Ecological Indicators 77 (2017) 67–79

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Research paper

Food-web indicators accounting for species interactions respond to multiple pressures

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ARTICLE INFO

Article history:
Received 6 October 2016
Received in revised form 23 January 2017
Accepted 26 January 2017
Available online 17 February 2017

Keywords:
Marine Strategy Framework Directive (MSFD)
Descriptor 4 (food-webs)
Multivariate autoregressive models
MAR models
Density-dependence
Predator-prey interaction
Pelagic fish
Baltic Sea
Ecosystem approach to fisheries management (EAFM)

ABSTRACT

Food-web indicators for marine management are required to describe the functioning and structure of marine food-webs. In Europe, the Marine Strategy Framework Directive (MSFD), intended to lead to a 'good environmental status' of the marine waters, requires indicators of the status of the marine environment that also respond to manageable anthropogenic pressures. Identifying such relationships to pressures is particularly challenging for food-web indicators, as they need to be disentangled from linkages between indicators of different functional groups caused by species interactions. Still, such linkages have not been handled in the indicator development. Here we used multivariate autoregressive time series models to identify how fish indicators in an exploited food-web relate to fishing, climate and eutrophication, while accounting for the linkages between indicators caused by species interactions. We assembled 31-year long time series of indicators of key functional groups of fish in the Central Baltic Sea pelagic food-web, which is characterized by strong trophic links between cod (*Gadus morhua*) and its main fish prey sprat (*Sprattus sprattus*) and herring (*Clupea harengus*). These food-web indicators were either abundance-based indicators of key piscivores (cod) and zooplanktivores (sprat and herring) or size-based indicators of the corresponding trophic groups (biomass of large predatory fish (cod $\geq$ 38 cm) and biomass of small prey fish (sprat and herring <10 cm)). Comparative analyses of models with and without linkages among indicators showed that for both types of indicators, linkages corresponding to predator-prey feedbacks and intra-specific density-dependence were essential to explain temporal variation in the indicators. Thus, no indicator-pressure relationships could be found that explained the indicators' variation unless such linkages were accounted for. When accounting for these, we found that the indicators overall respond to multiple pressures acting simultaneously rather than to single pressures, as no pressure alone could explain how the indicators developed over time. The manageable pressures fishing and eutrophication, as well as the prevailing hydrological conditions influenced by climate, were all needed to reproduce the inter-annual changes in these food-web indicators combined, although individual relationships differed between the indicators. We conclude that our innovative indicator-testing framework can therefore be used to identify responses of food-web indicators to manageable pressures while accounting for the biotic interactions in food-webs linking such indicators.
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1. Introduction

The development and application of indicators of the status of marine living resources have become increasingly important in the last decade scoping an ecosystem approach to fisheries management (Food and Agriculture Organization of the United Nations, 2003). In Europe, indicator development has recently progressed as part of the implementation of the Marine Strategy Framework

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http://dx.doi.org/10.1016/j.ecolind.2017.01.030
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Directive (MSFD), to aid the achievement of 'good environmental status (GES)' of European marine waters (European Union Directive 2008/56/EC). Different indicator-testing frameworks have been suggested for development of MSFD indicators (e.g. Piroddi et al., 2015; Lynam et al., 2016). However, indicators of the functioning and structure of marine food-webs (MSFD Descriptor 4), coupled to manageable pressures remain few. Synthesizing the status of dynamic and complex marine food-webs into single indicators is challenging (Rombouts et al., 2013), especially as interactions between species lead to continuous change in food-web composition and trophic cascades are common (Pace et al., 1999; Worm and Duffy, 2003; Frank et al., 2005; Casini et al., 2008, 2012). Hence, understanding how food-web indicators at different trophic levels are linked to each other is critically important to aid the development of relevant food-web indicators (Link, 2005). For example, indicators of predator species and of their prey are linked via predation mortality and energy gain from feeding. But the nature of this linkage is not straightforward, as it depends on the dominating interactions and can be modified by indirect effects via other trophic groups. For example, predation would lead to inverse relationships between indicators of the predator and of the prey, whereas the energy gain from resources would make indicators at the level of predators positively correlated to their prey species (Abrams, 2000). In addition to inter-specific interactions, populations are regulated by intra-specific density-dependent processes (Rose et al., 2001; De Roos et al., 2007; Casini et al., 2014). To our knowledge, such linkages among food-web indicators due to species interactions have so far not been accounted for despite their importance for the status of marine food-webs and their responses to management (Gårdmark et al., 2013).

Indicators intended to guide management actions need to both describe the state of a relevant food-web component and have a clear relationship to manageable external pressures. Overfishing is one of the major human-induced threats acting directly on the top of marine food-webs by removing large predatory fish (Pauly et al., 1998; Jackson et al., 2001). When translating these responses into food-web indicators, we would intuitively expect that top-down regulation caused by increased fishing mortality would have a negative effect on indicators relating to predator abundance and a positive effect on indicators relating to prey abundance due to lower predation mortality. However, the response to decreasing fishing pressure on predatory fish need not be the opposite, as it depends on the type and strength of species interactions (Van Leeuwen et al., 2014; Gårdmark et al., 2015). Furthermore, increased fishing mortality may lead to a shift in the body size distribution of target species to lower mean body sizes by removing large individuals. On the other hand, this size-selective removal of individuals may also result in an increase in mean body size of the species due to increased individual growth rates as a result of relaxed competition (Shin et al., 2005; Huss et al., 2014). Likewise, changes in other natural drivers, e.g. those linked to climate change, can modify food-web dynamics by both bottom-up and top-down forcing (Brown et al., 2010) as well as induce shifts in the regulation in food-webs (Möllmann et al., 2009). For example, nutrient enrichment has become a serious environmental concern altering marine food-webs by triggering bottom-up effects, mediated by harmful algae blooms and anoxia in deep waters (Smith, 2003; Llope et al., 2011; Lindegren et al., 2012). Similarly, warming is documented to positively affect the coupling between predators and prey through bottom-up effects (Jochum et al., 2012). On the other hand, warming has in experiments also been shown to strengthen top-down control (Kratina et al., 2012), with differing responses depending on food-chain length (Hansson et al., 2013), and also to directly affect the length of food-chains (Svensson et al., in press). Thus, responses to environmental changes inherently depend on interactions between species and functional groups in the food-web. For all environmental effects aforementioned, we still lack a good understanding of how species interactions may modify the relationships between external pressures and indicators within and across trophic levels.

The implementation of MSFD has promoted the development of a number of food-web indicators, for instance the survey-based Large Fish Indicator (LFI) (e.g. Greenstreet et al., 2011; Shephard et al., 2011; Gascuel et al., 2014; Modica et al., 2014; Engelhard et al., 2015; Adams et al., 2016), the Trophic Level of the surveyed fish community (TLco) (Shannon et al., 2014; Kleisner et al., 2015; Large et al., 2015; Coll et al., 2016) and the catch-based indicator Marine Trophic Index (MTI) (Shannon et al., 2014; Fu et al., 2015). These indicators were all developed to describe the composition of the fish community. As a complement, core indicators of the abundance of key functional groups (such as piscivores fish, top predators or species with high turn-over rate), have also been proposed (Rogers et al., 2010; Baltic Marine Environment Protection Commission HELCOM, 2013). All of these indicators are, however, primarily aimed to track the effects of fishing (Reed et al., 2016) and, more importantly, have ignored the role of species interactions for responses to this pressure. Interactions between species lead both to correlations among indicators across trophic levels, but can also mediate indirect responses to external pressures such as fishing (Shin et al., 2005; Daan et al., 2005). Therefore, to develop indicators across different trophic levels capable of assessing the impact of external pressures on the food-web while accounting for species interactions is essential to provide better assessments of food-web status.

In order to develop food-web indicators and identify their relationships to pressures, multivariate autoregressive models (MAR) might provide an appropriate framework. The main advantage of adopting this approach is that these multivariate statistical time series models allow for a concurrent estimation of inter-dependencies of indicators (arising from, for example, inter-specific competition, predation and intra-specific density-dependence) and their relation to environmental conditions (Ives et al., 2003). Thereby, the combination of linkages among indicators and of pressures they respond to can be found that best explain the temporal variation of all included food-web indicators. In addition, it does so while accounting for that these indicators are repeatedly sampled from the same population(s), i.e. includes autoregressive terms. This approach also enables the quantification of sources of uncertainties (both sampling and process errors), an important gap in some previous approaches (Jones and Cheung, 2015; Piroddi et al., 2015). MAR modelling has been used extensively as a tool to understand the dynamics of e.g. freshwater plankton communities and their coupling with the environment (e.g. Mac Nally et al., 2010; Hampton et al., 2013; Francis et al., 2014), as well as of exploited fish communities (Lindegren et al., 2009, 2014) and marine food-web dynamics (Griffiths et al., 2015). Recently, univariate autoregressive models have also been used to develop leading indicators of regime change in lakes (Francis et al., 2014 and references therein). However, this framework has not been applied so far to investigate how marine food-web indicators across different trophic levels relate to each other and to external pressures.

We aim to identify how food-web indicators across two trophic levels relate to variables related to fishing, climate and eutrophication, while accounting for the linkages between indicators caused by species interactions. To this end, we applied MAR models to 31-year long time series of two sets of indicators of three well-monitored fish species representing the pelagic marine food-web of the Bornholm Basin (Central Baltic Sea). In this region, these species are known to be controlled both by multiple external pressures and strong species interactions (Österblom et al., 2007; Casini et al., 2009; Möllmann et al., 2009; Gårdmark et al., 2015). The fish indicators proposed here include both indicators of key functional

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