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Ecosystem indicators-accounting for variability in species' trophic levels

Reed Jodie [1, 2, 3, 4], Shannon Lynne [1], Velez Laure [3, 4], Akoglu Ekin [5], Bundy Alida [6], Coll Marta [1, 2, 3, 7], Fu Caihong [8], Fulton Elizabeth A. [9], Gruss Arnaud [10, 11], Halouani Ghassen [12, 13], Heymans Johanna J. [14], Houle Jennifer E. [15], John Emma [16], Le Loc'h Francois [13], Salihoglu Baris [5], Verley Philippe [3], Shin Yunne-Jai [1, 2, 3, 4, *]

[1] Univ Cape Town, Marine Res Inst, Private Bag X3, ZA-7701 Rondebosch, South Africa.
[2] Univ Cape Town, Dept Biol Sci, Private Bag X3, ZA-7701 Rondebosch, South Africa.
[3] Inst Rech Dev, Res Unit, MARBEC, UMR 248, Ave Jean Monnet,CS 30171, F-34203 Sete, France.
[4] Univ Montpellier, Pl Eugene Bataillon,Batiment 24,CC,093, F-34095 Montpellier 05, France.
[5] Middle East Tech Univ, Inst Marine Sci, POB 28, TR-33731 Erdemli, Mersin, Turkey.
[6] Fisheries & Oceans Canada, Bedford Inst Oceanog, 1 Challenger Dr, Dartmouth, NS B2Y 4A2, Canada.
[7] CSIC, Inst Marine Sci ICM, Passeig Maritim Barceloneta,37-49, Barcelona 08003, Spain.
[8] Fisheries & Oceans Canada, Pacific Biol Stn, Nanaimo, BC V9T 6N7, Canada.
[9] CSIRO Oceans & Atmosphere, GPO Box 1538, Hobart, Tas 7001, Australia.
[10] Univ Miami, Rosenstiel Sch Marine & Atmospher Sci, Cooperat Inst Marine & Atmospher Studies, 4600 Rickenbacker Causeway, Miami, FL 33149 USA.
[11] Southeast Fisheries Sci Ctr, Sustainable Fisheries Div, 75 Virginia Beach Dr, Miami, FL 33149 USA.
[12] Inst Natl Agron Tunisie, UR Ecosyst & Ressources Aquat 03AGRO1, 43 Ave Charles Nicolle, Tunis 1082, Tunisia.
[13] UBO, IRD, Ifremer, CNRS,UMR 6539,Lab Sci Environm Marin,Inst Univ Eu, Technopole Brest Iroise,Rue Dumont Urville, F-29280 Plouzane, France.
[14] Scottish Marine Inst, SAMS, Oban PA37 1QA, Argyll, Scotland.
[15] Queens Univ Belfast, Sch Biol Sci, 97 Lisburn Rd, Belfast BT9 7BL, Antrim, North Ireland.
[16] Univ Sheffield, Dept Anim & Plant Sci, Sheffield S10 2TN, S Yorkshire, England.

* Corresponding author : Yunne-Jai Shin, email address : yunne-jai.shin@ird.fr

Abstract :

Trophic level (TL)-based indicators are commonly used to track the ecosystem effects of fishing as the selective removal of organisms from the food web may result in changes to the trophic structure of marine ecosystems. The use of a fixed TL per species in the calculation of TL-based indicators has been questioned, given that species' TLs vary with ontogeny, as well as over time and space. We conducted a model-based assessment of the performance of fixed TL-based indicators vs. variable TL-based indicators for tracking the effects of fishing pressure. This assessment considered three TL-based indicators (the trophic level of the landed catch (TLc), the marine trophic index (MTI) and the trophic level of the surveyed community (TLsc)), three fishing scenarios that targeted specific model groups (the low TL scenario (LTL), the high TL scenario (HTL) and a scenario encompassing broad-scale exploitation

(ALL)) and ten contrasting marine ecosystems with four types of ecosystem modelling approaches that differ in their structure and assumptions. Results showed that, overall, variable TL-based indicators have a greater capacity for detecting the effects of fishing pressure than fixed TL-based indicators. Across TL-based indicators, TLsc displayed the most consistent response to fishing whether fixed or variable species' TLs were used, as well as the highest capacity for detecting fishing effects. This result supports previous studies that promote the use of survey-based indicators over catch-based indicators to explore the impacts of fishing on the structure of marine ecosystems. Across fishing scenarios, the low trophic level fishing scenario (LTL) resulted in the lowest consistency between fixed and variable TL-based indicator responses and the lowest capacity of TL-based indicators for detecting fishing effects. Overall, our results speak to the need for caution when interpreting TL-based indicator trends, and knowledge of the broader context, such as fishing strategies and exploitation history.

Keywords : ecosystem indicators ecosystem models, fishing effects, fishing scenarios, trophic level-based indicators

Introduction

Ecosystem indicators are quantitative measurements of select characteristics that are used to gauge the status of marine ecosystems, and to track (i.e. detect, monitor and measure) the effects of anthropogenic and environmental stressors on these ecosystems (Cury and Christensen, 2005; Jennings, 2005; Shin and Shannon, 2010; Shin *et al.*, 2010; Heymans *et al.*, 2014). Multiple indicators are needed to synthesize ecosystem characteristics and include environmental, species-based, size-based and trophic-based indicators (Cury and Christensen, 2005; Fulton *et al.*, 2005; Shin *et al.*, 2005).

Ecosystem indicators are invaluable tools in an Ecosystem Approach to Fisheries (EAF) to guide management decisions, as well as for monitoring the efficacy of management measures (Jennings, 2005). To progress towards an EAF, emphasis has been placed on the development of indicators, and, to this end, the IndiSeas Program was initially established in 2005 under the auspices of the European Network of Excellence EurOceans (Shin and Shannon, 2010; Shin *et al.*, 2012; http://www.indiseas.org/). The aim of IndiSeas is to perform comparative analyses of ecosystem indicators to improve our understanding of fishing and environmental impacts on the structure and functioning of exploited marine ecosystems (Shin and Shannon, 2010; Shin *et al.*, 2010, 2012; Bundy *et al.*, 2012). The ecosystem indicators considered within the IndiSeas Program are formulated so that high fishing pressure should, theoretically, cause a decline in indicator values. However, ecosystem indicators often respond to more than one pressure, have variable behaviour under different ecological conditions and exploitation strategies and therefore require contextualisation (Travers *et al.*, 2006; Branch *et al.*, 2010; Heymans *et al.*, 2014; Shannon *et al.*, 2014; Coll *et al.*, 2016).

By selectively removing organisms from the food web, fishing modifies the trophic structure and the function of aquatic ecosystems (Pauly *et al.*, 1998). TL-based indicators are commonly used to track such changes in the food web (Pauly *et al.*, 1998; Branch *et al.*, 2010; Shannon *et al.*, 2014). The trophic level (TL) of an organism is defined by its position in the food web, first described by Lindeman (1942), and later adapted by Odum and Heald (1975) to account for omnivory. By convention, primary producers and detrital material are assigned to the first TL and consumers are assigned to TLs equal to one plus the mean TL of their prey, weighted by the proportion of prey biomass in the consumer's diet (Pauly *et al.*, 2000a). At the level of the community, TL-based indicators reflect the species composition of the community and are conventionally calculated using a single fixed TL per species. The species' TLs can be obtained from a variety of sources ranging from empirical sources such as stomach content analyses (Hyslop, 1980) and stable isotope analyses (Vinagre *et al.*, 2012), modelled using trophic models such as Ecopath with Ecosim (Christensen and Pauly, 1992), and most often extracted from global information systems such as FishBase (Froese and Pauly, 2015) and SeaLifeBase (Palomares and Pauly, 2015).

Global decreasing trends in the mean trophic level of commercial landings were defined by Pauly *et al.* (1998) as 'fishing down' the food web, whereby the abundance of high TL, piscivorous fish decreases over time, such that fishing increasingly targets lower TLs. Alternate hypotheses have also been proposed to describe these patterns. The 'fishing through' the food web hypothesis suggests that the decline in the mean TL of landings may, in some cases, be due to the addition of lower TL species to the landings (Essington *et al.*, 2006). 'Fisheries expansion' is another concept, whereby the expansion of fisheries offshore and/or into deeper waters leads to the addition of high TL species to the landings, thereby stabilising or increasing the mean TL of landings (Morato *et al.*, 2006).

The hypothesis of 'fishing down' the food web received much critique, most notably by Caddy *et al.* (1998), who suggested that 'bottom-up' effects (i.e. the changes in the structure of ecosystems derived from increased primary productivity) can result in large fluctuations in the biomass of small pelagic planktivores and should be taken into account in studies evaluating the mean TL of landings. These controversies led to the development of a variant of the mean TL of landings, namely the marine trophic index (MTI), which is simply the mean TL of landings excluding low-TL species, conventionally those species with TLs lower than 3.25 (Pauly and Palomares, 2005; Pauly and Watson, 2005).

Further, the use of landings data to calculate TL-based indicators has raised concern, since landings are influenced by shifts in global fishing strategies and markets (Caddy *et al.*, 1998; Munyandorero and Guenther, 2010). Changes in the mean TL over time (trends) computed from landed commercial catch data have been shown to diverge from those calculated from survey data, and may not adequately reflect ecosystem changes because they do not factor in marine organisms that are not landed by fisheries (Branch *et al.*, 2010). However, based on the assessment of a variety of TL-based indicators using model-, survey- and landings-based data, Shannon *et al.* (2014) found that these three data sources are complementary in detecting ecosystem changes due to fishing.

Finally, caution has been suggested in the use of a fixed, average TL per species to calculate TL-based community indicators, as this is thought to introduce bias, given that the TL of a marine organism can vary significantly from one individual to another (Caddy *et al.*, 1998). Variability in species' TLs is a consequence of body size (ontogenetic or intra-specific TL variability), but also of changes in the marine environment over time and space (Jennings *et al.*, 2002; Chassot *et al.*, 2008; Vinagre *et al.*, 2012), such as changes in community composition and prey availability. Pauly and Watson (2005) suggested that intraspecific TL variability has a minor effect on the trends exhibited by TL-based indicators compared with the changes in community composition that TL-based indicators are intended to track. However, the effect of species' TL variability has never been quantified.

Therefore, the central question examined in this paper is whether adopting a fixed TL per species in the calculation of TL-based indicators is meaningful for tracking the effects of fishing pressure on the structure of marine ecosystems. The aim of this study is to compare the ability of fixed TL-based indicators vs. variable TL-based indicators to track the effects of fishing on ecosystems, using a model-based simulation approach. The advantage of using this approach is that it allows species' TLs to vary in response to varying modelled controlled conditions (Shannon *et al.*, 2014).

Methods

The performance of three TL-based indicators (the trophic level of the landed catch (TL_c), the marine trophic index (MTI) and the trophic level of the surveyed community (TL_{sc})) was explored using four different ecosystem models, representing 10 contrasting marine ecosystems. Model simulations were conducted for each ecosystem under three contrasting fishing scenarios that targeted specific model groups (the low TL scenario (LTL), the high TL scenario (HTL) and a scenario encompassing broad-scale exploitation (ALL)) and a wide range of fishing mortalities.

Models and ecosystems

Four ecosystem modelling approaches were used to run simulations for the present study: Ecopath with Ecosim (EwE) (Pauly *et al.*, 2000b; Christensen and Walters, 2004), OSMOSE (Shin and Cury, 2001, 2004; Travers *et al.*, 2009), Atlantis (Fulton *et al.*, 2004, 2007, 2011) and a multispecies size-spectrum (SS) model (Andersen and Pedersen, 2010; Hartvig *et al.*, 2011). The four models differ in their structure and assumptions, which are fully documented in the supplementary material (Table S1). Ten ecosystems, with different environmental conditions, fishing history and community composition, were modelled using one of these four models. The ecosystems modelled were the following: the Black Sea (EwE) (Akoglu *et al.*, 2014), the Gulf of Gabes (OSMOSE) (Halouani *et al.*, 2016), the North Sea (SS) (Blanchard *et al.*, 2014), the South Catalan Sea (EwE) (Coll *et al.*, 2008, 2013), South-east Australia (Atlantis) (Fulton *et al.*, 2007), the Southern Benguela (EwE) (Shannon *et al.*, 2004, 2008; Smith *et al.*, 2011), the West coast of Canada (OSMOSE) (Fu *et al.*, 2012), the West coast of Scotland (EwE) (Alexander *et al.*, 2015), the West Florida Shelf (OSMOSE) (Grüss *et al.*, 2016) and the Western Scotian Shelf (EwE) (Araújo and Bundy, 2012) (Figure 1). Applying the same set of simulation experiments in various case studies with different modelling approaches is intended to generalize the indicator results with a broader perspective, and to account for uncertainties due to model and ecosystem structures.

Fishing Scenarios

Three contrasting fishing strategies were considered in this study, each of which targeted specific model groups. The low TL fishing scenario (LTL) targeted low TL forage species retained in commercial or subsistence fisheries, and excluded pre-recruit stages, where possible (model dependent). The high TL fishing scenario (HTL) targeted high TL predatory species, including large demersal and large pelagic species retained in commercial or subsistence fisheries, which mainly feed on fish species. The final fishing scenario encompassed broad-scale exploitation and targeted all species (ALL) retained in commercial or subsistence fisheries. Note that marine mammals, marine turtles and seabirds were not targeted under the HTL and ALL fishing scenarios. The species/groups considered in each modelled ecosystem and the fishing scenario targeting each are documented in the supplementary material (Table S2).

Simulations

For each exploited species, F_{MSY} (Fishing mortality rate at maximum sustainable yield) was estimated within each model while keeping the fishing mortality of all other species constant at their respective current fishing mortality rates. For each of the fishing scenarios (i.e. LTL, HTL and ALL), the species targeted by the fishing scenario were fished at a fishing rate equal to a given multiplier times their F_{MSY}, while the species not targeted by the fishing scenario were fished at their current fishing mortality rates. Twenty different multipliers of F_{MSY} were applied to the species targeted by the fishing scenario, ranging from 0 to 5.

Each of the three fishing scenarios was run under each of the 20 F_{MSY} multipliers for an explicit simulation time, which was specific to each model and case study. This time dimension was not identical in all models due to the internal model dynamics as some models require a burn-in period (to remove undue influence of initial conditions). Furthermore, some models quickly approach an equilibrium state (e.g. EwE) whereas other models take time to reach a ‘steady state’ even under constant forcing (e.g. Atlantis, which never completely converges to a single value per species under constant forcing but bounces around with a relatively stable band of biomass values). Consequently, the simulation time had to allow for a burn-in period and then span several decades during which a constant F_{MSY} multiplier was applied; this treatment period also had to run long enough to ensure the model had reached an equilibrium (or “steady”) state. The simulated TL values considered during the analysis (and reported in the results section) were averaged over the last 10 years of the simulations in all cases. There is no time dimension in the results reported.

Species’ TLs

In all the models, the TL of each species was calculated as:

$$TL_s = 1 + \sum_i (TL_i\, DC_{si})$$

with TL_i being the fractional TL of prey *i*, and DC_{si} the proportion of prey *i* in the diet of species *s*. These TLs are generated by the ecosystem models for each species for each year of a simulation and change with the species' biomasses (as the proportions of the prey species in the predators' diets change and thus so too do the TLs). The reported TLs were generated from the ecosystem models' output by averaging the TL of each species over the last ten years of simulation.

Two forms of the TLs were considered in this assessment: (1) a "fixed" reference TL per species, where the TL of the species from the ALL fishing scenario with F_{MSY} multiplier equal to 1 was taken as the definitive TL for that species and used to calculate the “fixed case” version of the various indicators; and (2) "variable" TLs of each species that were calculated using the dynamic TLs for each species, scenario and F_{MSY} combination.

Indicators

Three different TL-based indicators were calculated from model outputs under each of the three fishing scenarios (LTL, HTL and ALL) and across the range of F_{MSY} multipliers: (1) the TL of the (simulated) landed catch (TL_c); (2) the marine trophic index computed for (simulated) landed species with a TL greater than 3.25 (MTI); and (3) the TL of the (simulated) surveyed community (TL_{sc}). TL-based indicators are calculated as the mean trophic position of all species, weighted by the relative biomass of each species in the landings or in the surveyed community. Thus TL_c is given by:

$$TL_c = \frac{\sum_s Y_s \,.\, TL_s}{\sum_s Y_s}$$

where Y_s is the landings of species *s*, and TL_s is the trophic level of species *s*; MTI is given by:

$$MTI = \frac{\sum_{s(TL>3.25)} Y_s \,.\, TL_s}{\sum_{s(TL>3.25)} Y_s}$$

where Y_s is the landings of species with a TL greater than 3.25, and TL_s is the trophic level of species with a TL greater than 3.25; and TL_{sc} is estimated as:

$$TL_{sc} = \frac{\sum_s B_s \,.\, TL_s}{\sum_s B_s}$$

where B_s is the biomass of species *s*, and TL_s is the trophic level of species *s*. The species considered in the calculation of TL_{sc} were those which are sampled during routine surveys (as opposed to species sampled in catches by commercial fishing vessels), and included demersal and pelagic fish species (bony and cartilaginous, small and large), as well as commercially important invertebrates (squids, crabs, shrimps, etc.). Intertidal and subtidal crustaceans and molluscs such as abalones and mussels, mammalian and avian top predators, and turtles were not considered for the calculation of TL-based indicators in this study (Shin *et al.*, 2010) .

Analyses across modelled ecosystems

For the 10 ecosystems, the agreement between the fixed TL and each of the variable TLs of modelled species was assessed by plotting the standardized difference between the measurements (variable TL-fixed TL) against the fixed TL value. This allowed for a comparable assessment of the variability of TLs at a species level across modelled ecosystems.

The agreement between each fixed TL-based indicator and corresponding variable TL-based indicator was assessed by producing Bland-Altman plots, i.e. by plotting the difference between the two measurements against the mean of the two measurements (Bland and Altman, 1986). This allowed for comparable assessment of the level of agreement and for investigation of any relationships between the difference between the two measurements and the mean of the measurements. In a modelled ecosystem exhibiting strong agreement between fixed TL-based indicators and variable TL-based indicators, the mean difference between the two measurements would be low, indicating low bias. Each of the three indicators was plotted separately to allow for comparison.

The proportion of negative significant correlations with fishing pressure can be used as a gauge of the ability of a TL-based indicator to detect the effects of fishing on the structure of marine ecosystems, as TL-based indicators are, theoretically, expected to decrease with fishing pressure (Pauly *et al.*, 1998). Across all modelled ecosystems, we examined the degree of correlation between TL-based indicators (MTI, TL_c, TL_{sc}) and fishing pressure (F_{MSY} multiplier) to establish whether there was consistency in the responses of indicators to fishing, as well as any differences in the capacity of indicators to demonstrate negative correlations with fishing pressure. All correlations were evaluated using Spearman's rank order correlation coefficient, a non-parametric measure of statistical dependence between two independent variables (Spearman, 1904).

We also studied the consistency of response of each TL-based indicator to fishing whether fixed or variable species' TLs are used by considering pairs of variable-TL and fixed-TL indicators in each fishing scenario and each modelled ecosystem. Within each pair of indicators, we evaluated whether the correlations to fishing had the same significance (both significant or both non-significant), and whether the significant correlations with fishing had the same sign (both positive, or both negative).

Results

The averages and dispersion of differences between the fixed and variable TLs of species varied across modelled ecosystems (Figure 2). In four ecosystems (Black Sea, North Sea, South Catalan Sea and Southern Benguela), the average differences between fixed and variable simulated TLs and the dispersion of these differences were both high. In three ecosystems (West coast of Canada, West coast of Scotland and Western Scotian Shelf), the average differences between fixed and variable simulated TLs were low, while the dispersion of these differences was generally low, with a few species displaying higher dispersions of TL differences. In the Gulf of Gabes and the West Florida Shelf, the average differences between the fixed and variable simulated TLs of species and the dispersion of these differences were very low. In the Western Scotian Shelf, the dispersion of differences between fixed and variable simulated TLs increased with fixed TL. In contrast, the average differences between fixed and variable TLs and the dispersion of these differences decreased with fixed TL in the South-east Australia modelled ecosystem, i.e. they were very high in lower TL species but low in higher TL species.

The mean differences and the distribution of differences between variable and fixed TL-based indicators varied across modelled ecosystems (Figure 3). In five ecosystems (Gulf of Gabes, West coast of Canada, West coast of Scotland, West Florida Shelf and Western Scotian Shelf), the mean differences were low and their confidence intervals narrow. In three ecosystems (South Catalan Sea, South-east Australia and Southern Benguela), the mean differences as well as their confidence intervals were moderate. In the Black Sea and the North Sea, the mean differences as well as their confidence intervals were large.

The patterns in the distributions of differences between fixed and variable TL-based indicators for the three indicators considered (TL_c, TL_{sc} and MTI) also varied across modelled ecosystems (Figure 3). In the Gulf of Gabes and West Florida Shelf, the dispersion of differences was very low across simulated indicators. In four ecosystems (South Catalan Sea, West coast of Canada, West coast of Scotland and Western Scotian Shelf), the TL_{sc} indicators displayed lower differences than the TL_c and MTI indicators, reflecting a higher level of agreement between fixed and variable TL_{sc} indicators. The TL_{sc} values in those modelled ecosystems were also lower than the TL_c and MTI values, which was indicative of the higher abundance of low TL species in the community than in the landings. In the Southern Benguela, no distinct pattern in level of agreement was apparent and TL_c, TL_{sc} and MTI displayed similar dispersions of differences between fixed and variable TL-based indicators.

In the South-east Australia modelled ecosystem, the TL_c and the TL_{sc} indicators displayed two groups, with one being characterized by low indicator values and another higher indicator values. TL_c values were lower under the LTL fishing scenario, while TL_{sc} values were lower under the HTL fishing scenario (Supplementary Figure S1).

In the Black Sea and the North Sea, differences between fixed and variable simulated TL-based indicators generally increased with the value of indicators. In the North Sea this pattern was displayed across all three simulated indicators, but was clearer in the ALL fishing scenario with a quasi-linear increase which was due to increased fishing pressure. In the Black Sea simulations, this pattern was only displayed in the MTI indicator (Supplementary Figure S1).

In certain modelled ecosystems, the high dispersion of differences between the fixed and variable TLs of species indicated that the range of variable TLs was wider than in modelled ecosystems with low dispersions of differences (Figure 2). These patterns in the average differences and their dispersion were also reflected in the TL-based indicators (Figure 3). On one hand, the five modelled ecosystems that displayed the lowest average differences between the fixed and variable TLs of species and dispersion of differences also displayed the lowest mean and dispersion of differences between fixed and variable TL-based indicators (Gulf of Gabes, West coast of Canada, West coast of Scotland, West Florida Shelf and Western Scotian Shelf). On the other hand, the five modelled ecosystems with higher average differences between fixed and variable simulated TLs of species and dispersion of differences also displayed higher mean and dispersion of differences between fixed and variable simulated TL-indicators (Black Sea and North Sea, and to a lesser extent South-east Australia, South Catalan Sea and Southern Benguela).

Across modelled ecosystems, fishing scenarios and indicators, the percentage of significant correlations between TL-based indicators and fishing pressure was higher for the fixed TL-based indicators (75% versus 70%). However, the percentage of negative significant correlations was higher for the variable TL-based indicators (47% versus 42%), indicating their higher capacity to detect changes (assumed to be deleterious) due to increasing fishing pressure. Across fishing scenarios, the ALL and HTL fishing scenarios exhibited patterns that mirrored patterns described above (Figure 4a). In the LTL fishing scenario, for both fixed and variable TL-based indicators, a lower percentage of significant correlations with fishing was detected than in the HTL or ALL scenarios. The percentage of negative significant correlations in the LTL fishing scenario was lower for fixed than for variable TL-based indicators (21% and 27%, respectively). Across indicators, TL_{sc} displayed the highest percentage of significant and negative significant correlations with fishing, and the percentage of negative significant correlations was lower for the fixed TL-based indicators (57% versus 70%, Figure 4a). Similarly, TL_c displayed a lower percentage of negative significant correlations for fixed TLs (31% versus 43%), while the MTI showed the opposite pattern with a higher percentage of negative significant correlations when calculated with fixed TLs (38% versus 27%). When these patterns were examined at the ecosystem level, the results were less consistent. In 40% of the modelled systems (Black Sea, Gulf of Gabes, North Sea and Western Scotian Shelf), significant negative correlations with fishing were more prevalent when using variable species' TLs, they were less prevalent for 40% of the systems (South Catalan Sea, South-east Australia, Southern Benguela and West coast of Canada), and in 20% of the systems, there was no difference (West coast of Scotland and West Florida Shelf, Figure 4a). In the North Sea, the percentage of significant correlations with fishing was the same for fixed and variable TL-based indicators (67%), but there were a much greater number of significant negative correlations for the variable TL-based indicators.

Across modelled ecosystems, fishing scenarios and indicators, the percentage of pairs of fixed and variable TL-based indicators that displayed the same significance of correlation with fishing was 76%, whether correlations in each pair were significant or non-significant. This suggested a high level of agreement (consistency) in the significance (or lack thereof) of a given indicator calculated using fixed vs. variable species' TLs. Across fishing scenarios, the LTL fishing scenario displayed the lowest percentage of pairs of correlations with the same significance (68%), while the ALL and HTL fishing scenarios displayed higher percentages of pairs of correlations with the same significance (80%, Figure 4b). Across the three different TL-based indicators, the TL_{sc} displayed the highest percentage of pairs of correlations with the same significance (90%), while the MTI and TL_c displayed lower percentages of pairs of correlations with the same levels of significance (66% and 72% respectively, Figure 4b). Across modelled ecosystems, all displayed higher percentages of pairs of correlations with the same significance, than pairs of correlations with different significance (Figure 4b). The West coast of Canada displayed the highest percentage of pairs of correlations with the same significance (100%) while the West Florida Shelf displayed the lowest percentage (56%).

A closer inspection of the pairs of indicators where both correlations were significant revealed that 83% of these pairs of correlations were of the same sign (meaning that an indicator responded negatively [positively] to fishing pressure irrespective of whether fixed or variable species' TLs were assumed). This indicates a high level of consistency (agreement) of the direction of response to fishing pressure by a TL-based indicator calculated using fixed or variable species' TLs (i.e. same direction of change in the TL-based indicator pairs in response to increased fishing pressure). Across fishing scenarios, the ALL and HTL fishing scenarios displayed higher percentages of pairs of significant correlations of the same sign (80% and 90%, respectively) than the LTL scenario (77%, Figure 4b). Across indicators, the TL_{sc} displayed a high percentage of pairs of significant correlations of the same sign (92%) than the MTI and TL_{sc} (73% and 78%, respectively, Figure 4b). Across modelled ecosystems, all pairs of significant correlations were of the same sign except in the Black Sea, Gulf of Gabes and the North Sea (67%, 57% and 20%, respectively, Figure 4b).

The Spearman's correlation coefficients between TL-based indicators and fishing pressure (Supplementary Table S3) revealed that correlations in all three TL-based indicators were opposite in sign between fixed and variable TL-based indicators in the LTL scenario in the Black Sea and in the ALL scenario in the Gulf of Gabes. Similarly, in the North Sea modelled ecosystem, opposite correlations were found in TL_c and MTI under the HTL and ALL fishing scenarios, and in TL_c for the LTL scenario in the South Catalan Sea.

In summary, these model simulation results indicate that the TL_{sc} displayed the greatest consistency (agreement) between fixed and variable species' TL with increasing fishing pressure and yielded more negative correlations than non-significant or positive correlations with increasing fishing pressure. Across fishing scenarios, the LTL fishing scenario displayed the lowest consistency between fixed and variable TL-based indicators and yielded the fewest significant negative correlations between fishing pressure and the three TL-based indicators considered.

Discussion

TL-based indicators are increasingly being used by institutions such as the Convention on Biological Diversity (CBD) and others, to assess the ecosystem effects of fishing (CBD, 2004). However, TL-based indicators have been subject to criticism. The main goal of this study was to scrutinize whether one particular critique, the use of a fixed trophic level per species, would invalidate their utility for ecosystem-based assessments. Using model-based simulations, we tested whether considering the variability of species' TL vs. a fixed species' TL would change the response of TL-based indicators to fishing. Our results indicate that overall, variable TL-based indicators are more effective at detecting the ecosystem effects of fishing, and survey-based TL-indicators are preferable to catch-based TL-indicators.

In our simulation tests, we found that the differences between indicators calculated using fixed vs. variable species' TLs varied across modelled ecosystems, indicators and fishing scenarios. Although the mean difference between fixed and variable TL-based indicators aggregated across all modelled ecosystems was low (0.017), the 95% confidence interval was high (0.625), particularly as fixed TLs considered in this study ranged from 2.0 (Red Mullet from the Black Sea modelled ecosystem) to 5.28 (Saithe from the North Sea modelled ecosystem). Pauly & Watson (2005) argued that the magnitude of the effect of species TL variability is low in comparison with the impact on change in community composition; however, our results support the view that the effects of species TL variability can be important (Caddy *et al.*, 1998; Jennings *et al.*, 2002; Vinagre *et al.*, 2012).

While TL-based indicators are expected to decrease with fishing pressure (Pauly *et al.*, 1998), it is important to note that, in certain cases, this does not occur (Branch *et al.*, 2010; Shannon *et al.*, 2014). The direction of change in ecosystem indicators is specific to both the multispecies assemblages and the fishing scenario under consideration (Travers *et al.*, 2006), as well as to other factors at play (such as environmental influences and exploitation history). Our simulation results indicate that overall, variable TL-based indicators are better able to detect negative significant correlations with fishing pressure, and therefore better able to detect the impacts of fishing on the structure of marine ecosystems than fixed TL-based indicators. However, our simulation results also show that in a high proportion of cases, fixed TL-based indicators do a reasonable job at capturing fishing effects.

Across modelled ecosystems and fishing scenarios, the differences between fixed and variable TL-based indicators varied. In some of the modelled ecosystems (Gulf of Gabes, West coast of Canada, West coast of Scotland, West Florida Shelf and the Western Scotian Shelf), the differences between fixed and variable simulated TL-based indicators were low, and their consistency was high, suggesting that using fixed TL-based indicators may not bias the assessment of fishing impacts in these ecosystems. In the Southern Benguela, South-east Australia and the South Catalan Sea modelled ecosystems, the differences between fixed and variable TL-based indicators were moderate. However, in these three modelled ecosystems, the capacity for the simulated indicators to detect negative correlations with fishing pressure was not increased with the use of variable species' TL, and the consistency between indicators was high. Finally, the largest differences between fixed and variable TL-based indicators were observed in the Black Sea and the North Sea simulation results. In these two modelled ecosystems, the consistency between fixed and variable TL-based indicators was low, while the capacity of variable TL-based indicators to detect negative impacts of fishing on ecosystem structure was much higher than that of fixed TL-based indicators. This suggests cautious use of fixed TL-based indicators for the assessment of fishing effects on the structure of these ecosystems.

In addition to variation in indicator responses across modelled ecosystems when fixed vs. variable species' TLs are used, differences are also likely to arise due to model and modeller effect. By this we mean to draw due attention to the influence of model type (Supplementary Table S1) as well as the way in which these models have been constructed e.g. the degree of species aggregation into functional groups, model parameterization, etc. For example, in the OSMOSE models of the Gulf of Gabes and West Florida Shelf, aggregated benthic and planktonic compartments have been designed as potential food resources for the other species in the model, that are the focus of the model and are explicitly modelled with full life cycles. In these model applications, the absence of feedback from the fish populations to the benthic and planktonic compartments partly explains the low variability in species' TL.

Across modelled ecosystems, the patterns displayed by the differences between fixed and variable species' TLs (Figure 2) were generally similar to those displayed by the differences between fixed and variable TL-based indicators (Figure 3). The South-east Australia modelled ecosystem is the only system where only a few species were responsible for the dispersion patterns of the indicators' difference. As this was the only system modelled using Atlantis, it is unclear whether this is due to the model used or the nature of the ecosystem being represented (which is different in structure, with a much higher reliance on invertebrate and mesopelagic food sources, and a much lower productivity, than the other systems). To resolve this the analysis would need to be repeated in one of the systems considered here where an Atlantis model also exists (e.g. the North Sea or Southern Benguela).

Across the fishing scenarios modelled, the TL-based indicators assessed under the LTL scenario showed fewest negative responses to increased fishing pressure. The consistency between fixed and variable species TL responses to fishing pressure was also the lowest, suggesting that under this fishing scenario, the performance of TL-based indicators in detecting modelled fishing effects is reduced. TL-based indicators were originally formulated so as to detect the "fishing down the food web" impact where HTL species are targeted, then decline, leading to fishing of species lower in the food web (Shannon *et al.*, 2014). In the HTL scenario, the direct fishing effect of HTL removal is synergistic with the indirect effect on the upsurge of LTL species due to less predation pressure. In the context of the LTL scenario, the response of TL-based indicators reflects the direct decrease in LTL species biomass but the signal is countered by the indirect responses of the fish community. Smith et al. (2011) found that the simulated impacts on other ecological groups were both positive and negative when harvesting LTL species, and that the effects could be large, especially when the LTL species comprised a large proportion of the biomass in a model ecosystem, or were highly connected in the food web. The LTL species play an important role in marine food webs as they are the primary route of energy flow through the trophic web from plankton to larger predatory fish (Pikitch *et al.*, 2014). Concern has been raised about the impacts of harvesting these species on higher TL species, particularly in “wasp waist” systems, such as the Southern Benguela, where a large proportion of the plankton production is channelled through a small number of these LTL species to higher TLs (Cury *et al.*, 2000; Shannon *et al.*, 2000). Our simulation results suggest that under the LTL fishing scenario, changes to the trophic structure are complex (see Travers-Trolet *et al.*, 2014): TL-based indicators may not decrease with increasing fishing pressure, and this may not appropriately track the impacts of fishing on the structure of marine ecosystems. This concurs with previous comparative analyses performed under the IndiSeas programme (Shannon *et al.*, 2010, 2014; Coll *et al.*, 2016).

Differences between TL-based indicators calculated from the simulated biomass of the surveyed community (TL_{sc}) and the simulated catch data (TL_c, MTI) concur with previous studies that promote the use of survey-based indicators over catch-based indicators. This is because survey-based indicators account for changes to the community and there is no confounding effect with fishing strategy (Branch *et al.*, 2010; Shannon *et al.*, 2014).

Although both TL_c and MTI displayed similar consistencies in significance and sign of correlations with fishing pressure, the total number of pairs of significant correlations was lower in MTI indicators. The MTI was introduced in an attempt to prevent 'bottom-up' effects from biasing the calculation of the TL_c. Yet, in certain ecosystems dominated by LTL species, such as upwelling systems, the inclusion of low TL species in TL-based indicator assessments of the ecosystem is important to correctly capture the functioning of the underlying ecosystem (Cury *et al.*, 2005; Shannon *et al.*, 2014).

To conclude, the refinement of TL-based indicators to track the effects of fishing is necessary as we progress towards an EAF worldwide. Our comparisons of modelled fixed and variable TL-based indicators suggest that overall, variable TL-based indicators may perform better than fixed TL-based indicators in detecting changes in the structure of marine ecosystems due to fishing. In most modelled ecosystems examined here there was high consistency between fixed and variable TL-based indicators, supporting the default use of fixed TLs per species, which are more readily available. However, in other modelled ecosystems where the difference between fixed and variable TL-based indicators was high and the consistency in indicator responses was low, the uncertainty in TL variability must be taken into account. This study quantified such levels of uncertainty in species' TL, as well as their correlations with fishing pressure. This study also suggests that, where possible, TL-based indicators derived from the biomass of the surveyed community should be monitored in addition to TL-based indicators derived from the landed commercial catch, as the capacity of the former to detect changes in ecosystem structure due to fishing is greater. Finally, our results reiterate that indicators cannot be applied blindly and wherever possible they should be used with careful attention to context. In particular, our results indicate that caution be used when interpreting TL-based indicators under fishing strategies targeting primarily forage fish, as their ability to detect the effects of fishing is to some degree restricted.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Figures

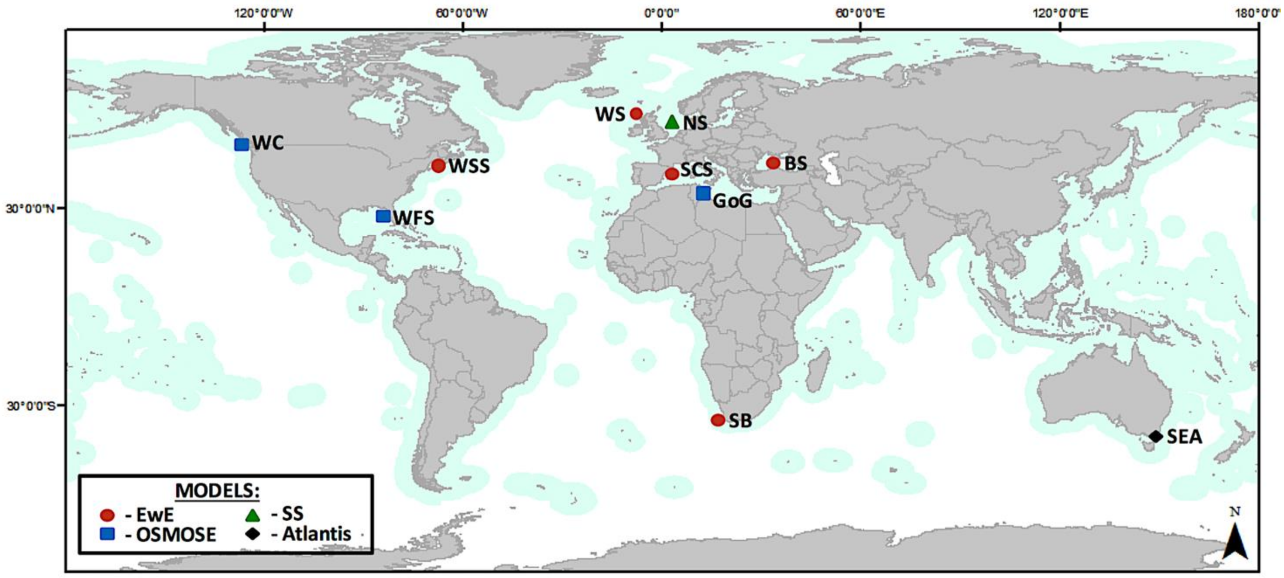

Figure 1. Location of the marine ecosystems considered with symbols indicating modelling approaches. The exclusive economic zones are indicated in the map as shaded areas around coasts (Ecosystems: BS, Black Sea; GoG, Gulf of Gabes; NS, North Sea; SCS, South Catalan Sea; SEA, South-east Australia; SB, Southern Benguela; WC, West coast of Canada; WS, West coast of Scotland; WFS, West Florida Shelf; WSS, Western Scotian Shelf; Models: EwE, Ecopath with Ecosim, SS, multispecies size-spectrum model).

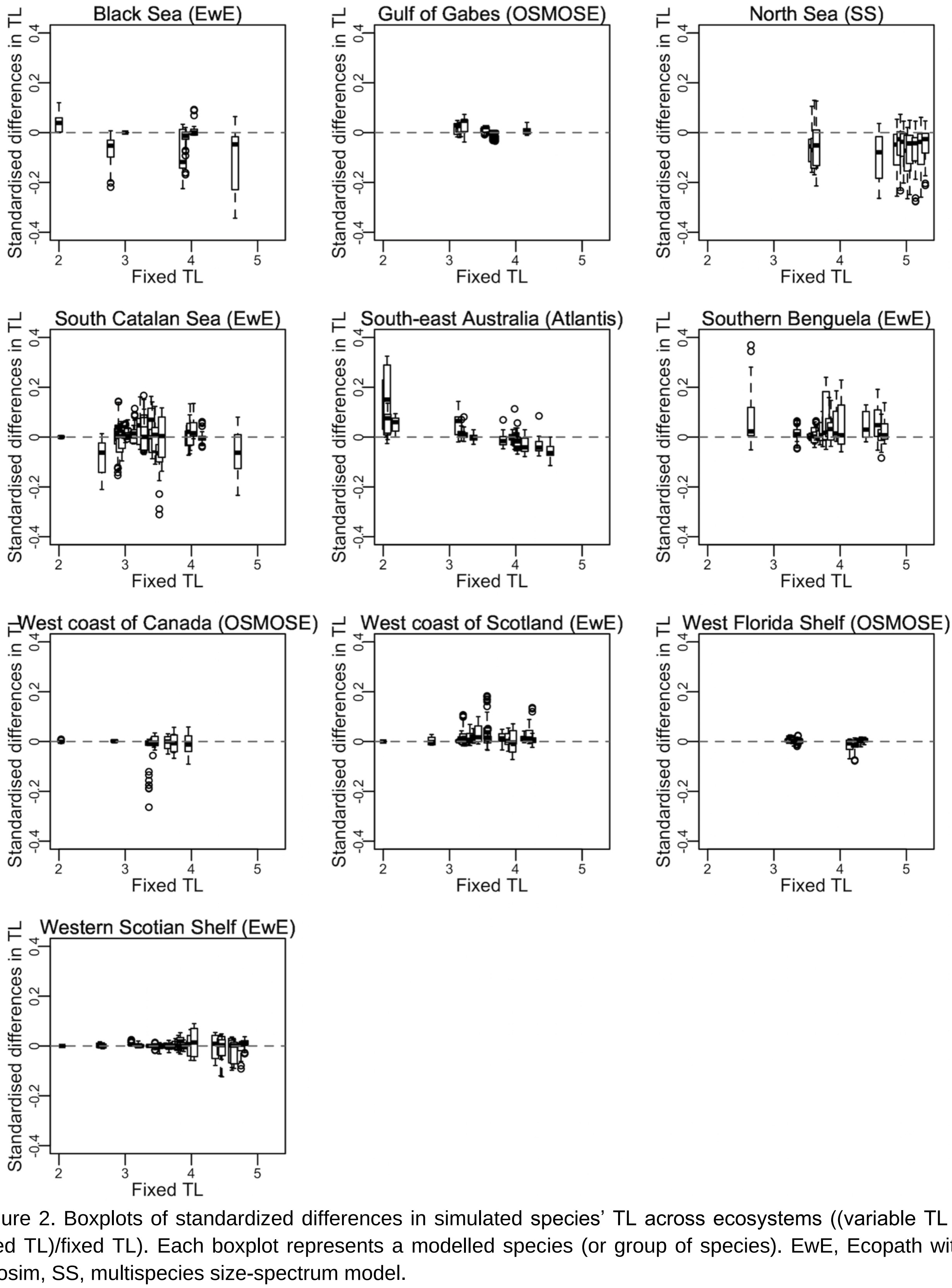

Figure 2. Boxplots of standardized differences in simulated species' TL across ecosystems ((variable TL – fixed TL)/fixed TL). Each boxplot represents a modelled species (or group of species). EwE, Ecopath with Ecosim, SS, multispecies size-spectrum model.

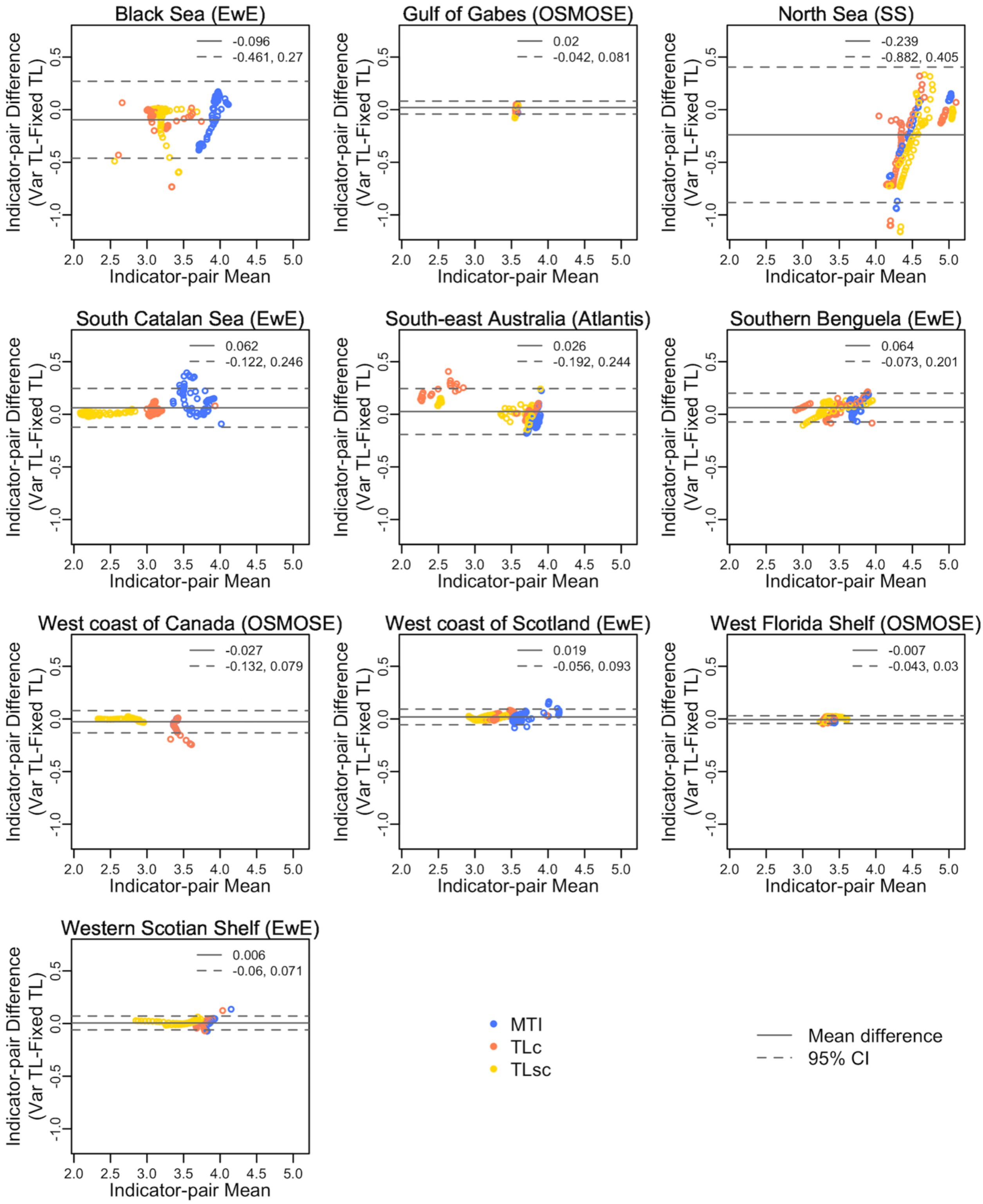

Figure 3. Standardized differences in variable and fixed simulated TL-based indicators across ecosystems (variable TL-based indicator – fixed TL-based indicator), with data points coloured by indicator type. Data points from the three fishing scenarios considered in the present study were plotted together. Each modelled ecosystem includes 180 data points, some of which may overlap: 20 F_{MSY} multipliers * 3 Fishing Scenarios (LTL, HTL & ALL) * 3 TL-based indicators (MTI, TL_c & TL_{sc}). The solid line represents the mean difference and dashed lines represent the 95% confidence interval around the mean. MTI, marine trophic index; TL_c, trophic level of the landed catch; TL_{sc}, trophic level of the surveyed community; EwE, Ecopath with Ecosim; SS, multispecies size-spectrum model.

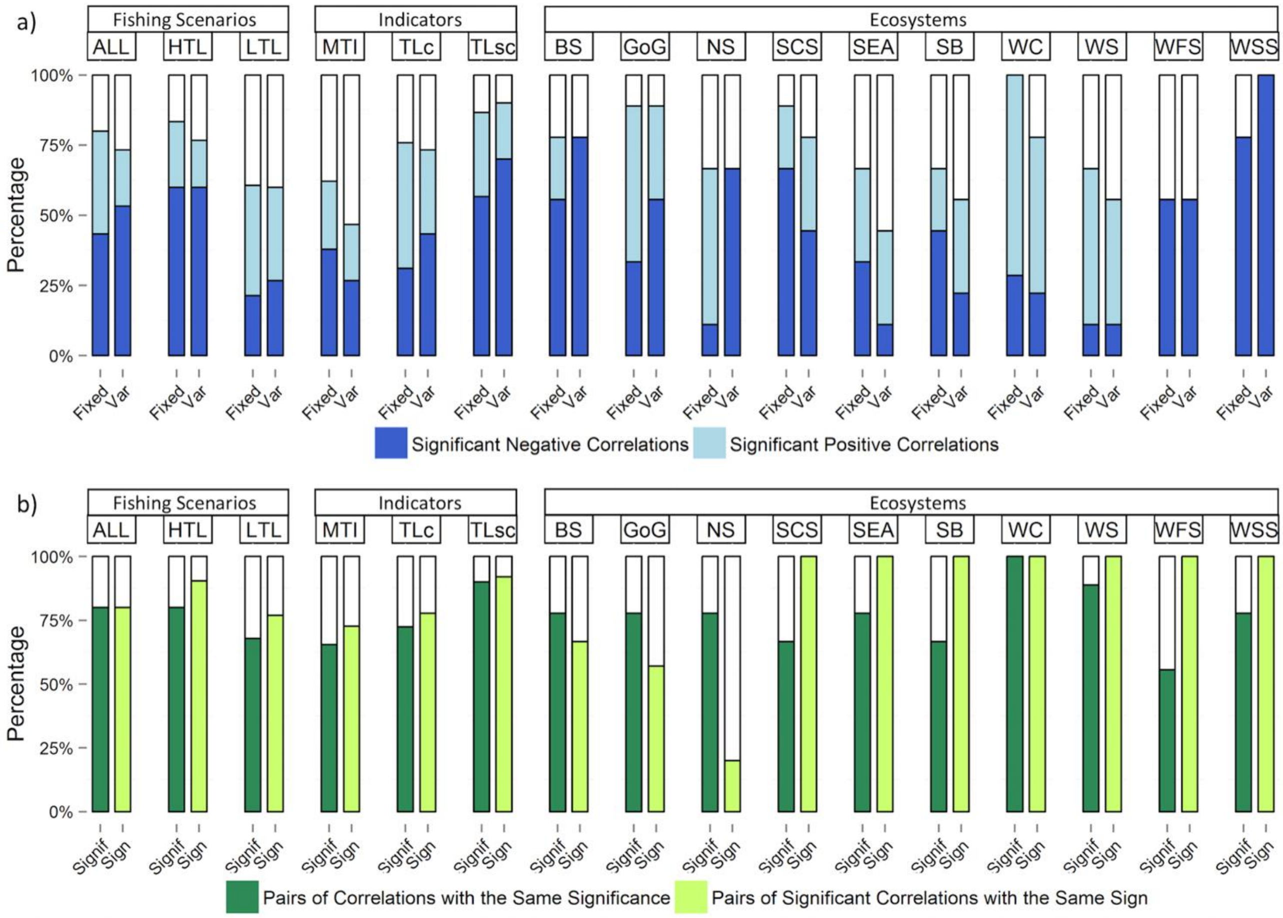

Figure 4. a) Percentage of significant Spearman's rank correlations between fishing and fixed TL-based indicators (Fixed) vs. variable TL-based indicators (Var). Significant correlation coefficients are positive or negative. The comparison of significant correlations is made across fishing scenarios (left panel), simulated indicators (middle panel) and ecosystems (right panel); b) Percentage of pairs of fixed and variable TL-based indicators (for example the pair (TL_c-fixed and TL_c-variable) from the Benguela EwE model for the HTL scenario calculated with fixed vs variable species' TLs) where both indicators have the same correlation significance to fishing (Signif) and same sign for the significant correlation coefficients with fishing pressure (Sign). The comparison is made across fishing scenarios (left panel), simulated indicators (middle panel) and ecosystems (right panel). The significance of pairs of correlation coefficients (Signif) includes whether both correlations are significant or both correlations are non-significant. Fishing Scenarios: ALL = scenario encompassing broad-scale exploitation, HTL, scenario targeting high TL species; LTL, scenario targeting low TL species; Indicators: MTI, marine trophic index; TL_c, trophic level of the landed catch; TL_{sc}, trophic level of the surveyed community; Ecosystems: BS, Black Sea (EwE); GoG, Gulf of Gabes (OSMOSE); NS, North Sea (SS); SCS, South Catalan Sea (EwE); SEA, South-east Australia (Atlantis); SB, Southern Benguela (EwE); WC, West coast of Canada (OSMOSE); WS, West coast of Scotland (EwE); WFS, West Florida Shelf (OSMOSE); WSS, Western Scotian Shelf (EwE); Models: EwE, Ecopath with Ecosim; SS, multispecies size-spectrum model.