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Risky business: The combined effects of fishing and changes in primary productivity on fish communities

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ABSTRACT

There is an increasing need to understand ecosystem responses to multiple stressors in that such complex responses depend not only on species-level responses, but also on species interactions and ecosystem structure. In this study, we used a multi-model ecosystem simulation approach to explore the combined effects of fishing and primary productivity on different components of the food-web across a suite of ecosystems and a range of model types. Simulations were carried out under different levels of primary productivity and various fishing scenarios. In addition to exploring synergistic, additive or antagonistic combined effects of multiple stressors, we included a fourth category "dampened", which refers to less negative or less positive impacts compared to additive ones, and in contrast to previous studies, we explicitly considered the direction (positive or negative) of the combined effects. We focused on two specific combined effects (negative synergism and positive dampened) associated with the risk of resultant lower fish biomass than expected under additive effects. Through a meta-analysis of the multi-models' simulation results, we found that (i) the risk of negative synergism was generally higher for low-trophic-level (LTL) taxa, implying that following an increase of fishing pressure on a given LTL stock, the subsequent decrease of biomass under low primary productivity would be larger than expected under additive effects and (ii) the risk of positive dampened effects was generally higher for high-trophic-level (HTL) taxa, implying that given a management measure aimed at reducing the impact of fishing on HTL stocks, the subsequent rebuilding of these stocks would be slower than expected. Our approach to categorizing and exploring cumulative effects can be applied to evaluate other community properties, and provide guidance for fisheries management.

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1. Introduction

Extensive studies have been conducted using empirical data from marine ecosystems to investigate individual effects of various stressors, particularly of fishing and environmental change (e.g., Fu et al., 2015; Shackell et al., 2012). Yet, research into the cumulative and interactive impacts of multiple stressors on marine ecosystems is more limited. Moreover, most studies analyzing the cumulative and interactive effects of stressors on marine ecosystems focus on impacts at the single-species level (Crain et al., 2008). However, impacts of multiple stressors on marine ecosystems depend not only on species-level responses to stressors, but also on species interactions, species diversity and redundancy, and ecosystem structure (Vinebrooke et al., 2004; Crain et al., 2008; Planque et al., 2010). This highlights the need to understand community-level and whole-ecosystem responses to multiple stressors (Breitburg et al., 1998).

Empirical studies exploring the effects of fishing and environmental change often assume that the combined effects of these two stressors are additive (e.g., Halpern et al., 2007, 2008; Link et al., 2010; Miller et al., 2011), i.e., that they are equal to the sum of the individual stressor impacts. However, Crain et al. (2008) found after reviewing 171 studies, mostly experimental ones and manipulating two or more stressors in marine and coastal systems, that the combined effects of stressors varied across studies, manifesting as additive (26% of the studies), synergistic (36%), or antagonistic effects (38%). Synergism is used to define a combined effect of multiple stressors that is greater than the addition of effects produced by the stressors acting in isolation. Antagonism is a cumulative effect with a lower magnitude than the sum of isolated effects (Folt et al., 1999; Darling and Côté, 2008). However, antagonism specifically designates situations where the pressures act effectively in opposition, or where the combined effect is opposite to the additive effect. In conservation science, it is commonly believed that ecological synergies are associated with deleterious consequences for ecological systems (Paine et al., 1998; Sala et al., 2000; Harley et al., 2006; Halpern et al., 2008; Brook et al., 2008) and that they have the potential to either reduce ecosystem resilience or push ecosystems into alternative states that would not have been reached with individual stressors acting in isolation (McClanahan et al., 2002; Folke et al., 2004).

However, in the applied context of fisheries management, synergistic or antagonistic combined effects may have different implications, depending on the response direction (positive or negative) of the combined effects. These management implications were not addressed in the afore-mentioned studies. Understanding that a conceptually robust definition and systematic classification of synergism and antagonism is a prerequisite for improving the ability to predict and manage the interactive effects of multiple stressors, Piggott et al. (2015) re-conceptualized synergism and antagonism by combining both the magnitude and response direction of combined effects, and illustrated how the traditional direction-independent classification of these terms may prove problematic. Travers-Trolet et al. (2014) introduced dampened effect as a third category of combined effects, in addition to synergism and antagonism, referring to less negative or to less positive impacts on a given ecosystem component. In this study, we further categorized the three types of combined effects (synergism, dampened effect, and antagonism) according to their direction (positive or negative) and ecological consequence (risk, being defined as combined effect resulting in lower fish biomass than expected under additive effects). See Section 2.5 for detailed definitions of the different categories of combined effects.

Empirically, it is difficult to draw general conclusions about the frequency with which synergistic, antagonistic and additive effects may be expected in the presence of multiple stressors, given the diversity of stressor combinations that can potentially co-occur across a broad range of marine ecosystems (Crain et al., 2008; Darling and Côté, 2008; Halpern et al., 2008; Costello et al., 2010). Ecosystem simulation models, such as Ecopath with Ecosim (EwE) (Christensen and Walters, 2004; Mackinson et al., 2009), OSMOSE (Shin and Cury, 2004; Travers et al., 2009; Travers-Trolet et al., 2014) and Atlantis (Fulton et al., 2004; Griffith et al., 2011, 2012), are increasingly being used worldwide to investigate impacts of fishing and environmental change on marine ecosystems. They are useful for the study of potential synergistic or antagonistic effects of stressors in marine ecosystems, since they can be employed as virtual laboratories where stressors can be controlled and dynamics can be tracked at different aggregation levels (i.e., at the species, community and ecosystem levels) (e.g., Griffith et al., 2012; Travers-Trolet et al., 2014). Using an Atlantis model of the southeastern Australian marine ecosystem, Griffith et al. (2012) found that the different trophic levels of a marine community responded differently to combined changes in fishing and environment – with benthic invertebrates responding antagonistically to the combination of ocean warming, ocean acidification and fishing pressure, while both top predator and planktonic groups responded synergistically. Practically, this would mean that pelagic and demersal fisheries should be managed differently under environmental change. Travers-Trolet et al. (2014) also suggested differential types of response depending on the trophic level considered; using an OSMOSE model of the Southern Benguela ecosystem, they suggested that small pelagic species were more prone to detrimental combined effects of fishing and environmental change than other trophic levels. Heymans and Tomczak (2016), using an EwE model of the Northern Benguela ecosystem, found that while the main driver of demersal species was fishing, for pelagic species it was fishing and climate, which caused changes in network structure.

Simulating interaction effects of multiple stressors on marine ecosystems is at its infancy. There is ample scope to improve, broaden and generalize the outcome of these recent modelling studies by developing more realistic end-to-end models (e.g., Travers et al., 2007; Rose et al., 2010), addressing uncertainty by comparing simulations across ecosystems and models, or refining the scenarios. In this study, we explored two stressors: fishing and changes in primary productivity, with the latter representing one aspect of environmental change, across nine marine ecosystems, using ecosystem models that differ in their structure and assumptions. We specifically investigated the combined effects of these two stressors on fish biomasses at different trophic levels.

Given recent empirical studies showing that the response of ecosystem indicators to individual stressors was dependent on the fishing strategy and history (Shannon et al., 2014), it is critical to explore different fishing strategy scenarios when investigating the combined impacts of fishing and environment on ecosystems. Therefore, ecosystem simulations in this study were carried out using different fishing strategies – where either all-trophic-level (ALL), high-trophic-level (HTL), or low-trophic-level (LTL) taxa (i.e., species or groups) were subjected to various levels of fishing mortality. Abiding by our new categorization of combined effects, we specifically explored negative synergism and positively dampened effects, and contrasted relative risks of these two effects between HTL and LTL taxa in a meta-analysis context (Koricheva et al., 2013). These analyses aimed at enhancing our understanding of the combined effects of fishing and primary productivity and providing guidance for fisheries managers.

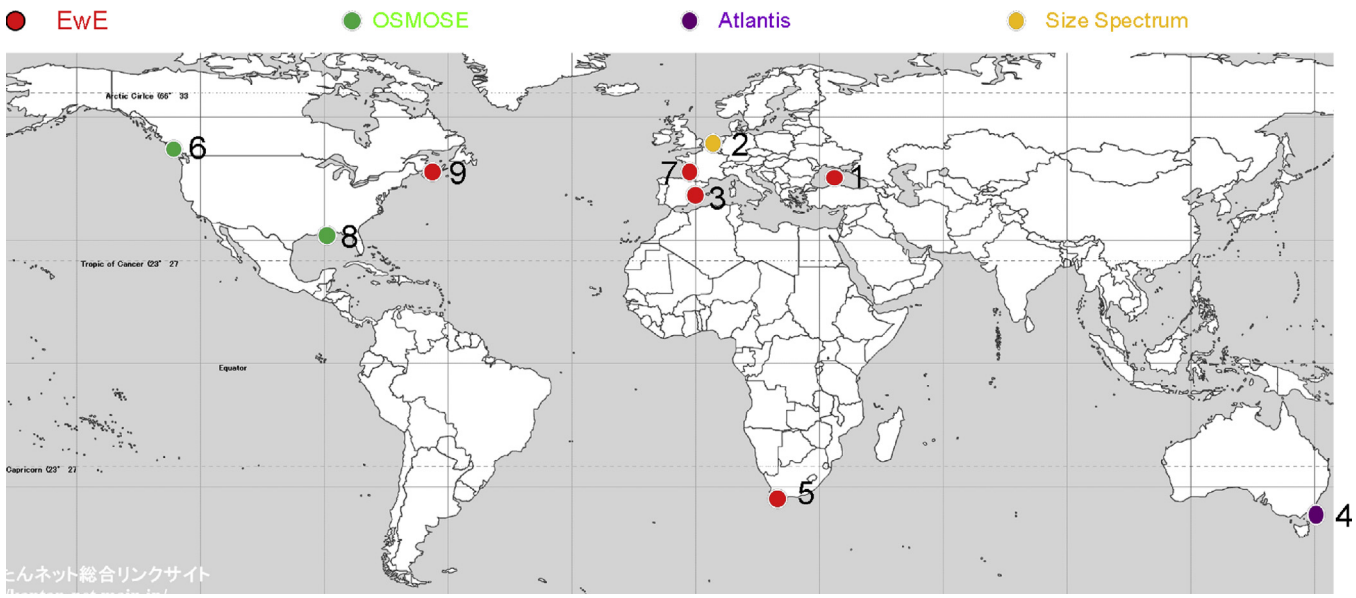


Fig. 1. Ecosystems studied with colours representing the different types of ecosystem models (EwE, OSMOSE, Atlantis, and Size Spectrum). 1: Black Sea, 2: North Sea, 3: Southern Catalan Sea, 4: Southeastern Australian, 5: Southern Benguela, 6: West Coast Canada, 7: Western Scotland, 8: West Florida Shelf, and 9: Western Scotian Shelf.

2. Materials and methods

2.1. Ecosystem models

Nine ecosystems are represented using one of four different ecosystem modelling approaches (Fig. 1): Ecopath with Ecosim (EwE, Christensen and Walters, 2004), OSMOSE (Shin and Cury, 2004), Atlantis (Fulton et al., 2004), and a size spectrum model (Blanchard et al., 2014). Five ecosystems were modelled with EwE: the Black Sea (Akoglu, 2013), the Southern Benguela (Shannon et al., 2004, 2008; Smith et al., 2011), the Southern Catalan Sea (Coll et al., 2006; Coll et al., 2013), the Western Scotian Shelf (Araújo and Bundy, 2011, 2012), and Western Scotland (Alexander et al., 2015). OSMOSE was used to model two ecosystems: West Coast Canada (Fu et al., 2013) and the West Florida Shelf (Grüss et al., 2016). The Southeastern Australian ecosystem was modelled with Atlantis (Fulton et al., 2014) and the North Sea was modelled with a size spectrum model (Blanchard et al., 2014). All models used in the present study have been published and validated against observations of abundance, biomass, and/or catch data.

2.2. Fishing strategies

Prior to simulation runs, fishing mortality corresponding to the maximum sustainable yield (F_{MSY}) was estimated in each ecosystem for each exploited taxon by reconstructing the yield to fishing mortality curve (catch as a function of fishing mortality rate) while holding the fishing mortality of all other taxa in the ecosystem constant at their respective current fishing mortality rates (F_{curr}). For each ecosystem, we separated all taxa into two categories, i.e., focus and non-focus taxa, with a focus taxon i being fished at $F_i = \lambda F^i_{MSY}$ (year^{-1}) and a non-focus taxon j being fished at its respective F^j_{curr}. By varying the multiplier λ, we implemented different levels of fishing mortality on focus taxa. Within each ecosystem, we investigated three different fishing strategies: an "all-trophic-level" (F_all) strategy, a "high-trophic-level" (F_htl) strategy, and a "low-trophic-level" (F_ltl) strategy. While the F_all strategy represents broad-scale exploitation, where the focus taxa are all taxa retained in commercial or subsistence fisheries, the F_htl strategy focuses on predatory taxa, which include large demersal and large pelagic taxa. The F_ltl strategy focuses on all forage taxa retained in commercial or subsistence fisheries. Here, forage taxa are defined as pelagic taxa, which as adults mainly feed on plankton (phyto-, zoo-, or ichthyoplankton). Any pre-recruit stages that are represented in the models are excluded from the fishing scenarios, as are air-breathing animals (i.e., marine mammals, marine turtles, and seabirds). For each fishing strategy, we experimented with a range of multipliers $\lambda \in \{0.25, 0.5, 0.75, 1, 1.25, 1.5\}$, covering a representative range of the yield-fishing mortality curve. The multiplier approach allows comparability across ecosystems.

2.3. Primary productivity

Because physical drivers were not explicit in all ecosystem models, we forced changes in phytoplankton biomass to represent changes in primary productivity (one of the few aspects of environmental change that are comparable across all ecosystem models). In EwE and OSMOSE, we forced phytoplankton biomass directly. In the size spectrum model, the plankton carrying capacity parameter was adjusted, because plankton biomass emerges in this model rather than being set directly. In Atlantis, nutrient inputs from point sources and upwelling were forced so that the resulting change in phytoplankton matched what would have occurred if the primary production had been forced directly. We represented directional primary productivity change by simply applying a multiplier $\gamma \in \{0.85, 0.9, 0.95, 1, 1.05, 1.1\}$ directly to modelled phytoplankton biomass. This range of variability encompasses the range of changes observed in the last decade in the ecosystems studied here (Boyce et al., 2014).

2.4. Response variables

In parallel to the trophic grouping used for the fishing strategies, the response variables used here are the aggregated biomass of ALL, HTL, or LTL taxa, averaged over the last ten years of simulation, after a spin-up time that is specific to each model. For each trophic taxa and each fishing strategy in an ecosystem, we analyzed 36 scenarios (= 6 F_{MSY} multipliers × 6 multipliers of phytoplankton biomass). The control scenario has both the F_{MSY} and phytoplankton biomass-multipliers set to 1 with resultant biomass B_C. Within each scenario k, the relative change in biomass is calculated as: $\Delta B^{Com}_k = \frac{B_k - B_c}{B_c}$ for

the combined effects with both fishing and phytoplankton biomass varying simultaneously. The relative biomass change for additive effects ΔB_k^{Sep} is the sum of relative biomass change with each of the two factors varying independently while the other remains at its control level.

2.5. Types of combined effects and risk

To characterize the types of effects resulting from the combination of fishing and phytoplankton biomass change, we adopted the following definitions of the different types of combined effects with risk zones defined where combined effects result in lower fish biomass than expected under the assumption of additive effects (the 1:1 line in Fig. 2). Aside from additive effects (1:1 line), the combined effects are as follows:

(i) When both ΔB_k^{Com} and ΔB_k^{Sep} are positive (in Quadrant I): if $\Delta B_k^{Com} > \Delta B_k^{Sep}$, the combined effects are considered positive synergistic, otherwise positive dampened. While positive synergism results in higher fish biomass than expected under the assumption of additive effects, positive dampened effect results in lower biomass, thus constituting a risk.

(ii) When both ΔB_k^{Com} and ΔB_k^{Sep} are negative (in Quadrant III): if $\Delta B_k^{Com} < \Delta B_k^{Sep}$, the combined effects are considered negative synergistic, otherwise negative dampened. Negative synergism exacerbates the reduction of fish biomass compared with the additive effects, so it is considered a risk; a negative dampened effect results in higher biomass than expected under additive effects.

(iii) In this study, effects on fish biomass are categorized as antagonistic when the combined effects and the sum of separate effects have opposite directions of change. In this sense, the definition of antagonism is more specific than that used in other studies (e.g., Crain et al., 2008). In the case where $\Delta B_k^{Com} > 0$ and $\Delta B_k^{Sep} < 0$ (in Quadrant II), the combined effects are positive antagonistic; otherwise, negative antagonistic (in Quadrant IV). Since positive antagonism results in higher fish biomass than expected under additive effects, there is no risk associated with it; on the contrary, negative antagonism falls within the risk area.

Based on the types of combined effects defined above, we assigned each scenario to one of the six categories (positive synergism, positive dampened, positive antagonism, negative synergism, negative dampened and negative antagonism) to report the frequency (based on occurrence) and intensity of each effect. The intensity of an effect is represented by the absolute difference between ΔB_k^{Com} and ΔB_k^{Sep}. In order to reflect both occurrence and intensity of the combined effects, weighted frequency (i.e., frequency*intensity) is used for the following analyses.

2.6. Meta-analysis

While we appreciate that using statistics on model data breaks the fundamental assumption that the underlying model is unknown, it is often still a useful approach for summarizing ecosystem model results. Moreover, in this case a statistical approach is particularly appropriate as calculating the true underlying model across the entire ensemble of models is extremely difficult. To compare combined effects of fishing and phytoplankton biomass change across ecosystems, fishing strategies and trophic groups, we adopt a meta-analytic approach. While traditional statistical reports include information on significance such as *p*-value, such values do not tell the size of a difference between two measures, nor can it easily be compared across studies. In contrast, in any meta-analysis, the relevant results of each study are expressed in terms of an outcome measure putting the results on a common scale. This common outcome measure is called the effect size, and it is the magnitude of the effect size that is compared and combined across studies.

In this study, the relative risk (*RR*) is used as the effect size. We specifically aimed at comparing the *RR* between the LTL and HTL groups to determine if these two trophic groups respond differently to the fishing and phytoplankton biomass changes explored, and if they have different levels of ecological risk – thereby requiring separate consideration, treatment and advice in fisheries management. We compared the nine ecosystems under the three fishing strategies. The *RR* value is computed as: $RR = P_1/P_2$. For the first type of ecological risk (negative synergism), for instance, P_1 is the proportion of negative synergism for the LTL group; P_2 is the proportion for the HTL group. Following the standard practice, the statistical analysis was performed on the logarithms of the ratios since

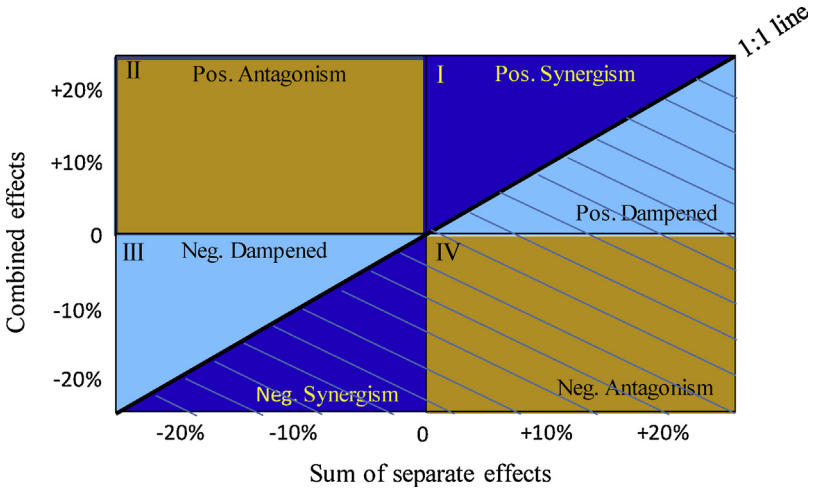


Fig. 2. Schematic comparison of the combined versus additive separate effects. Effects are presented as relative change in biomass occurring when fishing and phytoplankton biomass change act simultaneously (combined effect, y-axis) versus acting separately (x-axis). The 1:1 line represents combined effects being equal to additive effects. The zones below the 1:1 line are considered as risk zones, including negative synergistic (Neg. Synergism), negative antagonistic (Neg. Antagonism), and positive dampened (Pos. Dampened) effects.

$\ln(RR)$ is nearly normal and the standard error of $\ln(RR)$ is estimated as: $SE = \left(\frac{1-P_1}{n_1 P_1} + \frac{1-P_2}{n_2 P_2}\right)^{1/2}$ (Fleiss and Berlin, 2009).

To summarize results from the nine ecosystems quantitatively, we used a random-effects model (a full model without discriminating fishing strategies) to determine the level of heterogeneity among the ecosystems that could be introduced by the different ecosystem structures and/or different modelling approaches. In addition, a likelihood-ratio test between the full model and a reduced model that included fishing strategy as a moderator was conducted to indicate if fishing strategy mattered to the results. According to Koricheva et al. (2013), the random-effects model can be written as: $\theta_i = \ln(RR) + u_i$, where θ_i is the estimated effect size of the true effect size $\ln(RR)$ for ecosystem i, and $u_i \sim N(0, \tau_i^2)$ with τ^2 representing the amount of heterogeneity among the true effects. If $\tau^2 = 0$, then there is no heterogeneity among true effects (i.e., $\theta_1 = \theta_2 = \cdots = \theta_k \equiv \theta$), so that $\ln(RR) = \theta$ denotes the true effect. Following Raudenbush (2009), the best estimate of $\ln(RR)$ (noted $\ln(\hat{RR})$) is the average of θ_i weighted by precision (i.e., the reciprocals of the variance τ_i^2), i.e.,

$$\ln(\hat{RR}) = \sum_{i=1}^{k} \frac{\theta_i}{\tau_i^2} \Big/ \sum_{i=1}^{k} \frac{1}{\tau_i^2},$$

where $\left(\sum_{i=1}^{k} \frac{1}{\tau_i^2}\right)^{-1}$ is the variance.

The null hypothesis of homogeneity is tested using Cochran's Q-test:

$$Q = \sum_{i=1}^{k} \frac{(\theta_i - \ln(\hat{RR}))^2}{\tau_i^2}.$$

If the null hypothesis is rejected based on a given p value, the extent of heterogeneity among the true effects is represented by

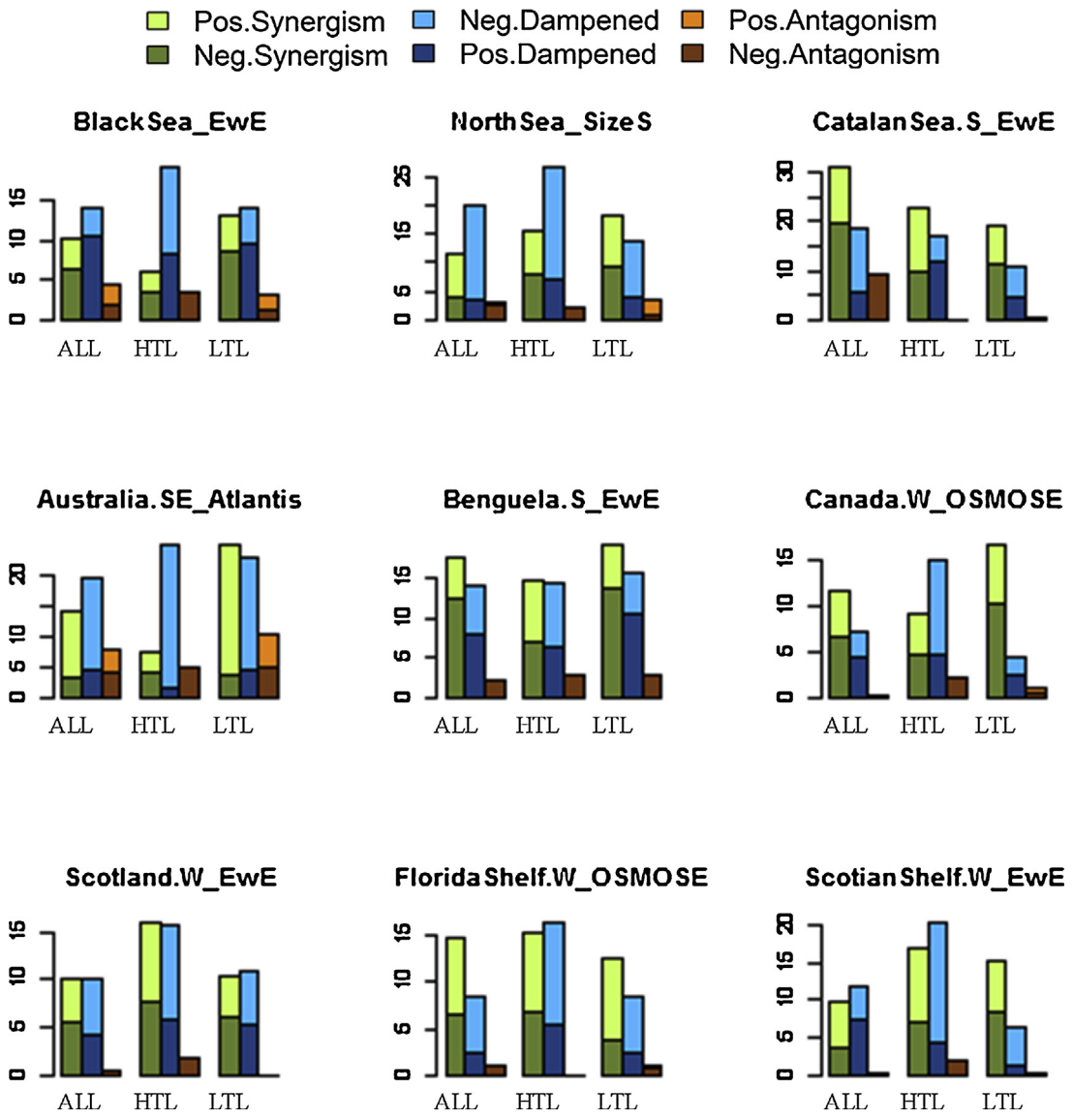


Fig. 3. Intensity-weighted frequencies of the six combined effects of fishing and phytoplankton biomass change on aggregated fish biomass for all- (ALL), high- (HTL), and low-trophic-level (LTL) groups recorded over all fishing strategies simulations, with combined effects being arranged according to the traditional definition of synergism (first stacked bar), dampened effect (second stacked bar), and antagonism (third stacked bar).

the simple ratio: $H = Q/(k-1)$. Under the null hypothesis of homogeneity, H has an expected value of unity; an H value of 2 implies that the variation in the estimated effect size θ_i is twice what would be expected under the null hypothesis. The meta-analysis was conducted using the "metafor" package (Viechtbauer, 2010).

3. Results

The combined effects of fishing and phytoplankton biomass change on fish biomass varied among the different trophic groups (LTL, HTL, and ALL) within each ecosystem (Fig. 3). In particular, the most frequently occurring effect differed between HTL and LTL groups in each ecosystem with only three exceptions (the Black Sea where dampened effects occurred more frequently for both HTL and LTL groups; the Southern Catalan Sea and the Southern Benguela where synergistic effects occurred more often). Across all the ecosystems, the HTL group was

most likely subjected to dampened effects; the LTL group on the other hand was more prone to synergistic effects. The intensity of synergistic effects was generally larger than that of dampened effects (Fig. 4). Antagonistic effects, particularly positive antagonism, were the least frequent in our simulation experiments; however the intensity of this effect tended to be larger than those from the synergistic and dampened effects (Fig. 4), implying that when antagonism happens, the resulting response of the fish community could be much larger than what would be expected under other types of combined effects.

Because the different directions of the synergistic, dampened, and antagonistic effects have different ecological risks, presenting different implications for fisheries management, we organized the combined effects based on their risk or non-risk feature. With two exceptions (West Coast Canada and Western Scotland), all ecosystems either had more or less risky combined effects for both HTL and LTL groups (Fig. 5). The non-risky combined effects (i.e., positive synergism, negatively dampened effects and positive antagonism) were predominant for both HTL and LTL groups in several ecosystems (e.g., the North Sea, the Southeastern Australian ecosystem, and the West Florida Shelf). In contrast, the risky combined effects (i.e., negative synergism, positively dampened effects and negative antagonism) played important roles in some other ecosystems (e.g., the Black Sea, the Southern Catalan Sea, and the Southern Benguela).

In order to differentiate the different types of risky combined effects, we contrasted the LTL and HTL groups to determine how prone they were to each of the ecological risks within each ecosystem and under each fishing strategy. Most $\hat{RR}$ values of negative synergistic effects were at or above 1 (Fig. 6). The $\hat{RR}$ value averaged over all ecosystems and fishing strategies was significantly greater than 1 with $p = 0.021$ (Table 1). This suggested that the risk of a negative synergistic interaction between fishing and phytoplankton biomass change was significantly higher for the LTL group than for the HTL group. The p-value for the likelihood- ratio test between the full model (shown in Fig. 6) and the reduced model was 0.939, indicating the conclusion drawn here was irrespective of fishing strategy. The ratio of total heterogeneity to total variability was 53% (Table 1), indicating more than half of the variability was due to heterogeneity across the ecosystem simulation models. The H value of 2.279 (Table 1) implied that the variation in $\hat{RR}$ was more than double of what would be expected under the null hypothesis of homogeneity.

In contrast, most $\hat{RR}$ values of positive dampened effect were at or below 1 (Fig. 7). The $\hat{RR}$ value averaged over all the ecosystems and fishing strategies was significantly less than 1 (i.e., 0.752) with $p = 0.006$ (Table 1). This suggested that the risk of positive dampened effects was lower for the LTL group than for the HTL group.

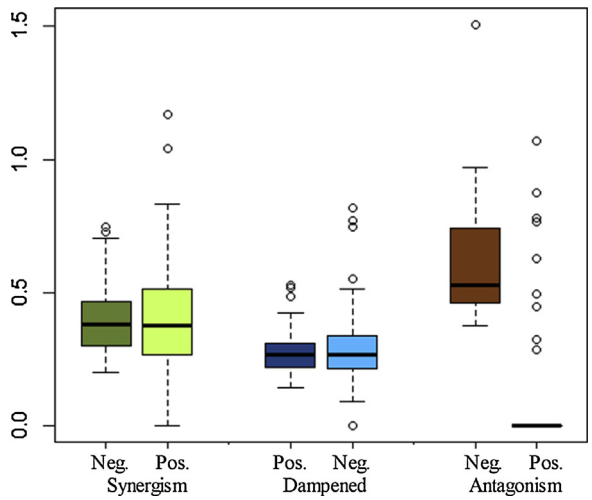


Fig. 4. Boxplot of intensity (i.e., the absolute difference of relative change in fish biomass between combined and separate effects) for synergism (negative: Neg. and positive: Pos.), dampened (positive: Pos. and negative: Neg.), and antagonism (negative: Neg. and positive: Pos.) across all fishing strategies, models and ecosystems examined.

The likelihood-ratio test ($p = 0.476$) between the full model (shown in Fig. 7) and the reduced model indicated that fishing strategy was not a factor affecting the conclusion drawn here. The amount of heterogeneity was high (74%) compared to the total variability, again indicating significant heterogeneity across the ecosystem simulation models.

When we explored the risk of relative biomass change falling below the additive 1:1 line, i.e., negative synergistic, positive dampened, and negative antagonistic effects, the $\hat{RR}$ value averaged over all ecosystems and fishing strategies was 0.903, not significantly different from 1 at p value of 0.05 (Table 1). Because the relative risk of negative synergism and that of positive dampened was opposite, the combination of these two types of risk would not be significantly different between the HTL and LTL groups. In addition, the fact that the $\hat{RR}$ value was slightly less than 1 could be solely a result of the Southeastern Australia ecosystem where the $\hat{RR}$ values were significantly less than 1 under all three fishing strategies (Fig. 8), meaning for this ecosystem the risk of having detrimental combined effects for HTL species was globally higher than for LTL species.

4. Discussion

With the growing need to apply ecosystem-based approaches to marine resource management, research on cumulative impacts from multiple stressors has become a focal topic in marine science (Rosenberg and McLeod, 2005; Leslie and McLeod, 2007), particularly under the current situation where both climate change and overfishing are affecting the productivity and structure of marine ecosystems at unprecedented rates (Kirby et al., 2009). While interactions between fishery exploitation and environmental change may result from combinations of various environmental variables that operate through different pathways, as an initial step, we investigated variation in primary productivity as representing one aspect of environmental change. Our research employed a multi-model ecosystem simulation approach to explore the combined effects of fishing and primary productivity on different components of the food-web. While combined effects of fishing and environmental change on fish communities have been investigated within a single ecosystem using a single ecosystem model (Griffith et al., 2011, 2012; Travers-Trolet et al., 2014), this research is the first to

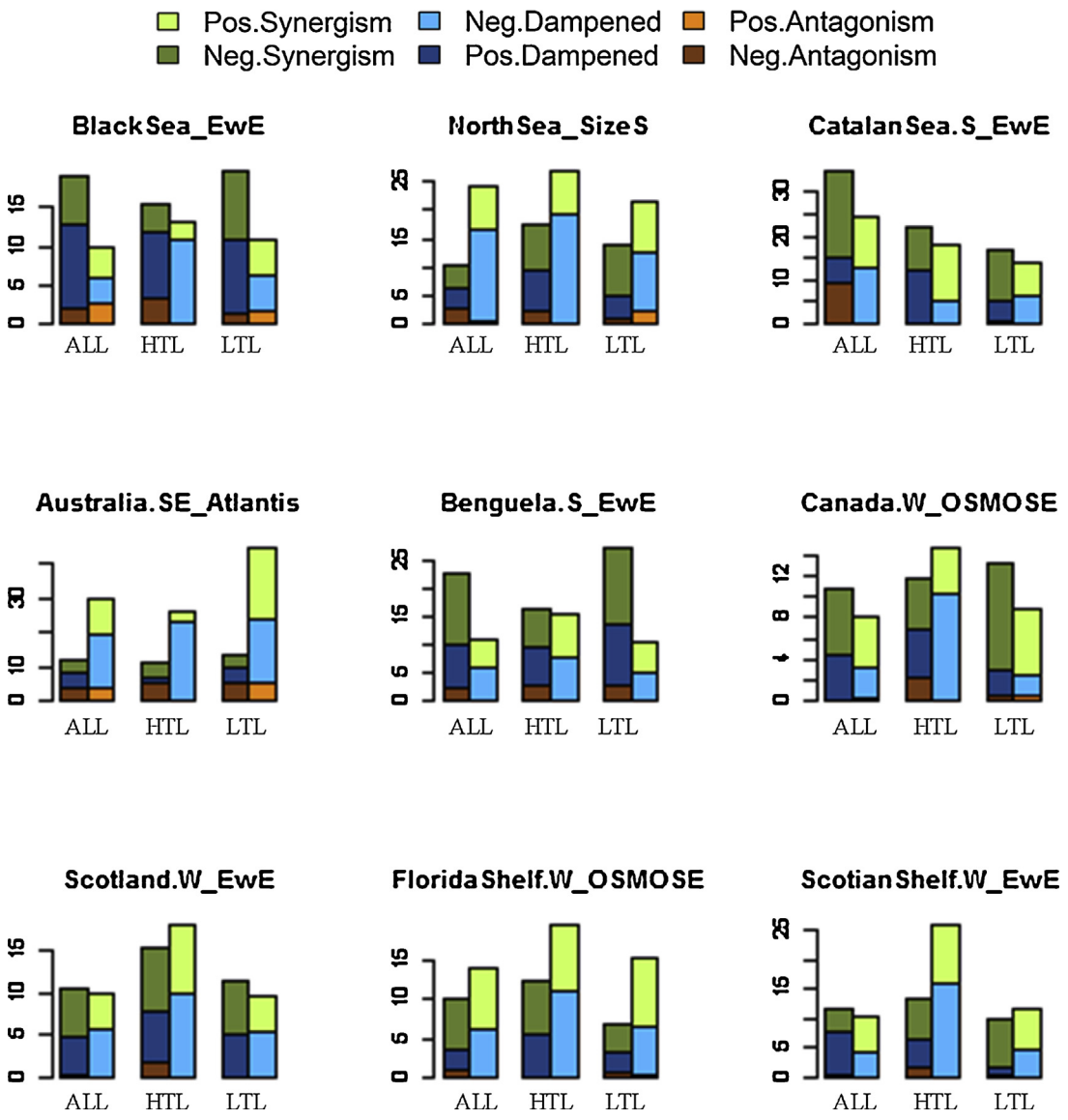


Fig. 5. Intensity-weighted frequencies of the six combined effects of fishing and phytoplankton biomass change on aggregated fish biomass for all- (ALL), high- (HTL), and low-trophic-level (LTL) groups recorded over all fishing strategies simulations, with combined effects being arranged according to the risk (first stacked bar: negative antagonism, positive dampened, and negative synergism) or non-risk (second stacked bar: positive antagonism, negative dampened, and positive synergism) feature.

Table 1
The relative risk ($\hat{RR}$) of negative synergism, positive dampened, and lower biomass averaged over 9 ecosystems and 3 fishing strategies for the low-trophic-level group versus for the high-trophic-level group. Along with $\hat{RR}$ are SE (standard error of $\hat{RR}$ estimate), p value (p-val) indicating the significance level for the null hypothesis of $\hat{RR} = 1$, and the lower (CI.lb) and upper bounds (CI.ub) of 95% confidence intervals. The test of heterogeneity informs whether the $\hat{RR}$ estimates are homogeneous (null hypothesis) with τ^2 measuring the amount of heterogeneity, and H (in a ratio term) indicating the variation in the $\hat{RR}$ estimates in relation to what would be expected under the null hypothesis.

	Relative Risk					Test for Heterogeneity				
	$\hat{RR}$	SE	p-val	CI.lb	CI.ub	τ^2	total heterogeneity/total variability	p-val	Q	H
Neg. Synergism	1.298	1.119	0.021	1.041	1.618	0.167 (SE = 0.091)	52.70%	0.000	59.260	2.279
Pos. Dampened	0.752	1.110	0.006	0.612	0.923	0.209 (SE = 0.082)	73.96%	<0.0001	90.605	3.485
Lower Biomass	0.903	1.059	0.075	0.808	1.010	0.057 (SE = 0.024)	65.96%	<0.0001	78.343	3.013

investigate the combined effects across a diverse series of marine ecosystems and models.

Following the traditional classification of combined effects without considering the direction of change triggered, we found that the HTL group was most likely subjected to dampened effect and the LTL group to synergistic effect across all the ecosystems. The least frequent combined effect was antagonism, suggesting that, whether adverse or positive, effects of fishing and phytoplankton biomass change rarely cancel one another out. Since we classified as antagonistic effects only those cases where the combined effects and the separate effects occurred in opposite directions, the result derived here concerning the frequency of antagonism is not comparable with previous studies (e.g., Crain et al., 2008; Rosenblatt and Schmitz, 2014). The infrequent occurrence of antagonism accompanied with its significantly larger intensity (absolute difference between ΔB_k^{Com} and ΔB_k^{Sep}) could be related to "ecological sur-

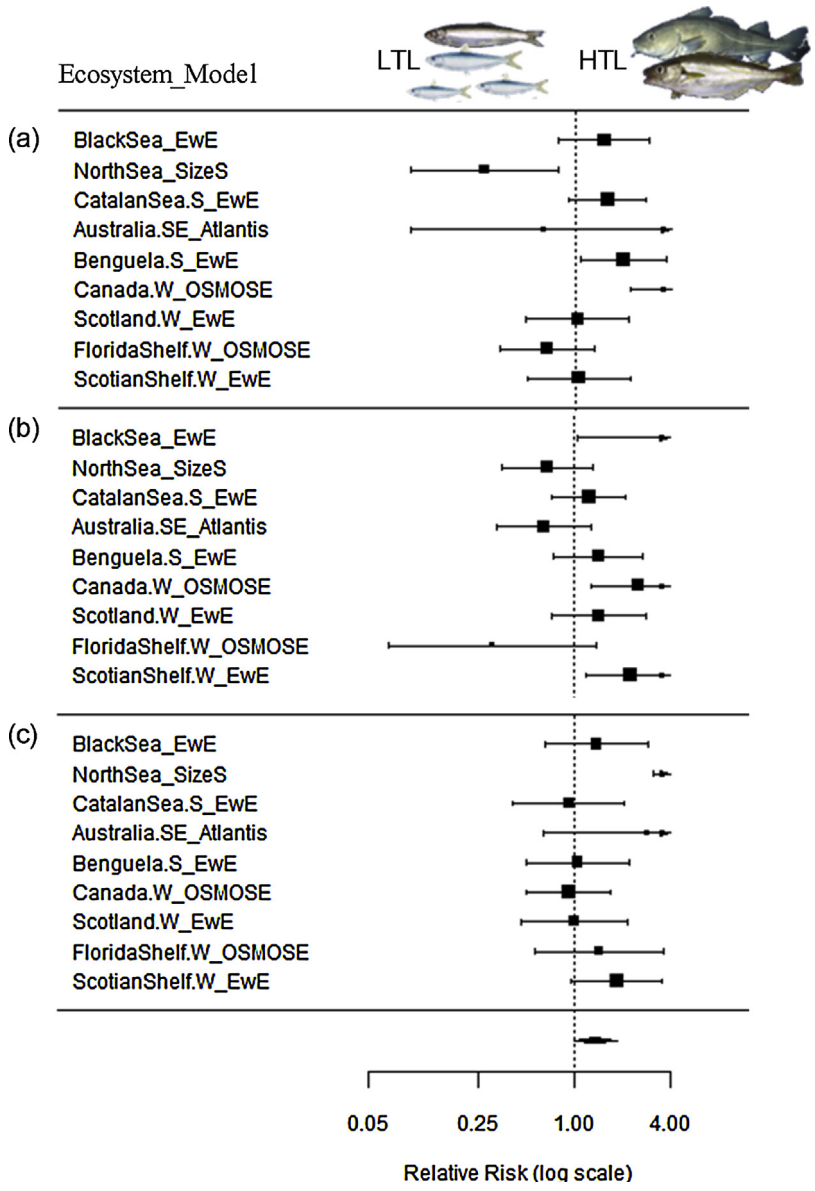


Fig. 6. Forest plot showing the relative risk of negative synergistic effects for the low trophic level (LTL) group versus the high trophic level (HTL) group under three fishing strategies: (a) F_all, focusing on all trophic level; (b) F_htl, focusing on high trophic level; and (c) F_ltl, focusing on low trophic level taxa. The points are the mean values for individual ecosystems; the estimated average relative risk across ecosystems is indicated at the bottom.

prises" reported in natural systems (Lindenmayer et al., 2010) or particularly in marine ecosystems and fisheries management, when the response of target populations to specific management measures, such as rebuilding measures, are contrary to predictions and counter intuitive (Pine et al., 2009). Our results suggest we could better understand ecological surprises if essential drivers are explicitly taken into account and the appropriate scenarios are tested with models incorporating those drivers. Managers are often bound to assess the consequences of ecological surprises a posteriori. Their capacity to be prepared for such events would increase if our capacity to predict those rare events is improved. Such efforts can forewarn managers about potential future states and rare events, so managers can trigger appropriate management responses that are robust to such conditions.

Across ecosystems and fishing strategies, dampened effects were rather common, although all previous research, with the exception of Travers-Trolet et al. (2014), had classified this effect as antagonism because directional change had not been considered in earlier studies. One example of such a dampening process is when the food-web is under organizational control of key LTL taxa, known as wasp-waist control (Cury et al., 2000; Bakun, 2006). In this case, the availability of the LTL taxa may absorb the stressors and typically determines the fate of the predatory fish stocks in conjunction with the effects of fishing pressure upon them. Therefore, any bottom up or top-down cascading impact is likely to be dampened in the food-web. This is true even though the LTL taxa tend to be under heavy fisheries exploitation. Only when the impact of a driver is so strong that it undermines the resilience of the trophic groups, do the combined effects appear to act synergistically on the ecosystem, as evidenced by the infamous *Mnemiopsis*-anchovy shift in the Black Sea in 1989 (Akoglu et al., 2014) or the shift from anchovy/sardine to goby/jellyfish in the Northern Benguela ecosystem (Heymans and Tomczak, 2016).

In contrast to previous studies, we explicitly considered the direction of the combined effects and specifically associated each direction-dependent combined effect with ecological risk. While the frequencies of the traditionally defined synergism, dampened effects and antagonism in an ecosystem often display irregular pat-

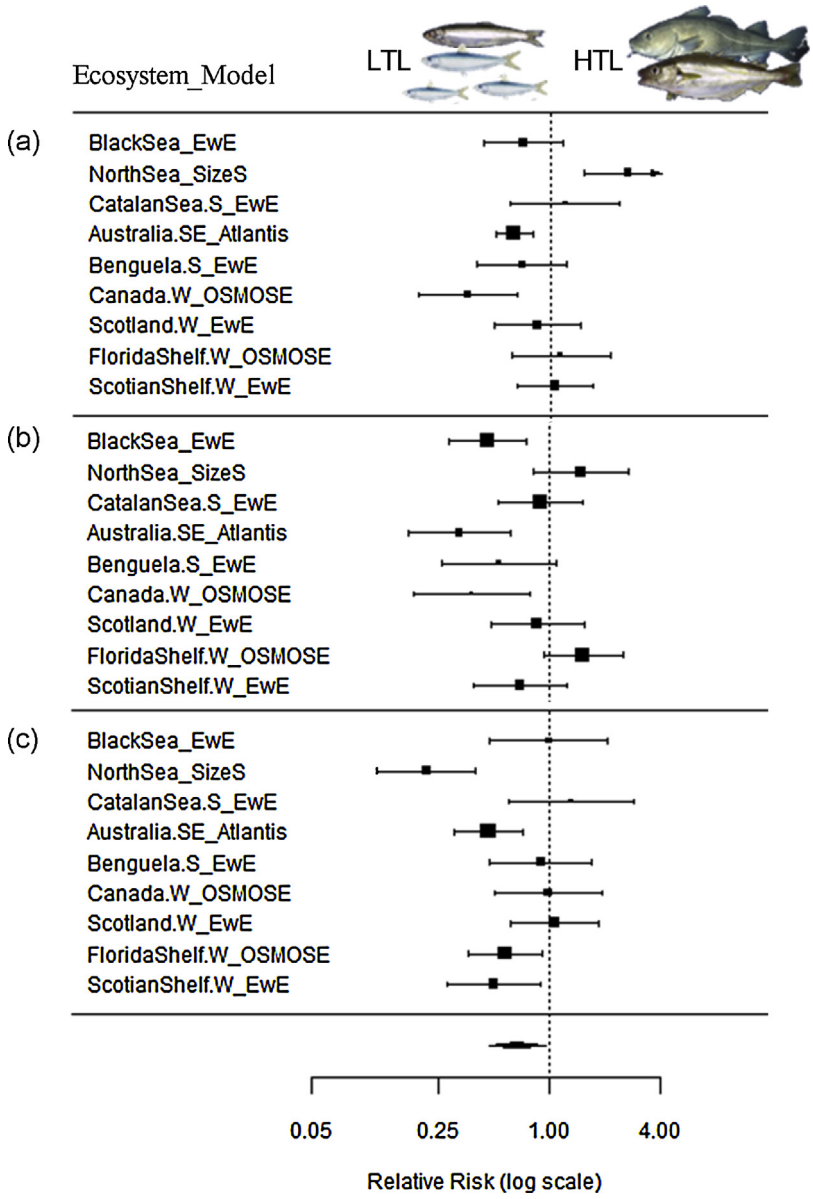


Fig. 7. Forest plot showing the relative risk of positive dampened effects for low-trophic-level group versus high-trophic-level group under three fishing strategies: (a) F_all, focusing on all trophic level; (b) F_htl, focusing on high trophic level; and (c) F_ltl, focusing on low trophic level taxa. The points are the mean values for individual ecosystems; the estimated average relative risk across ecosystems is indicated at the bottom.

terns (Fig. 3), the frequencies of risky and non-risky combined effects tend to have similar patterns between the HTL and LTL groups (Fig. 5), implying if risky combined effects dominate for the HTL group, so do for the LTL group. This indicates that it is useful to classify the combined effects according to the risk and non-risk categories because this classification reveals an ecosystem's vulnerability to risks irrespective of the trophic groups examined. Therefore, this classification boosts confidence in determining the risky business related to combined effects.

Through specifically contrasting the LTL and HTL groups in relation to a specific risky combined effect, we obtained findings that have important implications for fisheries management. First, the risk of negative synergism is significantly higher for the LTL group than for the HTL group, whatever the fishing strategy considered. This implies that following an increase of fishing pressure on a given LTL stock, the subsequent decrease of biomass under low phytoplankton biomass will be higher than that expected if only the fishing driver is taken into account in the assessment. Second, the risk of positive dampened effect is significantly higher for the HTL group than for the LTL group, whatever the fishing strategy considered. This means that given a management measure for reducing the impact of fishing on HTL stocks, the subsequent rebuilding of these stocks will be slower than expected under an assessment taking into account the fishing driver only. Third, the overall risk of relative biomass change falling below that expected under additive effects is not significantly different between the HTL and LTL groups due to the fact that the relative risk of negative synergism and that of positively dampened effect cancel one another out. This indicates the importance of differentiating the different types of risk when exploring the combined effects of multiple stressors in fisheries management.

In order to better understand triggers causing the risky combined effects (i.e., negative synergism, positively dampened effects and negative antagonism), we further explored the occurrences of these risky combined effects over the multiplier spaces of fishing mortality and phytoplankton biomass under different fishing

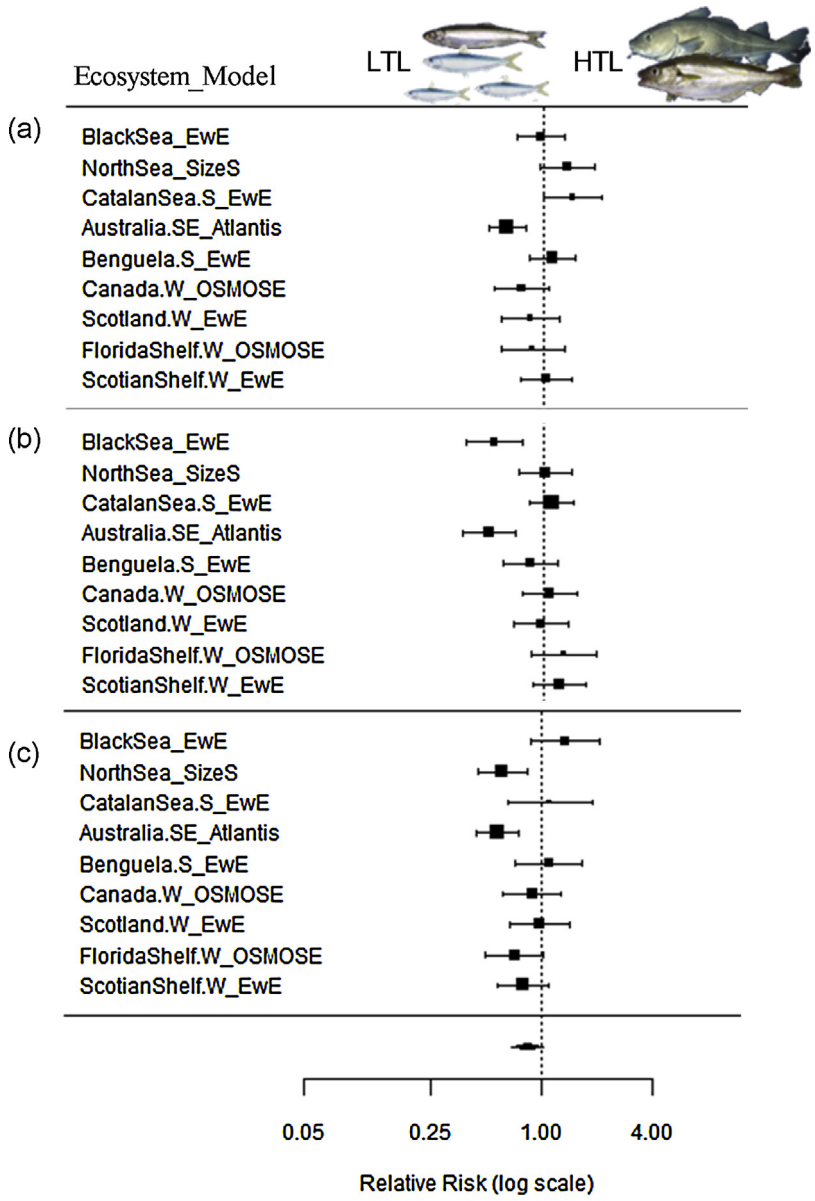


Fig. 8. Forest plot showing the relative risk of relative biomass falling below the 1:1 line for low-trophic-level versus high-trophic-level group under three fishing strategies: (a) F_all, focusing on all trophic level; (b) F_htl, focusing on high trophic level; and (c) F_ltl, focusing on low trophic level taxa. The points are the mean values for individual ecosystems; the estimated average relative risk across ecosystems is indicated at the bottom.

strategies (See Appendix B for more details). As expected, risky combined effects generally occur at low phytoplankton biomass and high fishing mortality. However, under fishing strategy F_htl, the ALL and LTL groups are more likely subject to negative synergism and positively dampened effects at low fishing mortality and low phytoplankton biomass. This is likely due to the fact that lower fishing mortality on the HTL group results in higher HTL biomass and thus higher predation mortality on the LTL group. Such findings have been made possible by employing the ecosystem models that detail the dynamics of different trophic groups and fishing strategies at different trophic levels. Future research on the development and application of more scenarios of ecosystem dynamics and services using these ecosystem models across broad spatial scales will be beneficial for moving toward ecosystem-based approaches to marine resource management.

Aside from the general patterns across the ecosystems related to the combined effects, understanding how the characteristics of the different ecosystems are related to combined effects is also beneficial. We attempted to functionally link the obtained simulated patterns to features of ecosystem structure (See Appendix C for more details). Further research is warranted in order to achieve more definite conclusions.

Overall, meta-analysis has allowed us to compare combined effects across different ecosystems through comparable simulation experiments with differences existing in both the ecosystem structure and model structure. Such comparison provides us with good opportunities to explore commonalities and divergences among various ecosystems, both of which will lead to greater understanding of the combined effects. However, due to the small number of simulation scenarios, the confidence intervals of the estimated relative risk (Figs. 6–8) were rather wide. Future simulations and comparisons can be improved by implementing significantly more scenarios of interactions between fishing mortality and phytoplankton biomass change and by including a range of feasible parameterizations per model (to capture ecological uncertainty around individual system function and responses). The finding

that more than half of the variability was due to heterogeneity across the ecosystem simulation models indicates that a broader scale of comparison is warranted in order to verify the conclusions drawn from this study. Future comparisons can be done within a single ecosystem but employing a variety of ecosystem models or across different ecosystems but using the same ecosystem model in order to address uncertainties in either ecosystem structure or model structure. Nevertheless, the current study has taken a positive step forward by convening research scientists across different continents to carry out unified simulation experiments using existing modelling capacities. Future research will benefit from comparative modelling approaches running common scenarios and methods across the growing library of extant and validated ecosystem models.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolmodel.2017.12.003.

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