17.90	2	100.00	12.78	2	100.00	Adult herring (49, 3.28), adult cod (29, 4.26)	Dommasnes et al. (2001)
63 Eastern Scotian Shelf (1995–2000)	Low exploitation after collapse of groundfish stocks	3.26	12.3	0.54	2	95.90	1.28	2	95.97	Juvenile silver hake (31.15, 3.59), bivalve molluscs (16.35, 2.00), adult silver hake (12.26, 4.1), large crabs (7.1, 3.03), shrimps (7.0, 2.45)	Bundy (2005)

Table 2. (continued)

No. Ecosystem model	Information	TL _c	TE	PPR _a	EO _a	P _{assist, a} (%)	PPR _b	EO _b	P _{sustb} (%)	Fishery	Source
64 West coast of Vancouver Island (1950)	Highly exploited	3.66	13.7	33.35	1	22.57	22.38	1–2	35.94	Adult herring (52.30, 3.61), demersal fish (42.09, 3.67)	Martell (2002)
65 West Greenland trawling area (1994)	Shift regime from cod to shrimp. Important amount of cod bycatch	3.25	7.10	3.57	2	95.81	2.64	2	96.19	Shrimp (80.29, 3.13), redfish (11.68, 3.66)	Pedersen & Zeller (2001)
Tropical shelves and seas											
66 Campeche Bank of Yucatan shelf (1990s)	Highly exploited with some overexploited resources	4.11	17.6	50.39	1	14.07	37.59	1	19.04	Groupers (33.33, 4.64), octopus (22.22, 4.1), snappers (11.11, 4.56), sharks (11.11, 4.94), herring (11.11, 3.17), porgies (11.11, 3.42)	Arreguín-Sánchez et al. (1993b)
67 Continental shelf of southern Brazil (1990s)	Highly exploited	3.37	11.8	-	-	-	3.3	2	94.70	Whitemouth croaker (23.4, 3.06–3.23), Argentine croaker (19.2, 3.13), South American striped weakfish (14.89, 3.64–3.20), skipjack tuna (10.64, 3.42)	Velasco Canziani (2004)
68 Bali Strait (1990s)	Heavily exploited, sardine could be overexploited	2.91	11.7	6.90	2–1	50.14	3.99	2	66.90	Small pelagics (83.91, 2.8), medium pelagics (12.02, 3.66)	Buchary et al. (2002)
69 Gulf of Thailand (1973)	Moderate fishing	2.73	5.6	3.04	2	95.02	2.29	2	95.97	Trashfish (27.82, 2.56), shellfish (17.34, 2.2), shrimp (8.87, 2.35)	FAO/FISHCODE (2001)
70 Gulf of Thailand (1993)	Highly exploited	2.76	5.3	2.84	2	95.56	2.2	2	96.04	Small pelagic (18.96, 2.90) mackerel (15.15, 2.97), small demersal (11.55, 3.18) trashfish (7.84, 2.56)	Fisheries Centre (2007)
71 Kuala Trengganu (1980s)	Moderate fishing	3.41	17.8	26.13	1	0.00	35.67	1	0.00	Pelagic fishes (59.72, 3.17), intermediate predators (18.16, 4.27), small demersal zoobenthonic feeders (12.92, 3.39)	Pauly & Christensen (1993)
72 Tampa Bay (1950)	Moderate fishing	2.56	8.6	0.72	2	95.14	0.61	2	95.97	Mullet (72.12, 2.03–2.91), blue crab (9.62, 2.65)	Walters et al. (2005)
Coastal areas											
73 Beach seine fishery area of Gulf of Mexico (1990s)	Fishing pressure has declined	3.06	16.1	51.99	1	0.00	44.38	1	0.00	Pigfish (35.27, 3.09), herring (28, 2.92), pinfish (8.51, 3.06), grunt (8.3, 3.3)	Vega-Cendejas et al. (1993)
74 Floreana rocky reef, Galapagos (1999–2000)	Highly exploited	2.27	13	6.7	1	0.00	4.31	1	5.39	Sea cucumbers (70.36, 2.06), detritivorous mullets (15.42, 2.12)	Okey et al. (2004)

Table 2. (continued)

No. Ecosystem model	Information	TL _c	TE	PPR _a	EO _a	P _{sust, a} (%)	PPR _b	EO _b	P _{sust, b} (%)	Fishery	Source
75 Great Barrier Reef, prawn ground of Far North (1994–1996)	Trawl resources fully-exploited	2.37	11.5	7.89	1	0.00	13.89	1	0.00	Small omniv. fishes (33.88, 2.71), herbivore fishes (33.88, 2.01), sessile invertebrates (18.97, 2.05)	Fisheries Centre (2007)
76 North coast of central Java (1979–1980)	Highly fished	3.04	11.8	11.41	1	28.46	10.05	1	31.01	Small pelagics (24.488, 2.94–3.44), demersal fishes (16.7, 3.09–3.12), large pelagics (15.20, 3.19), mackerel (13.49, 3.15)	Nurhakim (2003)
77 Schlei Fjord (1984)	Highly fished small pelagics	3.08	7.40	43.40	1	24.03	71.8	1	12.51	Temporal planktivorous (80.14, 3), medium predators (13.24, 3.51)	Christensen & Pauly (1992)
78 Shallow areas of Gulf of Thailand (1979)	Small scale fisheries	2.64	6.8	2.63	2	94.12	2.88	2	87.45	Molluscs & jellyfish (38.66, 2.13), crustaceans (30.67, 2.55), small demersal fishes (22.70, 3.29)	Pauly & Christensen (1993)
Coastal lagoons											
79 Celestun lagoon, Mexico (1990s)	Healthy exploited	3.24	6.4	7.74	2	95.34	7	2	95.97	Lutjans (49, 3.44), <i>Arius</i> sp. (16, 3.35)	Chávez et al. (1993)
80 Chicú lagoon, Taiwan (1996–1997)	Highly fished	2.4	13.1	47.27	1	0.00	68.22	1	0.00	Herbivorous fishes (41.79, 2), oysters (28.03, 2.1), benthic fishes (19.50, 3.2)	Lin et al. (1999)
81 Etang de Thau, France (1980s)	Moderate – highly exploited	2.19	10.80	2.65	1	22.61	10.77	1	0.00	Molluscs (96.42, 2.14)	Palomares et al. (1993)
82 Laguna de Bay, Philippines (1968)	Some degradation and pollution of water	2.26	15.5	14.57	1	0.00	9.19	1	0.00	Snails (58.81, 2), shrimp (16.76, 2.46), therapon (16.21, 2.73)	Delos Reyes & Martens (1994)
83 Laguna de Bay, Philippines (1980)	Degradation and pollution of water	2.08	12.4	24.72	1	0.00	19.94	1	0.00	Snails (71.10, 2), milkfish (14.83, 2), therapon (6.59, 2.72)	Delos Reyes & Martens (1994)
84 Orbetello lagoon (1995)	Stressed ecosystem	3.01	9.2	9.26	2	63.22	6.3	2	69.82	Pleustophytes (97, 1), mullet (1.4, 2.26–2.36)	Brando et al. (2004)
85 Orbetello lagoon (1996)	Stressed	1.13	9.6	8.68	1	0.00	6.07	1	0.00	Pleustophytes (93.8, 1), seabream (2.49, 3.74), mullet (2.18, 2.26–2.36)	Brando et al. (2004)
Upwelling ecosystems											
86 California upwelling (1965–1972)	Sardine and mackerel stocks breakdown	2.98	3.9	1.67	2	100.00	1.25	2	100.00	Hake/whiting (53.68, 3.17), anchovy (32.63, 2.56), demersal fishes (12.63, 3.23)	Jarre-Teichmann (1998)
87 California upwelling (1977–1985)	Fish and marine mammals increasing	2.86	4	3.94	2	95.84	2.92	2	96.23	Anchovy (53.55, 2.56), hake/whiting (19.13, 3.17), demersal fishes (13.66, 3.23), mackerel (13.66, 3.18–3.27)	Jarre-Teichmann (1998)

Table 2. (continued)

No. Ecosystem model	Information	TL _c	TE	PPR _a	EO _a	P _{sust,a} (%)	PPR _b	EO _b	P _{sust,b} (%)	Fishery	Source
88 NW Africa upwelling (1972–1979)	Highly fished	3.059	6.1	12.4	2	93.39	9.38	2	94.36	Horse mackerel (25, 3.28), sardine (17.14, 2.22), demersal fishes (14.21, 3.23), sardinella (13.51, 2.83), other pelagics (23.89, 2.83–3.21)	Jarre-Teichmann (1998)
89 Peru upwelling (1960–1969)	Highly fished	2.22	3.9	10.63	1–2	32.68	7.18	2–1	62.14	Anchovy (98.51, 2.44)	Jarre-Teichmann et al. (1991)
90 Peru upwelling (1964–1971)	Before collapse of anchovy. Highly fished	2.45	3.9	12.36	2	62.16	9.07	2	68.69	Anchovy (60.90, 2.44), sardine (24.59, 2.89)	Jarre-Teichmann (1998)
91 North Benguela upwelling (1971–1977)	Highly fished	2.85	7.9	4.98	2	77.00	10.17	2	65.05	Sardine (36.63, 3.1), hake (26.42, 3.4), horse mackerel (17.21, 2.2), anchovy (16.66, 3.4)	Heymans et al. (2003)

representing the North Sea, the Western Vancouver Island coast, the Southern Benguela and the Eastern Tropical Pacific. These models are provided with time series of biological data, vulnerability settings, environmental forcing functions and changes of fishing pressure for simulating dynamics of marine populations. A mass-balance Ecopath model was saved for each simulated year, thus obtaining annual estimates of the input variables for calculating L and p_{sust} over time. Moreover, keeping all the environmental factors constant and changing the fishing pressure exerted by chosen fleets, 6 future scenarios were explored for the North Sea model (Christensen et al. 2002), thus obtaining insights into the sustainability of alternative management policies.

- (3) Data sets with different degrees of aggregation of landings for various marine areas were used to estimate the L index and p_{sust}. Aggregated data for main marine ecosystem types (open oceans, upwellings, tropical shelves, temperate shelves and coastal areas and reefs) were taken from Pauly & Christensen (1995) for the years 1988 to 1991. Disaggregated landing statistics for the Mediterranean basin and the Black Sea enabled estimation of TL_c and PPR by means of equations proposed by Pauly et al. (1998a) and Pauly & Christensen (1995), respectively. Data included official landings, discards and illegal, unregulated or unreported catches (IUU). PP estimates were taken from published data and a characteristic TE for each ecosystem type was estimated from the set of 91 ecosystem models (Appendix 2).

Given a reference level of p_{sust} = p, the relative target value L_p can be achieved with different strategies combining appropriate values of TL_c, %PPR, TE and P₁. Assuming a constant fishing strategy fishery (i.e. TL_c constant) and ecosystem functioning (i.e. TE and P₁ constant), target %PPR_p can be estimated by inverting Eq. (6). On the basis of target and actual PPR (%PPR_p, %PPR⁰ respectively) along with actual catches (Y⁰), the corresponding ecosystem-based maximum sustainable catches (EMSC_p) (Tudela et al. 2005) can be estimated as:

$$EMSC_p = \frac{\%PPR_p}{\%PPR^0} \cdot Y^0 = \frac{(-L_p \cdot \ln TE \cdot TE^{1-TL_c})}{\%PPR^0} \cdot Y^0 \quad (8)$$

EMSC_p represents the maximum catch that allows the ecosystem to achieve a given reference level of p_{sust} = p. Therefore EMSC₇₅ and EMSC₉₅ for the 2 reference values chosen (p_{sust} = 75%, 95%) represent a practical, though approximate, guide for fishery management.

RESULTS

Ecosystem-based reference framework for fisheries management

Fig. 2 shows the 3D plot of %PPR_a, TL_c and TE values for the 51 classified models and surfaces that represent points with equal loss in secondary production, i.e. with equal probabilities of the ecosystem being sustainably fished ($p_{\text{sust}} = 0$ and 100%).

Reference values and confidence intervals for the L index are estimated applying Eq. (7) and the jackknife method to the well-studied and classified models (Table 1) obtaining $L_{50\%} = 0.054 \pm 0.014$, $L_{75\%} = 0.021 \pm 0.013$ and $L_{95\%} = 0.007 \pm 0.007$ using %PPR_a; and $L_{50\%} = 0.050 \pm 0.010$, $L_{75\%} = 0.019 \pm 0.014$ and $L_{95\%} = 0.009 \pm 0.008$ using %PPR_b. Fig. 3 reports the relationship between L and p_{sust} found using PPR_a.

Comparison between the exploitation status based on detailed information available (column 3, EO, Table 1) with the exploitation status estimated on the basis of the L index (Columns 7, EO_a, and 10, EO_b, Table 1) provides a basis for inferring the usefulness of this novel index in quantifying ecosystem overfishing. This comparison results in a different status with respect to the preliminary classification for a few models mainly represented by reconstruction of past eco-

systems (Eastern Bering Sea 1950s, Newfoundland 1900 and Northern British Columbia 1900) and upwelling areas (North Benguela 1978 to 1983, Peru 1973 to 1981). Other ecosystems show correct classification within the confidence interval: the North Sea (1981), the Northern British Columbia (1950 and 2000), the Bay of Bengal (1984 to 1986) and the Gulf of Thailand (1980s). However, 80% of the models are correctly classified in this calibrating procedure.

Assessment of ecosystem exploitation levels

The calculation of the L index and estimation of p_{sust} values for the 40 unclassified ecosystem models (Table 2) produces a quantification of the sustainability of fisheries that is consistent with the partial information available for more than 75% of the cases. Clear exceptions are the West Greenland model of the shrimp trawling areas (1994) for temperate areas, the continental shelf of southern Brazil (1990s), the Gulf of Thailand (1993) and Kuala Trengganu (1980s) among tropical areas, Celestun lagoon among lagoons, and California (1965 to 1972) among upwellings. Among the 40 represented ecosystems, 16 are assessed as overfished and 24 as sustainably exploited.

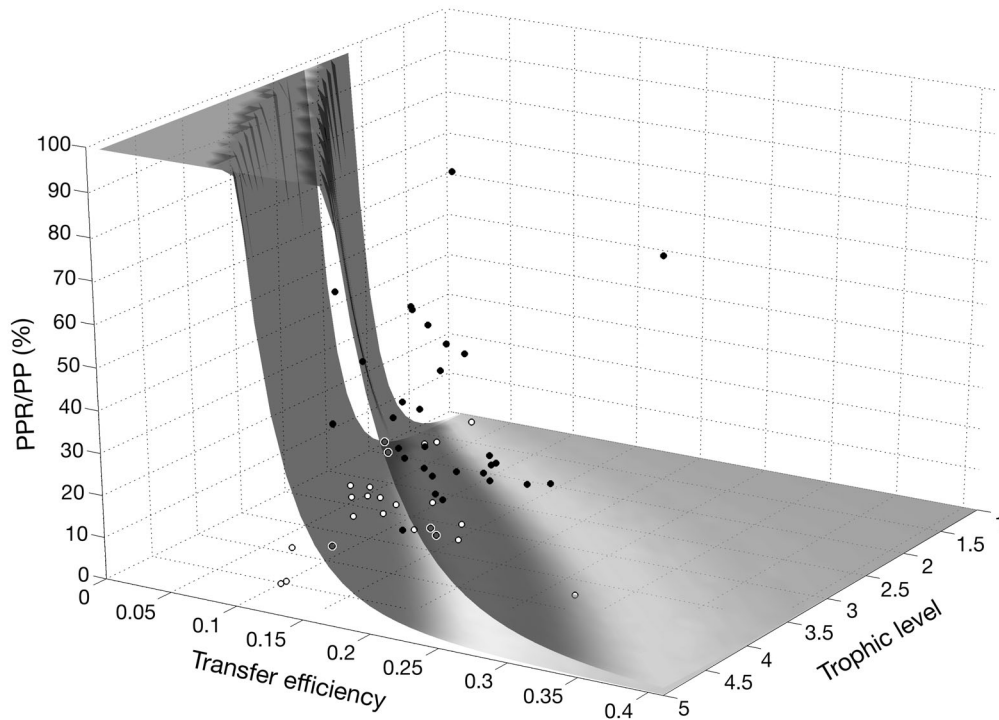


Fig. 2. Percent of primary production required to sustain the fishery (%PPR_a), trophic level of the catches and transfer efficiency data for the ecosystem models classified as sustainably fished (open circles, shaded when below surfaces) and overfished (black circles). Reference surfaces, L₀% (left) and L₁₀₀% (right) are also represented. The space above the right hand curve includes all points of surely overfished ecosystems, while the space below the left hand curve defines sustainably fished ecosystems with a 100% probability

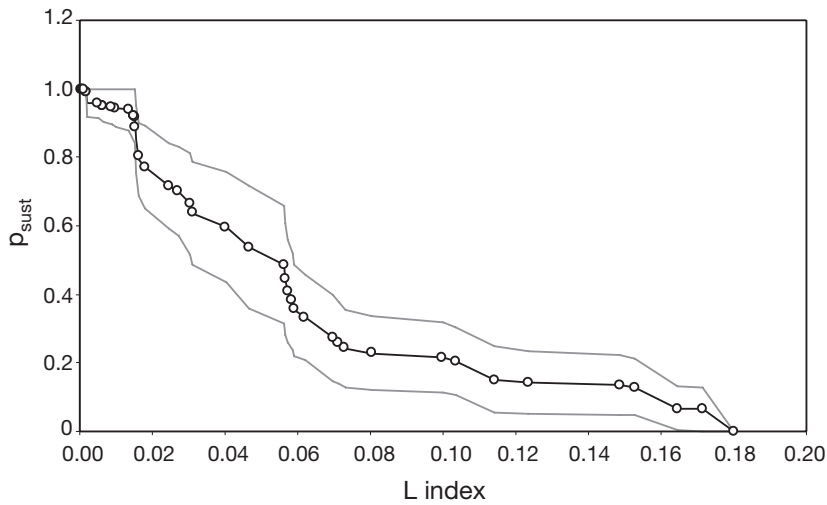


Fig. 3. Values indicating the probability of an ecosystem being sustainably fished (p_{sust}) vs. L index obtained by application of the index to classified models. Nominal values refer to the 51 classified models (O), while averages (—) and confidence intervals (—) are obtained by applying the resampling method. This plot, referring to PPR_a (percentage of primary production required to sustain the fishery from primary producers only), can be used for assessing the current level of exploitation for an ecosystem, once provided with an estimate of the L index, and for estimating ecosystem-based maximum sustainable catches (EMSC) once a p_{sust} value is fixed as reference limit

Fig. 4 reports L values over time estimated by using the 4 dynamic ecosystem models. South Benguela is sustainably fished throughout all the years analysed. Eastern Tropical Pacific is in a sustainable framework but L has a positive trend, indicating a decrease in sustainability. The North Sea is overexploited throughout the whole time series, indicating that the fisheries are non-sustainable. However, the negative trend in L indicates that this ecosystem may be moving towards relatively more sustainable fishing levels. West Coast Vancouver Island shows high variability in the L index and a prevalence of periods of overexploitation. However, sustainability increased over the last 10 yr (p_{sust} increases).

All the alternative scenarios simulated for the North Sea (Fig. 5) show an increase in the sustainability of fishing activities at the ecosystem level. Scenario 6 (which implied a 20% reduction on all

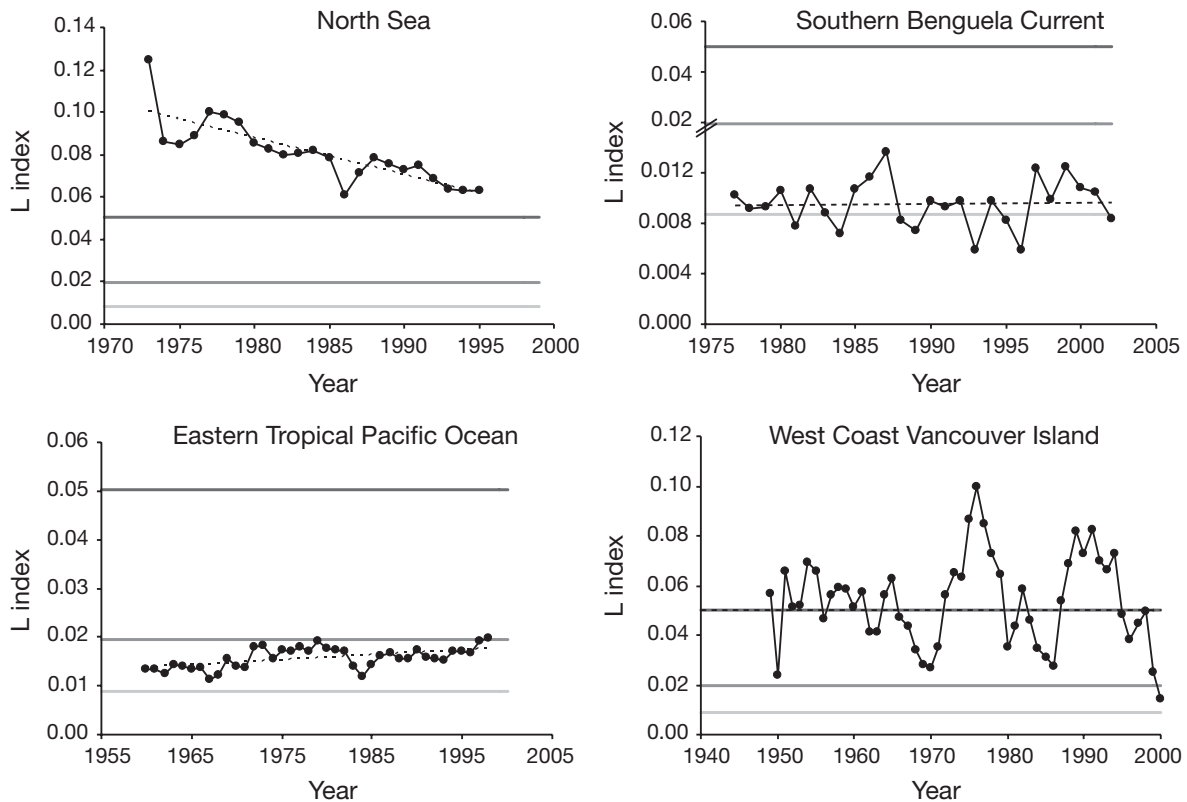


Fig. 4. Estimation of the L index of ecosystem overfishing over time for 4 ecosystem models. The index data (●) is estimated on the basis of dynamic modelling simulations of previously calibrated models using PPR_b (percentage of primary production required to sustain the fishery, including the detritus-based food web). Analysis done for PPR_a (see Fig.3) gave analogous results. Dotted line: L index trend; along with the reference levels for the L values: $L_{50\%}$ (dark grey), $L_{75\%}$ (medium grey) and $L_{95\%}$ (light grey)

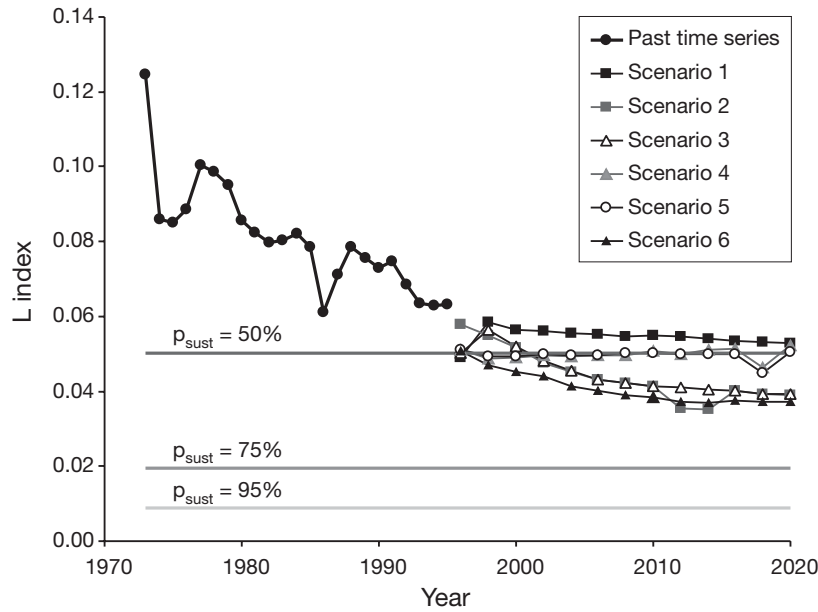


Fig. 5. L index estimated over time using PPR_b from a dynamic model of the North Sea ecosystem using past fishing pressure (1973–1995) and under 6 alternative future scenarios of fishing (1996–2020). Scenarios represent: (1) no fishing on juvenile groups from 1999; (2) no fishing on small pelagic fishes from 1999; (3) no fishing on juvenile groups or small pelagic fishes from 1999; (4) 20% reduction on all fished groups from 1999; (5) 20% reduction on all fished groups, no fishing on juveniles from 1999; and (6) 20% reduction on all fished groups, no fishing on small pelagic fishes from 1999; P_{sust} defined in Fig. 3 legend

fished groups and no fishing on small pelagic fish) shows the best results in terms of sustainability of the fishery.

Values of the L index and p_{sust} by ecosystem type (Table 3) indicate high sustainability levels for open oceans ($p_{sust} = 100\%$), low sustainability for upwelling and tropical shelves ($p_{sust} = 35.36$ and 33.19% , respectively) and particularly low sustainability for coastal areas (21.57%). Intermediate exploitation levels are estimated for temperate shelves (53.78%) and for global data (53.77%). Application of the L index to the Mediterranean and Black seas highlights intermediate sustainability levels (53.77 and 53.78% , respectively) when considering the systems as a whole. Sustainability levels departing from the intermediate values are found in subsystems such as the Northern and Central Adriatic Sea (77.05%) and the Southern Catalan Sea (35.34%) (see Table 1). Using PPR_b , sustainability of fishery decreases dramatically both in the Catalan and the Adriatic Seas (28.60 and 37.90% , respectively).

Table 3. Estimated probabilities of the ecosystem to be sustainably fished (p_{sust}) and ecosystem-based maximum sustainable catches (EMSC) by ecosystem type and for Mediterranean regional data with $\%PPR_a$ (see Fig. 3 legend). Transfer efficiency (TE) estimated from average ecosystem types values (see Appendix 2, Table A2) if not otherwise indicated; input data (PP, TL_c , catches and discards) from Pauly & Christensen (1995) for 1988–1991 if not otherwise indicated; catches modified to consider discards and illegal, unregulated or unreported catches (IUU); $change_{75}$ and $change_{95}$ indicate percentage reduction of catches needed from actual value to $EMSC_{75}$ and $EMSC_{95}$, respectively

	TE (%)	PP ($gC\ m^{-2}\ yr^{-1}$)	TL_c	Catches and discards ($t\ km^{-2}\ yr^{-1}$)	PPR (%)	p_{sust} (%)	EMSC ₇₅ \pm SD ($t\ km^{-2}\ yr^{-1}$)	Change ₇₅ (%)	EMSC ₉₅ \pm SD ($t\ km^{-2}\ yr^{-1}$)	Change ₉₅ (%)
Ecosystem type										
Open oceans	12	103	4.0	0.012	1.75	100.00	0.171 ± 0.11	—	0.062 ± 0.057	—
Upwellings	5	973	2.8	25.560	39.31	35.36	8.699 ± 5.606	–66	3.133 ± 2.918	–88
Tropical shelves	10	310	3.3	2.871	28.95	33.19	0.926 ± 0.597	–68	0.334 ± 0.311	–88
Temperate shelves	14	310	3.5	2.306	12.92	53.78	0.973 ± 0.627	–58	0.35 ± 0.326	–85
Coastal areas and reefs	13	890	2.5	10.510	4.40	21.57	2.113 ± 1.362	–80	0.761 ± 0.709	–93
Global data (1988–1991)	12	126	2.8	0.260	4.71	53.77	0.108 ± 0.07	–58	0.039 ± 0.036	–85
Mediterranean data										
Mediterranean Sea (2001)	12	142 ^c	3.08 ^e	0.637 ^e	8.60	53.77	0.263 ± 0.169	–59	0.095 ± 0.088	–73
Black Sea (2001)	12	322 ^e	3.04 ^e	1.644 ^e	7.50	53.78	0.714 ± 0.46	–57	0.257 ± 0.24	–72
South Catalan Sea (1994–2000)	13 ^a	157 ^d	3.12 ^a	5.356 ^a	9.45–10.6	35.34–33.15	1.777 ± 1.145	–67	0.64 ± 0.596	–79
Northern & Central Adriatic Sea (1990s)	10 ^b	115 ^b	3.07 ^b	2.445 ^b	6.59–15.0	77.05–53.74	2.04 ± 1.315	–17	0.735 ± 0.684	–46
^a Coll et al. (2006) ^b Coll et al. (2007) ^c Bosc et al. (2004) ^d Estrada (1996) ^e Sea Around Us (2007)										

Estimated $EMSC_{75\%}$ (Table 3) is substantially lower than current catches for upwelling regions (–66%), tropical shelves (–68%), temperate shelves (–58%) and coastal areas (–80%). Adopting a reference of $p_{sust} = 95\%$, the difference with current catches is about 85 to 90% for all ecosystem types. In order to reach sustainability levels of $p_{sust} = 75$ and 95%, catches at a global scale need to be decreased by 58 and 85%, respectively.

A reference probability of $p_{sust} = 75\%$ is achieved through reduction of catches by 59% for the whole Mediterranean basin, by 57% for the Black Sea and by 67 and 17% for the South Catalan and Adriatic Seas, respectively. Reduction of catches by 73, 72, 79 and 46%, respectively, are needed to reach the reference probability of 95%, i.e. $EMSC_{95\%}$.

DISCUSSION

Loss in secondary production takes into account both features of exploitation activities (TL_c and PPR) and ecosystem properties (PP and TE) and provides an ecological basis for defining the L index, an original composite measure of the ecosystem effects of fishing. Loss in production has emerged from a comprehensive integration of recent ecological principles and ideas applied for evaluating fishery impacts (Pauly & Christensen 1995, Pauly et al. 1998a) and represents a further step of ideas proposed in Tudela et al. (2005). The inclusion of TE accounts for differences in ecosystem functioning, thus allowing for the consistent application of the L index to different ecosystem types for a broad assessment of ecosystem effects of fisheries.

Performance of the L index

Loss in secondary production estimated for the set of previously classified models highlights the ability of the L index to characterize systems as overexploited or sustainably fished. The high classification success of previously classified ecosystems (80%, Table 1) and the high consistency of classification with respect to the fragmentary information available for other ecosystem models (Table 2) validate our initial assumption that the relative loss in secondary production can be a proxy for the impact of fishing on the ecosystem.

Inconsistencies emerging in the calibration process regard mainly past ecosystem models (eastern Bering Sea [1950s], Newfoundland [1900] and northern British Columbia [1900]) that are considered sustainably exploited on the basis of available information, but that our assessment evaluates as overexploited (Table 1).

Such disagreement can be explained by the high degree of uncertainty embedded in the reconstruction of historical ecosystems (Heymans 2003) and by the fishing pressure on marine mammals, which was higher in the past (Tudela et al. 2005). The L index application assesses the Newfoundland ecosystem as sustainably fished from 1985 to 1987 ($p_{sust} = 88.96$ to 78.61%), in contrast with available information (Table 1) but in agreement with biomass estimates for *Gadus morhua* (Atlantic cod) and *Pandalus borealis* (northern shrimp) obtained from research surveys and CPUE data (Worm & Myers 2003). The relatively high biomass of cod at the end of the 1980s allowed fishing operations to maintain a high fishing pressure on this species. However, Northern cod collapsed in the early 1990s, followed by a regime shift (Steele 1998) with an increase in northern shrimp. This brought the ecosystem to a highly overfished situation in the 1990s ($p_{sust} = 13.6$ to 12.8%), resulting in the closure of the fishery in 1992 (Hilborn et al. 2003).

Some of the inconsistently classified models have p_{sust} close to 50% or within the confidence interval. Thus, their misclassification has low reliability. Strong disagreement between our assessment and previous evaluations (see Hilborn et al. 2003, Worm & Myers 2003, Myers & Worm 2005) consist of a few cases such as the West Greenland trawling area, the Faroe Islands seas, the Adriatic Sea and upwelling areas. The West Greenland shrimp trawling area (Model 65), Faroe Islands seas (Model 59) and upwellings (Models 86 to 91) are ecosystems where environmental factors (e.g. climate variability) could have produced negative effects (Pedersen et al. 2004) masking a sustainable exploitation as estimated by the index (Table 2). The Faroe Islands seas are assessed by the L index as exploited at very low levels of sustainability, while estimates of spawning stock biomass for cod suggested that they were not very depleted with respect to virgin biomass (Myers & Worm 2005). However, climatic variability has a major impact on fish landings in the region (Jakupsstovu & Reinert 1994).

In the case of the Adriatic Sea, the assessment is in contrast with information collected when using PPR_a , but not when considering PPR_b (Table 1). Since a relevant fraction of energy for the food web comes from non-living organic matter in this ecosystem (Coll et al. 2007), this result highlights the importance of considering sources of energy other than primary production.

Despite these exceptions, the evaluation of the sustainability of fisheries through the L index is consistent with published analyses conducted using single species or community data. Very low sustainability of fisheries in the Gulf of Mexico (Models 28, 66, 73) agrees with low shark biomass assessed on the basis of pelagic longline logbooks (Baum & Myers 2004; Tables 1 & 2).

Non-sustainability of fisheries in Newfoundland from 1995 to 2000, in the North Sea in 1981, in the Baltic Sea in 1974 (Models 11, 15, 53) and sustainability of fisheries for the eastern Scotian Shelf from 1980 to 1985, the Gulf of Saint Lawrence from 1985 to 1987 and Iceland in 1997 (Models 20, 22, 61) is consistent, for the respective periods, with evaluations based on the status of large predatory fishes (Myers & Worm 2005) and on a meta-analysis of time series of cod and shrimp biomass (Worm & Myers 2003; Tables 1 & 2). Stable cod biomass over time for Iceland and the Norwegian Barents Sea (Worm & Myers 2003) is in agreement with our findings (Models 61 & 62; Table 2). The increase of cod stock for Skagerrak–North Sea (Worm & Myers 2003)—now rebuilding (Hilborn et al. 2003)—agrees with the increasing sustainability of fisheries found in our analysis for North Sea models representing different periods (Models 13, 14, 15; Table 1). Assessment of very low sustainability levels for northern British Columbia and the west coast of Vancouver Island (Models 18, 19, 64; Tables 1 & 2) is in accordance with the evidence of failure of fishery management based on single stock assessment (Hilborn et al. 2003). High variability estimated for cod and shrimp biomass in Gulf of Maine (Worm & Myers 2003) might explain the result presented for this ecosystem (Model 60; Table 2).

When applied to mass balance model results, the L index only refers to the time period specified by the model. Thus, in the case of the eastern Scotian Shelf for example, the ecosystem is assessed as sustainable for 1980 to 1985, when groundfish stocks were high. However, other assessments over a longer period of time indicate that by 1992, the Atlantic cod stock had collapsed and the ecosystem had fundamentally changed (Worm & Myers 2003, Bundy et al. 2005). A second model for the eastern Scotian Shelf for 1995 to 2000 (Bundy 2005) again indicates a sustainable system. However, in this case, since the groundfish fishery was closed in 1993, fishing activity was refocused on invertebrate fisheries which are still healthy. By looking at 2 snapshots, the transition between the 2 states was missed. Thus, in order to follow trends in the L index, it should be applied to a continuous series of landings data or to a dynamic model.

Regional and global quantification of ecosystem overfishing

Application of the index to ecosystem dynamics obtained from EwE model simulations provides insights on the sustainability of fisheries over time. Our results from such an application agree with other evaluations based on field data. The Southern Benguela has been suggested to be moderately exploited (Shannon et al.

2004). Exploitation of the eastern tropical Pacific Ocean seems to be limited by physical and technological factors although sustainability of this open sea decreases over time due to excessive pressure on high trophic levels (Cox et al. 2002). West Coast Vancouver Island is subjected to high fishing pressure under high environmental variability, represented in the dynamic model through a forcing function on primary production (Martell 2002). Management of the North Sea ecosystem has been implemented, increasing the sustainability of exploitation (Hilborn et al. 2003).

However, simulations of different future scenarios of fishing activities in the North Sea (Christensen et al. 2002) show that a further increase in the sustainability of exploitation can be achieved only through a substantial reduction of catches and increase of TL_c , which is not necessarily obtained through increased fishing of higher TLs, but instead, by decreasing the proportion of low TL species in the catches (Fig. 5).

Application of the index to global landing data sets provides a basis for inferring that coastal areas, coral reefs and upwellings show very low probabilities of being sustainably fished, while temperate and tropical shelves show intermediate probabilities. High sustainability of the fisheries found for open oceans is consistent with the relatively low yields and high trophic levels of the catches taken from this environment. Open oceans are subjected to lower fishing pressure compared to coastal systems (Caddy et al. 1998) and they represent the upper reference for sustainably exploited systems in the presented analysis. However, as previously discussed, the eastern tropical Pacific Ocean shows a continuous increase with time in the L index, implying a decrease in sustainability, in accordance with the observed decline of top predators (Myers & Worm 2003, 2005). Therefore, the assessment obtained for open oceans should be used cautiously, especially since only 2 oceanic ecosystems were included in the analysis. More robust estimates will depend on the future availability of more data.

The important risks of ecosystem overfishing found for upwelling, coastal and shelf areas are in accordance with the concentration of marine catches in these marine environments (Pauly & Christensen 1995). These risks underline the need for a dramatic reduction of the catches.

Application of reference targets to areas for which detailed descriptions of fisheries are available (in terms of catches, discards and IUU, such as the Mediterranean Sea), confirms the need for a substantial decrease in yield and points to a serious risk of overfishing, which arises from intense current and historical fishing pressure and exploitation (Bas et al. 1985). At the global scale, a 58% reduction in catches would be needed in order to reach a $p_{\text{sust}} = 75\%$.

Properties and limitations

A suitable ecosystem-based indicator should be: (1) quantitative and sensitive to changes in the structure and functioning of ecosystems induced by fishing activities; (2) easy to calculate, in order to facilitate its application in data-poor cases; (3) low-cost to allow its application in developing countries; and (4) practical for defining reference values (Link 2002). Analyses, applications and results presented in this work provide evidence that the L index matches these requirements. In particular, estimated reference levels for sustainable exploitation provide quantitative, practical information (in terms of reduction of catches) for management. Moreover, although trophodynamic EwE models can provide a platform for evaluating alternative management solutions, the L index is not dependent on these models. Thus, its application can be generalized to different modelling approaches or to catch data, providing estimates of PP, TE, TL_c are available.

The loss in production is theoretically derived as a deterministic function of %PPR, TL_c and TE. Thus, the L index integrates the properties of these indicators. It accounts for changes in nutrients and PP, the effects of which propagate upwards throughout the trophic web (Pace et al. 1999), and captures the negative effects expected when fishing down the food web (Pauly et al. 1998a).

The %PPR and TL_c can be estimated from catch statistics or from ecosystem models (Pauly & Christensen 1995, Stergiou & Karpouzi 2002), but not TE. This appears to be a weak point of the proposed index. However, using a wide set of ecosystem models, it was possible to estimate standard values of TE by ecosystem type (Appendix 2). Although an overall single value of TE for a given ecosystem is an approximation of the efficiencies of all processes, results of the sensitivity analysis show that improvements in the TE estimate only provide moderate improvement in estimates of loss in secondary production (Appendix 1).

However, the sensitivity analysis also showed that a 1% change in TL_c produces approximately a 5.8% change in the L index. The high sensitivity of the L index to errors in TL_c and the uncertainty that characterizes TL estimates (Pinnegar et al. 2002) may explain some of the observed inaccuracies of the index in evaluating the ecosystem exploitation status. The above implies that particular attention should be paid to calculating TL_c as accurately as possible.

Some limitations in the use of the L index might be identified on the basis of assumptions and hypotheses pointed out in the theoretical derivation. The L index is identified at steady state. Therefore, it should not be applied to situations with very sharp changes in exploitation or primary production. Scaling PPR on

actual P_1 allows us to take into account variability in production, and dynamic simulations have been used to show that the index can correctly identify overexploited and sustainably fished years when modifying fishing intensity. This scaling reduces the L index to a relative measure and enables the application of the index to data expressed in any unit. The reference values developed here are for weight or carbon units only and should only be (cautiously) applied to systems using the same units.

The L index might not take into account the compensatory effects that arise when changing fishing pressure. Removal of part of the production by the fishery would leave more resources available to the remaining individuals, resulting in lower mortality rates, for example. Such an effect, although considered common (Walters & Martell 2004), seems less important than the direct effect of the removal of production on the upper TLs (Walters et al. 2005), thus justifying our disregard of compensatory effects at the ecosystem scale. Moreover, the index does not account for the delayed effects such as those on upper TLs due to changes in primary production and on lower TLs due to changes in fishery structure. Compensatory and time delayed effects can be included in the estimation of the L index when a dynamic model is used.

The L index might not correctly describe the depletion due to the massive removal of keystone species that would produce disproportionate or magnified effects on the trophic web, as would be the case for top predators in oceanic ecosystems (Libralato et al. 2006). However, the identified relationship between biodiversity and production (Tilman et al. 1997, Worm & Duffy 2003) implies that the L index indirectly takes into account the decrease of biological diversity and the risk of extinction (Murawski 2000).

Directions for future research

The ecologically broad meaning of the L index necessarily implies a broad range of management solutions to accomplish with reference levels (e.g. increase in TL_c , decrease in catches, decrease in discards). Therefore, although results highlight the usefulness of the L index for quantitative ecosystem-based fisheries management, traditional stock-by-stock evaluations (Hilborn et al. 2003, Worm & Myers 2003) should continue to play an important role in fisheries management. Nevertheless, the comparison between results obtained by applying of the L index and analyses based on traditional fish stocks data presented in this study highlights the complementary nature of the 2 approaches, thus supporting their combined use for quantitative ecosystem-based fisheries management

(Pauly et al. 2002). Future research should point toward the use of a set of indicators for evaluating the effects of fishing at different ecological hierarchical levels (population, community, ecosystem), thus coupling single stock assessments with broad ecosystem-based evaluations (Link 2002, Bundy et al. 2005).

New assessments for well-studied ecosystems, easily done by estimating the L index using values of PPR, P_1 , TL_c and TE, would provide more evidence of its accuracy in quantifying the ecosystem effects of fishing. However, the performance of the L index in evaluating these effects should be validated by applying it to data-rich areas where assessment based on commonly available data (e.g. catches) can be compared with that based on experimental surveys. This validation should necessarily account for spatial and temporal patterns of ecosystem properties and fishing pressures. Spatio-temporal resolution of datasets might represent a limit for validation.

The L index has the advantage of being calculated directly from landing statistics by applying empirical formulas for estimating %PPR and TL_c (Pauly & Christensen 1995, Pauly et al. 1998a). However, PPR should preferably be estimated using diet composition (DC) of the landed fishes (i) and TL of their prey (j). The equation provided by Pauly & Christensen (1995) can be reformulated as:

$$PPR = \frac{1}{9} \sum_i \left[y_i \cdot \sum_j DC_{ij} \cdot \left(\frac{1}{TE} \right)^{TL_j - 1} \right] \quad (9)$$

This formula, due to a wide variation in TL for landed species (i), yields more precise estimates of PPR. Similarly, the L index should be estimated using the formulation proposed in the left side of Eq. (6), while the simplification represented by the right side should be used for facilitating graphic representation and for assessments based on aggregate datasets.

The high sensitivity of the L index to the TL_c necessitates the use of techniques that provide accurate and reliable TL estimates for marine species (Pinnegar et al. 2002). In cases where the confidence interval of TL_c is wide, i.e. when fisheries operate on a broad spectrum, accuracy of the fishing status and EMSC estimates should be considered carefully. In order to obtain an accurate and reliable estimation of the ecosystem overfishing status, the index should be estimated by including discards and IUU in the PPR estimates, as they frequently comprise an important proportion of the catch (Alverson et al. 1994, Pauly et al. 2002).

In general, methods for estimating PPR, TL_c and TE with low error imply the use of quantitative ecosystem modelling (Christensen & Walters 2004), which allows the inclusion of a large body of information and the direct quantification of input parameters for the

L index, avoiding empirical formulae and standard values. Availability of more ecological models for highly studied ecosystems will allow improvement both in the definition of reference values of the L index and in the accuracy of results provided. However, dramatic consequences of environmental fluctuations, ecological unpredictability and the unavoidable uncertainty associated with data still imply a broad use of the precautionary approach.

CONCLUSIONS

Theoretical loss in secondary production is used as a proxy for quantifying ecosystem effects of fishing and is formulated in a new index of ecosystem overfishing: the L index. The approach proposed integrates and complements previous analyses (Pauly & Christensen 1995, Pauly et al. 1998a, Myers & Worm 2003, Tudela et al. 2005), allowing a broad and general application of the index using both landings data and ecosystem models. The L index allows the estimation of ecosystem-based maximum sustainable catches that, when compared with current catches, might give approximate but direct and practical information regarding the degree of intervention required. Results show that moderate %PPR values are only compatible with fisheries harvesting the higher part of the food web. This raises serious concern in the sustainability of current fishing regimes that, after having depleted stocks of large predators (Pauly et al. 1998a), are mainly characterised by strategies based on low TL_c and high %PPR (Pauly et al. 2002). In the framework of sustainable exploitation of biological resources, the approach proposed here represents a first broad estimation of sustainable reference levels for an ecosystem-based management of fisheries and is compatible with other approaches focusing on lower hierarchic levels (e.g. community, species).

Acknowledgements. We thank all the authors that kindly supplied the information and their personal experience concerning ecosystem models. We wish to acknowledge V. Christensen and C.J. Walters (UBC, Canada) for providing the model database and for giving useful advice. We thank E. Morello (ISMAR – CNR, Italy), A. Pastore and R. Pastres (Università Ca' Foscari, Italy) and C. Solidoro (OGS, Italy) for comments and suggestions. We thank A. Bundy (DFO, Canada) and 2 anonymous reviewers for helpful comments and corrections.

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Appendix 1. Local sensitivity analysis of the L index

In order to explore the propagation of uncertainty of each of the input variables (PPR, P_1 , TE and TL_c) to the value of the L index, analytical and numerical sensitivity analyses were carried out (Saltelli et al. 2000a). Absolute local sensitivity $s_{L,j}$ is defined as the first order derivative of the index L with respect to the input variable ($j = \text{PPR}, P_1, \text{TE}, TL_c$) and is an approximation of the absolute change of the index due to a small change on the input variable's value (Saltelli et al. 2000b). Relative sensitivities ($\tilde{s}_{L,j}$), obtained by multiplying absolute sensitivity for the nominal value of the input variable and dividing by the output variable (the L index), represent the percentage change in the index due to a 1% change in the variable, simplifying the comparison among sensitivities of different input variables (Saltelli et al. 2000b). Therefore, sensitivities express the error in the output variable (L index) due to the error in the input variables and have a powerful role in uncertainty analysis (Turányi 1990). In general, sensitivities are functions of the input variables. Thus, they are estimated for nominal values chosen to be

representative of the ranges commonly observed. Here, nominal values are chosen as $\text{PPR}^* = 70 \text{ gC m}^{-2} \text{ yr}^{-1}$, $P_1^* = 200 \text{ gC m}^{-2} \text{ yr}^{-1}$, $\text{TE}^* = 10\%$ and $TL_c^* = 2.5$. Results show that PPR and P_1 have an opposite influence on the L index and that their relative sensitivity is constant (Table A1). Thus, the L index does not depend on the chosen nominal values PPR^* and P_1^* . Although a first glance at the relative sensitivity shows that TE has non-linear effects on the L index, in practice, it is very close to linearity and almost constant at different values of TE (this was proven with the numerical sensitivity application as well). Conversely, the sensitivity of the L index due to errors in TL_c appears to be linear, as can be seen from relative sensitivity formulation, with sensitivity proportional to values of TL_c with the coefficient $\ln(\text{TE})$. This shows the high changes in sensitivity due to changes in TL_c . Therefore TL_c appears to be the most sensitive input variable in the L index formulation: a 1% change in its value produces the highest fractional change in L (5.756%).

Table A1. Local sensitivity analysis applied to the L index. Absolute and relative sensitivities are calculated for nominal values of input parameters (PPR = primary production required to sustain fishery; P_1 = production at first trophic level; TE = transfer efficiency; TL_c = trophic level of catches) as reported in the second column. Generally, sensitivities depend on parameter reference value used, however, it should be noted that relative sensitivity due to PPR and P_1 are constant

Input parameter	Nominal value	Absolute local sensitivities		Relative local sensitivities	
		Formulation	Value	Formulation	Value
PPR	$70 \text{ gC m}^{-2} \text{ yr}^{-1}$	$s_{L,\text{PPR}} = \frac{dL}{d\text{PPR}} = -\frac{1}{P_1} \cdot \frac{\text{TE}^{TL_c-1}}{\ln \text{TE}}$	6.9×10^{-5}	$\tilde{s}_{L,\text{PPR}} = 1$	1
P_1	$200 \text{ gC m}^{-2} \text{ yr}^{-1}$	$s_{L,P_1} = \frac{dL}{dP_1} = \frac{\text{PPR}}{P_1^2} \cdot \frac{\text{TE}^{TL_c-1}}{\ln \text{TE}}$	-2.4×10^{-5}	$\tilde{s}_{L,P_1} = -1$	-1
TE	10%	$s_{L,\text{TE}} = \frac{dL}{d\text{TE}} = \frac{\text{PPR}}{P_1} \cdot \frac{\text{TE}^{TL_c-2}}{[\ln \text{TE}]^2} \cdot [1 - (TL_c - 1) \cdot \ln \text{TE}]$	0.093	$\tilde{s}_{L,\text{TE}} = \left[\frac{1}{\ln \text{TE}} - (TL_c - 1) \right]$	1.93
TL_c	2.5	$s_{L,TL_c} = \frac{dL}{dTL_c} = -\frac{\text{PPR}}{P_1} \cdot \text{TE}^{TL_c-1}$	-0.011	$\tilde{s}_{L,TL_c} = \ln \text{TE} \cdot TL_c$	-5.76

Appendix 2. Transfer efficiency for ecosystem types

Table A2. Summary statistics of transfer efficiency (TE) estimated for ecosystem type on the basis of model data sets

	N	Mean	SE	Median	Mode	SD	Variance	Range	Min	Max	Chosen value ^a
Temperate shelves and seas	39	14.25	0.97	13.7	14.3	6.03	36.33	34.59	3.5	38.1	14
Tropical shelves and seas	21	10.32	0.80	9.7	13.5	3.66	13.39	12.60	5.2	17.8	10
Coastal areas and coral reefs	13	12.91	1.19	13.0	—	4.30	18.50	13.80	6.8	20.6	13
Upwellings	9	5.09	0.52	4.0	3.9	1.56	2.44	4.30	3.6	7.9	5
Lagoons	9	10.97	1.05	10.8	—	3.16	9.96	9.10	6.4	15.5	11
Total	91	11.92	0.57	11.8	—	5.45	29.73	34.59	3.5	38.1	12

^aCharacteristic value of TE for ecosystem type is chosen between mean value for all ecosystems. Chosen values are rounded at the proximate integer according to the average SE observed