



## Full length article

## Evaluating fishing effects on the stability of fish communities using a size-spectrum model

Chongliang Zhang<sup>a</sup>, Yong Chen<sup>b,c</sup>, Binduo Xu<sup>a</sup>, Ying Xue<sup>a</sup>, Yiping Ren<sup>a,c,\*</sup><sup>a</sup> College of Fisheries, Ocean University of China, 216, Fisheries Hall, 5 Yushan Road, Qingdao, 266003, China<sup>b</sup> School of Marine Sciences, University of Maine, 216, Libby Hall, Orono, ME, 04469, USA<sup>c</sup> National Laboratory for Marine Science and Technology, 1, Wenhai Road, Aoshanwei Town, Qingdao, 266000, China

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## ABSTRACT

Effects of fishing on the stability of fish populations have been examined in numerous studies; however, species interactions and their changes with life history stages may complicate such effects at the community level, which has not been well understood. We simulated trophic interactions within fish communities using a size-spectrum model and examined the effects of fishing on community stability for a variety of scenarios. We focused on two characteristics of community stability, the level of fluctuations in community status and recovery rates after perturbation, measured by spawning stock biomass (SSB) and two size-based indicators, mean body size (MW) and slope of the size spectrum (Slope). Increasing variability of fishing pressure was found to lead to linear increases in the variation of community status, whereas the impact was limited on integrated indicators such as MW, Slope and total SSB. The interaction of fishing pressure with given levels of recruitment variability amplified the fluctuations in SSB, but reduced those in MW and Slope. For a variety of random perturbations, all scenarios showed similar recovery trajectories, in which MW and Slope showed a steep decrease and slow recovery. Fishing pressure had substantial influences on the recovery of SSB and MW, but less effects on Slope, except for the non-fishing scenarios. The recovery time of SSB was highly variable among species and decreased with the increasing fishing pressure in general. The indirect effect of fishing on stability could be largely attributed to the changes in feeding conditions. Our stability evaluations have several implications for fisheries management, suggesting the potential and challenge for the recovery of depleted fisheries stocks in the absence of environmental changes.

## 1. Introduction

Stability is a central topic to ecology and many studies have explored the relationships among stability, diversity and ecosystem structure. It has been well-acknowledged that ecosystems are not necessarily stable (Levin and Lubchenco, 2008), and the potential existence of multiple states is important for management (Scheffer et al., 2001). There is increasing evidence for marine regime shifts worldwide (Jiao, 2009; Gårdmark et al., 2014; Levin and Mollmann, 2014; Mollmann et al., 2014), with a trend that is likely to be made worse by climate changes, acidification, pollution, and overfishing (Folke et al., 2004; Vasilakopoulos and Marshall, 2015). Given mankind's reliance on marine ecosystem services and ever increasing impacts on the marine environment, we need to pay special attention to ecological stability (Gunderson, 2000; Worm et al., 2006; Levin and Lubchenco, 2008).

Ecosystem stability is a complex and multidimensional concept, involving definitions such as *variability*, *resistance*, *resilience*, *persistence*

and *robustness* (Donohue et al., 2013). There are two perspectives of stability among studies, related to external environmental drivers and internal biotic interactions of ecosystems, respectively (Beisner et al., 2003). Studies that focus on the second perspective suggest that overall stability depends on the structure of ecosystems, such as types of interaction (e.g., predation, mutualism, or competition, Allesina and Tang, 2012; Mougi and Kondoh, 2012), topology (e.g., the level of connectedness within the food web, Dunne et al., 2002; Dunne, 2006), the strengths of predator-prey interactions (McCann et al., 1998), and the position of particular species within the food-web structure (James et al., 2015). For example, Allesina and Tang (2012) found that whilst predator-prey interactions were stabilizing forces, mutualism and competition led to destabilizing effects. Dunne (2006) and McCann et al. (1998) found that food webs could be stabilized by connectance, with a large number of weak links being particularly important. Here we focus on two, but important, aspects of community stability, the level of fluctuations in community status and recovery rates after

\* Corresponding author at: College of Fisheries, Ocean University of China, 216, Fisheries Hall, 5 Yushan Road, Qingdao, 266003, China.  
 E-mail address: [renyip@ouc.edu.cn](mailto:renyip@ouc.edu.cn) (Y. Ren).

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perturbations. The former aims to examine the fluctuations of fishery stocks, and the latter follows the concerns of *engineering resilience* (Angeler and Allen, 2016).

There have been concerns regarding fishing effects on the stability or sustainability of fisheries (Beddington et al., 1977), which suggests that exploited populations may show more fluctuations (Anderson et al., 2008). However, studies commonly focus on the stability of single species and tend to ignore overall ecosystem effects (Goñi, 1998; Anderson et al., 2008). Marine fishes exhibit complex trophic interactions, which lead to diverse indirect effects, particularly trophic cascades (Pace et al., 1999). In addition, marine species grow through several orders of magnitude from egg to adult (Neuheimer et al., 2015). As body sizes increase, individuals experience remarkable changes in life-history traits (Werner and Gilliam, 1984; Barnes et al., 2008) and shifts in ecological roles, i.e., “ontogenetic niche shifts” (Werner and Gilliam, 1984), wherein trophic interactions may change substantially. These dynamic and life-stage-dependent species interactions should receive more attentions in the evaluation of ecological stability (Emmerson and Raffaelli, 2004; Blanchard et al., 2011; Gilljam et al., 2015).

In the present study, we use a size-spectrum model to simulate the dynamic trophic interactions within fish communities and examine the fishing effects on community stability using species biomass and two community indicators. Several simulation scenarios were considered to evaluate direct and indirect effects of fishing pressure on the fluctuations and recovery of community status. This study intends to clarify the effects of fishing on the stability of fish communities and suggest adaptive management strategies to enhance ecosystem stability.

## 2. Materials and methods

### 2.1. Size-spectrum model

Size-spectrum models are developed to reflect the complexity of trophic interactions based on theoretical and empirical studies (Silvert and Platt, 1978; Benoît and Rochet, 2004; Andersen and Beyer, 2006; Hartvig et al., 2011; Andersen et al., 2016a). This approach characterizes life-history traits with individual body size and allows for the emergence of trophic interactions from underlying physiological processes (Andersen et al., 2016b). The size-spectrum approach has been used to evaluate fishing impacts, management strategies (Andersen and Pedersen, 2010; Rochet and Benoît, 2012; Blanchard et al., 2014; Jacobsen et al., 2014; Thorpe et al., 2017), and the steady state of marine communities, and suggest that the stability can be enhanced by small predator-prey mass ratios, wide diet selection, high feeding efficiency (Datta et al., 2011; Plank and Law, 2011), trait diversity (Zhang et al., 2013), and the inclusion of maintenance respiration and reproduction (Capitán and Delius, 2010).

Size-spectrum models are built on the basis of the regularity of size-abundance distributions, i.e., a linear relationship in double logarithmic size spectra (Sheldon et al., 1972; Sprules et al., 2016). The size-spectrum model used in this study has three fundamental assumptions (Andersen et al., 2016b): (i) energy flows at the community level are driven by individual-level energy budgets; (ii) predator-prey size ratios primarily determine trophic interactions; and (iii) vital rates are closely correlated to individual body sizes, i.e., the allometric scaling law that can be applied for estimating biological rates (Kleiber, 1932; Brown et al., 2004). These assumptions allow dynamic growth, reproduction, and mortality rates to emerge from trophic interactions (Andersen et al., 2009; Hartvig et al., 2011).

The model formulates the size spectrum as a function of mortality ( $\mu$ ) and growth rate ( $g$ ) using the McKendrick-von Foerster equation (M1 in Table 1) (McKendrick, 1925; von Foerster, 1959). Feeding kernel is governed by the size ratio between predators and prey (M2), described by a log-normal function (Ursin, 1973). The amount of encountered food is the product of available prey density and a size-specific search

rate (M3 and M4). Food consumption is limited by a size-dependent maximum consumption rate (M5 and M6). The assimilated food is primarily used to fuel standard metabolism (M8), and the remaining energy is split between somatic growth (M9) and reproduction (M10). The recruitment of larvae depends on egg production (M11) and is constrained by a Beverton–Holt-type density-dependent function (M12), in which the maximum recruitment ( $R_{\max}$ ) is derived from equilibrium solution of the model (M13) (Andersen et al., 2016b) or calibrated empirically (Blanchard et al., 2014) as is the case in this study. Three sources of mortality are included in the model, background (intrinsic) mortality (M14), predation mortality (M15) and fishing mortality (M16), in which fishing mortality is determined by fishing effort, size selection and species catchability. A background resource is incorporated into the model to provide food for the smallest individuals, described by a semi-chemostat equation (M17).

The size-spectrum modelling is implemented with R package “mizer” (Scott et al., 2014). The model was calibrated with data collected in a trawl survey program conducted from 2009 to 2015 for the fish community in Haizhou Bay, China. The model development is detailed in Zhang et al. (2016), and the model parameters were updated with additional data available to this study as shown in the Supplementary materials (Section A. Model parameterization).

### 2.2. Simulation scenarios

We evaluated the direct and indirect effects of fishing on community stability for various simulation scenarios,

- (1) Variable fishing pressure was simulated to examine the direct effects of fishing on the fluctuations of community status. Fishing effort was assumed to follow a normal distribution in this scenario, i.e.,  $Ef \sim N(Ef_0, \sigma_f^2)$ , in which the standard deviations  $\sigma_f$  range from 0 to 0.4, and  $Ef_0$  was  $1.77 \text{ year}^{-1}$ , constant among scenarios ( $Ef_0$  was estimated from the seasonal trawl and stow-net fishery survey in Haizhou Bay from 2011 to 2015; details in the Supplementary materials). The model was run for 300 years and each level of  $\sigma_f$  was run for 200 times.
- (2) The interactions between fishing and recruitment variability were simulated to examine the indirect fishing effects on community fluctuations. We assumed that the community fluctuations arise from recruitment variability in this scenario and tested whether fishing pressure could amplify or suppress such effects (Anderson et al., 2008). Recruitment variability was simulated by multiplying the deterministic recruitment with a stochastic term (M12), which followed a lognormal distribution,  $\log(\xi) \sim N(0, \sigma_r)$ . The standard deviation  $\sigma_r$  was set to 0.5 to simulate a medium level of recruitment variability (Blanchard et al., 2014) and different levels of  $\sigma_r$  generally showed a consistent pattern (Supplementary Materials, Fig. S3). Fishing efforts ranged from 0 to 2 times of  $Ef_0$  in this scenario to test the indirect effects of fishing. The model was run for 300 years and each level of  $Ef$  (21 levels from 0 to 2  $Ef_0$  in total) was run for 200 times.
- (3) Perturbations on fish communities were simulated to test fishing effects on community recovery. The models were run for 200 years to an equilibrium status, and therein perturbations were introduced to the community. The perturbations resulting from fishing activities represent various possible combinations of catchability, size selectivity and fishing effort (M16). We simulated a wide range of random demographic variations instead of explicit fishing scenarios. Specifically, we multiplied random errors to the equilibrium abundance of each species and size class. The error term followed a beta distribution  $beta(2,8)$  with a mean of 0.2 to simulate a moderate level of stock depletion. The models were run for additional 100 years after perturbations to allow the community to recover. We monitored the recovery trajectories to examine the existence of alternative stabilities caused by fishing (Gellner et al., 2016). The

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