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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 community-level or whole-ecosystem responses to multiple stressors since the impacts of multiple stressors on marine systems 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 (targeting different trophic levels). Previous work exploring the effects of multiple stressors often assumed that the combined effects of stressors are additive, synergistic or antagonistic. In this study, we included a fourth category "dampened", which refers to less negative or to less positive impacts on a given ecosystem component compared to additive effects, and in contrast to previous studies, we explicitly considered the direction of the combined effects (positive or negative). We focused on two specific combined effects (negative synergism and positive dampened) associated with the ecological 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 higher than expected when fishing is the sole driver 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 if only fishing were considered. Our approach

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to categorizing and exploring cumulative risk can be applied to evaluate other community properties and indicators and our findings could provide guidance in fisheries management.

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