

Trend analysis of indicators: a comparison of recent changes in the status of marine ecosystems around the world

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Time-series of ecological and exploitation indicators collected from 19 ecosystems were analysed to investigate whether there have been temporal trends in the status of fish communities. Using linear and non-linear statistical methods, trends are reported for six indicators (mean length of fish in the community, mean lifespan, proportion of predatory fish, total biomass of surveyed species, mean trophic level of landings, and inverse fishing pressure), and the redundancy of these indicators across ecosystems is evaluated. The expected direction of change for an ecosystem that is increasingly impacted by fishing is a decline in all indicators. A mixture of negative and positive directions of change is recorded, both within and among all ecosystems considered. No consistent patterns in the redundancy of the ecological indicators across ecosystems emerged from the analyses, confirming that each indicator provided complementary information on ecosystem status. The different trends in indicators may reflect differing historical exploitation patterns, management, and environmental regimes in these systems. Commitment to monitoring programmes and development of system-specific baseline, target, and threshold reference levels are required. Improved understanding of the responsiveness and performance of ecological indicators to management actions are needed to address adequately whether ecosystems are recovering from, or being further impacted by, fishing, and whether management targets are being met. The relative effects of multiple environmental and ecological processes as well as multiple human-induced stressors that characterize exploited ecosystems also need to be quantified.

Keywords: community, ecological indicators, ecosystem-based fisheries management, ecosystem effects of fishing, natural resource management.

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Introduction

An ecosystem approach to fisheries (EAF) requires basic understanding of the important processes controlling marine ecosystem productivity. A necessary first step towards understanding any ecosystem in this context is to determine key indicators of aspects of ecosystem state that respond to fishing pressure (Trenkel and Rochet, 2003; Jennings, 2005; Link, 2005). Obtaining such understanding has proved difficult because of the complexity of marine ecosystems, their many components and different drivers, and the sheer volume of data required. Ecosystem considerations in a marine scientific and management context have been extant for more than a century (Baird, 1873), but making them operational in the context of EAF has remained a key challenge. One approach has been to examine patterns in

indicators of ecosystem structure and functioning over time (size-based, species-based, and trophodynamic indicators) to determine whether changes have been consistent with theoretical expectations for highly impacted, exploited systems. Research needs to be extended, however, to consider a suite of ecological indicators that encompass the key processes of exploited ecological systems with an improved understanding of their link to fishing pressure. Ultimately, we need to seek general relationships between pressure and state in the world's marine ecosystems; explicit use of indicators can facilitate this understanding.

The comparative approach has provided significant insights into understanding marine ecosystem functioning, with states (Hunt and Megrey, 2005; Moloney *et al.*, 2005; Coll *et al.*, 2006; Shin *et al.*, 2010a) and trends (Bianchi *et al.*, 2000; Shannon

et al., 2009) having been compared among ecosystems. In many respects, comparisons among a wide range of ecosystems can serve as *ad hoc* replicate responses akin to an experiment, highlighting common basic features as well as key differences, and giving insight into the effects of pressures that influence ecosystem processes. Such comparative analyses allow an opportunity for taking a broader ecosystem perspective and permit the drawing of generalizations about responses that will help identify ecosystem indicators and also help to support implementation of an EAF.

Using the comparative approach, we explore temporal variation in a set of ecosystem indicators: mean length of fish in the community, mean lifespan, proportion of predatory fish, total biomass of surveyed species, mean trophic level of landings, and inverse fishing pressure. We investigate two specific features, the trends of indicators over time and the similarities (or redundancies) of temporal responses the indicators may display under the same fishing pressure. Various methodological approaches to deal with trend analyses have been proposed and applied to ecological data. The significance of the trend (whether the predicted slope is significantly different from zero) and the direction of the trend are key parameters in characterizing whether fishing pressure is likely to be increasingly impacting ecosystems or whether there are signs of recovery. As ecological time-series often cover relatively short periods, are frequently characterized by strong autocorrelation attributable to various underlying ecological processes, and contain non-linearities, any single statistical method may (or may not) be appropriate.

The overall objectives of this work are to (i) explore the recent changes of ecosystem indicators using both linear and non-linear statistical methods for quantifying trends, (ii) compare and contrast trends in indicators across ecosystems, and (iii) address the redundancies and/or complementarities of indicators by looking at similarities in their temporal dynamics.

Methods

In all, 19 exploited ecosystems were included in this analysis (Table 1). They were upwelling, high latitude, temperate, and tropical marine ecosystems, and covered a range of low to highly productive areas, located in the Atlantic, Pacific, and Indian Oceans, and in the Mediterranean Sea. A description of each ecosystem is provided in *Shin et al.* (2010b) and *Shannon et al.* (2010) for upwelling and comparable systems. A set of six indicators was analysed to calculate the trends: the mean length (referred to as fish size) and mean lifespan (lifespan) of surveyed species, the proportion of predatory fish (% predators), the trophic level of landed catches (trophic level), the total biomass of surveyed species (biomass), and biomass/landings (inverse fishing pressure). A description of how to quantify and analyse these indicators is presented in *Shin et al.* (2010b), and a description of the origin of the data in www.indiseas.org. The list of indicators, their equations, expected direction of change following increased exploitation, and corresponding management objectives, are provided in Table 2.

Standardization and scaling of indicator time-series

When assessing temporal trends, the associated time-scale must be specified (e.g. the whole time-series or a recent period). Usually, the term trends implicitly refers to a linear approximation of time-series. Here, however, trend refers to either a significant linear or non-linear change in an indicator over the past 10 years (1996–2005), although for comparison we also estimate trends over a

Table 1. Ecosystems considered in this study (for further details see *Shin et al.*, 2010b, and Table 2).

	Ecosystem	Geographic area	Large marine ecosystem
1	Barents Sea	Northeast Atlantic	Barents Sea
2	Bay of Biscay	Northeast Atlantic	Iberian Coastal
3	Bering Sea, Aleutian Islands	Northeast Pacific	East Bering Sea
4	Central Baltic Sea	Northeast Atlantic	Baltic Sea
5	Eastern Scotian Shelf	Northwest Atlantic	Scotian Shelf
6	Guinean EEZ	East Central Atlantic	Guinea Current
7	Irish Sea	Northeast Atlantic	Celtic–Biscay Shelf
8	Mauritanian EEZ	East Central Atlantic	Canary Current
9	North-central Adriatic Sea	Central Mediterranean	Mediterranean
10	Northeast United States	Northwest Atlantic	Northeast US continental shelf
11	North Sea	Northeast Atlantic	North Sea
12	Northern Humboldt	Southeast Pacific	Humboldt Current
13	Portuguese EEZ	Northeast Atlantic	Iberian Coastal
14	Morocco (Sahara coastal)	East Central Atlantic	Canary Current
15	Senegalese EEZ	East Central Atlantic	Canary Current
16	Southern Benguela	Southeast Atlantic	Benguela Current
17	Southern Catalan Sea	Northwest Mediterranean	Mediterranean
18	Southern Humboldt	Southeast Pacific	Humboldt Current
19	West coast Canada	East Central Pacific	Gulf of Alaska

longer period (1980–2005, or the full length of the time-series where this is shorter). The choice of the length of time-series was a compromise guided by preliminary results. Short-term trends over the past 5 years were mostly non-significant. For most indicators, trends were not detectable across a 5-year period for several reasons: some ecosystems are already severely impacted so we could not expect a clear trend, data are missing in some cases for recent years so the trend is actually estimated over less than 5 years, the variance of each indicator is high, and the statistical power for detecting trends is low for indicator series < 10 years (*Nicholson and Jennings*, 2004). On the other hand, time-series spanning the longer period (1980–2005) were not available for sufficient of the ecosystems to carry out full cross-comparisons (Figure 1). Therefore, we emphasized the 1996–2006 time-frame for comparative purposes, and report trends for the longer period.

Standardization of the indicators is essential for comparative purposes (inter-indicator and inter-ecosystem comparisons). All indicator time-series were normalized by subtracting the mean value of that indicator over the period examined and dividing by the standard deviation $(Y - Y_{\text{mean}})/Y_{\text{std}}$ (Figure 1). This enabled comparisons to be made between indicators (comparison of sensitivities) and ecosystems (comparison of fishing impacts). The slope of the trends obtained from normalized values is equivalent to the slope obtained from the original values when they are expressed as a ratio of the standard deviation (Y/Y_{std}) .

Table 2. List of ecosystem indicators used in trend analyses, along with the expected trends from increasing exploitation and corresponding management objectives.

Indicator	Headline label	Calculation, notations (units)	Expected trend	Management objectives	Management direction
Total biomass of species surveyed	Biomass	B (t)	D	RP	Reduction in overall fishing effort and quotas
1/(landings/biomass)	Inverse fishing pressure	B/Y retained species	D	RP	Reduction in overall fishing effort and quotas
Mean length of fish in the community	Fish size	$\sum_i L_i/N$ (cm)	D	EF	Reduction in overall fishing effort, decreased fishing effort on large fish species
TL landings	Trophic level	$\sum_s(TL_s Y_s)/Y$	D	EF	Decreased fishing effort on predator fish species
Proportion of predatory fish	% predators	Proportion of predatory fish = biomass of predatory fish/biomass surveyed	D	CB	Decreased fishing effort on predator fish species
Mean lifespan	Lifespan	$\sum_s(\text{age}_{\max,s} B_s)/\sum_s B_s$	D	SR	Decreased fishing effort on long-lived species

L , length (cm); i , individual; s , species, N , abundance; B , biomass, Y , catch (t); D, decline over time; RP, resource potential; EF, ecosystem structure and functioning; CB, conservation of biodiversity; SR, ecosystem stability and resistance to perturbations.

Tests to detect trends

Generalized least-squares and autoregressive error analysis

Time-series of ecosystem indicators are relatively short, and frequently characterized by strong autocorrelation, imposed as a consequence of the ecosystem dynamics. A linear-trend model was fitted to each of the indicator time-series using a generalized least-squares regression framework, which models the temporal correlations in the error using a two-stage estimation procedure (Coll *et al.*, 2008). Trends were estimated for two separate periods, as stated above: 1996–2005 and 1980–2005 (or for the whole time-series if shorter). The two-stage estimation procedure was used to take account of autocorrelation in the residuals and to satisfy regression assumptions. The significance of the estimated trend (whether the predicted slope is significantly different from zero) was then assessed. This allowed for valid inference to assess the significance of the trend.

The procedure was as follows:

Stage 1: an ordinary least-squares (OLS) regression model was used to fit the straight-line model $y = \beta_0 + \beta_1 x + \varepsilon$, expressed in matrix notation as $y = Xb + e$, where $e \sim N(0, \sigma^2 I)$, which assumes independent and identically distributed errors. Analysis of residuals $\hat{e} = y - \hat{y}$ was carried out to determine whether statistical assumptions were met. When autocorrelated errors were present (defined as a p -value of >0.05 in a two-sided Durbin–Watson test), we proceeded to Stage 2 below.

Stage 2: generalized least-squares regression was used to fit the straight-line model with more flexible assumptions about the error terms, i.e. $e \sim N(0, \Sigma)$. Here, Σ is a covariance matrix based on the assumption of e having a temporal-dependence structure following an autoregressive process of order 1 [AR(1)]. The significance of the trend is assessed by testing $H_0: \beta_1 = 0$ vs. $H_1: \hat{\beta}_1 \neq 0$, with the test statistic $t^* = \hat{\beta}_1 / \text{s.e.}(\hat{\beta}_1)$.

This two-stage procedure was generally sufficient for trend estimation; the time-series are relatively short and there is considerable flexibility in realizations of the autocorrelated AR(1) errors.

We did, however, identify cases where it proved not entirely adequate (because of the potential for non-constant variance, non-linearity, or leftover autocorrelation).

Intersection–union test

A second method for detecting trends from time-series was developed by Trenkel and Rochet (2009). It consists of fitting a non-linear smoother to the whole indicator series to remove random sampling noise and, if the smoother has sufficient goodness-of-fit, calculating first and second derivatives from the smoothed time-series and carrying out a series of tests formulated as an intersection–union test. A parametric bootstrap is then used for taking uncertainty in the indicator time-series into account. The non-linear smoother is fitted as a generalized additive model, using a thin-plate regression spline with automatic estimation of the degree of smoothness using generalized cross-validation (Wood, 2006). The null hypothesis in an intersection–union test is a union of type $H_0: \theta \in \bigcup_{\gamma \in \Gamma} \Theta_\gamma$, where θ is the vector of parameters of interest and Θ_γ the set of values allowed under the null hypotheses of each of the $\gamma = 1, \dots, \Gamma$ tests (Casella and Berger, 1990). The alternative hypothesis is expressed as the intersection $H_1: \theta \in \bigcap_{\gamma \in \Gamma} \Theta_\gamma^c$ with Θ_γ^c the set of values of the individual alternative hypotheses. Then, the global null hypothesis is rejected only if the null hypotheses for all Γ tests are rejected.

Given the time-scale considered here, specific null hypotheses were developed with separate tests for increasing and decreasing time-trends. These hypotheses and the resulting tests are described below. The condition for a significant decrease or no change in the smoothed indicator time-series over a given time-horizon is met, i.e. the null hypothesis of an increase is rejected if the following two conditions are met:

- C1: the maximum smoothed indicator value $\max(\hat{I}_j)$, for $j = T - m + 1, \dots, T$, is not found within the most recent m years, i.e. in years $T - 4, \dots, T$ for $m = 5$; and
- C2: $f \times n_j$ of all annual slopes ordered by increasing size are negative $\hat{I}_j \leq 0$, for $j = 1, \dots, f \times n$,

where \hat{I}_j is the smoothed indicator value for year j , T the total number of years in the time-series, f the proportion of years within the n years considered in the test, and \dot{I}_j the first derivative of the smoothed indicator time-series for year j , which will be referred to as the annual slope. Condition C1 allows the whole time-series to be incorporated into the test, even if only a shorter recent period is being considered, e.g. $n = 10$ and $T = 26$. Condition C2 states that the first $f \times n$, e.g. $0.8 \times 10 = 8$, annual slopes of the slopes arranged in increasing order are negative or zero.

The two conditions lead to the definition of null and alternative hypotheses for each subtest. For example, a decreasing time-trend over the study period is declared significant if all null hypotheses of subtests T1 and T2 corresponding to conditions C1 and C2 are rejected (intersection condition).

In a T1 test on the location of the maximum:

$$H_{01}: \hat{I}_{\max} \in \{\hat{I}_{T-m+1}, \dots, \hat{I}_T\}, \quad \text{and} \\ H_{11}: \hat{I}_{\max} \in \{\hat{I}_1, \dots, \hat{I}_{T-m}\},$$

H_{01} is rejected if the maximum value is not situated during the final m years. In a T2 test for values of the first $f \times n$ annual slopes sorted in increasing order:

$$H_{02}: \bigcup_{t=T-n+1}^T \hat{I}_t > 0, \quad \text{and} \quad H_{12}: \bigcap_{j=1}^{f \times n} \hat{I}_j \leq 0.$$

For testing an increasing time-trend, the null and alternative hypotheses are formulated in a similar manner. For a significant increase in the smoothed indicator time-series, the maximum in C1 is replaced by the minimum, and in C2 \leq by \geq . Given that the tests are carried out on smoothed (predicted) indicator values, years with missing data are not a problem. For a more exhaustive explanation of the application of intersection–union tests for detecting time-trends, see [Trenkel and Rochet \(2009\)](#).

The method was applied for detecting time-trends over two time-horizons: over the past 10 years ($n = 10$, $f = 1$) of the indicator time-series, i.e. the period 1996–2005, and for a longer period ($n = 26$) corresponding to the years 1980–2005, or the whole available time-series if shorter. Note that the same period was considered for all indicators, even if a longer series existed for a subset. In both cases, m was set to 5. For the longer period, several values of f were tested, $f = \{0.65, 0.75, 0.85\}$. Hence eight tests (four for increasing and four for decreasing time-trends) were carried out for each indicator time-series for each system. A risk level of $\alpha = 0.05$ was used for all tests. In the parametric bootstrap, given that indicator time-series had no associated measures of uncertainty, a coefficient of variation (CV) of 3% was assumed for all years and indicators.

Tests to detect redundancy between indicators

Multivariate analysis of indicator time-series

Redundancy of indicators can be assessed in a simple manner based on the pairwise correlation of indicators. In a given ecosystem, any two indicators that are strongly correlated (regardless of the direction) can be classified as redundant, and the strongly correlated indicator can safely be excluded from further consideration because it does not contain extra

information. Assessing the redundancy of multiple indicators across multiple ecosystems can be done using some multivariate techniques. To assess the redundancy of indicators, two steps were followed. The initial step involves computing pairwise correlations (Pearson's product moment correlation), taking the whole time-series of each indicator. The multivariate pairwise correlations across ecosystems were translated into inter-ecosystem resemblance matrices using Euclidean distance as a measure of resemblance. The resulting inter-ecosystem distances among the ecosystems were then summarized visually using non-metric multidimensional scaling (MDS). MDS is one of the various ordination techniques used in ecological studies. MDS attempts to map n -dimensional (n , number of variables; variables in this case are a pair of ecosystem indicators) distribution of samples (in this case ecosystems) into smaller dimensions (usually 2–3). It is an iterative process. The stress value indicates how well the n -dimensional distance between ecosystems is preserved in the two- or three-dimensional representation of the relative location of ecosystems. A higher stress value is an indication of poor representation in the lower dimension. If the stress value is >0.2 , two-dimensional representation is generally not recommended ([Clarke and Warwick, 2001](#)). The analysis was done in R and PRIMER-E statistical software ([Clarke and Gorley, 2006](#)).

Mutual-information analysis

Measuring mutual information involves comparing the rhythms of two time-series to quantify their degree of dynamic cohesion ([Cazelles, 2004](#)). High values of mutual information mean that the two time-series fluctuate at the same pace, showing either synchronized or opposing phases. For a pair of ecosystem indicators, mutual information can be interpreted as a measure of redundancy, because it represents the extent of common information the two variables carry.

Calculating mutual information is straightforward. The respective rhythm of two time-series $X(t)$ and $Y(t)$ is found by translating their fluctuations into “peak”, “trough”, “decrease”, and “increase” symbols ([Haydon et al., 2003](#)). From the corresponding symbolic series obtained, $S(t)$ and $U(t)$, mutual information is given by the equation:

$$I_{SU} = H_S + H_U - H_{SU},$$

with H_S and H_U the entropy of S and U , and H_{SU} their joint entropy. The equations for entropy and joint entropy are

$$H_S = - \sum_{i=1}^k p(S_i) \log_2[p(S_i)],$$

with k the total number of symbols and $p(S_i)$ the probability of observing the symbol i along the symbolic series S , and

$$H_{SU} = - \sum_{i=1}^k \sum_{j=1}^k p(S_i, U_j) \log_2[p(S_i, U_j)],$$

where $p(S_i, U_j)$ is the probability of observing at the same time the symbol i on the symbolic series S and j on the symbolic series U .

Statistical significance was computed by generating sets of surrogate data from the original time-series under the null hypothesis that any co-occurrence of peaks, troughs, increases, and decreases

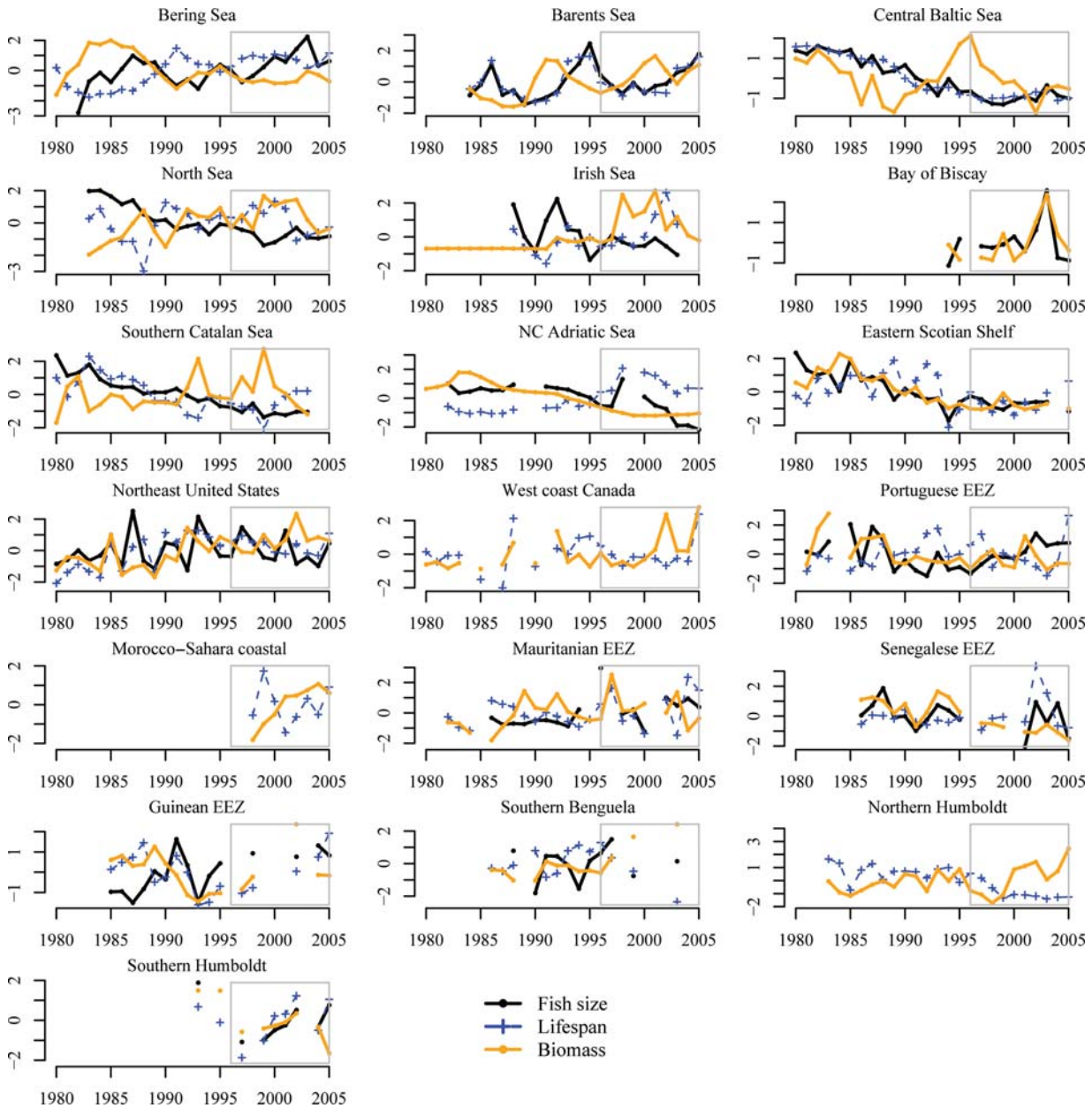


Figure 1. Normalized time-series (1980–2005) of indicators for several high-latitude, temperate, tropical, and upwelling ecosystems in the study. The box indicates the period used for short-term trend analysis. Note that short-term (1996–2005) time-series were normalized separately for analyses, but that the plots show the normalized medium-term time-series (1980–2005).

can be explained by chance only. A null distribution of mutual information is then built, from which 95% quantiles are extracted (see Cazelles, 2004, for more detail).

Results

Trends

Linear fits to time-series of ecological and exploitation indicators revealed a mixture of negative and positive trends along with the absence of temporal change, after correcting for autocorrelation where necessary (Figure 2). In 7 of the 19 ecosystems, there were significant negative trends in the indicators ($\alpha = 0.05$). Only one

of the ecosystems, the southern Benguela, experienced significant negative trends in more than one indicator over the period 1996–2005 (lifespan, proportion of predators, and trophic level of catch). However, of these indicators, only trophic level had a contiguous dataseries with >4 years. In contrast, ten of the ecosystems experienced significant positive trends in at least one indicator. Moreover, all ecosystems demonstrated a mixture of positive and negative changes in the indicators, except the west coast Canada (all positive) and the North Sea, both of which experienced reductions (although not significant at $\alpha = 0.05$) in all ecological indicators, and a significant increase in one exploitation indicator (inverse fishing pressure). The significance level

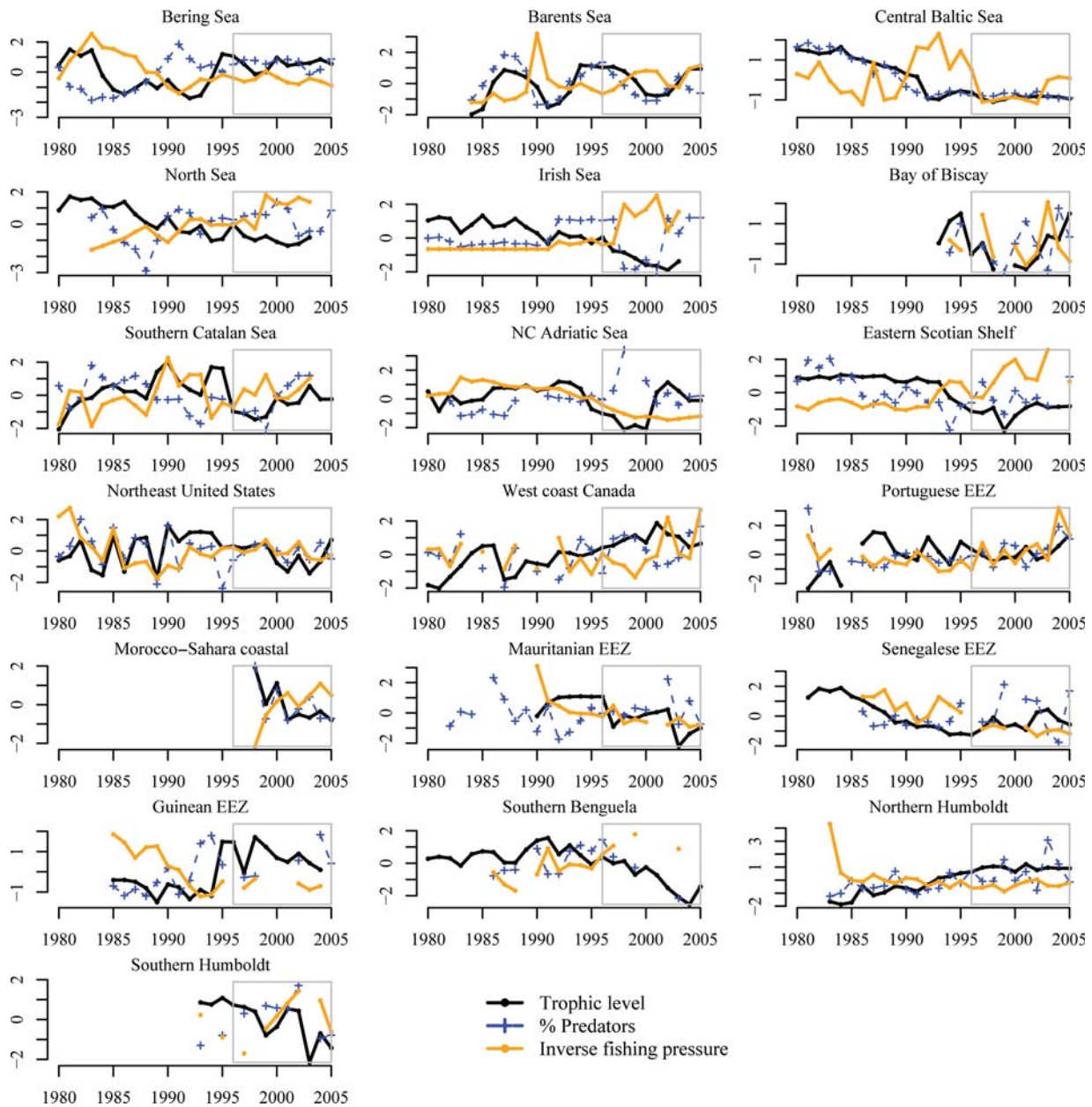


Figure 1. Continued.

affects whether or not a linear trend is detected. At a significance level of $\alpha = 0.1$, there was a higher incidence of negative (14) and positive (19) trends in total for all indicators and ecosystems (Table 3). When the medium-term period (1980–2005) was used for detecting linear trends, more trends were detected ($\alpha = 0.05$), with a much higher prevalence of declining trends (Figure 3). Short-term trends were generally steeper than medium-term trends.

Several reasons may have influenced the statistical ability to detect trends. First, the time-series were relatively short, and short-term trends are likely to capture recent variability better than the long-term gradual change. Second, 12% of the indicator time-series violated the assumption of normality required for OLS regression, and 5% did not follow the linearity assumption. In

35% of the indicators, autocorrelation needed to be taken into account (Table 3). In all, 20% of the trends were identified to be significant at $\alpha = 0.05$ (22 indicators across 19 systems, and 6 indicators each, with 4 values missing).

The intersection–union test method revealed even fewer significant changes in indicators over the 10-year period (8 years for the Morocco–Sahara coastal ecosystem; Table 4): across the 19 systems and 6 indicators, just 14 time-trends were significant, belonging to ten systems, with mainly one significantly changing indicator per system. No significant time-trend in any indicator was found for the north-central Adriatic Sea, the Baltic Sea, the Barents Sea, the southern Benguela, the Bering Sea, the southern Catalan Sea, the Mauritanian EEZ, and the Saharan coastal ecosystems. The length of the available time-series

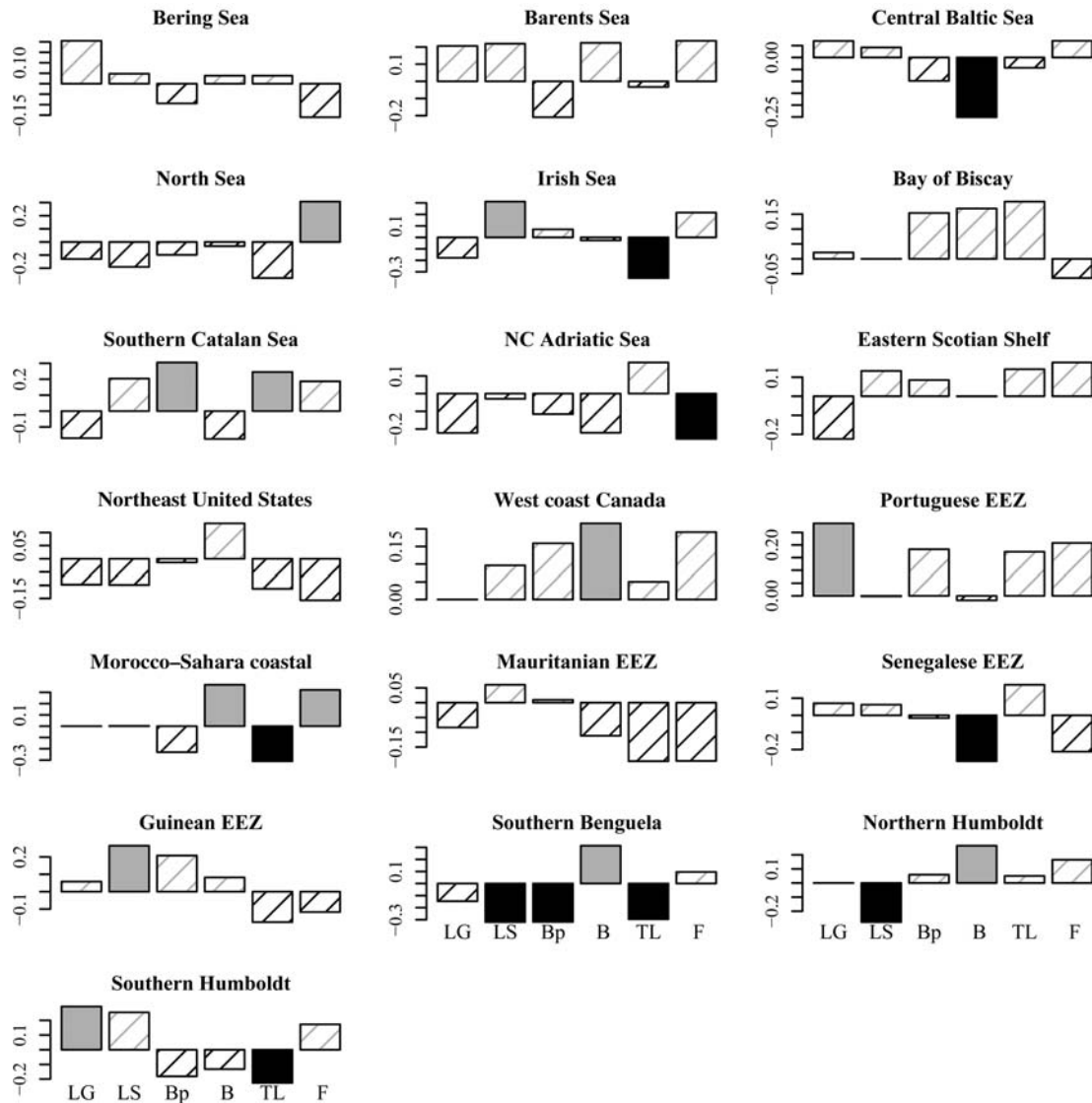


Figure 2. Linear trends of indicators over the short term (1996–2005) for each ecosystem, using generalized least-squares and autoregressive error (Table 2). Grey represents an increasing and black a decreasing trend over time. Solid boxes indicate that trends were significantly different from zero ($\alpha = 0.05$) and hatched boxes indicate otherwise. LG, mean length; LS, mean lifespan; Bp, percentage predators; B, total biomass; TL, mean trophic level of landed catch; F, inverse fishing pressure.

varied considerably between systems, only five systems spanning the longer period 1980–2005 (Table 4). Hence, when considering time-trends over longer periods, the results cover different time-spans. Taking all test results together across systems and indicators, a clear negative relationship between the number of years considered in the hypothesis test ($f \times n$ in T2) and the proportion of significant time-trends was found, indicating that the conditions used for building the null hypotheses for the intersection–union test are more suited for shorter-term trends. Therefore, this method was used for evaluating trends for the period 1996–2005 only.

Redundancy

Except the widespread correlation between biomass and the exploitation indicator (inverse fishing pressure), the pattern of redundancy between all other indicators varied among ecosystems.

Therefore, any two indicators could be redundant (strongly correlated positive or negative) in certain ecosystems, while remaining weakly correlated in others. For example, the cross-correlations between fish size, trophic level, lifespan, and % predators were strong in the Baltic Sea (see Figure 1 for a comparison of time-series). In the North Sea, Irish Sea, Baltic Sea, and eastern Scotian Shelf, correlations between fish size and trophic level were strong. Correlations between fish size and biomass were positive in the north-central Adriatic Sea, the eastern Scotian Shelf, the southern Humboldt, and the Senegalese EEZ, but were negative in the southern Catalan Sea, the North Sea, and the Irish Sea. The MDS results were fairly inconclusive in terms of representing clear-cut groupings of similarities in pairwise indicator correlations across systems in two dimensions. A relatively high stress-value (0.18) indicated that a two-dimensional representation may not be adequate. The results of principal components

Table 3. Trends (reported as slopes) in ecosystem indicators over 10 years (1996–2005) using generalized least-squares and autoregressive error.

Ecosystem	Fish size	Lifespan	% predators	Biomass	Trophic level	Inverse fishing pressure
NC Adriatic Sea	−0.22a	−0.03a	−0.12	−0.22a,n,l	0.18a	−0.26a
Central Baltic Sea	0.07	0.04	−0.10	−0.25a	−0.04a	0.07a
Barents Sea	0.21a,n	0.22a	−0.21a,n	0.22a,n	−0.03a	0.24a
Bay of Biscay	0.02	–	0.15	0.17	0.19a	−0.06
Southern Benguela	−0.15	−0.32a	−0.32	0.31a	−0.30	0.10a,l
Bering Sea	0.21	0.05a,l,n	−0.09	0.04	0.04	−0.16
West coast Canada	–	0.10a,l,n	0.16a	0.22	0.05	0.19
Southern Catalan Sea	−0.17	0.20a,n	0.31	−0.18	0.25	0.19
Southern Humboldt	0.29	0.25	−0.18	−0.13a	−0.23	0.17a,l,n
Guinean EEZ	0.06	0.27a	0.21	0.08a	−0.18	−0.12
Irish Sea	−0.18	0.31	0.07a	−0.03	−0.35a,n	0.22
Mauritanian EEZ	−0.08	0.06	0.01	−0.11	−0.20	−0.20
Morocco coastal	–	0.00	−0.23	0.37a	−0.31	0.32a,n
North Sea	−0.13a,n	−0.19	−0.10	−0.03a	−0.28a	0.31
Northern Humboldt	–	0.28a,n	0.06	0.27a,n	0.05	0.17
Portuguese EEZ	0.29	0.00a,n	0.18	−0.02	0.17a	0.21
Eastern Scotian Shelf	−0.22a	0.13	0.08	0.00	0.14	0.18
Senegalese EEZ	0.07	0.06	−0.02	−0.27	0.18	−0.21
Northeast United States	−0.10	−0.10	−0.01	0.14	−0.11	−0.16

Significance levels are shown emboldened ($\alpha = 0.1$) and underlined ($\alpha = 0.05$). a, adjusted for autocorrelation; n, normality assumptions violated; l, linearity assumptions violated.

analysis (PCA) on pairwise correlations by ecosystem type matrix were also examined and revealed a similar representation of ecosystems in two dimensions, with less than half the variability (46%) explained by the first two principal components (not shown).

Mutual information, in terms of peaks and troughs of indicators, was significant in at least one pair of indicators for all ecosystems considered. Five of the indicator pairs were significant in five or more ecosystems (Table 5). Four of the 19 ecosystems (Barents Sea, Bering Sea, southern Benguela, and southern Humboldt) had strong associations in five or more indicator pairs. The highest prevalence of mutual information was between inverse fishing pressure and biomass, largely because the latter indicator is used as part of the calculation of inverse fishing pressure. Other pairs of indicators expected to be complementary in ecological terms included % predators and lifespan. However, according to the mutual-information approach, a number of indicators that intuitively should be related (although these were correlated), such as fish size and trophic level, were non-redundant.

To evaluate whether ecosystems could be grouped based on similarity of temporal trends, results for the periods 1980–2005 and 1996–2005 for linear and 1996–2005 for non-linear trends were combined into a matrix, where significant ($\alpha = 0.05$) trends were coded as either -1 or $+1$ for each ecosystem, and non-significant trends were coded as 0 . The same approach was used to group based on both sets of redundancy results, where pairwise correlations >0.5 and significant mutual information between the two indicators were coded as 1 and 0 otherwise. A dissimilarity matrix based on Euclidean distances was then computed followed by hierarchical cluster analysis with the R packages “hclust” and “pvclust”, using the “ward” agglomeration method. Figure 4a shows that ecosystems could be grouped into three clusters, although the strength of these clusters was weak ($p < 0.2$). The first group consisted of ecosystems located in high latitude, temperate, and tropical regions. These were ecosystems that did not

experience drastic changes in the indicators during the time-windows considered. This group also contained the southern Humboldt, north-central Adriatic Sea, the eastern Scotian Shelf, the Baltic Sea, the southern Catalan Sea, and the Portuguese EEZ. All the latter ecosystems experienced changes in fish size and biomass. The second group contained the northern Humboldt, West coast Canada, and the Guinean EEZ ecosystems, which all experienced increases in the trophic level of catch. Finally, the southern Benguela and Saharan coastal ecosystems experienced declines in the trophic level of the catch. The Northeast United States, North Sea, and Irish Sea all experienced decreases in fish size accompanied by increases in biomass over time.

Figure 4b shows that two groups emerged based on both sets of redundancy analyses ($p < 0.10$). The first group tended to have greater overlap in the redundancy lifespan and % predators, and either lifespan and fish size or trophic level indicators. The second group tended to have a greater degree of redundancy between fish size and inverse fishing pressure, fish size and trophic level, and fish size and biomass. The two groups overlapped in their redundancy between inverse fishing pressure and biomass.

Discussion

All the ecosystems considered in this study were exploited long before the beginning of the time-series considered here (Bundy *et al.*, 2010). Therefore, the focus of this study was to identify whether there have been further decreases in the indicators during the most recent time-frame (1996–2005), as opposed to the general detection of impacts. Using multiple methods and a cross-ecosystem comparative approach revealed that recent trends in ecosystem indicators are not all unanimous or synchronously declining. However, significant decreases in one or more of the ecological indicators during the years 1996–2005 from either the linear or non-linear methods were detected for many of the ecosystems: the central Baltic Sea, the southern Benguela, the

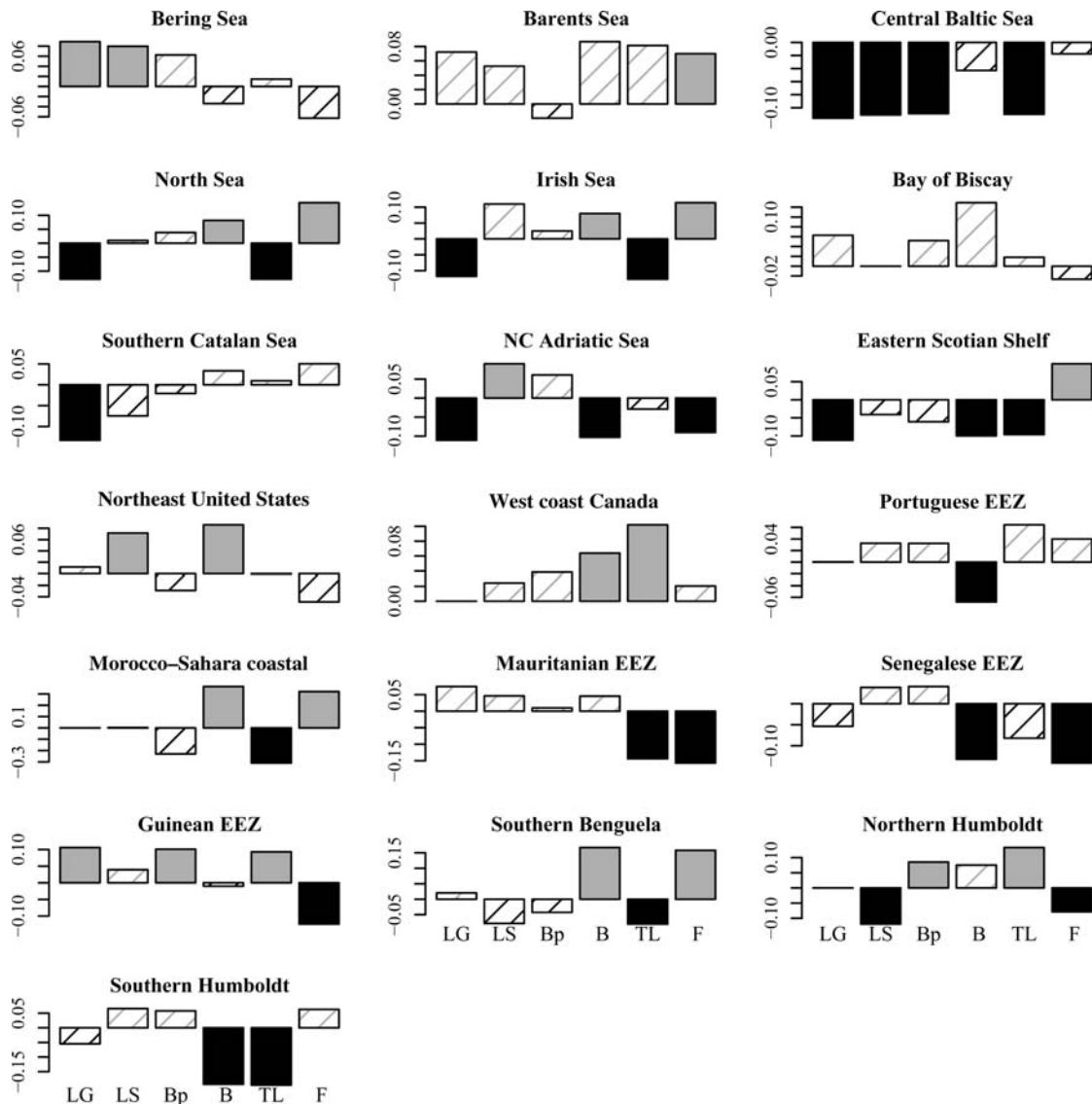


Figure 3. Linear trends of indicators over the medium term (1980–2005) for each ecosystem, using generalized least-squares and autoregressive error. Grey represents an increasing and black a decreasing trend over time. Solid boxes indicate that trends were significantly different from zero ($\alpha = 0.05$) and hatched boxes indicate otherwise. LG, mean length; LS, mean lifespan; Bp, proportion of predators; B, total biomass; TL, mean trophic level of landed catch; F, inverse fishing pressure.

southern Catalan Sea, the southern Humboldt, the Irish Sea, Saharan coastal, the northern Humboldt, the eastern Scotian Shelf, the Senegalese EEZ, and the Northeast US shelf (Table 6). This could suggest that these ecosystems are still experiencing increases in pressure and that current management plans are not stringent enough or have not been established long enough to promote recovery.

No significant recent changes were detected for the Barents Sea, the Bay of Biscay, or the Bering Sea ecosystems over the period 1996–2005, suggesting that increasing pressure has been halted but that there is no sign of recovery. It may be that a stable alternative state has been reached (Choi *et al.*, 2004), recovery is very slow, or that changes were not detected for other reasons (low statistical power, observation error, environmental forcing, data quality; Jouffre *et al.*, 2010).

Positive trends were detected either in isolation or in combination with declines in other indicators. Positive trends were

detected for West coast Canada (biomass, % predators), Guinean EEZ (lifespan, fish size), Portuguese (fish size, biomass), and the North Sea (biomass, inverse fishing pressure), and a mixture of positive and negative trends were detected for many of the ecosystems. It is important to note that this does not necessarily imply recovery, because in cases where ecosystems are mainly exploited for their small pelagic fish or invertebrates, increasing % predators, mean trophic level of the catch, mean length, and mean lifespan will result when these organisms are depleted. This appears to be the case for the southern Catalan (biomass⁻, % predators⁺, trophic level⁺), and possibly also the northern Humboldt (lifespan⁻, biomass⁺, % predators⁺) and southern Humboldt (trophic level⁻, fish size⁺) ecosystems (Arancibia and Neira, 2005), but see Coll *et al.* (2010) for further discussion. In the North Sea and Irish Sea, biomass has increased alongside a reduction in fishing pressure and a continued decline in fish size. This could be due to the indirect effects of fishing that have caused prey release

Table 4. Trends in ecosystem indicators over 10 years (1996–2005) using intersect–union tests ($\alpha = 0.05$).

Ecosystem	Fish size	Lifespan	% predators	Biomass	Trophic level	Inverse fishing pressure	N
NC Adriatic Sea							24
Baltic Sea							26
Barents Sea							22
Southern Benguela							16
Bering Sea							24
Biscay of Biscay		NA				–	12
Southern Catalan Sea							26
Guinean EEZ	+						13
Irish Sea		+					16
Mauritanian EEZ							16
Morocco coastal	NA						8
Northeast United States	–			+			26
Northern Humboldt	NA		+				23
North Sea				+			21
Portuguese EEZ						+	25
Scotian Shelf		–				+	26
Senegalese EEZ						–	20
Southern Humboldt					–		13
West coast Canada	NA		+			+	26

Blanks, non-significant changes; NA, no data available; +, significant increase; –, significant decrease; N, total length of time-series considered (including missing years).

Table 5. Number and names of ecosystems in which redundancy was significant ($\alpha = 0.05$) for each pair of indicators, based on mutual information.

Redundant indicators	Ecosystems
Lifespan vs. fish size	4 = Barents Sea, Mauritania, southern Benguela, southern Humboldt
% predators vs. fish size	3 = Senegalese EEZ, southern Benguela, southern Catalan Sea
% predators vs. lifespan	6 = Bering Sea, central Baltic Sea, Mauritania, North Sea, southern Benguela, southern Catalan Sea
Biomass vs. lifespan	5 = Bering Sea, eastern Scotian Shelf, Irish Sea, southern Benguela, southern Humboldt
Biomass vs. % predators	4 = Bering Sea, southern Benguela, southern Catalan Sea, Barents Sea
Trophic level vs. fish size	1 = Bay of Biscay
Trophic level vs. lifespan	1 = Northeast United States
Trophic level vs. % predators	1 = Central Baltic Sea
Inverse fishing pressure vs. lifespan	5 = Bering Sea, eastern Scotian Shelf, Northeast United States, Morocco (Sahara coastal), southern Humboldt
Inverse fishing pressure vs. biomass	10 = Barents Sea, Bering Sea, Guinean EEZ, Irish Sea, north-central Adriatic Sea, Northeast United States, North Sea, southern Humboldt, northern Humboldt, West coast Canada
Biomass vs. fish size	5 = Mauritania, southern Catalan Sea, southern Humboldt, Baltic Sea, Guinean EEZ
Trophic level vs. biomass	4 = Barents Sea, Bay of Biscay, northern Humboldt, eastern Scotian Shelf
Inverse fishing pressure vs. fish size	4 = Guinean EEZ, Portuguese EEZ, Senegalese EEZ, southern Humboldt
Inverse fishing pressure vs. % predators	2 = Barents Sea, Bering Sea
Inverse fishing pressure vs. trophic level	2 = Bering Sea, southern Benguela

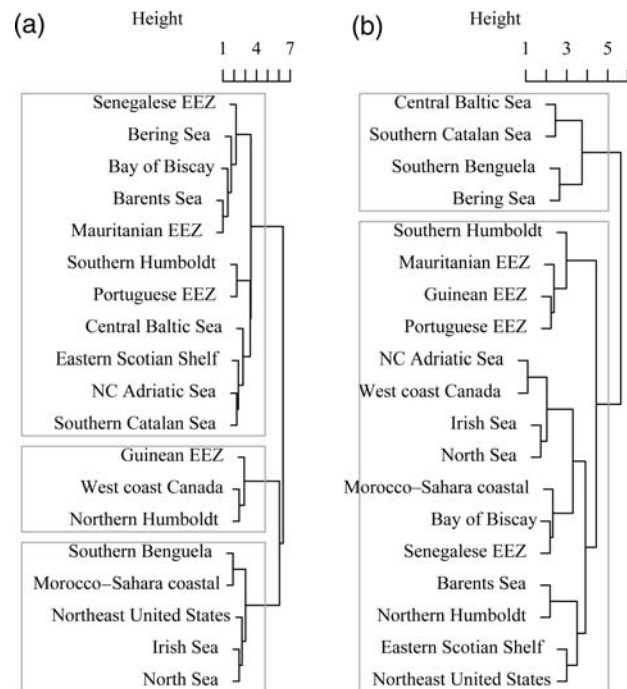


Figure 4. Cluster dendrograms of ecosystems based on (a) all indicator trend results (1980–2005 and 1996–2005 for linear, 1996–2005 for non-linear-trend analyses), and (b) both sets of redundancy results (correlation of indicators and mutual information). Trends were coded as +1, –1, or 0, and redundancy was coded as either 1 or 0. Euclidean distance and Ward agglomeration methods were used. Percentage *p*-value thresholds for the groups in (a) and (b) were weak and were 80 and 90%, respectively.

and/or enhanced survival of recruits (Blanchard *et al.*, 2005; Daan *et al.*, 2005) rather than biomass recovery.

Conclusions on whether or not the ecosystem indicators were decreasing over time rely heavily on the type and power of the

Table 6. Summary and comparison of short-term (1996–2006) trends detected (significance level, $\alpha = 0.05$) using both linear and non-linear (intersection–union) methods in the ecological indicators (excluding inverse fishing pressure) for the 19 ecosystems.

Ecosystem	Decrease		Increase		Overall direction	n
	Linear	Non-linear	Linear	Non-linear		
NC Adriatic Sea						5
Central Baltic Sea	Biomass				D	5
Barents Sea						5
Bay of Biscay						4
Southern Benguela	Lifespan % predators, trophic level		Biomass		D > I	5
Bering Sea						5
West coast Canada			Biomass	% predators	I	4
Southern Catalan Sea		Biomass	% predators, trophic level		I > D	5
Southern Humboldt	Trophic level	Trophic level	Fish size		D > I	5
Guinean EEZ			Lifespan	Fish size	I	5
Irish Sea	Trophic level		Lifespan	Lifespan	I > D	5
Mauritanian EEZ						5
Morocco SC	Trophic level		Biomass		D = I	4
North Sea				Biomass	I	5
Northern Humboldt	Lifespan		Biomass	% predators	I > D	4
Portuguese EEZ			Fish size	Biomass	I	5
Eastern Scotian Shelf		Lifespan			D	5
Senegalese EEZ	Biomass				D	5
Northeast United States		Fish size		Biomass	D = I	5

The overall direction of change was established by dominance of the number of decreasing (D) vs. increasing (I) indicators detected across all indicators and methods for each ecosystem. Blank cells indicate no significant change in direction. *n*, total number of indicators considered.

statistical test carried out. All ecosystems, except the Morocco (Sahara coastal) ecosystem ($n = 8$), had time-series at least 10 years long. Increasing the number of years included in the time-window greatly affects the ability of statistical power to detect a trend (Nicholson and Jennings, 2004). For example, in the North Sea, the central Baltic, the Irish Sea, the southern Catalan Sea, the north-central Adriatic Sea, and the eastern Scotian Shelf, there were significant declines in fish size over the past 25 years—this type of pattern is well-documented by other studies (Jennings *et al.*, 1999, 2002; Daan *et al.*, 2005). Over the short term, some of these declines were still evident from a negative slope, but they were not always significant. We cannot know until future data are collected whether this difference is attributable to a real slowing down (and eventual cessation or reversal) of the trend as the community recovers, or whether it is simply attributable to a lower statistical power.

The detection of trends in ecological and exploitation indicators is difficult for several other reasons. First, the pressure–state relationships between exploitation and ecological indicators are not necessarily linear, so reference trends can be misleading. Second, the responsiveness (time of response) of ecological indicators to fishing pressure may vary for different indicators and in some cases is difficult to determine. In addition, the responsiveness of an indicator may vary depending on which fishing effects are actually occurring during the period. When smaller sizes and lower trophic levels are targeted preferentially, an increase in the indicators rather than expected decreases will result. Also, the speed of change in average length will depend on the part of the size distribution that changes: changes in small sizes are expected to move the average faster than larger ones.

Spatial heterogeneity and shifts attributable to climate change in fish communities as well as in fishing effort can also conceal correlations, or on the contrary can bias the analysis (Blanchard *et al.*, 2005, 2008; Perry *et al.*, 2005). It is therefore important to be able to monitor indicators that match both the spatial distribution of

the resources of interest and of fishing activity ideally for sufficiently long periods of time (10+ years). Moreover, because they do not concern the same life stages and species, and because fishing patterns can change, ecological indicators calculated from survey or from catch data do not necessarily change in the same direction, nor do they have the same time and amplitude of response to a change in fishing pressure.

Indicator dataserries are also prone to differences caused by the quality of the underlying survey data, different calculation methods employed for a single indicator, or differences in the different survey gear and/or sampling seasons (Trenkel *et al.*, 2004). Even if the indicators used in this study have been chosen to be as simple as possible and are based on readily available data, in practice the quality of the data depends much on the whole data-collection process, which varies across the ecosystems. Currently, we lack specific meta-information and studies to assess the quality of the indicator estimates, e.g. to quantify the ranges of the sampling errors in each of the indicator series. We assume that the sampling uncertainties remain lower than natural (real) variations of the sampled variables. In certain cases and/or on certain indicators, this assumption may not hold. Perhaps this could explain why some expected trends are not observed, or conversely that certain unexpected trends are observed as a result of sampling artefacts (Jouffre *et al.*, 2010).

Although there was no consistent pattern in redundancy of the ecological indicators, inverse fishing pressure (the only exploitation indicator) and biomass carry mutual information in 12 of 19 ecosystems, and 13 of 19 were positively correlated with coefficients >0.5 . This is not surprising because fishing pressure was calculated by dividing total landings by biomass to standardize for different levels of productivity across the systems to facilitate cross-system comparisons (Shin *et al.*, 2010b). The reason for including inverse fishing pressure in the indicator suite was to obtain a standardized measure of exploitation pressure across ecosystems that also changed in the same direction as the other

indicators in the suite (negative), purely for ease of visual interpretation. It is important to note that as an exploitation indicator, our inverse fishing pressure indicator is not ideal because it confounds both the changes attributable to pressure and ecological status (biomass). Ideally, information on fishing effort for each ecosystem would allow for standardization of total landings time-series. Unfortunately, this information was not available for all the ecosystems analysed here.

There were no clear patterns in the redundancy of the remaining five ecological indicators, suggesting that as a suite they capture complementary information on ecosystem structure and function. The varying degree of redundancy in the indicators across ecosystems might be a reflection of different historical fishing or management patterns. For example, in ecosystems where management action has been stringent, there could be a reversal in one of indicator (positive trend), but a lag or continued decline in others. Such could be the case if a reduction in overall effort resulted in an increase in biomass but perhaps not in fish size, which could take longer to reverse especially if phenotypic and/or genetic changes were a product of size-selective fishing practices (Law, 2000). More work is needed to improve understanding on how sensitive and responsive each indicator is in its ability to detect changes in ecosystem structure and functioning as a consequence of changes in fishing pressure.

The influence of environmental variability and forcing is likely to mask the effects of fishing or cause a mixture of responses attributable to multiple causal mechanisms and stressors on ecosystems (Halpern *et al.*, 2008). This is especially the case for short time-series and for eastern ocean boundary ecosystems, where upwelling is an important process, e.g. the southern Benguela, the southern and northern Humboldt, Portugal, and West coast Canada (Shannon *et al.*, 2010). In those systems, a strong influence of environmental drivers on the suite of indicators has been identified (Link *et al.*, 2010). Other human-induced factors (pollution, climate) causing changes in nutrients and influencing the productivity of ecosystems may be acting more strongly on some of the indicators (such as biomass) than the effect of fishing alone. More research is clearly needed on the dominance of causal stressors and the cumulative impacts of multiple human activities on the dynamics of ecosystems.

Conclusions, limitations, and future work

This exploratory study is one of the first undertaken to cross-compare recent trends of ecosystem indicators worldwide. Overall, the results are not encouraging in that there were no consistent patterns across ecosystems and indicators, making it difficult to identify underlying broad-scale relationships between exploitation and ecological indicators or to generalize across systems. In some systems, there is evidence of increasing indicator trends; in others, unfortunately, declines are still prevalent. There is a clear need for management strategies to be identified that will reverse or (at worst) halt the direction of declining trends in ecological state. To do this, we need a clearer understanding of the sensitivity and responsiveness of these indicators to fishing pressure and management actions, while taking into consideration natural background variability, other potential concurrent and cumulative impacts, and uncertainty. In other words, how much does fishing need to be reduced in order for there to be a change in ecological state, and how well can each of these indicators actually represent changes in ecological state? In order for

an EAF to be successful, system- and indicator-specific baseline, target, and threshold reference points need to be developed for a change in a particular indicator to be meaningful and interpretable for management. Objectives at the EAF level need to be clarified, and appropriate types and levels of management intervention need to be defined to meet the objectives. Finally, there needs to be a reliable long-term quality-assessed monitoring procedure in place, as well as information systems that allow for both ecological and fisheries (and other impact) data to be collected and maintained at the same spatial and temporal scales. Without such information, it will not be possible to assess adequately any improvements in ecosystem status, or whether EAF management objectives are being met.

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References

- Arancibia, H., and Neira, S. 2005. Long-term changes in the mean trophic level of central Chile fishery landings. *Scientia Marina*, 69: 295–300.
- Baird, S. F. 1873. Report on the condition of the sea fisheries of the south coast of New England in 1871 and 1872. Report of the United States Fish Commission, 1. GPO, Washington, DC.
- Bianchi, G., Gislason, H., Graham, K., Hill, L., Koranteng, K., Manickchand-Heileman, S., Payá, I., *et al.* 2000. Impact of fishing on size composition and diversity of demersal fish communities. *ICES Journal of Marine Science*, 57: 558–571.
- Blanchard, J. L., Dulvy, N. K., Jennings, S., Ellis, J. R., Pinnegar, J. K., Tidd, A., and Kell, L. T. 2005. Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? *ICES Journal of Marine Science*, 62: 405–411.
- Blanchard, J. L., Maxwell, D. L., and Jennings, S. 2008. Power of monitoring surveys to detect abundance trends in depleted populations: the effects of density-dependent habitat use, patchiness, and climate change. *ICES Journal of Marine Science*, 65: 111–120.
- Bundy, A., Shannon, L. J., Rochet, M.-J., Neira, S., Shin, Y.-J., Hill, L., and Aydin, K. 2010. The good(ish), the bad and the ugly: a tripartite classification of ecosystem trends. *ICES Journal of Marine Science*, 67: 745–768.
- Casella, G., and Berger, R. L. 1990. *Statistical Inference*. Duxbury Press, Belmont, CA. 650 pp.

- Cazelles, B. 2004. Symbolic dynamics for identifying similarity between rhythms of ecological time series. *Ecology Letters*, 7: 755–763.
- Choi, J. S., Frank, K. T., Leggett, W. C., and Drinkwater, K. 2004. Transition to an alternate state in a continental shelf ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 505–510.
- Clarke, K. R., and Gorley, R. N. 2006. *PRIMER v6. User Manual/Tutorial*. PRIMER-E, Plymouth.
- Clarke, K. R., and Warwick, R. M. 2001. *Changes in Marine Communities: an Approach to Statistical Analysis and Interpretation*, 2nd edn. PRIMER-E, Plymouth.
- Coll, M., Palomera, I., Tudela, S., and Dowd, M. 2008. Food-web dynamics in the South Catalan Sea ecosystem (NW Mediterranean) for 1978–2003. *Ecological Modelling*, 217: 95–116.
- Coll, M., Shannon, L. J., Moloney, C. L., Palomera, I., and Tudela, S. 2006. Comparing trophic flows and fishing impacts of a NW Mediterranean ecosystem with coastal upwellings by means of standardized ecological models and indicators. *Ecological Modelling*, 198: 53–70.
- Coll, M., Shannon, L. J., Yemane, D., Link, J. S., Ojaveer, H., Neira, S., Jouffre, D., et al. 2010. Ranking the ecological relative status of exploited marine ecosystems. *ICES Journal of Marine Science*, 67: 769–786.
- Daan, N., Gislason, H., Pope, J. G., and Rice, J. C. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES Journal of Marine Science*, 62: 177–188.
- Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., et al. 2008. A global map of human impact on marine ecosystems. *Science*, 319: 948–952.
- Haydon, D. T., Greenwood, J. J. D., Stenseth, N. Ch., and Saitoh, T. 2003. Spatio-temporal dynamics of the grey-sided vole in Hokkaido: identifying coupling using state-based Markov-chain modelling. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 270: 435–445.
- Hunt, G. L., and Megrey, B. A. 2005. Comparison of the biophysical and trophic characteristics of the Bering and Barents Seas. *ICES Journal of Marine Science*, 62: 1245–1255.
- Jennings, S. 2005. Indicators to support an ecosystem approach to fisheries. *Fish and Fisheries*, 6: 212–232.
- Jennings, S., Greenstreet, S. P. R., Hill, L., Piet, G. J., Pinnegar, J. K., and Warr, K. J. 2002. Long-term trends in the trophic structure of the North Sea fish community: evidence from stable-isotope analysis, size-spectra and community metrics. *Marine Biology*, 141: 1085–1097.
- Jennings, S., Greenstreet, S. P. R., and Reynolds, J. D. 1999. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology*, 68: 617–627.
- Jouffre, D., Borges, M. F., Bundy, A., Coll, M., Diallo, I., Fulton, E. A., Guitton, J., et al. 2010. Estimating EAF indicators from scientific trawl surveys: theoretical and practical concerns. *ICES Journal of Marine Science*, 67: 796–806.
- Law, R. 2000. Fishing, selection and phenotypic evolution. *ICES Journal of Marine Science*, 57: 659–668.
- Link, J. S. 2005. Translation of ecosystem indicators into decision criteria. *ICES Journal of Marine Science*, 62: 569–576.
- Link, J. S., Yemane, D., Shannon, L. J., Coll, M., Shin, Y-J., Hill, L., and Borges, M. F. 2010. Relating marine ecosystem indicators to fishing and environmental drivers: an elucidation of contrasting responses. *ICES Journal of Marine Science*, 67: 787–795.
- Moloney, C. L., Jarre, A., Arancibia, H., Bozec, Y. M., Neira, S., Roux, J-P., and Shannon, L. J. 2005. Comparing the Benguela and Humboldt marine upwelling ecosystems with indicators derived from inter-calibrated models. *ICES Journal of Marine Science*, 62: 493–502.
- Nicholson, M. D., and Jennings, S. 2004. Testing candidate indicators to support ecosystem-based management: the power of monitoring surveys to detect temporal trends in fish community metrics. *ICES Journal of Marine Science*, 61: 35–42.
- Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate change and distribution shifts in marine fishes. *Science*, 308: 1912–1915.
- Shannon, L. J., Coll, M., and Neira, S. 2009. Exploring the dynamics of ecological indicators using food web models fitted to time series of abundance and catch data. *Ecological Indicators*, 9: 1078–1095.
- Shannon, L. J., Coll, M., Yemane, D., Jouffre, D., Neira, S., Bertrand, A., Diaz, E., et al. 2010. Comparing data-based indicators across upwelling and comparable systems for communicating ecosystem states and trends. *ICES Journal of Marine Science*, 67: 807–832.
- Shin, Y-J., Bundy, A., Shannon, L. J., Simier, M., Coll, M., Fulton, E. A., Link, J. S., et al. 2010a. Can simple be useful and reliable? Using ecological indicators for representing and comparing the states of marine ecosystems. *ICES Journal of Marine Science*, 67: 717–731.
- Shin, Y-J., Shannon, L. J., Bundy, A., Coll, M., Aydin, K., Bez, N., Blanchard, J. L., et al. 2010b. Using indicators for evaluating, comparing, and communicating the ecological status of exploited marine ecosystems. 2. Setting the scene. *ICES Journal of Marine Science*, 67: 692–716.
- Trenkel, V. M., Pinnegar, J. K., Rochet, M-J., and Rackham, B. D. 2004. Different surveys provide similar pictures of trends in a marine fish community but not of individual fish populations. *ICES Journal of Marine Science*, 61: 351–362.
- Trenkel, V. M., and Rochet, M-J. 2003. Performance of indicators derived from abundance estimates for detecting the impact of fishing on a community. *Canadian Journal of Fisheries and Aquatic Sciences*, 60: 67–85.
- Trenkel, V. M., and Rochet, M-J. 2009. Intersection–union tests for characterising recent changes in smoothed indicator time series. *Environmental Indicators*, 9: 732–739.
- Wood, S. N. 2006. *Generalized Additive Models: an Introduction with R*. Chapman and Hall/CRC Press, Boca Raton, FA. 391 pp.

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