



Biomass accumulation across trophic levels: analysis of landings for the Mediterranean Sea

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ABSTRACT: The need to implement Ecosystem-Based-Management (EBM) in marine ecosystems and the recent adoption of European Union directives, such as the Marine Strategy Framework Directive (MSFD), make indicators that are able to describe ecosystem state particularly relevant. The trophodynamic context is promising in that it can define integrative ecosystem indicators from modelling and field data. Here we analyze energy accumulation across trophic levels (TLs), i.e. the accumulation of energy in various biomass components of an ecosystem. The analysis of biomass accumulation across TLs, previously applied to surveys and model output data, was applied to a time series (1970 to 2010) of landings in the Mediterranean Sea and its 8 sub-areas. The standardized cumulative biomass versus TL curves for each year were fit to a logistic function, revealing that the accumulation pattern was detectable using landings data and confirming prior patterns. Parameters describing the curve shape, i.e. basal biomass, inflection point and steepness, were considered as possible indicators for assessing changes of ecosystem state through time. These parameters were able to detect systems modification in terms of both space and time and exhibited differential sensitivity to external drivers. The inflection point was mainly fishery-driven, whereas steepness seems to respond to environmental features, indicating an ability to discriminate across major ecosystem drivers. The application of Monte Carlo uncertainty analysis showed that all of the parameters are sufficiently robust to possible sampling errors in the TL assignment to the different taxa. Collectively, these results confirm the robustness of patterns for cumulative biomass across TL curves seen in a growing number of marine ecosystems. These emergent features suggest that this approach could produce useful ecosystem indicators for the implementation of EBM and the MSFD.

KEY WORDS: Trophodynamic indicators · Trophic level · Cumulative biomass curve · Landings data · Environmental factors · Sensitivity analysis · Mediterranean Sea

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INTRODUCTION

Concepts such as 'ecological status' and 'reference conditions' remain among the most important issues which require precise definition in the context of marine environmental management. In particular, with the implementation of the Madrid Protocol for Integrated Coastal Zone Management (ICZM; UNEP/

MAP/PAP, 2008) and declaration of European Union (EU) directives such as the Habitats Directive (92/43/EC), the Water Framework Directive (WFD; 2000/60/EC) and the Marine Strategy Framework Directive (MSFD; 2008/56/EC), the need for ecosystem management is crucial. These directives require the definition and implementation of appropriate ecological indicators that are able to convey complex

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information to a range of different stakeholders (Rice 2003, Rice & Rochet 2005, Jørgensen et al. 2010, Link et al. 2010). For example, the MSFD requires that EU member states achieve 'good environmental status' (GES) of the marine environment by 2020, highlighting the need not only for indicators but also for reference conditions thereof.

Much of the work in the last decade has endeavoured to define optimal features for indicators, including the need to be feasible, reliable, applicable and effective (Rochet & Trenkel 2003, Jennings 2005, Link 2005, Rice & Rochet 2005). Apart from a few exceptions (Blanchard et al. 2010, Bundy et al. 2010), considerable effort has been devoted to analyzing indicator performance at lower hierarchical levels, from individuals to populations and communities (Gislason 1999, Jennings & Dulvy 2005, Shin et al. 2005). Nevertheless, a system-level approach can be more attractive than species-oriented approaches because both the direct and indirect effects of disturbance can be considered in a single interaction network (Raffaelli 2005). Furthermore, system-level indicators integrate across a range of ecosystem functions and processes and can detect major changes that warrant attention more robustly than indicators that focus on specific taxa, habitats or features of the ecosystem and that often have higher inter-annual variance (Link 2010). However, at the ecosystem scale, any impact might potentially cause diffuse and emergent changes in food webs (Layman et al. 2005, Raffaelli 2005); thus, ecosystem indicators need to discriminate responses to different specific pressures, such as anthropogenic (e.g. exploitation pressure) or environmental (e.g. climate), and distinguish them from trophodynamic functional effects (due to ecological interactions) (Link et al. 2010, 2012a).

Ecosystem-emergent properties can be a useful means of describing ecosystem function as well as deriving indicators (Cropp & Gabric 2002). Trophodynamic studies have developed considerably since Lindeman (1942) and Odum & Heald (1975) proposed an energetic context for evaluating ecosystem function. In particular, they have addressed the assessment of fishery impacts on marine ecosystems as well as how the trophodynamic functioning of a system can be measured and how it responds to such impacts (e.g. Cury et al. 2005, Gascuel et al. 2005, 2008, Libralato et al. 2008, Shin et al. 2010a). The proposed measures are promising integrative indicators that reflect a systemic response to external pressures but often require intensive modelling or are focused on one facet of the ecosystem response to

one type of perturbation (Bundy et al. 2005, Coll et al. 2008, 2010a, Shannon et al. 2010, Shin et al. 2010b). Overall, considering the complexity and associated high functional diversity in marine ecosystems, the practical application of system-level indicators remains a challenge.

In this context, the analysis of total biomass in the ecosystem and its distribution across trophic levels (TLs) may be an interesting alternative approach. According to Holling et al. (1995), ecosystem biomass is a conservative property, which in marine environments exhibits an accumulation at intermediate TLs (Link et al. 2009). Changes to this accumulation have been suggested as reflective of shifts in ecosystem structure (Sosa-López et al. 2005).

Recently, Pranovi et al. (2012) proposed using parameters associated with and estimated from cumulative biomass (cumB) across TL curves as an integrative ecosystem indicator. Here, we extend this method and test it using landings data for different areas of the Mediterranean Sea.

The Mediterranean Sea is a semi-enclosed water body comprised of a series of other semi-enclosed basins and, as such, is characterized by peculiar morphological-topographical features. Water circulation is driven mainly by the presence of physical thresholds, such as Gibraltar and the Sicilian Channel. This structuring results in strong environmental gradients in both space (latitude and longitude) and time (seasons). The Mediterranean is also recognized as an important biodiversity hotspot (Bianchi & Morri 2000, Coll et al. 2010b). This sea has been subjected to high fishing pressure, resulting in a general overexploitation of renewable resources (STECF 2010, Colloca et al. 2011). Yet as in many other seas, the Mediterranean has recently shown clear signs of changes related to other external drivers, including pollution, climate and eutrophication (Blondel & Aronson 2005, Coma et al. 2009, Coll et al. 2010b). Given these features, the Mediterranean could serve as an important study site for testing measures derived from the cumB vs. TL method (Link et al. 2009, Pranovi & Link 2009, Pranovi et al. 2012) as possible ecosystem indicators.

Our specific aims were to (1) calculate parameters derived from the cumB-TL curve applied to Mediterranean landings and test their applicability as ecosystem indicators, (2) assess the sensitivity of curve parameters to possible 'sampling errors' in terms of TL assignment to each species, and (3) analyze relationships between curve parameters and different external drivers (both natural and anthropogenic).

MATERIALS AND METHODS

Landings data sets

Other applications of the cumB-TL approach (Pranovi & Link 2009, Pranovi et al. 2012) used extant fishery-independent survey or model-derived data sets. However, as synoptic and long-term time series data of biomass estimates are not available for all areas of the Mediterranean Sea, we explored the use of landings data as a proxy for biomass. We are cognizant of the limitations of using landings as an index of biomass (c.f. Pauly et al. 2013) but also wanted to explore the utility of the approach for fishery-dependent data to determine if the overall systemic response could be detected using such a data time series. This use is appropriate, since we are not looking for a single species assessment but rather ecosystem-wide changes that might be embedded in aggregative landings data.

The time series of landings were reconstructed using the General Fishery Commission for the Mediterranean (GFCM) capture database for the period 1970 to 2010 from the 8 major fishing areas of the Mediterranean Sea designated by the Food and Agriculture Organization of the United Nations (FAO) (Fig. 1). The scientific names of targeted taxa were assigned to each commercial category, where possible, excluding cases of large categories including multispecies assemblages, such as 'Fish', 'Mollusks', etc. This allowed us to assign to each taxon an appropriate TL first on the basis of published data for this region (Stergiou & Karpouzi 2001) and then by consulting FishBase (Froese & Pauly 2000; see Table S1 in the Supplement at

www.int-res.com/articles/suppl/m512p201_supp.pdf). Landings data per TL were used to estimate the relative cumB across TLs for each year in each area.

CumB vs. TL model

To obtain comparable cumB-TL curves (in both space and time) and to estimate the curve parameters, the landings data for each year in each area were fitted to a 5-parameter logistic nonlinear regression model (Ricketts & Head 1999):

$$\text{Biomass} = c + \frac{d - c}{1 + f \cdot e^{b_1[\log(\text{TL}) - \log(e)]} + (1 - f) \cdot e^{b_2[\log(\text{TL}) - \log(e)]}} \quad (1)$$

$$\text{where } f = \frac{1}{1 + e^{\left(\frac{2b_1b_2}{|b_1+b_2|}\right) \cdot [\log(\text{TL}) - \log(e)]}} \quad (2)$$

and c is the minimum plateau (or y -axis intercept), d is the maximum plateau (here set to 1, since we used cumB relative to the maximum), b_1 and b_2 are coefficients related to the slope of the curve, and e is the inflection point in terms of the x -axis (Ricketts & Head 1999).

From these equations, 3 different properties were derived (Fig. 2):

(1) 'Basal biomass' (that is, the y -axis intercept) represents the contribution, in terms of cumB, of the lowest TLs available in the analyzed sample; since landings data were used in this application, this parameter can be interpreted as the incidence of low TL taxa (TL < 2.5) in the total catches.

(2) 'Trophic level of the inflection point' (that is, the projection of the inflection point on the x -axis) represents the point of change in the slope sign of the sigmoid curve. It corresponds to the peak in catches of the dome-shaped curve resulting from the trophic spectra analysis (for details, see Libralato & Solidoro 2010). In this case, however, it can be analytically estimated and expressed in terms of TL and level of cumB (projection on the y -axis; not applied in the present study). It identifies the middle of the interval at which the maximum biomass (in this case, catches) accumulation is observed and can therefore be considered the modal point of the exploitation activities.

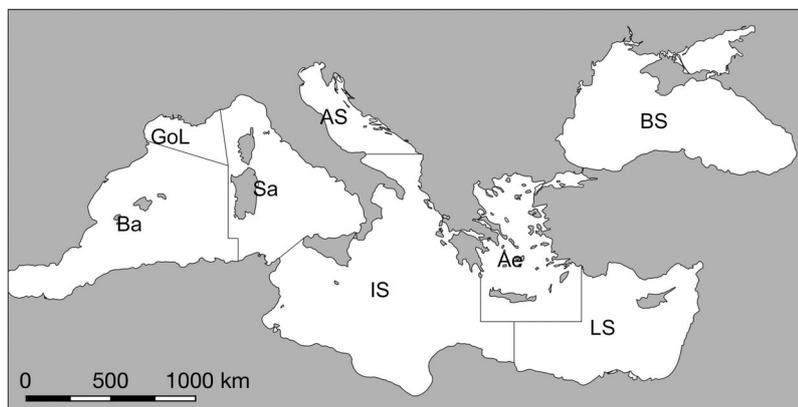


Fig. 1. Subdivision of the Mediterranean Sea according to the Food and Agriculture Organization of the United Nations-General Fisheries Commission for the Mediterranean. Ae = Aegean Sea, AS = Adriatic Sea, Ba = Balearic Sea, BS = Black Sea, GoL = Gulf of Lion, IS = Ionian Sea, LS = Levant Sea, Sa = Sardinia

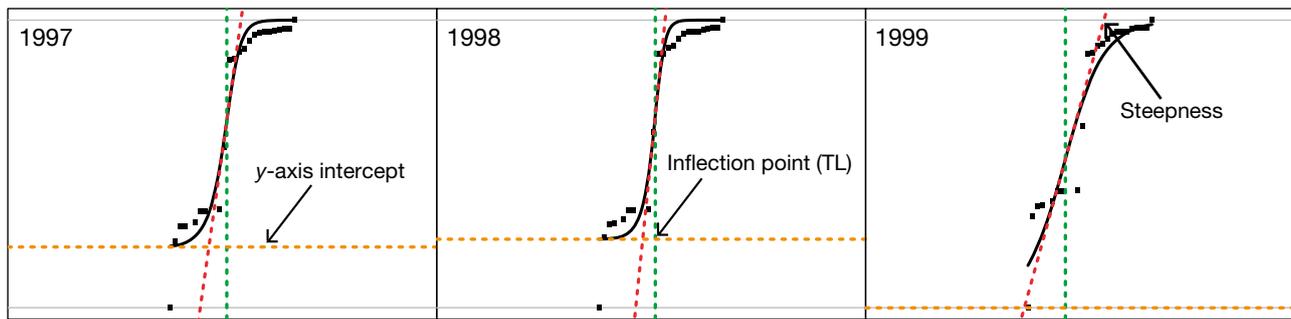


Fig. 2. Parameters of the non linear logistic curve (black line) fitting the cumulative catch data at trophic level (dots). The y -axis intercept (orange dashed line) is the intersection of the curve with the y -axis, i.e. the basal biomass; the inflection point (TL) (green dashed line) represents the projection of the inflection point of the curve onto the x -axis, i.e. the trophic level of the inflection point; the steepness (red dashed line) represents the slope of the tangent to the fitting curve at the inflection point

(3) 'Steepness' represents the slope of the tangent passing through the inflection point; it can be considered an integrative parameter of the general curve shape.

The curve fitting of landings data, i.e. the estimation of parameters, was performed using the 'drm' package (Ricketts & Head 1999) within the R statistical environment (v. 2.15.1; R Development Core Team 2012).

Uncertainty analysis

One of the critical points of the method and, more generally, of all TL-based indicators is the assignment of a fixed TL to each species. The same species, in fact, can exhibit a high TL variability in both space and time and across life-history stages (Feyrer et al. 2003, Sarà & Sarà 2007, Hammerschlag et al. 2010). To assess the robustness of cumB vs. TL and derived indicators to variability in TL, a Monte Carlo uncertainty analysis was conducted. In each area and for each year, 1000 iterations were performed by randomly sampling the TL of each species from normal distributions $N(m,s)$ where m = mean TL of the species and s = standard deviation of the TL calculated by applying a $CV = s/m$ of 4.76% (average value calculated on the basis of the values reported by Stergiou & Karpouzi [2001] for Mediterranean Sea species). This approach allowed us to take into consideration not only the uncertainty of TLs but also the increase of variability with increasing TL value (Stergiou & Karpouzi 2001). At each Monte Carlo iteration, data were fitted using Eq. (1) and the curve parameters estimated. In this way, for each iteration it was possible to obtain a new time series of parameters to be compared to the original one (nominal parameter estimates).

Explanatory variables and relationships with curve parameters

To assess the relationships of the derived parameters with different explanatory variables, a set of 18 environmental and anthropogenic variables was initially considered (Table 1). Some were time-invariant, such as those related to the geomorphology of the area, whereas others were temporally dynamic, such as those related to climate, primary production and fishing impact (Table 1).

After a preliminary analysis was carried out for each variable and each area (see Table S2 in the Supplement), the variables originally identified were reduced to 9 by choosing only one among those subsets that exhibited high Spearman cross-correlations (Table 1; Table S2 in the Supplement). These selected variables were then tested for possible relationships with the temporal trends of curve parameters using generalized additive mixed models (GAMMs; Hastie & Tibshirani 1990, Wood 2006). In particular, different alternative correlations and heterogeneity structures were evaluated following the protocol proposed by Zuur et al. (2009). After choosing the optimal random structure, the models were fit by considering a thin-plate regression with a shrinkage component (Wood 2008) so that not only the shape but also the selection of variables was fully data-driven. Since chl a was available only for a subset of years (1997 to 2010), the analysis was carried out on both the long and short time series (by excluding and including chl a , respectively). Calculations were carried out using the 'mgcv' package (Wood 2011) within the R statistical environment (v. 2.15.1; R Development Core Team 2012).

Table 1. Explanatory variables initially considered for testing relationships with the cumulative biomass (cumB) vs. trophic level (TL) curve parameters. Italics indicate formally tested variables. References are only reported where necessary to explain the respective variable

Category	Estimated variable	Indicator description	Period	Reference
Geo-morphological				
Latitude	Max	N-coordinate of polygon centroid (highest point)	Invariant	
	<i>Central</i>	N-coordinate of polygon centroid (middle point)	Invariant	
	Min	N-coordinate of polygon centroid (lowest point)	Invariant	
Longitude	<i>Central</i>	E-coordinate of polygon centroid (middle point)	Invariant	
Depth	<i>Mean</i>	Isobaths interpolation	Invariant	
	Median	Isobaths interpolation	Invariant	
	<i>Max depth (range)</i>	Maximum depth of the area	Invariant	
Surface	<i>Area</i>	Polygon area	Invariant	
Climatic				
Sea surface temperature	Annual mean	Mean SST value on annual basis	1970–2010	
	<i>Annual anomaly</i>	Deviation from the 1970–1990 mean value	1970–2010	
Atmospheric pressure	NAO (winter)	Normalized sea level pressure difference between Lisbon (Portugal) and Reykjavik (Iceland)	1970–2010 ^a	
	WeMOi	Normalized sea level pressure difference between Padua (Italy) and San Fernando (Cádiz, Spain)	1970–2010 ^b	Martín-Vide & Lopez-Bustins (2006)
	<i>MOI1</i>	Normalized sea level pressure difference between Algiers (Algeria) and Cairo (Egypt)	1970–2010 ^c	Palutikof et al. (1996), Palutikof (2003)
	MOI2	Normalized sea level pressure difference between Gibraltar's northern frontier and Lod Airport in Israel	1970–2010 ^d	Palutikof et al. (1996), Palutikof (2003)
Primary production	<i>Chla</i>	Satellite imagery (SeaWifs/Modis A)	1997–2010	
	PAR	Satellite imagery (SeaWifs/Modis A)	1997–2010	
Anthropogenic				
L-index derivatives	<i>Lindex</i>	Loss in production index, estimating the reduction of energy availability, due to fishing activities	1997–2010	Libralato et al. (2008)
	Psust	Probability of being sustainably fished, estimated according to the L-index value	1997–2010	Libralato et al. (2008)
^a North Atlantic Oscillation (NAO): www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml ^b Western Mediterranean Oscillation index (WEMOI): www.ub.edu/gc/English/wemo.htm ^c Mediterranean Oscillation Index (MOI): www.cru.uea.ac.uk/cru/data/moi ^d Sea surface temperature (SST): www.ncdc.noaa.gov/ersst/				

RESULTS

General patterns

The landings database was composed of 195 taxa belonging to the Mollusca, Crustacea and Pisces groups (for the complete list of taxa and their presence in the 8 areas, see Table S1 in the Supplement). At the level of the Mediterranean Sea, landings are dominated by Pisces followed by Mollusca and Crustacea (Table 2). This pattern is found in all of the areas, although the relative composition varies (Table 2), from the Black Sea, dominated by Pisces (97.4%), to the Adriatic Sea, with the lowest contribution by Pisces (68.0%) and a large fraction (24%) of Mollusca. In terms of preferred macrohabitat, pelagic organisms are the dominant group at the

Mediterranean level and in the Adriatic Sea, Aegean Sea, Balearic Sea, Black Sea, Gulf of Lion, and Sardinia areas (ranging from 96.4% in the Black Sea to 51.4% in Sardinia). Conversely, in the Ionian and Levant areas, these proportions are inverted, with catches dominated by demersal species (56.2 and 71.6%, respectively) (Table 2).

Application of the method showed that the consistency of the sigmoidal logistic pattern in the cumB vs. TL curve applied to landings, both across time (1970 to 2010) and space (all 8 GFCM areas in the Mediterranean Sea) (Fig. 3). The plots highlighted the presence of inter- and intra-area differences, such that specific temporal dynamics can be observed (Fig. 3). Important modifications to the logistic curve over time are suggestive of systemic-level changes (e.g. Balearic Sea, Black Sea, Gulf of Lion). There were

Table 2. Proportion of major groups in the fisheries landings (as %), in terms of major taxonomic groups and macrohabitat preference, for the 8 analyzed areas and the entire Mediterranean Sea. Values refer to the median and the interquartile range (in parentheses) for 1970 to 2010

	Adriatic Sea	Aegean Sea	Balearic Sea	Black Sea	Gulf of Lions	Ionian Sea	Levant Sea	Sardinia	Mediterr. Sea
Pisces	68 (62.2–75.1)	90.3 (86.1–94.2)	92.2 (91.1–92.8)	97.4 (95.4–97.9)	90.6 (89.3–92.3)	77 (74.5–78.3)	93.2 (90.0–94.7)	78.9 (65.7–82.5)	86.9 (85.8–88.8)
Mollusca	24 (21.1–28.5)	5.4 (3.5–7.1)	5.3 (4.6–5.9)	1.2 (0.0–5.5)	7.5 (6.2–8.9)	13.3 (11.7–16.1)	4.2 (3.5–5.2)	12.1 (11.2–14.3)	8.1 (7.1–9.0)
Crustacea	7 (3.7–8.5)	4.3 (1.7–5.5)	2.5 (2.3–2.9)	0.4 (0.5–2.4)	1.9 (0.6–2.0)	9.7 (8.7–11.1)	2.6 (1.4–4.0)	9 (6.3–21.0)	4.4 (3.6–5.6)
Pelagic	73.1 (68.8–76.9)	69.5 (67.3–71.8)	81.1 (79.0–83.0)	96.4 (94.7–97.6)	72 (67.7–78.2)	43.8 (37.3–45.0)	28.4 (23.1–34.4)	51.4 (44.0–57.9)	76.9 (75.2–79.2)
Demersal	26.9 (23.1–31.1)	30.5 (28.2–32.7)	18.9 (17.0–21.0)	3.6 (2.4–5.3)	28 (21.7–32.3)	56.2 (55.0–62.7)	71.6 (65.6–76.9)	48.6 (42.1–55.9)	23.1 (20.8–24.8)

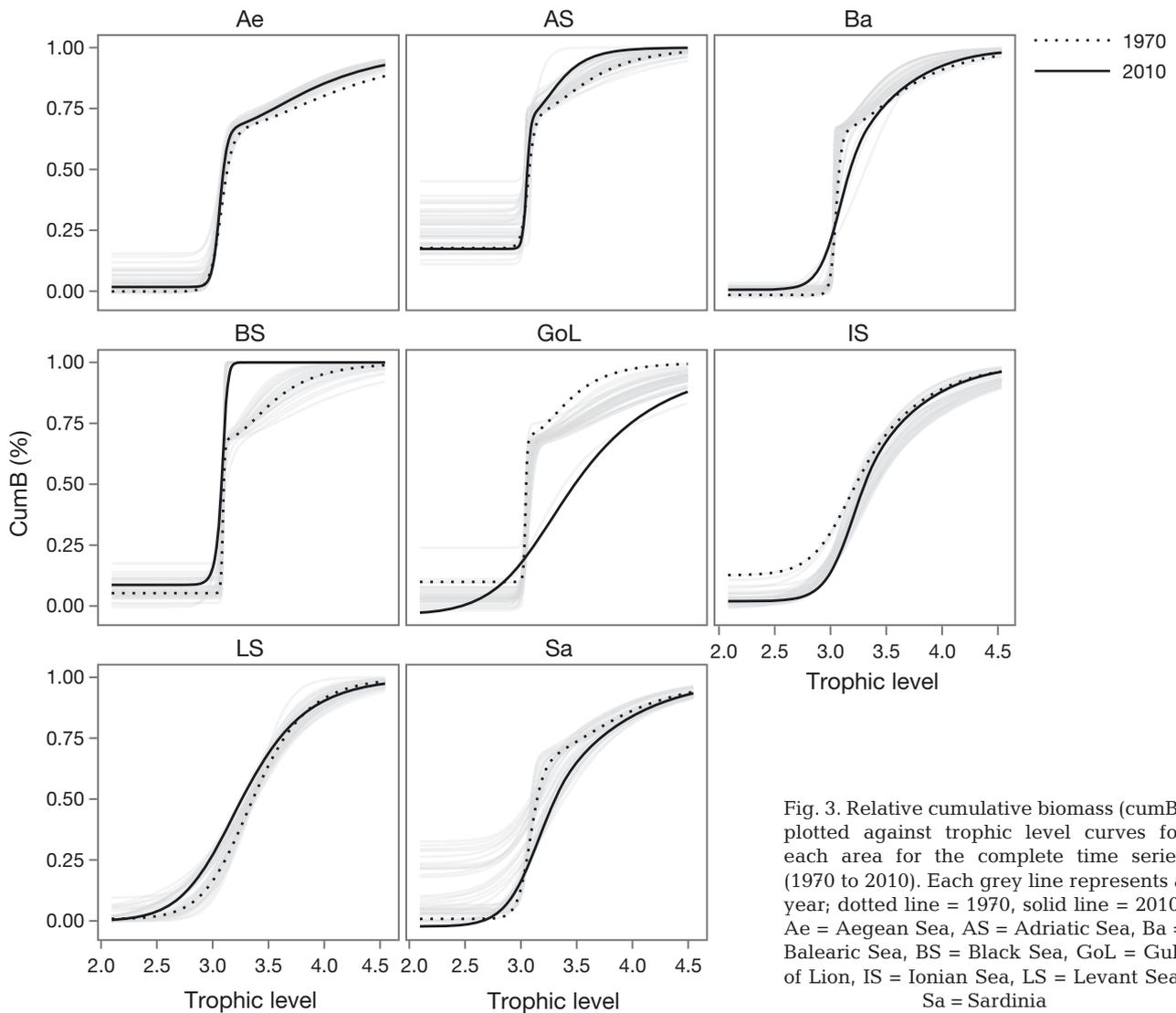


Fig. 3. Relative cumulative biomass (cumB) plotted against trophic level curves for each area for the complete time series (1970 to 2010). Each grey line represents a year; dotted line = 1970, solid line = 2010. Ae = Aegean Sea, AS = Adriatic Sea, Ba = Balearic Sea, BS = Black Sea, GoL = Gulf of Lion, IS = Ionian Sea, LS = Levant Sea, Sa = Sardinia

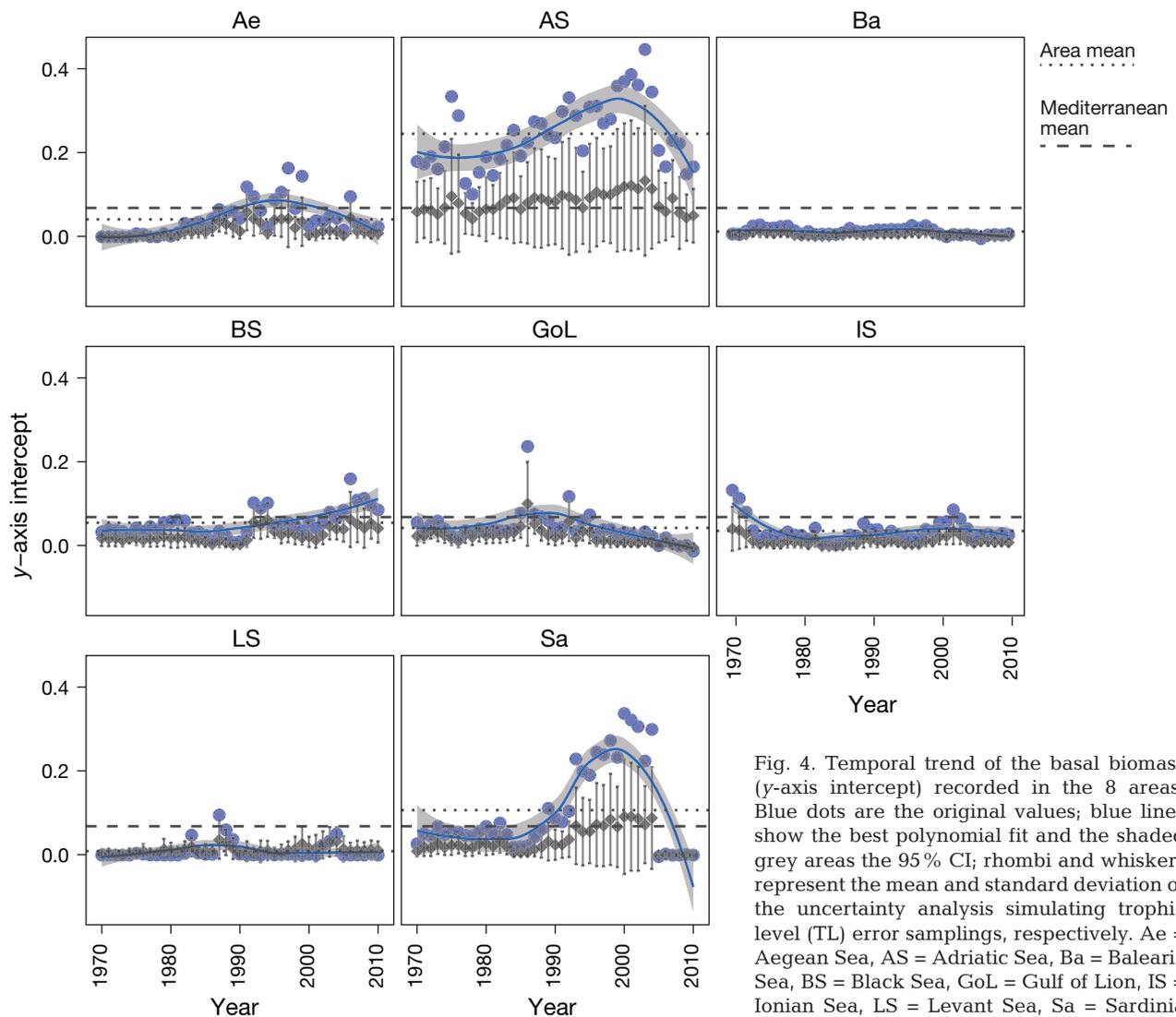


Fig. 4. Temporal trend of the basal biomass (y-axis intercept) recorded in the 8 areas. Blue dots are the original values; blue lines show the best polynomial fit and the shaded grey areas the 95% CI; rhombi and whiskers represent the mean and standard deviation of the uncertainty analysis simulating trophic level (TL) error samplings, respectively. Ae = Aegean Sea, AS = Adriatic Sea, Ba = Balearic Sea, BS = Black Sea, GoL = Gulf of Lion, IS = Ionian Sea, LS = Levant Sea, Sa = Sardinia

also modifications over time concentrated in specific portions of the curve, i.e. high variability over time across the lower TLs (e.g. Sardinia) or higher TLs (Gulf of Lion, with the exception of the last 2 yr), suggestive of more targeted responses in the systems, but no hypothesis of possible causes can be posed at this level of analysis. Fig. 3 shows the different shape between the first and the last year of the time series for the Balearic Sea, Black Sea and Gulf of Lion; other areas, such as the Adriatic, Aegean and Levant, exhibited similar curve shapes between the beginning and the end of the series.

Changes in the shape of the cumB-TL curve result in differential effects on the estimated parameters. In particular, the stretching of the curve generally produced a decrease in steepness. Subsequently, shifts in steepness can either not affect the inflection point

(e.g. Gulf of Lion, with the exception of the last 2 yr) or notably alter it as in the Balearic Sea. The implication of these shifting parameters is that certain drivers have been impacting the system, albeit with differing responses.

Temporal trends (Figs. 4 to 6) highlighted that each curve parameter showed specific patterns, depending on the area (Table 3). In general, basal biomass appears to be relatively stable through time in almost all of the areas, even if different mean values are observed across the areas. The exceptions are the Adriatic Sea and Sardinia, which exhibit higher mean values (Table 3) and a higher inter-annual variability, with a peak in 2004 (Fig. 3). This parameter, reflecting the catch composition, can be useful in detecting changes in exploitation at the low TL species level.

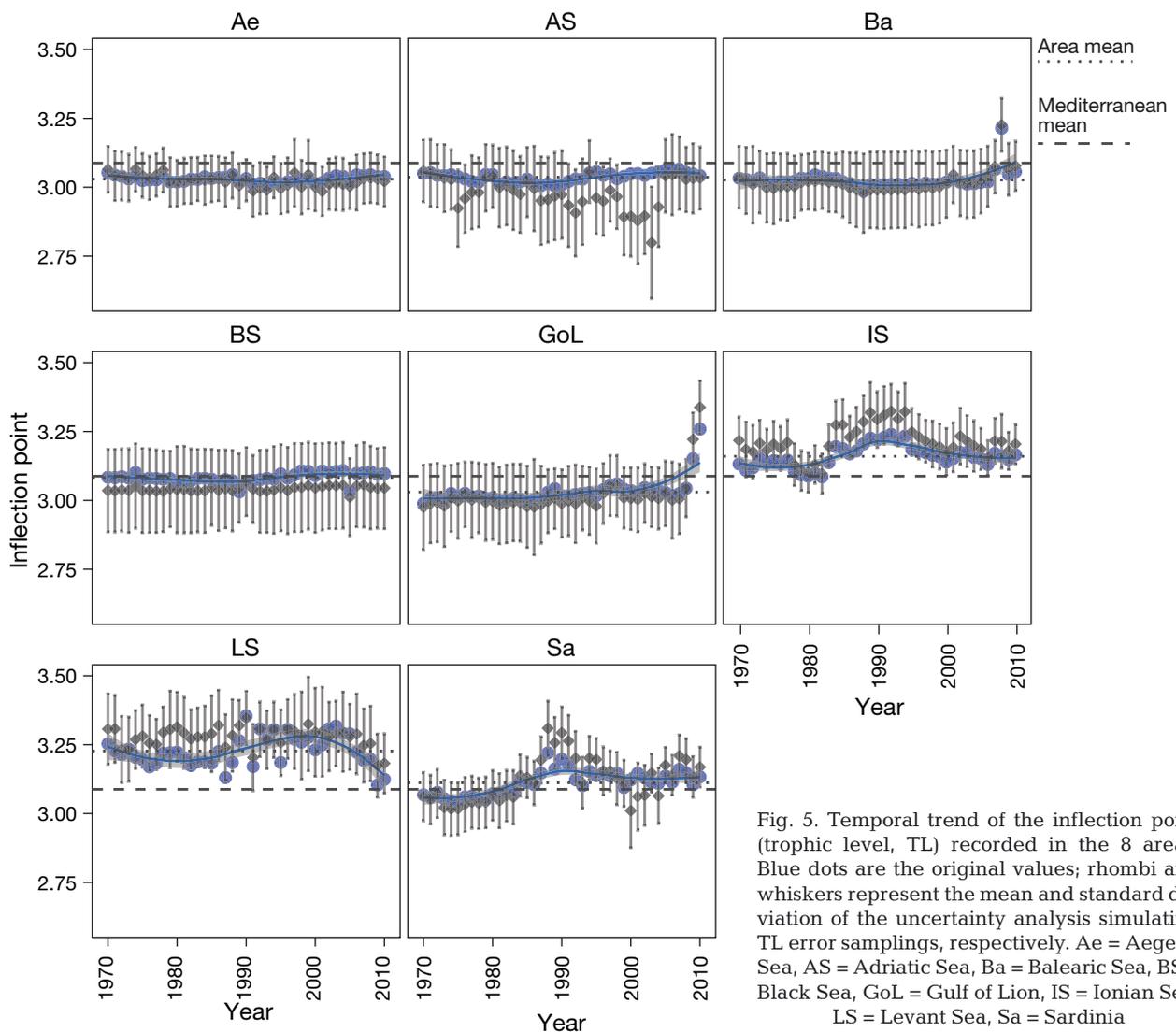


Fig. 5. Temporal trend of the inflection point (trophic level, TL) recorded in the 8 areas. Blue dots are the original values; rhombi and whiskers represent the mean and standard deviation of the uncertainty analysis simulating TL error samplings, respectively. Ae = Aegean Sea, AS = Adriatic Sea, Ba = Balearic Sea, BS = Black Sea, GoL = Gulf of Lion, IS = Ionian Sea, LS = Levant Sea, Sa = Sardinia

The inflection point (with respect to TL) also exhibits relatively low inter-annual variability, with a notable pattern only in the Ionian, Levant and Sardinia areas, which showed an increase in the 1990s followed by a decline (Fig. 5). Steepness is the most variable parameter, showing high variability across the areas in terms of both mean values (Table 3) and temporal dynamics. With the exception of the Ionian and Levant areas, steepness showed periodical fluctuations, culminating in a general decrease in the last years (Fig. 6). This variability both within and among areas could be useful in detecting the effects of external drivers acting on the ecosystems.

The analysis for the entire Mediterranean showed few temporal variations in the basal biomass and TL inflection point but a more dynamic pattern for steepness, thus confirming patterns observed at the indi-

vidual area level (Fig. 7). All 3 parameters showed 2 clearly distinguishable periods, i.e. before and after the beginning of the 1990s. The second period is characterized by a decrease of steepness, an increase of basal biomass (peaking at the end of the 1990s) and a rather stable trend of the inflection point with only a slight increase in the last years.

Uncertainty analysis

Results of the uncertainty analysis showed limited differences in terms of both direction and range of variation in parameter estimates relative to nominal estimates (Figs. 4 to 6), even if with some exceptions (see the case of basal biomass in Sardinia). This indicates that the method can be considered sufficiently

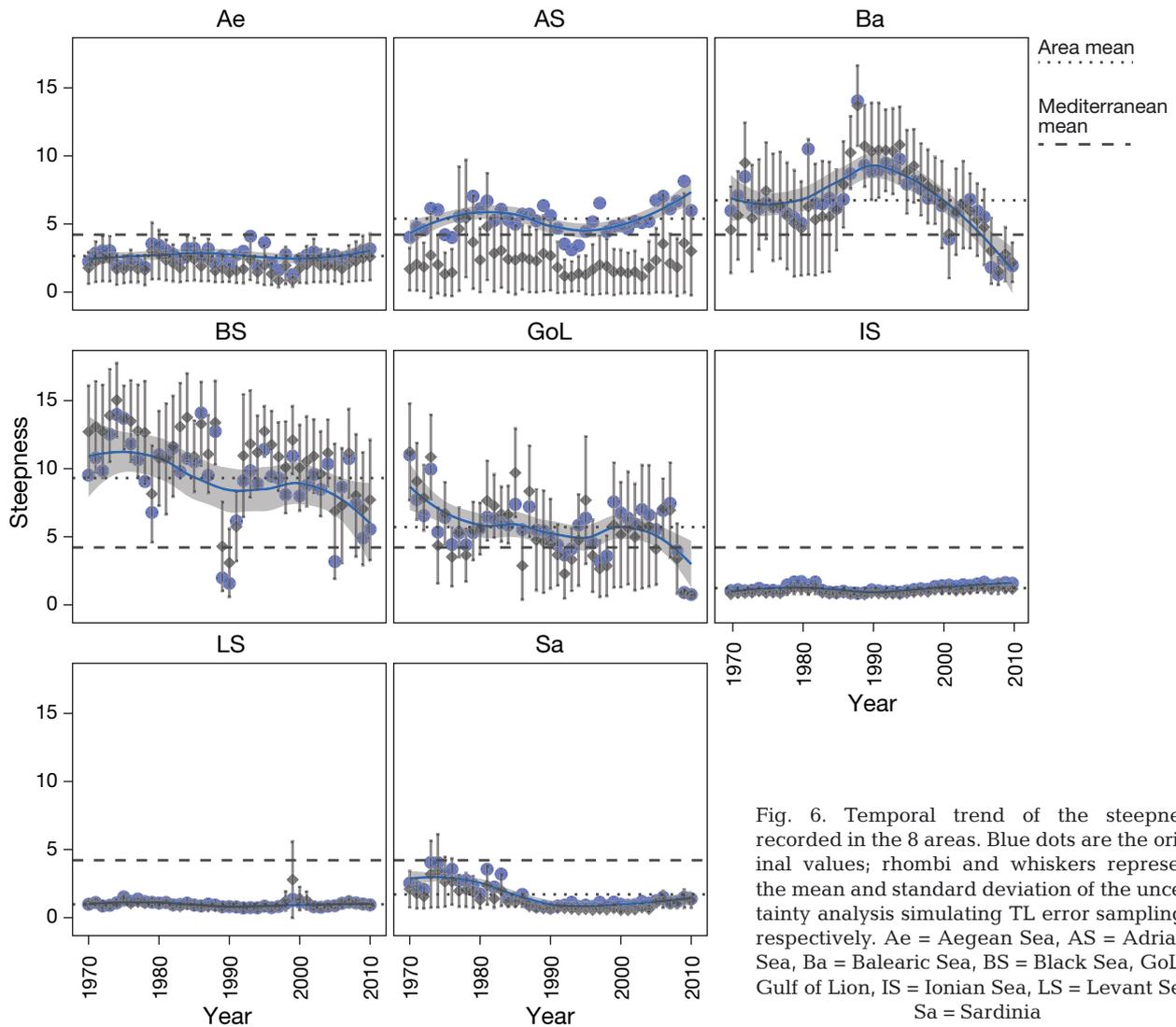


Fig. 6. Temporal trend of the steepness recorded in the 8 areas. Blue dots are the original values; rhombi and whiskers represent the mean and standard deviation of the uncertainty analysis simulating TL error samplings, respectively. Ae = Aegean Sea, AS = Adriatic Sea, Ba = Balearic Sea, BS = Black Sea, GoL = Gulf of Lion, IS = Ionian Sea, LS = Levant Sea, Sa = Sardinia

robust to possible ‘sampling errors’ in terms of the TL attribution. In general, the dispersion estimated by the Monte Carlo analysis is proportional to the difference between mean values obtained from the uncertainty analysis and nominal values. The salient point is that TL assignment did not affect the trend detection capability.

Explanatory variables and relationships with curve parameters

The GAMM analysis had the same optimal random structure for the 3 curve parameters in all areas, with a first-order autocorrelation term and a random intercept term. The proportion of explainable variance was approximately 40% for all parameter combinations. All results in terms of the response shape between

Table 3. Mean values (\pm SD) of curve parameters (average 1970 to 2010) obtained by fitting raw data in the 8 areas and in the entire Mediterranean Sea

Area	Basal biomass	Inflection point	Steepness
Adriatic Sea	0.24 \pm 0.08	3.04 \pm 0.02	5.39 \pm 1.07
Aegean Sea	0.04 \pm 0.04	3.03 \pm 0.01	2.72 \pm 0.77
Balearic Sea	0.01 \pm 0.01	3.02 \pm 0.03	6.74 \pm 2.40
Black Sea	0.05 \pm 0.03	3.08 \pm 0.02	9.31 \pm 2.87
Gulf of Lion	0.04 \pm 0.04	3.03 \pm 0.04	5.71 \pm 1.91
Ionian Sea	0.03 \pm 0.03	3.16 \pm 0.04	1.23 \pm 0.27
Levant Sea	0.01 \pm 0.02	3.23 \pm 0.05	0.98 \pm 0.19
Sardinia	0.11 \pm 0.10	3.11 \pm 0.04	1.71 \pm 0.98
Mediterranean Sea	0.07 \pm 0.02	3.06 \pm 0.01	4.65 \pm 1.55

each curve parameter and the different drivers are reported in the Supplement (Figs. S1 to S4); Table 4 summarizes only those that are significant.

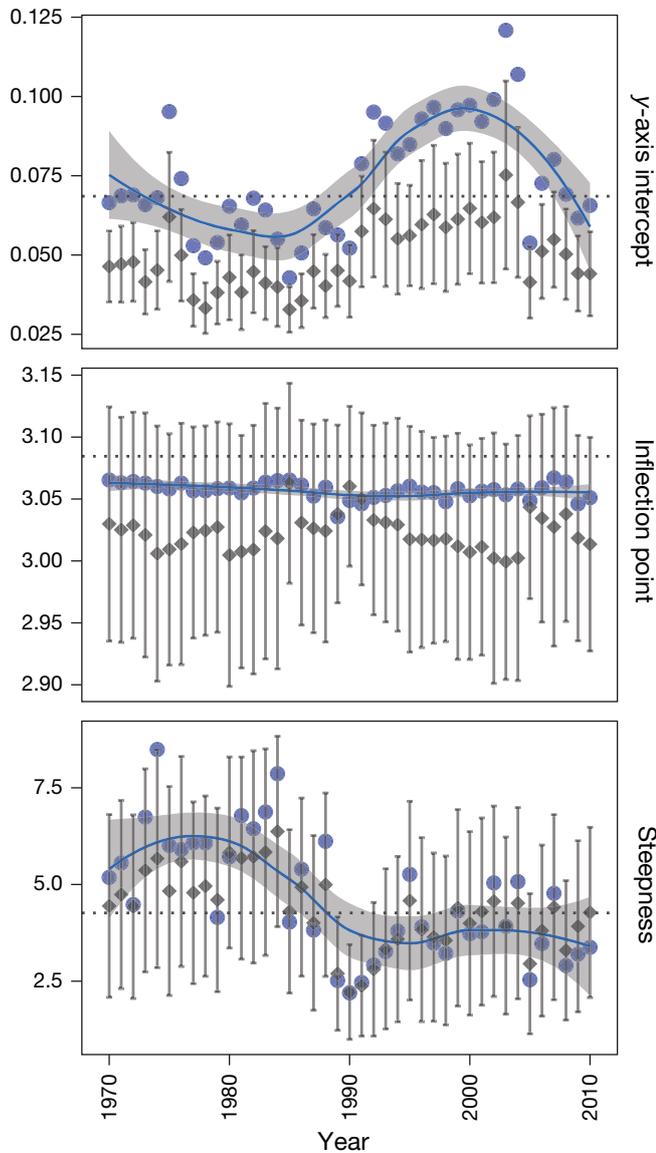


Fig. 7. Temporal trend of the curve parameters estimated for the entire Mediterranean Sea. (A) Basal biomass; (B) inflection point (trophic level, TL); and (C) steepness. Blue dots are the original values; rhombi and whiskers represent the mean and standard deviation of the uncertainty analysis simulating TL error samplings, respectively; dotted lines show Mediterranean means

Basal biomass was related to mean area depth in both the long and short time series analyses, implying an increase of the incidence of herbivorous and detritivorous taxa (TL < 2.5) in total catches in shallower seas. Commercial species at such TLs are usually benthic invertebrates that are mainly exploited in shallow fishing grounds (Table 4).

The inflection point (with respect to TL) was positively correlated with the area surface in both the short and long analyses and also with the L-index in

the short time series (Table 4). The L-index can be considered a measure of fishing pressure, and the total surface of the area can be interpreted as a proxy for the availability of fishing grounds, which can be interpreted either as allowing fishermen to have a broader fishing area or as increasing the incidence of higher TL species in the catches. This implies that the inflection point seems to be largely related to fishery-driven considerations. The inflection point was stable through time and, hence, was used as an estimate of the overall fishing effects (see significant relationship with the L-index; see Table 4).

Steepness was negatively correlated with area latitude and positively correlated with maximum depth in the long time series analysis (sea surface temperature [SST] and L-index are marginally significant at the 0.1 p-level); it was positively correlated with SST, chl a and L-index in the short time series (Table 4). This parameter is a measure of 'dispersion' of catches around the TL of biomass accumulation. As a consequence, it is reasonable to expect that the parameter is simultaneously affected by both bottom-up environmental (geographic and primary production) and top-down anthropogenic (fishery-dependent) drivers.

DISCUSSION

Emergent properties deserve particular attention in the development of indicator frameworks. Gunderson & Holling (2002) note that emergent ecosystem properties can be considered stable and robust features through both space and time. As suggested by the goal functions theory (Müller & Leupelt 1998), these are the objectives that tend to be optimized and saturated in all ecological systems (Cropp & Gabric 2002). From this perspective, indicators based on these emergent properties are expected to be quite effective in detecting significant state variations of complex systems such as these Mediterranean ecosystems.

In particular, total system biomass is quite a conservative property, changing very slowly through time in a wide variety of ecosystems (Holling et al. 1995). This is directly linked to both (1) species functional redundancy (Peterson et al. 1998, Loreau et al. 2002), which allows a species to substitute for another in the same ecological role; and (2) the homeostatic capabilities of food webs, which can react to external perturbations by rearranging the topology (links and nodes) and energy flows (McCann & Rooney 2009, Vallina & Le Quéré 2011). As these properties tend to

Table 4. Correlation between curve parameters and external drivers (only parameters showing significant relationships are reported). The analysis was carried out for all systems combined, with and without chl *a* (i.e. short and long time series, respectively). +: significant ($p < 0.05$) positive relationship; -: significant ($p < 0.05$) negative relationship; (+): significant ($p < 0.1$) positive relationship; Chl *a*: chlorophyll concentration; SST: sea surface temperature; TL: trophic level

Curve parameter	Area depth	Area surface	Area max. depth	Area latitude	SST	Chl <i>a</i>	L-index
Without chl <i>a</i>							
Basal biomass	-						
Inflection point (TL)		+					+
Steepness			-	+	(+)		(+)
With chl <i>a</i>							
Basal biomass	-						
Inflection point (TL)		+					
Steepness					+	+	+

be conservative because of the resilience of ecological systems (sensu Holling 1996), detecting changes to them could be difficult and, once detected, could be too late for mitigation or recovery (Gunderson & Holling 2002). In this context, it is crucial to understand which types of drivers an indicator is sensitive to and how robust an indicator is in relation to modifications of the external conditions and/or the system state.

Meaning of indicators derived from biomass accumulation across TLs

The analysis of the biomass distribution across TLs (cumB-TL) combines 2 of the most important emerging properties of an ecosystem (energy structure and storage, expressed as biomass), allowing for an improvement in the 'resolution power' of the indicator. Indeed, within the context of the relationship between diversity and ecosystem functioning (Chapin et al. 1997, Tilman et al. 1998, Schwartz et al. 2000, Naeem 2002, Micheli & Halpern 2005), we recommend further analysis of 'functional diversity' related not to taxonomic but to system operational categories. In a trophodynamic context, these categories would be better defined in terms of trophic composition ('vertical diversity', Duffy et al. 2007) and then combined with an emergent property, such as what we have shown here as system biomass. From our work, we note that the metrics associated with the cumB-TL curve encapsulate a suite of realized ecosystem functions. The 3 curve parameters, which are differentially sensitive to different external

drivers, collectively appear to capture different aspects of ecosystem functioning. They also appear to exhibit different responses to changes in ecosystem state, all desirable features for ecosystem indicators (Rice & Rochet 2005, Link et al. 2010).

For instance, the basal biomass for the Mediterranean appears to represent a measure of the prevalence of herbivorous and detritivorous species as part of total biomass. As such, it can be considered a structural parameter related to both fisheries dynamics and features of the area, particularly depth. Within the context of the present application to the Mediterranean Sea, this parameter was typically quite stable through time, with

similarly low values across different areas. This indicates the rare occurrences of lower TL invertebrates in catches. However, for those parts of the Mediterranean where there was a somewhat higher prevalence of lower TL invertebrates in the catch, this parameter readily captured such distinctions across areas. This is also true for temporal dynamics. Accordingly, the trend recorded for the Adriatic Sea can be explained by the high level of bivalve exploitation (mainly razor and striped Venus clams), with a peak recorded at the end of the 1990s followed by a decrease of the resource (Romanelli et al. 2009). The variations in basal biomass over time in the Sardinia area are mainly related to mussels that for a period were considered within the landings statistics by FAO. These examples show the capabilities of basal biomass to capture the changes in the landings.

The inflection point represents an estimate of the TL at peak catches. The parameter is, at least in the Mediterranean, mainly fishery-driven, given its association with proxy variables for fishing emerging from the GAMM analysis. The parameter was also mostly stable through time and can be interpreted as an indicator of overall fishing effects (e.g. to assess the presence of fishing down effects; Pauly et al. 1998).

Steepness synthesizes environmental and anthropogenic processes; it is the parameter that integrates across the cumB-TL curve, measuring the strength of biomass accumulation. In this case, a flattening of the cumB-TL curve (resulting in a decrease of the steepness) can be considered a negative response of the ecosystem to both natural and anthropogenic drivers. The parameter was significantly correlated to 2 driv-

ers, chl *a* and SST, which are important in determining the production regime of the system, similar to high-latitude systems (Pranovi et al. 2012).

Regarding temporal dynamics, the steepness and inflection point showed an inverse pattern, but both indicators exhibited the highest variability in the areas known to have experienced the most perturbations. Inflection points showed high temporal variability in the 3 areas (Ionian Sea, Levant Sea, Sardinia) that presented a peak in landings at the end of the 1980s and beginning of the 1990s, which might be related to the peaks in exploitation. Steepness, on the other hand, showed a pattern more clearly explainable with broad ecosystem changes. In the Adriatic Sea, the steepness pattern appeared to highlight the crisis at the end of the 1980s and a slow recovery in the following period; in the Balearic Sea, the pattern showed a decrease of environmental 'quality' in the last decade as highlighted in previous works (e.g. Coll et al. 2006); and in the Black Sea, the readily observed dramatic reduction in steepness is connected with the regime shift recorded for 1988 to 1989, in relation to the ctenophore alien species invasion (Daskalov 2002).

Uncertainty and reliability of indicators derived from CumB vs. TL

The use of trophic composition analysis, applied to landings data in particular, is still a highly debated issue (Branch et al. 2010). That general debate raises concerns about the difficulties of correctly assigning a TL to different taxa because of the high observed variability of diet in both time (e.g. ontogenetic shifts) and space plus concerns over using landings data to represent biomass of 'real communities' (see Pauly et al. 2013). We trust the work here reasonably addresses and even mitigates some facets of these concerns. In particular, the sensitivity analysis showed little change in response across levels of TL assignment, suggesting that at least this method is robust to these TL assignments. The sensitivity analysis, in fact, revealed some level of robustness in relation to possible 'sampling errors' in the TL assignment to different taxa, showing that the main features of the temporal dynamics are maintained for the 3 parameters estimated from cumB-TL curves. Nevertheless, differences in sensitivity were detected among curve parameters, with the inflection point more stable than steepness and basal biomass. Regarding the representativeness of real communities, it has to be considered that landings could be biased by different

factors. Unreported catches, missing entire compartments or key species simply not targeted by fisheries (such as many lessepsian species) all represent important issues in the Mediterranean Sea. From an ecosystem services perspective, however, the quality of a supplied service (in this case, the exploitable biomass) is directly dependent on the ecological status, and analysis of landings variations through time can be considered a proxy of the entire system functioning. In addition, landings often represent the only data source available on a time series basis.

Until now, the biomass accumulation across TL method has been applied to survey data (Pranovi et al. 2012) and model output data (Link et al. 2012b). Yet the patterns shown here are similar to those observed for fishery-independent data (Pranovi et al. 2012, Pranovi & Link 2009, Link et al. 2012b), suggesting that this approach can readily use a wider range of data to capture main emergent ecosystem properties. The consistency of the pattern with that emerging from the use of other kinds of data (Pranovi et al. 2012, Pranovi & Link 2009, Link et al. 2012b) may also indicate an inherent robustness of the cumB-TL method. Further, these curves were estimated in terms of relative biomass values, mitigating possible effects on landings data as representative of biomass. Therefore, parameters estimated on relative curves were comparable in both space and time, even in the absence of reliable data on the fishery features to correct for the absolute value of landings. The consistency of the biomass accumulation pattern across TLs, independent of the type of data used (e.g. fishery-independent or fishery-dependent), may also be viewed as a confirmation that, to some extent, landings represent a reliable proxy for understanding changes in exploited marine communities (sensu Pauly et al. 2013).

The patterns we observed highlight the presence of biomass accumulation at intermediate TLs (between TL 2.8 and 3.3), confirming previous findings (Pranovi et al. 2012) and theoretical expectations (Link et al. 2009). General patterns for cumB-TL curves were consistent in both space (across the 8 analyzed areas) and time (through the entire time series, 1970 to 2010), but the indicators were able to capture spatiotemporal dynamics in terms of catch composition, which can also reflect dynamics of the trophic structure. Collectively, this provides further evidence that the biomass accumulation patterns at intermediate TLs can be considered an emerging property in all marine ecosystems, as suggested by Pranovi et al. (2012) and Link et al. (2012b). Emergent properties from the general cumB-TL curve

pattern (i.e. estimated curve parameters as basal biomass, inflection point and steepness) may be suitable as ecosystem indicators. The method used here for defining such indicators has the advantage of being applicable in many situations where only rudimentary fishery statistics are available (Pauly et al. 1998, Pauly & Maclean 2003). This would be of particular interest in areas characterized by high ecological heterogeneity and great differences in availability of scientific information, such as the Mediterranean Sea.

The comparison of these findings to those from high-latitude ecosystems (Pranovi et al. 2012) suggests some differences in biomass accumulation patterns. Biomass accumulation in the Mediterranean areas is lower than that in high-latitude ecosystems, as seen in the values of inflection point and steepness. Although the value of these parameters can be partially related to the type of data used (fishery-dependent vs. fishery-independent), an important interpretation may also lie in the differences in ecosystem structure across types of ecosystems and areas. Higher latitude systems should have a higher accumulation of biomass because their food webs are relatively simpler and the mean size of species is larger (e.g. see Heymans et al. 2012). Yet despite differences in actual values of these parameters, one common feature remains across the different types of ecosystems; the present work confirms findings reported in Pranovi et al. (2012) that fishing can notably affect the structure of marine ecosystems, with significant and detectable impacts on inflection point and steepness of the cumB-TL curve. However, contrary to previous findings from other ecosystems (Pranovi et al. 2012), the Mediterranean climate proxies (such as the North Atlantic Oscillation and different Mediterranean Oscillation indices) did not seem to play a direct role in affecting the cumB vs. TL curve shape. This could be related to the complicated effects of climatic changes on the Mediterranean area that can be only partially summarized by these proxies. That SST was related to the dynamics of these parameters in the Mediterranean suggests that there may indeed be some environmental relationships, which we have not fully captured here.

Potential indicators for ecosystem-based management

The cumB-TL curve and associated parameters demonstrated strong potential as good candidates for ecosystem indicators in an ecosystem-based man-

agement context. They showed desirable features such as low sensitivity to possible errors in assigning the TLs and a differential sensitivity to external drivers. Moreover, as noted above, we document that the cumB-TL approach is feasible using landings data. Thus, the associated parameters can be applied to different kinds of data (fishery-dependent and fishery-independent), making this approach widely applicable to a broader range of data sources. The approach is a relatively simple treatment of readily available data and does not require extensive food web modelling. This approach clearly captured modifications to catches over time as emergent in the ecosystem-level indicators. General expectations such as the flattening of cumB curves in relation to an increase of anthropogenic impacts (Link et al. 2009) were confirmed. For instance, the known regime shift recorded for 1988 to 1989 in the Black Sea (Daskalov 2002) was readily observed as a dramatic reduction in steepness for that system; similar patterns were observed for the Gulf of Lion in the last 2 yr, probably due to the sharp decrease of small pelagic abundance recorded in the area (European Commission 2010).

Even if a complete disentangling of drivers and responses is not possible, some discrimination between natural and anthropogenic parameters was discernible. Steepness was largely affected by environmental variables, whereas the inflection point was mostly fishery-driven. From this, we divide the 8 areas into 2 groups: (1) systems with almost stable steepness and high variability in the inflection point (Ionian Sea, Levant Sea and Sardinia), probably affected mainly by variations in the fisheries; and (2) systems showing high variability in steepness and a stability in the inflection point (Adriatic Sea, Balearic Sea, Black Sea, and Gulf of Lions), for which an effect of environmental drivers can be invoked. The ability to discriminate across main ecosystem drivers is not a trivial outcome when establishing indicators.

The comparison between results obtained at the regional (single area) and large marine ecosystem (LME; entire Mediterranean) scales highlighted the importance of the adoption of a refined, spatially explicit approach, since the analysis at the larger scale (LME) could often result in not only a loss of information (missing significant trends) but also misleading conclusions. For instance, contrasting indicator dynamics at regional scales that have significant ecological meaning can be lost when looking at aggregated values at the scale of the Mediterranean, missing the ability to detect ecological changes. As an example, the basal biomass and inflection point

analyzed at the Mediterranean level showed a stable pattern, suggesting a quite resilient situation in relation to fishing impact. Yet individual areas showed significant temporal variability. Steepness for the entire Mediterranean showed 2 clear phases before and after 1990, again suggesting a kind of ecological stability, at least on a decadal basis. Recent analyses, however, demonstrated exploited populations in recent times in some areas (Colloca et al. 2011), in agreement with our regional findings. Moreover, spatial heterogeneity in management planning always has to be taken into account (Giakoumi et al. 2013); thus, the regional (sub-area) scale also warrants examination.

As with other trophodynamic indicators that have been proposed and that are in development (Bundy et al. 2005, Coll et al. 2008, Libralato et al. 2008, Link et al. 2009, 2010, Shannon et al. 2010, Shin et al. 2010a), additional simulation and uncertainty testing is warranted before their use can become fully operational. Yet the cumB-TL parameters show promise as useful indicators in the context of MSFD Descriptor 4. Within this context, the proposed indicators seem to match many of the criteria suggested for ecosystem indicators selection (see Rice & Rochet 2005), as they are applicable to different kinds of data (from landings to model outputs), responsive on an appropriate time scale and offer the opportunity to define the magnitude and direction of change. For instance, these indicators can be analyzed to define relationships with the GES and the analysis of several systems with known status or with time series of known ecological status trajectories that will allow the development of thresholds. Thresholds could be defined by comparatively analyzing a couple of indicators (e.g. inflection point vs. steepness) for a large set of systems in which the ecological state is known. This will identify reference levels or at least values of the indicators that we want to avoid.

Evaluating thresholds was beyond the scope of the work here; nevertheless, desirable directions of change for these indicators have been highlighted. This represents an important first step that can be useful in systems for which reference conditions are lacking or difficult to determine, as is often the case for the application of some GES indicators by EU member states.

Several regulations (Habitats Directive 92/43/EC, WFD 2000/60/EC, MSFD 2008/56/EC) and agreements (including the Madrid Protocol and ICZM) require the implementation of ecosystem-based management that will necessarily require a suite of

robust indicators able to describe the ecosystem state. Particularly interesting are indicators that allow discrimination, at least partially, between different external drivers (e.g. natural vs. anthropogenic pressures). Therefore, we are confident that the measures proposed here represent a useful step towards that end.

LITERATURE CITED

- Bianchi CN, Morri C (2000) Marine biodiversity of the Mediterranean Sea: situation, problems and prospects for future research. *Mar Pollut Bull* 40:367–376
- Blanchard JL, Coll M, Trenkel VM, Vergnon R and others (2010) Trend analysis of indicators: a comparison of recent changes in the status of marine ecosystems around the world. *ICES J Mar Sci* 67:732–744
- Blondel J, Aronson J (2005) *Biology and wildlife of the Mediterranean region*. Oxford University Press, Oxford
- Branch TA, Watson R, Fulton EA, Jennings S and others (2010) The trophic fingerprint of marine fisheries. *Nature* 468:431–435
- Bundy A, Fanning P, Zwanenburg KCT (2005) Balancing exploitation and conservation of the eastern Scotian Shelf ecosystem: application of a 4D ecosystem exploitation index. *ICES J Mar Sci* 62:503–510
- Bundy A, Shannon LJ, Rochet MJ, Neira S, Shin YJ, Hill L, Aydin K (2010) The good(ish), the bad and the ugly: a tripartite classification of ecosystem trends. *ICES J Mar Sci* 67:745–768
- Chapin FS III, Walker BH, Hobbs RJ, Hooper DU, Lawton JH, Sala OE, Tilman D (1997) Biotic control over the functioning of ecosystems. *Science* 277:500–503
- Coll M, Palomera I, Tudela S, Sarda F (2006) Tropic flows, ecosystem structure and fishing impact in the south Catalan Sea, North Western Mediterranean. *J Mar Syst* 59:63–69
- Coll M, Libralato S, Tudela S, Palomera I, Pranovi F (2008) Ecosystem overfishing in the ocean. *PLoS ONE* 3:e3881
- Coll M, Shannon LJ, Yemane D, Link JS and others (2010a) Ranking the ecological relative status of exploited marine ecosystems. *ICES J Mar Sci* 67:769–786
- Coll M, Piroddi C, Steenbeek J, Kaschner K and others (2010b) The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS ONE* 5:e11842
- Colloca F, Cardinale M, Maynou F, Giannoulaki M and others (2011) Rebuilding Mediterranean fisheries: a new paradigm for ecological sustainability. *Fish Fish* 14: 89–109
- Coma R, Ribes M, Serrano E, Jiménez E, Salat J, Pascual J (2009) Global warming-enhanced stratification and mass mortality events in the Mediterranean. *Proc Natl Acad Sci USA* 106:6176–6181
- Cropp R, Gabric A (2002) Ecosystem adaptation: Do ecosystems maximise resilience? *Ecology* 83:2019–2026
- Cury PM, Shannon LJ, Roux JP, Daskalov GM, Jarre A, Moloney CL, Pauly D (2005) Trophodynamic indicators for an ecosystem approach to fisheries. *ICES J Mar Sci* 62:430–442
- Daskalov GM (2002) Overfishing drives a trophic cascade in the Black Sea. *Mar Ecol Prog Ser* 225:53–63
- Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thébaud E, Loreau M (2007) The functional role of biodiversity in

- ecosystems: incorporating trophic complexity. *Ecol Lett* 10:522–538
- European Commission (2010) Assessment of the status of the fishery dependent community, Sète, France. FISH/2006/09. European Commission, Brussels
- Feyrer F, Herbold B, Matern SA, Moyle PB (2003) Dietary shifts in a stressed fish assemblage: consequences of a bivalve invasion in the San Francisco Estuary. *Environ Biol Fishes* 67:277–288
- Froese R, Pauly D (eds) (2000) FishBase 2000: concepts, design and data sources. ICLARM, Los Baños, Laguna
- Gascuel D, Bozec Y, Chassot E, Colomb A, Laurans M (2005) The trophic spectrum: theory and application as an ecosystem indicator. *ICES J Mar Sci* 62:443–452
- 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
- Giakoumi S, Sini M, Gerovasileiou V, Mazor T and others (2013) Ecoregion-based conservation planning in the Mediterranean: dealing with large-scale heterogeneity. *PLoS ONE* 8:e76449
- Gislason H (1999) Single and multispecies reference points for Baltic fish stocks. *ICES J Mar Sci* 56:571–583
- Gunderson LH, Holling CS (eds) (2002) Panarchy: understanding transformations in human and natural systems. Island Press, Washington, DC
- Hammerschlag N, Ovando D, Serafy JE (2010) Seasonal diet and feeding habits of juvenile fishes foraging along a subtropical marine ecotone. *Aquat Biol* 9:271–290
- Hastie T, Tibshirani R (1990) Generalized additive models in S. Chapman & Hall, London
- Heymans JJ, Coll M, Libralato S, Christensen V (2012) Ecosystem theory, modelling, and application to coastal ecosystems. In: Wolanski E, McLusky D (eds) *Treatise on Estuarine and Coastal Science*. Elsevier, Amsterdam, p 93–113
- Holling CS (1996) Engineering resilience versus ecological resilience. In: Schulze PC (ed) *Engineering within ecological constraints*. National Academy Press, Washington, DC, p 31–43
- Holling CS, Schindler DW, Walker BW, Roughgarden J (1995) Biodiversity in the functioning of ecosystems: an ecological synthesis. In: Perrings CA, Maler KG, Folke C, Holling CS, Jansson BO (eds) *Biodiversity loss, ecological and economical issues*. Cambridge University Press, Cambridge, p 44–83
- Jennings S (2005) Indicators to support an ecosystem approach to fisheries. *Fish Fish* 6:212–232
- Jennings S, Dulvy NK (2005) Reference points and reference directions for size-based indicators of community structure. *ICES J Mar Sci* 62:397–404
- Jørgensen SE, Xu FL, Costanza R (2010) Handbook of ecological indicators for assessment of ecosystem health, 2nd ed. CRC Press/Taylor & Francis, Boca Raton, FL
- Layman CA, Winemiller KO, Arrington DA (2005) Describing a species-rich river food web using stable isotopes, stomach contents, and functional experiments. In: de Ruiter PC, Wolters V, Moore JC (eds) *Dynamic food webs: multispecies assemblages, ecosystem development and environmental change*. Academic Press, Boston, MA, p 395–406
- Libralato S, Solidoro C (2010) Comparing methods for building trophic spectra of ecological data. *ICES J Mar Sci* 67:426–434
- Libralato S, Coll M, Tudela S, Palomera I, Pranovi F (2008) Novel index for quantification of ecosystem effects of fishing as removal of secondary production. *Mar Ecol Prog Ser* 355:107–129
- Lindeman RL (1942) The trophic-dynamic aspect of ecology. *Ecology* 23:399–417
- Link JS (2005) Translating ecosystem indicators into decision criteria. *ICES J Mar Sci* 62:569–576
- Link J (2010) Ecosystem-based fisheries management: confronting tradeoffs. Cambridge University Press, Cambridge
- Link JS, Pranovi F, Coll M, Libralato S, Christensen V, Legault C (2009) Exploring novel metrics of ecosystem overfishing using energy budget model outputs. *Fish Cent Res Rep* 17:153
- Link JS, Yemane D, Shannon LJ, Coll M, Shin YJ, Hill L, Borges MF (2010) Relating marine ecosystem indicators to fishing and environmental drivers: an elucidation of contrasting responses. *ICES J Mar Sci* 67:787–795
- Link JS, Gaichas S, Miller TJ, Essington T and others (2012a) Synthesizing lessons learned from comparing fisheries production in 13 northern hemisphere ecosystems: emergent fundamental features. *Mar Ecol Prog Ser* 459:293–302
- Link JS, Pranovi F, Libralato S, Coll M, Christensen V, Legault C (2012b) Delineating marine ecosystem perturbation and recovery: theory and application of a trophic approach. *ICES Annu Sci Conf*, Sep 17–21, Bergen
- Loreau M, Naeem S, Inchausti P (eds) (2002) *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford
- Martín-Vide J, Lopez-Bustins JA (2006) The Western Mediterranean Oscillation and rainfall in the Iberian Peninsula. *Int J Climatol* 26:1455–1475
- McCann KS, Rooney N (2009) The more food webs change, the more they stay the same. *Philos Trans R Soc London B* 364:1789–1801
- Micheli F, Halpern BS (2005) Low functional redundancy in coastal marine assemblages. *Ecol Lett* 8:391–400
- Müller F, Leupelt M (1998) *Eco targets, goal function and orientors*. Springer-Verlag, Berlin
- Naeem S (2002) Disentangling the impacts of diversity on ecosystem functioning in combinatorial experiments. *Ecology* 83:2925–2935
- Odum WE, Heald EJ (1975) The detritus-based foodweb on an estuarine mangrove community. In: Cronin LE (ed) *Estuarine research*. Academic Press, New York, NY, p 265–286
- Palutikof JP (2003) Analysis of Mediterranean climate data: measured and modelled. In: Bolle HJ (ed) *Mediterranean climate: variability and trends*. Springer-Verlag, Berlin
- Palutikof JP, Conte M, Casimiro Mendes J, Goodess CM, Espírito Santo F (1996) Climate and climate change. In: Brandt CJ, Thornes JB (eds) *Mediterranean desertification and land use*. John Wiley & Sons, London, p 43–86
- Pauly D, Maclean J (2003) *In a perfect ocean: the state of fisheries and ecosystems in the North Atlantic Ocean*. Island Press, Washington, DC
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F Jr (1998) Fishing down marine food webs. *Science* 279:860–863
- Pauly D, Hilborn R, Branch TA (2013) Fisheries: Does catch reflect abundance? *Nature* 494:303–306
- Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6–18

- Pranovi F, Link JS (2009) Ecosystem exploitation and trophodynamic indicators: a comparison between the Northern Adriatic Sea and Southern New England. *Prog Oceanogr* 81:149–164
- Pranovi F, Link J, Fu C, Cook AM and others (2012) Trophic level determinants of biomass accumulation in marine ecosystems. *Mar Ecol Prog Ser* 459:185–201
- R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0, available at www.R-project.org/
- Raffaelli D (2005) Tracing perturbation effects in food webs: the potential and limitation in experimental approaches. In: de Ruiter PC, Moore JC, Wolters V (eds) *Dynamic food webs: multispecies assemblages, ecosystem development and environmental change*. Academic Press, Boston, MA, p 348–353
- Rice JC (2003) Environmental health indicators. *Ocean Coast Manage* 46:235–259
- Rice JC, Rochet MJ (2005) A framework for selecting a suite of indicators for fisheries management. *ICES J Mar Sci* 62:516–527
- Ricketts JH, Head GA (1999) A five-parameter logistic equation for investigating asymmetry of curvature in baroreflex studies. *Am J Physiol* 277:441–454
- Rochet MJ, Trenkel VM (2003) Which community indicators can measure the impact of fishing? A review and proposals. *Can J Fish Aquat Sci* 60:86–99
- Romanelli M, Cordisco CA, Giovanardi O (2009) The long-term decline of the *Chamelea gallina* L. (Bivalvia: Veneridae) clam fishery in the Adriatic Sea: Is a synthesis possible? *Acta Adriat* 50:171–205
- Sarà G, Sarà R (2007) Feeding habits and trophic levels of bluefin tuna *Thunnus thynnus* of different size classes in the Mediterranean Sea. *J Appl Ichthyol* 23:122–127
- Schwartz MW, Brigham CA, Hoeksema JD, Lyons KG, Mills MH, van Mantgem PJ (2000) Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* 122:297–305
- Shannon LJ, Coll M, Yemane D, Jouffre D and others (2010) Comparing data-based indicators across upwelling and comparable systems for communicating ecosystem states and trends. *ICES J Mar Sci* 67:807–832
- Shin YJ, Rochet MJ, Jennings S, Field JG, Gislason H (2005) Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J Mar Sci* 62:384–396
- Shin YJ, Bundy A, Shannon LJ, Simier M and others (2010a) Can simple be useful and reliable? Using ecological indicators to represent and compare the states of marine ecosystems. *ICES J Mar Sci* 67:717–731
- Shin YJ, Shannon LJ, Bundy A, Coll M and others (2010b) Using indicators for evaluating, comparing, and communicating the ecological status of exploited marine ecosystems. 2. Setting the scene. *ICES J Mar Sci* 67:692–716
- Sosa-López A, Mouillot D, Chi TD, Ramos-Miranda J (2005) Ecological indicators based on fish biomass distribution along trophic levels: an application to the Terminos coastal lagoon, Mexico. *ICES J Mar Sci* 62:453–458
- STECF (Scientific, Technical and Economic Committee for Fisheries) (2010) In: Casey J, Dörner H (eds) 35th plenary meeting report of the scientific, technical and economic committee for fisheries (PLEN-10-03), Nov 8–12 2010, Brussels. Publications Office of the European Union, Luxembourg
- Stergiou KI, Karpouzi VS (2001) Feeding habits and trophic levels of Mediterranean fish. *Rev Fish Biol Fish* 11: 217–254
- Tilman D, Lehman CL, Bristow CE (1998) Diversity-stability relationships: statistical inevitability or ecological consequence? *Am Nat* 151:277–282
- Vallina SM, Le Quéré C (2011) Stability of complex food webs: resilience, resistance and the average interaction strength. *J Theor Biol* 272:160–173
- Wood SN (2006) *Generalized additive models: an introduction with R*. Chapman & Hall/CRC, Boca Raton, FL
- Wood SN (2008) Fast stable direct fitting and smoothness selection for generalized additive models. *J R Stat Soc B* 70:495–518
- Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc B* 73:3–36
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York

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