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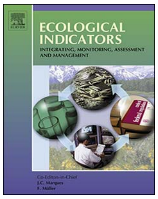

Original Articles

The specificity of marine ecological indicators to fishing in the face of environmental change: A multi-model evaluation

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ABSTRACT

Ecological indicators are widely used to characterise ecosystem health. In the marine environment, indicators have been developed to assess the ecosystem effects of fishing to support an ecosystem approach to fisheries. However, very little work on the performance and robustness of ecological indicators has been carried out. An important aspect of robustness is that indicators should respond specifically to changes in the pressures they are designed to detect (e.g. fishing) rather than changes in other drivers (e.g. environment). We adopted a multi-model approach to compare and test the specificity of commonly used ecological indicators to capture fishing effects in the presence of environmental change and under different fishing strategies. We tested specificity in the presence of two types of environmental change: "random", representing interannual climate variability and "directional", representing climate change. We used phytoplankton biomass as a proxy of the environmental conditions, as this driver was comparable across all ecosystem models, then applied a signal-to-noise ratio analysis to test the specificity of indicators with random environmental change. For directional change, we used mean gradients to apportion the quantity of change in the indicators due to fishing and the environment. We found that depending on the fishing strategy and environmental change, ecological indicators could range from high to low specificity to fishing. As expected, the specificity of indicators to fishing almost always decreased as environmental variability increased. In 55–76% of the scenarios run with directional change in phytoplankton biomass across fishing strategies and ecosystem models, indicators were significantly more responsive to changes in fishing than to changes in phytoplankton biomass. This important result makes the tested ecological indicators good candidates to support fisheries management in a changing environment. Among the indicators, the catch over biomass ratio was most often the most specific indicator to fishing, whereas mean length was most often the most sensitive to change in phytoplankton biomass. However, the responses of indicators were highly variable

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depending on the ecosystem and fishing strategy under consideration. We therefore recommend that indicators should be tested in the particular ecosystem before they are used for monitoring and management purposes.

1. Introduction

Indicators help policymakers make effective decisions by providing information about potential impacts of policy on an ecosystem. For example, ecological indicators are used to support biodiversity assessment for the UN Convention on Biological Diversity (Nicholson et al., 2012) and to characterise the health of exploited marine ecosystems in support of an ecosystem approach to fisheries (EAF; Garcia et al., 2003), as mandated by policies such as the EU Marine Strategy Framework Directive (Greenstreet et al., 2012, Probst et al., 2013, Piet and Hintzen, 2012). Given a policy or management objective, the selection of appropriate indicators is a complicated process whereby indicators must satisfy a number of criteria. These include well-accepted underlying ecological theory linking indicators to their policy objectives, their measurability, and public awareness (Rice and Rochet, 2005; Mace and Baillie, 2007; Borja and Dauer, 2008; Shin et al., 2010). Additionally, to be useful for decision-making, indicators should respond predictably with respect to a given pressure, otherwise they can be misinterpreted. In the context of EAF, it is essential for decision-makers that the response of indicators to changing fishing pressure is well characterised, because modifying fishing pressure (effort, gear type, mesh size, etc.) is one of the primary management "levers" of fisheries (Garcia et al., 2003). The performance of indicators can be quantified based on different facets, e.g. the rate and speed of response to change in fishing pressure, or the specificity of response to fishing among other drivers of change, and performance should, ideally, be tested before indicators are put into management practice in a particular ecosystem.

It is assumed that indicators in support of EAF respond to fishing in a predictable way and that they reflect the impact of fishing on ecosystem properties. As the evidence cannot be easily provided by empirical analyses, the few studies that quantified the response and performance of indicators to fishing have almost exclusively been based on a model-based simulations framework (Fulton et al., 2005; Travers et al., 2006; Houle et al., 2012; Fay et al., 2013; Lehuta et al., 2013). In addition, the performance of indicators has only been addressed in a purely fisheries context, while ignoring the environment at large. But as shown empirically, ecological indicators that were selected for reflecting ecosystem changes due to fishing also respond to other stressors such as environmental change (Blanchard et al., 2005; Link et al., 2010; Large et al., 2013; Fu et al., 2015). Therefore, it is important to fill the gap and test how specific the response of indicators is with regard to fishing in the face of environmental variability and change.

Indicators of ecosystem health status are generally assumed to have a negative response to fishing (Shin et al., 2010), but fishing history and the pattern of fishing affect indicator response and its robustness (Branch et al., 2010; Shannon et al., 2014; Coll et al., 2016). An indicator may have been developed to capture a specific fishing phenomenon which can be observed under certain conditions (e.g. to what extent decreasing trophic level of the catch reflects the "fishing down marine foodwebs" phenomenon; Pauly et al., 1998), but it may respond differently in other contexts, or under specific fishing strategies, such as a balanced fishing across trophic levels (Garcia et al., 2012). In addition, ecosystem features such as depth and latitude also influence indicator behaviour (Heymans et al., 2014). The response of indicators should therefore be tested and characterized under different fishing strategies in a variety of ecosystems, which feature different dominant processes and structures.

We tested the specificity of a set of indicators, i.e. the degree to which indicators respond to changes in fishing pressure compared to changes in primary production, chosen as one of the other key drivers that could impact fish dynamics. We adopted a comparative multi-modelling approach to explore the differential response of indicators to fishing, based on differences of fishing strategy and ecosystem features. Many uncertainties exist due to differences in ecosystems, but also due to the assumptions and structure of ecosystem models. We address this by covering a wide range of ecosystems and by using four different types of ecosystem models (Ecopath with Ecosim, Atlantis, Osmose, multi-species size-spectrum) with different underlying conceptual and structural premises (see supplementary material of Tittensor et al. (2017) and Reed et al. (2017) for a comparison of the models).

2. Materials and methods

2.1. Ecological indicators

We computed a suite of ecological indicators – a subset of the IndiSeas indicators (Shin et al., 2010; Coll et al., 2016) – that could be calculated from the output of the ecosystem models used in this study. All indicators were conceptually defined so that they are expected to decline with increasing fishing pressure. The following indicators were

Table 1

Summary of indicators calculated from model results.

Indicator	Definition[*]	Species included[†]	References
Mean length[‡]	$\frac{\sum_i L_i}{N}$ (cm)	All pelagic and demersal surveyed species	Shin et al. (2005)
Mean trophic level[¶] (community)	$\frac{\sum_s TL_s B_s}{\sum_s B_s}$	All pelagic and demersal surveyed species	Cury et al. (2005), Pauly et al. (1998)
Proportion of predatory fish	B (predatory fish)/B (surveyed)	All pelagic and demersal surveyed species	Shin et al. (2010)
Mean lifespan	$\frac{\sum_s \mathrm{age}_{\max,s} B_s}{\sum_s B_s}$ (years)	All pelagic and demersal surveyed species	Shin et al. (2010)
Biomass/landings	B/Y	All retained species	Shin et al. (2010)
Mean intrinsic vulnerability[§]	$\frac{\sum_s IVI_s Y_s}{\sum_s Y_s}$	All retained species	Cheung et al. (2007); Coll et al. (2016)
Marine trophic index[¶]	$\frac{\sum_s TL_s Y_s}{\sum_s Y_s}$, including only species with TL > 3.25	All retained species	Pauly and Watson (2005)

[*] L, length (cm); i, individual; s, species; N, abundance; B, biomass (tons); Y, catch (tons); TL, trophic level; $\mathrm{age}_{\max}$, maximum age (years); IVI, intrinsic vulnerability index.

[†] Definitions of pelagic, demersal, surveyed, and retained species are adopted from Shin et al. (2010); see summary in Appendix A in Supporting Information.

[‡] Mean length indicator may be calculated from all models except EwE.

[¶] A variable trophic level may be calculated by models, but here, to match empirical data, we use a fixed trophic level TL_s for each modelled species s.

[§] Intrinsic vulnerability scores only available for fish, not invertebrates, so only fish are included in this indicator.

considered (Table 1): mean length, mean trophic level (TL) of the community, proportion of predatory fish, mean lifespan, biomass/landings ratio, mean intrinsic vulnerability, and marine trophic index. In order to place our simulation experiments and subsequent analyses in the same conditions as the *in situ* collection of empirical data, only those species in the model that are actually surveyed in each ecosystem were used to calculate the community-based indicators (mean length, mean TL of the community, proportion of predatory fish, mean lifespan). Only those species in the model that are retained by fishing vessels were used to calculate the exploitation-based indicators (mean intrinsic vulnerability, marine trophic index). Both survey- and catch-based output were used to calculate the biomass/landings ratio. We acknowledge that restricting the indicators to a subset of species underutilises the potential of the models as data generators, but it is reflective of the kinds of empirical information immediately available in the different systems and thereby informative to local regulatory agencies. In future analyses, there remains the opportunity to test the entire set of models' output to devise the minimum data/indicator requirements across systems for universal observing programs and the like to fully capture the ecosystem effects of fishing.

2.2. *Ecosystem models*

To capture the wide range of uncertainties across ecosystems and different model structures, we used a multi-model ensemble that consisted of four different ecosystem models applied to seven marine ecosystems. Ecopath with Ecosim models (EwE; Christensen and Walters, 2004, Christensen et al., 2008) were used for the Black Sea (Akoglu, 2013), Southern Benguela (Shannon et al., 2004; Shannon et al., 2008; Smith et al., 2011), Southern Catalan Sea (Coll et al., 2008; Coll et al., 2013), and the Western Scotian Shelf/Bay of Fundy (Araujo and Bundy, 2011, Araújo and Bundy, 2012). Each of these models was previously fitted to time series of abundance and catch data, with the exception of the Southern Catalan Sea model, which was fitted to survey data only due to the poor quality of catch data in the Mediterranean Sea. We used the OSMOSE (Shin and Cury, 2001, 2004) model for the West Coast Canada ecosystem, calibrated to time-averaged biomass data (Fu et al., 2013). A size spectrum model, previously calibrated to time-averaged landings and spawning stock biomass data, was used for the North Sea (Blanchard et al., 2014). The Atlantis model was used to represent the Southeastern Australia ecosystem, which had been previously calibrated against historical survey and landing time series data (Fulton et al., 2005; Fulton et al., 2014).

2.3. *Representation of fishing pressure*

Within each ecosystem, we tested three different fishing strategies: a "low trophic level" (LTL) strategy, a "high trophic level" (HTL) strategy, and an "all species" (ALL) strategy. In a given fishing strategy, we distinguished two categories of retained species, i.e. the focus and the non-focus species. The focus species have their fishing mortality gradually increased, whereas the non-focus species undergo a constant fishing mortality which corresponds to the current fishing situation. The LTL strategy had a focus on LTL species: we made fishing mortality vary for forage species only, while holding present-day fishing levels for all other species that were retained in commercial or subsistence fisheries. Forage species were defined as pelagic species that feed mainly on plankton (phyto-, zoo-, or ichthyoplankton) as adults. The HTL strategy focused on predatory species that included large demersal and large pelagic species (including the largest predatory fish, chondrichthyans and large predatory invertebrates such as the giant squid) mainly feeding on fish and macroinvertebrate species and that were retained in commercial or subsistence fisheries. The ALL strategy represented broad-scale exploitation, where fishing mortality varied for all species that were retained in commercial or subsistence fisheries. Any pre-recruit stages that were represented in some of the models were excluded from the fishing scenarios, as well as any small invertebrates and (at the other extreme) air-breathing animals (i.e. marine mammals, marine turtles, and seabirds).

To make fishing strategies comparable across model systems, we implemented them with a multiplier of the fishing mortality corresponding to the maximum sustainable yield (F_{MSY}) of the focus species. This is to allow the evaluation of indicators across ecosystems, accounting for fishing impacts on intrinsic biological properties and dynamics of the species, but avoiding indicators' responses which would be too dependent on the fishing history in the different ecosystems. We prioritized the comparability of fishing pressure across ecosystems, rather than contrasting more detailed ecosystem-specific fishing strategies and intensities. MSY is a reference level which is generic across species and ecosystems, therefore implementing the fishing strategies HTL/LTL/ALL in different ecosystems relative to this reference level allows the evaluation of the specificity of indicators in a standardized way. Thus, before running the fishing strategies, the single species F_{MSY} was estimated in each ecosystem, by reconstructing the yield to fishing mortality curve for each species (catch as a function of fishing mortality rate), while holding the model fishing mortality of all other retained species constant at their respective current fishing mortality rates (F_{curr}). Then, the three fishing strategies (LTL, HTL, ALL) could be run, with a focus species i being fished at $F_i = \lambda\, F_{MSY,i}$ (year^{-1}) and a non-focus species j being fished at its respective current fishing rate $F_{curr,\,j}$. For each fishing strategy, we tested the range of F_{MSY} multipliers $\lambda = \{0.25, 0.5, 0.75, 1, 1.25, 1.5\}$, which covered a representative range of the yield-fishing mortality curve. The focus species in the same strategy were fished at the same proportion of their respective F_{MSY}. This multiplier approach allowed comparability across models and ecosystems when plotting indicators' responses, using the multiplier λ as the common x-axis.

2.4. *Representation of environmental change*

Modelled phytoplankton biomass, which was comparable across models and ecosystems, was used as a proxy for environmental change since explicit physical drivers were not available for all ecosystem models. In EwE and OSMOSE, we changed the input phytoplankton biomass directly. For the size spectrum model, we changed the plankton carrying capacity parameter because plankton biomass emerges from the model and is not set directly. Explicit nutrient cycling in Atlantis meant that direct forcing of phytoplankton was inappropriate. Therefore, nutrient inputs from point sources and upwelling were forced instead so that the resulting change in phytoplankton matched the magnitude of change represented in the phytoplankton biomass forcing used for the other model types.

To represent the effect of random environmental change on each model ecosystem, we forced modelled phytoplankton biomass by a random multiplier drawn from a lognormal distribution with a mean μ of 1 and a range of standard deviations σ. We ran a set of 30 random multipliers for each σ to adequately sample the random distribution. A lognormal distribution was chosen because in marine ecosystems, the distribution of biomass, including that of phytoplankton, across body size is thought to be even on a logarithmic scale (Sheldon et al., 1972). The standard deviations tested were consistent with observed variation in the IndiSeas environmental dataset (www.indiseas.org). For each ecosystem, we calculated the mean and standard deviation of the annual satellite-derived Chlorophyll *a* from the MODIS Aqua spectral data (Appendix B). In the data from 2003 to 2011, σ ranged from 0.01 to 0.69, with a mean of 0.21, so we took $\sigma = \{0.1, 0.2, 0.3\}$ as the values tested. For Atlantis, nutrient forcing values were generated to approximate the widths of a lognormal distribution in the resulting phytoplankton biomass.

We represented directional climate change in a simple and comparable way across all models, by applying a multiplier $\gamma \in \{0.85, 0.9, 0.95, 1, 1.05, 1.1\}$ directly to modelled phytoplankton biomass, without randomness. This range of variability encompassed the range of changes observed in the last decade in the ecosystems studied here (Boyce et al., 2014).

2.5. Scenario testing

We tested a set of scenarios in each modelled ecosystem following a multi-factorial simulation design: one simulation was run for each unique combination of fishing strategy (HTL, LTL, ALL), fishing mortality (varied using the F_{MSY} multiplier), type of phytoplankton biomass variation (random, directional) (Table 2). For random environmental change, we ran 30 random simulations for each combination of standard deviation σ, fishing strategy and F_{MSY} multiplier λ. For directional environmental change, we completed one simulation for each combination of phytoplankton multiplier γ, fishing strategy, and λ. For each simulation, we took the average of the outputs over the last ten years. In all cases this final decade of the simulation did not overlap with the (model specific) spin-up time required to reach a new equilibrium state after the application of the factors λ, γ, and σ. For OSMOSE, which is a stochastic model, 20 replicates were run for each simulation specified above. Outputs averaged over the 20 replicates were used as the simulation results for the purposes of the rest of the analyses.

2.6. Analysis methods

The specificity of indicators in the presence of random variation was analysed using the signal-to-noise ratio (Houle et al., 2012). In the simulation framework described above, a change of fishing mortality provides the input signal and the random variation of the phytoplankton biomass provides the noise. The signal-to-noise ratio for each F_{MSY} multiplier λ was calculated by taking the mean of the indicator at fishing multiplier $\lambda = 1$ (across the 30 simulations with random phytoplankton biomass) and subtracting the mean of the indicator at each λ and dividing the result by the standard deviation at each λ (Fig. 1). This was repeated for each ecosystem model, fishing strategy (HTL, LTL or ALL), indicator, and standard deviation σ of the phytoplankton biomass ($\sigma = 0.1$, 0.2 or 0.3). The signal-to-noise ratio is a standardised measure that can be directly compared across indicators and models. To undertake comparisons of the specificity of indicators to fishing, we took the absolute value of the slope of the best-fit regression line through the signal-to-noise ratio over the range of λ, since this represented the rate of change due to fishing and not due to the variability of phytoplankton biomass. We chose to use regression as it was a simple method with meaningful parameters (e.g. slope) that was easily comparable across ecosystems. The greater the absolute value of the slope, the more specific the indicator to fishing (Houle et al., 2012). However, there is no threshold applied to determine that one indicator is more specific to the signal (fishing) than to the noise (phytoplankton biomass). Rather, the slope of the SNR only serves to compare the specificity of an indicator to fishing relatively to another indicator in this model simulation framework.

For directional environmental change, we examined the specificity of indicators to fishing by comparing gradients of change of indicators in the fishing and the phytoplankton biomass directions. First, to make cross-comparisons possible, we standardised the indicators to the reference value of the indicator when the F_{MSY} multiplier $\lambda = 1$ and the phytoplankton multiplier $\gamma = 1$. To do this, we subtracted the reference value from the indicator and divided the result by the standard deviation of the indicator across λ and γ. We created a two-dimensional matrix (for fishing multiplier and phytoplankton multiplier) for each indicator, each ecosystem model and fishing strategy. Each element in the matrix was the value of the standardised indicator at each unique combination of λ and γ. We took the mean component of the gradient in each direction of this matrix to apportion, on average, how much variation in the indicator was due to changes in fishing and how much was due to changes in phytoplankton. The gradient in the λ direction is the approximate local first derivative (slope) of the fishing component, and similarly the gradient in the γ direction approximates the local first derivative of the phytoplankton component. Compared to a multivariate linear regression analysis, the advantage of the gradient method is that it assumes linearity only locally, and compared to a nonlinear regression analysis, it may be applied to a smaller dataset (here $n = 6$). The gradients in each direction were calculated by taking the backwards difference between each point for that direction (example provided in Appendix C). To determine specificity from this, we took the ratio of the |mean fishing component of the gradient| to the |mean primary production component of the gradient|. The greater the ratio is, the more specific the indicator to fishing. When the ratio is > 1 then fishing has a greater effect on the indicator response than changes in phytoplankton biomass.

3. Results

The results of testing specificity with random environmental change are summarised with the slopes of the regressions of the signal-to-noise ratio series (Fig. 2). Specificity of indicators was generally greater at lower standard deviation σ of phytoplankton: 88% of the indicators across all ecosystem models and fishing strategies were most sensitive to fishing (the slope of the signal-to-noise ratio series was highest) at the lowest σ (0.1). Indicators across ecosystem models and fishing strategies showed variation in specificity; many had large confidence intervals as fishing and phytoplankton biomass changed or had low specificity (slope of the signal-to-noise ratio series close to zero; Fig. 2), implying that indicators were sensitive to changes in both primary production as well as fishing.

Results of specificity with directional environmental change are summarised with the ratio of the |mean fishing component of the gradient| to the |mean phytoplankton component of the gradient| (Fig. 3). Similar to specificity with random environmental change, indicators showed differential specificity to directional change in the environment, across ecosystem models and fishing strategies. Overall, 75% of indicators across all ecosystem models and fishing strategies had absolute values of the ratio > 1, implying that most indicators in contrasted situations were more responsive to changes in fishing than to changes in primary production. However, the confidence intervals around the mean gradient were often large.

No general differences between size-structured ecosystem models (North Sea size spectrum, West Coast Canada OSMOSE and to a less extent Southeastern Australia Atlantis) and those with no size structure (Black Sea, Southern Benguela, Southern Catalan Sea, and Western Scotian Shelf EwE models) were apparent in specificity results with either random or directional environmental change. However, the response of indicators to fishing and environment was particular to each modelled ecosystem.

Many of the indicators calculated from the Southeastern Australia

Table 2

Crossed factorial simulation design conducted with each ecosystem model to test indicators' specificity to fishing. F_{MSY}: Annual fishing mortality rate at Maximum Sustainable Yield; σ: standard deviation of the lognormal distribution of phytoplankton biomass; γ: multiplier of phytoplankton biomass.

Factors			
Fishing strategy	F_{MSY} multiplier	Phytoplankton biomass variation	
		Random	Directional
Low trophic level	0.25	$\sigma = 0.1$ (30 runs)	$\gamma = 0.85$
High trophic level	0.5	$\sigma = 0.2$ (30 runs)	$\gamma = 0.9$
All trophic level	0.75	$\sigma = 0.3$ (30 runs)	$\gamma = 0.95$
	1		$\gamma = 1$
	1.25		$\gamma = 1.05$
	1.5		$\gamma = 1.1$

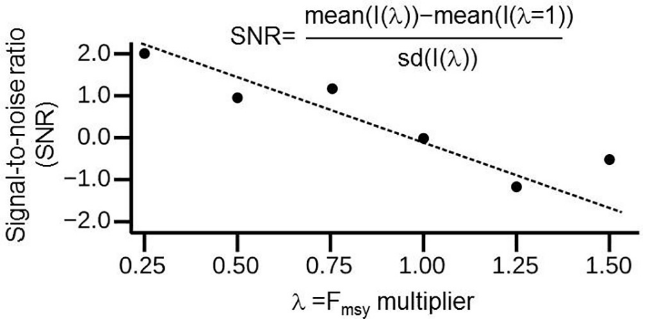

Fig. 1. Conceptual plot illustrating the calculation of the signal-to-noise ratio (SNR) for each indicator I as a function of λ the multiplier of fishing mortality (the signal). Such a SNR plot corresponds to one single indicator and one single scenario (e.g., fishing strategy HTL and 30 random phytoplankton biomass with sd = 0.1). The dashed line corresponds to a linear regression of the SNR as a function of λ.

Atlantis model showed moderate to high specificity (Figs. 2 and 3). The lowest specificity with both types of environmental change tended to be under the LTL strategy. The trophic-based indicators (TL of the community and the marine trophic index) showed some of the strongest responses across both types of specificity; however, their variability was still quite high so their reliability should be treated with caution. Similarly, the specificity of indicators was moderate to high in the Southern Benguela model (in general the ratio of the gradients > 1) especially in the HTL fishing scenario, and with lower variability in response than in the SE Australia model (Fig. 3).

Specificity of indicators to fishing from the Black Sea model was generally low for both types of environmental change (Figs. 2 and 3), in particular for the LTL strategy. In the LTL strategy, most Black Sea indicators did not follow the general trend of highest specificity at low standard deviation σ, particularly TL of the community and proportion of predatory fish (Fig. 2). For these indicators, the signal-to-noise ratio was positive and increased as fishing increased. Specificity with directional phytoplankton change was low (ratio of the gradients < 1) for most indicators in both the HTL and LTL strategies, but was high in the ALL fishing strategy (Fig. 3).

In the North Sea size spectrum model, most indicators (except biomass/landings and TL of the community) were very sensitive to changes in phytoplankton biomass (Figs. 2 and 3), and therefore were not as specific to fishing.

In the Southern Catalan Sea model, many indicators, such as mean TL of the community, proportion of predatory fish, and biomass/landings, had lower specificity to fishing compared to other ecosystems (Figs. 2 and 3). With directional environmental change, 56% of indicators had an absolute value of the ratio of the mean gradients < 1 (Fig. 3).

Indicators in the presence of both types of environmental change in the West Coast Canada OSMOSE model had varying degrees of specificity. For community-based indicators, the slope of signal-to-noise ratio tended to be the highest at $\sigma = 0.1$ and under LTL and ALL strategies (Fig. 2). Mean intrinsic vulnerability and marine trophic index could not be calculated in the LTL strategy because herring was the only exploited species in the LTL strategy and it has a TL < 3.25. Indicators with directional environmental change were generally specific to fishing (all ratios > 1), but in the LTL and ALL fishing scenarios, the degree of specificity was very different between indicators.

In the Western Scotian Shelf EwE model, there was considerable variation in specificity (Figs. 2 and 3) but generally, indicators displayed high specificity to fishing. With the exception of proportion of predatory fish under the LTL strategy, all other indicators showed greater specificity to fishing pressure than to directional change in phytoplankton biomass.

Given the variability of indicators' specificity across fishing strategies and ecosystems, we combined all simulation results and specifically compared the percentage of times when an indicator had either the highest or the lowest specificity to fishing in each scenario. Overall, it is interesting to note that two indicators exhibited consistent behaviour across all ecosystems and fishing strategies. Mean length of fish in the community had the lowest specificity to fishing in 67% and 56% of the scenarios where phytoplankton biomass was varied randomly or directionally, respectively (Fig. 4). Note that mean length could only be calculated for three ecosystem models (the non EwE models), therefore the set of scenarios in which the indicator could be compared to others was reduced to 9 (3 ecosystems and 3 fishing strategies) for random as well as for directional change in phytoplankton biomass. By contrast, the biomass over catch ratio had the highest specificity to fishing in 43% of all scenarios run (Fig. 4).

4. Discussion

Using a multi-model, multi-scenario approach for a range of exploited marine ecosystems, our results demonstrated that many of the indicators that we tested responded more to changes in fishing than to changes in phytoplankton biomass. In particular, the biomass over catch ratio indicator was the most specific to fishing. This result was robust to the fact that the specificity of indicators with random environmental change almost always decreased as variability increased. In a majority of the scenarios of combined directional changes in fishing and phytoplankton biomass, the tested indicators were able to detect the ecosystem effects of fishing more strongly than the change in phytoplankton biomass: the specificity of the indicators to fishing was more robust for biomass over catch ratio, mean life span, TL of the community and Marine Trophic Index (specific to fishing in 75–76% of the scenarios), and less robust for intrinsic vulnerability and proportion of predatory fish (specific to fishing in 55–56% of all scenarios) (Fig. 3). Likewise, a few empirical studies have shown that these ecological indicators and similar ones were sensitive to changes in the environment, but that fishing generally had a stronger effect, though this varies among ecosystems (Blanchard et al., 2005; Link et al., 2010). Supporting empirical evidence that indicator behaviours depend on ecosystem traits (Heymans et al., 2014), fishing history and the pattern of fishing (Shannon et al., 2014), our simulations showed that indicators were differentially specific to fishing across ecosystems and fishing strategies. Several lessons and/or limitations became apparent in the course of our comparative work.

4.1. Ecosystem traits influence indicator responses

There was no universal response of indicators to fishing in the presence of environmental change. Therefore the ability of indicators to monitor ecosystem effects of fishing must be anchored to a given ecosystem and fishing context, e.g. if the current level of fishing was very high, as in the Southern Catalan Sea, or if one particular fish species was especially sensitive to primary production, as in the North Sea. This makes expert interpretation of the results especially important, and this is a key part of the IndiSeas approach where local experts are involved in the interpretation of results in the context of the ecosystem (Shin and Shannon, 2010; Bundy et al., 2012; Shin et al., 2012; Coll et al., 2016). In the southeastern Australia ecosystem for example, the fact that the specificity of the indicators was highest under the HTL strategy could be due to the fact that it is mostly HTL species that are currently surveyed. Therefore, in this ecosystem, the community-based indicators responded more directly to fishing pressure with little dilution by planktivorous fish signals. Moreover, the dominant role of mesopelagic fish in the system (and their potential to dominate ecosystem outcomes in response to both phytoplankton and system productivity even with alternative levels of fishing) was not realistically reflected in the calculated indicators as mesopelagics are not surveyed in southeastern Australia.

In the Black Sea, the relatively low specificity of indicators can be

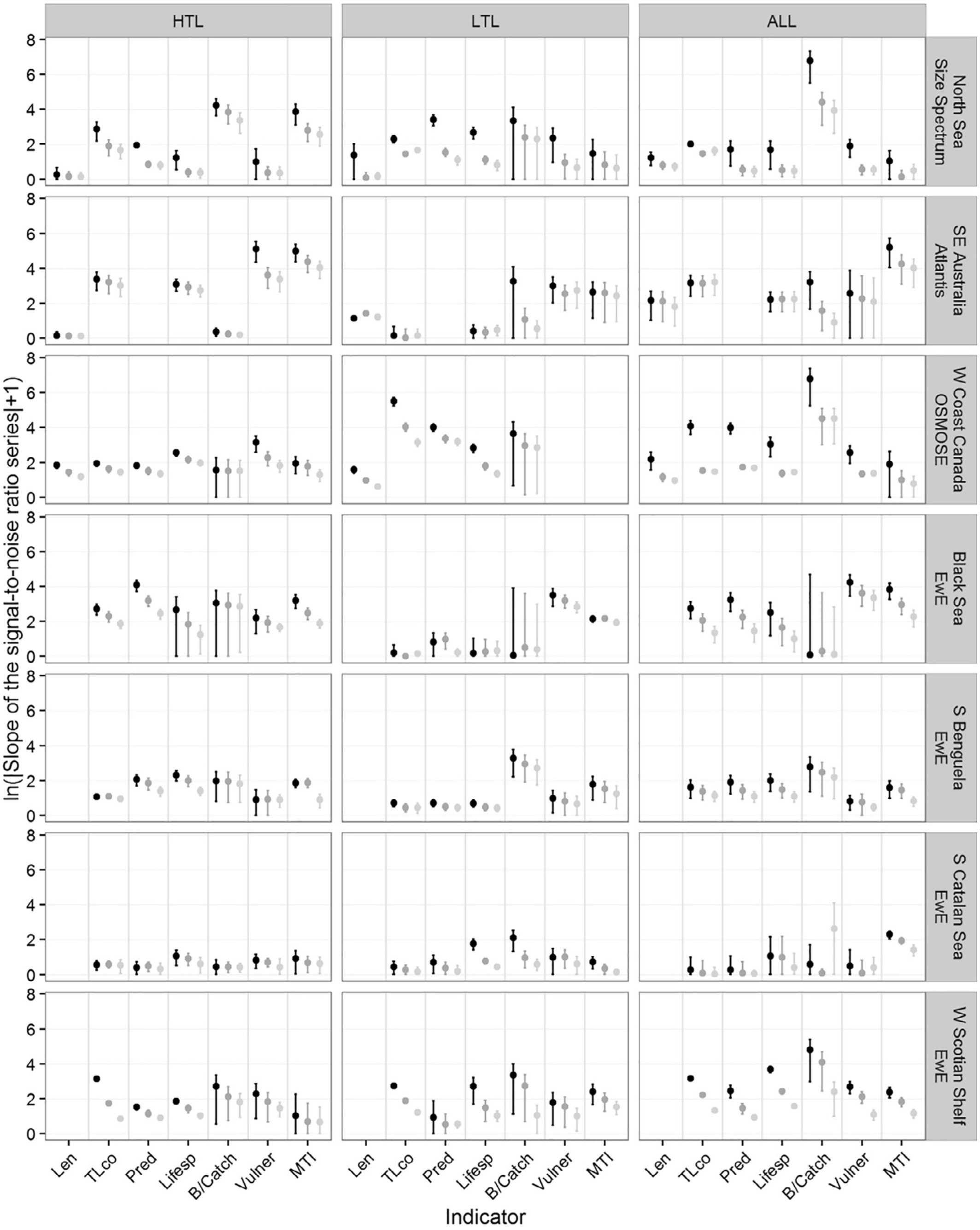

Fig. 2. Specificity of indicators to fishing with random variability in the phytoplankton biomass. The "random" specificity is measured as the absolute value of the slope of the linear regression of the signal-to-noise ratio—fishing mortality F_{MSY} multiplier series, for each standard deviation σ of the phytoplankton biomass ($\sigma = 0.1$, dark gray data points; $\sigma = 0.2$, black data points; $\sigma = 0.3$, light gray data points). Indicators are on x-axis (Len: Mean length of the community, TLco: Trophic level of the community, Pred: Proportion of predators, Lifesp: mean lifespan of the community, B/Catch: total biomass to landings ratio, Vulner: mean intrinsic vulnerability of the catch, MTI: Marine Trophic Index), ecosystem models are in rows, and fishing strategies in columns (HTL: High Trophic Level strategy, LTL: Low Trophic Level strategy, ALL: All trophic levels strategy). The greater the absolute value of the slope of the regression, the more specific the indicator is to fishing. Error bars are 95% confidence intervals of the slope estimate. Wide error bars reflect higher uncertainty in indicators' specificity and departure from the linearity assumption for the SNR curves. Mean length is not calculated by EwE models.

related to the model's sensitivity to changes in phytoplankton biomass. The nonlinear dynamics of the ecosystem are indeed driven by complex competition between the middle-TL groups for zooplankton, which is tightly coupled to primary production. By contrast, in the West Coast of Canada model, the high variability of indicators' specificity (Fig. 3) could be explained by the variation in response of LTL herring (*Clupea pallasii*), which is the most abundant species (almost 10 times more than some HTL species). When the phytoplankton multiplier was $\gamma = 1.05$ or 1.1, herring increased dramatically in response to the increase in phytoplankton and euphausiids, which resulted in a drastic increase of seal biomass and reduction of other species. Then when λ increased to 1.5, fishing played a dominant role and thus the advantage of having more phytoplankton to herring diminished and all fish behaved similarly.

In the North Sea, the low specificity of most indicators is to be interpreted in the light of the species composition. It is likely that changes in plaice abundance was dominating specificity of indicators, since plaice have a high growth rate and feed on macroinvertebrate and zooplankton which respond strongly to changes in primary production. In the Catalan Sea, the low specificity of indicators to fishing could be explained by bottom-up control of the foodweb combined with the high

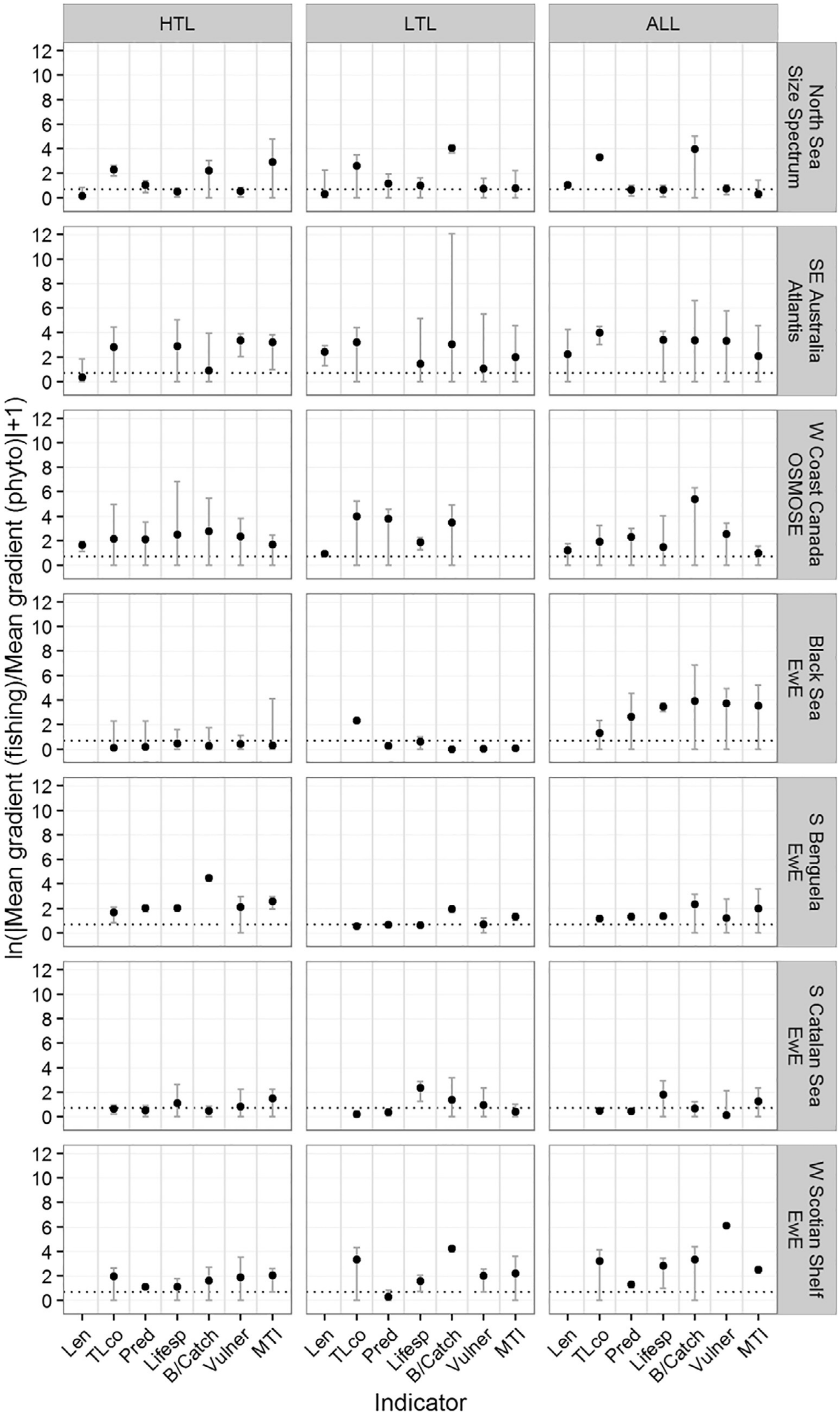

Fig. 3. Specificity of indicators to fishing, with directional change in phytoplankton biomass. The "directional" specificity is measured as the absolute value of the ratio of the mean fishing component of the gradient to the mean phytoplankton component of the gradient, for the standardized indicator response to changing fishing F_{MSY} multiplier λ and phytoplankton multiplier γ, for each ecosystem model (rows) and fishing strategy (columns; HTL: High Trophic Level strategy, LTL: Low Trophic Level strategy, ALL: All trophic levels strategy). The more specific an indicator is, the greater the absolute value of the ratio. The horizontal dotted line corresponds to a ratio of gradients equal to 1 (i.e. equal to log(2) with the log transformation used). Error bars are 95% confidence intervals of the ratio (n = 5 gradients ratios). Len: Mean length of the community, TLco: Trophic level of the community, Pred: Proportion of predators, Lifesp: mean lifespan of the community, B/Catch: total biomass to landings ratio, Vulner: mean intrinsic vulnerability of the catch, MTI: Marine Trophic Index.

current fishing mortality rate F_{curr} used in the model or due to a long history of fishing exploitation (Shannon et al., 2014; Coll et al., 2016), or to both. The current over-exploitation of the system, which has been documented to occur for a long period of time (Coll et al., 2008), could mean that the model system is stressed even when the fishing multiplier λ is low.

The strength of our simulation framework is that it allowed for specificity tests of a range of indicators across a variety of ecosystem

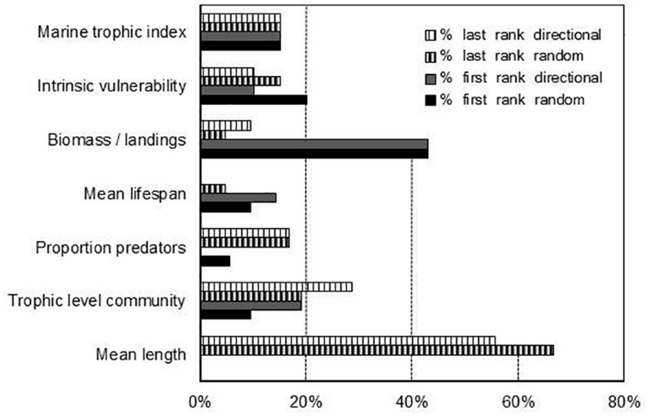

Fig. 4. Rank of indicators specificity, expressed as the % of times an indicator has the highest specificity to fishing in the random (absolute value of the slope of SNR; black bars) and directional variation (absolute value of the ratio of the gradients; dark grey) of phytoplankton biomass; or the lowest specificity (dark stripes for random, light stripes for directional change in phytoplankton biomass), across all scenarios and ecosystems.

and fishing contexts using standardized scenarios and specificity metrics. This comparative approach increased the robustness of the predictions of indicator responses by capturing a wide range of uncertainty associated with ecosystem and model uncertainties. However, a potential drawback is that the scenarios were not always realistic enough when focusing on the local ecosystem and fishing contexts. Even though most simulated fishing mortality values encompassed current estimated fishing mortality values (Appendix D), future ecosystem-specific work could test indicators' specificity with simulations based on the current fishing pressures, rather than using the idealised F_{msy} reference point which served to standardize scenarios across ecosystems. Also, non-independent fishing mortality values for different species could be potentially simulated in the case of mixed fisheries. Concerning the environmental variability and directional change, our phytoplankton biomass scenarios were overly simplified in the way of representing the broad-scale impacts of the environment on indicators' response to fishing. Again, this was constrained by the comparative approach, where we had to rely on a driver common to all the various ecosystem models used in our study. We recommend that further development of indicators' testing for a specific ecosystem should be underpinned by a set of relevant environmental drivers (e.g., sea temperature, primary production, salinity, oxygen concentration, mixed layer depth) that would be reflective of the local ecosystem dynamics and functioning.

4.2. Ecosystem models influence indicator responses

The multi-model, multi-ecosystem approach was useful for cross-comparison of indicator specificity across a range of ecosystem and model attributes. We used standardized changes in fishing mortality and phytoplankton biomass, so as to make indicators results comparable across ecosystems and models. However, differences exist in the way fishing and phytoplankton force the models, and impact the different species or functional groups. We selected model applications that were published and peer-reviewed, and fit to time series (EwE and Atlantis models) or time-averaged (size spectrum and OSMOSE models) biomass and landings data to ensure model credibility. However, it was not the purpose of this study to evaluate the degree of realism and confidence of each model used. We note that the variety of the models could make it difficult to discriminate between differences in indicator behaviour due to model or ecosystem properties. For example, the models represent life history differently with different mixes of species; many EwE models include both vertebrate and invertebrate species but are unstructured or only partially size-structured, whereas the size spectrum model includes only fish species but is fully size-structured. Although these differences in model structure can influence simulation outcomes (Heath et al., 2013), there were no clear differences in indicator specificity between size-structured and unstructured or partially size-structured models in our results. In future work, this should be addressed by using several models for a particular ecosystem (over a similar time series) to determine which behaviours were due to model attributes and which were due to system attributes. In particular, one limitation of our work was that only a few ecosystem models were able to produce size-based indicators, so the evaluation of the specificity of size-based indicators was limited to a few case studies. Finally, the set of models used are all dynamic so future work should go beyond our present comparative study based on equilibrium analyses. Indicators are used to monitor changes in the system attributes and are thus expected to be responsive in a relatively short time scale to changes in fishing pressure. The time of response, or responsiveness, of indicators is a property that clearly needs to be quantified so management decisions can be evaluated within an appropriate time frame. This is all the more critical for determining the duration of experimental measures, particularly when it comes to implementing marine protected areas.

4.3. The analysis of indicators of fishing effects must integrate the influence of a changing environment

Although a majority of the scenarios with directional change in phytoplankton biomass showed that indicators were more specific to fishing than to phytoplankton biomass, the responses were heterogeneous and were dependent on the ecosystem. The environmental influence on indicator specificity should therefore be accounted for when using indicators for management purposes. For example, differences in growth rate and productivity have been shown to influence ecosystem impacts of fishing (e.g. Bianchi et al., 2000). It is not safe to assume that reducing fishing pressure will improve an indicator value (and therefore the ecosystem status) if the primary production changes at the same time. Rather, this change in primary production should be accounted for. In addition, our results suggest that if primary production variability increases, which is likely to occur as a result of global change (Winder and Cloern, 2010), indicators may become less specific to fishing. This might be expected in the southern Benguela, for example, where variability in upwelling indices increased in the 1990s and 2000s (Blamey et al., 2012), whereas in the northern Benguela ecosystem, the reduction in fishing pressure in the 1990s was not followed by an increase in ecosystem health due to reduced primary production (Heymans and Tomczak, 2016). Our simulations unveiled the sensitivity of mean length of fish to variability and change in the phytoplankton biomass, highlighting that caution should be used in interpreting this indicator in the context of fisheries management. Fish mean length integrates major processes occurring in a global change context making it significant to monitor the health status of marine ecosystems. However, without a suite of complementary indicators informing on population and community changes (e.g., fish recruitment, length at age, mean maximum length), it is challenging to interpret its variations, and to disentangle whether the decrease in mean length is due to fishing (Shin et al., 2005) or to climate change (Cheung et al., 2013, Lefort et al., 2015), or on the contrary whether an increase is due to favourable environmental conditions (leading to recruitment success for example, or increased growth rate) or due to release of fishing pressure (Bundy et al., 2010).

For indicators to be useful in decision-making, there are other performance features apart from specificity, which need to be tested in a similar systematic way. Future work should provide more evidence for indicators' sensitivity (shape of response curves, range of sensitivity) and responsiveness (time of response) for quantifying overall indicators' performance and robustness in a variety of conditions. For general ecosystem-based management, system status and trends should be characterised and underlying causes identified so that appropriate management responses can be invoked accordingly. Changing attributes of fishing pressure (e.g. gear type, gear selectivity, effort, etc.) is the main management “lever” (Garcia et al., 2003), thus indicators that are sufficiently specific to fishing are required for management-relevant performance to be assessed (Rice and Rochet, 2005).

Our results have shown that the behaviour of ecological indicators needs to be interpreted in the context of the local ecosystem, such as accounting for exploitation history and physical and biological ecosystem characteristics. We did not find any indicator that was systematically more specific to fishing than to phytoplankton biomass across all scenarios in the ecosystem models we tested, confirming the need to examine a suite of indicators (e.g. Fulton et al., 2005; Link et al., 2010). The pattern across a suite of indicators can help to attribute changes in indicators to different drivers, where a single indicator cannot. However, our study has shown that some indicators, such as the biomass over catch ratio, seem to capture fishing effects more specifically even in the presence of environmental variability and change. In contrast, mean length of fish needs to be interpreted with much more caution, given its sensitivity to environmental perturbations. This study can be considered as one of the first milestones for testing the performance of indicators in order to build decision-making tools or management strategy evaluation based on ecosystem indicators for an EAF.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2018.01.010.

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