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The efficacy of fisheries closure in rebuilding depleted stocks: Lessons from size-spectrum modeling

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ABSTRACT

Fishery closure has increasingly been used for rebuilding depleted fish stocks; however, trophic interactions have rarely been included in studying stock rebuilding in fisheries management. This study used a size-spectrum modeling approach to explicitly capture the effects of trophic interactions in the evaluation of simulated fishery closure. We generalize model parameters to evaluate the influence of community complexity, life-history characteristics and fishing regimes. A target fish stock of large body size showed the potential to recover after being depleted; however, the timescale for recovery ranged from 10 to more than 100 years. Increased number of species could smooth community dynamics and prolong the duration for recovery. The fish species characterized by large body sizes or preference of small-sized prey tended to recover slowly. Bycatch rate had substantial influence on community structure and stocks recovery rate. We showed that an external modification of community size-structure could largely promote stock rebuilding. We conclude that community complexity, life-history characteristics and fishing regimes should be explicitly taken into account in the implementation of fisheries closure.

1. Introduction

Overfishing, increasingly occurring worldwide with the development of industrialized fishing capacity, has led to the collapse of many marine fisheries in the world (Hutchings, 2000; Jackson et al., 2001). It is estimated that the worldwide population of large predatory fish has been reduced to 10% of pre-industrial abundance levels (Myers and Worm, 2003). There is widespread desire and have been considerable management efforts to avoid overfishing and restore marine ecosystems (Rosenberg et al., 2006; Worm et al., 2009); however, objectives and solutions for developing sustainable fisheries are generally controversial with limited successes (Pitcher and Pauly, 1998; Hall and Mainprize, 2004; Murawski, 2010; Zhou et al., 2010).

Control of exploitation rates is a primary approach for the recovery of fishery stocks (Caddy and Agnew, 2004; Rosenberg et al., 2006), and various regulations have been developed for its implementation, including gear restrictions, protection of nursery habitat, species-specific fisheries, minimum legal size and controls of total allowable catch and total fishing effort (Worm et al., 2009). Fishery closure is a simple management approach that can control exploitation rates directly. Stock recoveries following fishery closures have been observed at the time of World Wars I and II, when fish populations generally increased rapidly after fisheries cessation (Borley, 1923; Margetts and Holt, 1948). There is also recent evidence showing the recovery of depleted stocks with formal rebuilding plans (Murawski, 2010). However, fishery closures are not always successful despite of considerable management efforts (Bundy and Fanning, 2005). For example, a comprehensive analysis of 90 marine fish stocks showed that 41% stocks continued to decline within 5 years of fishing reduction and 40% stocks was not recovered 15 years after their declines (Hutchings, 2000).

Many studies have evaluated fishery rebuilding plans with different concerns (e.g., Baskett et al., 2007; Worm et al., 2009). Studies of fishery closure were traditionally built on single-species framework, which lacks explicit considerations of species interactions and their roles in early-life mortality, recruitment and community structure (Pitcher, 2001; Caddy and Agnew, 2004; Micheli et al., 2004). Recent studies have been focused on ecosystem dynamics (Daskalov et al., 2007; Marzloff et al., 2009; Mollmann et al., 2014). Some studies suggest that new ecological states may be stabilized by ecological feedback loops, in which case ecosystems cannot recover to the former state despite of fisheries moratorium, i.e. "regime shift" (Scheffer et al., 2001; Gårdmark et al., 2014). Even if there is no regime shift and overfishing effects are reversible,

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species interactions still need to be considered in fisheries management as resultant ecosystem dynamics may substantially impact the efficiencies of management plans (Frank et al., 2011; Fung et al., 2013).

Trophic interactions have long been overlooked in fishery stock assessment (but see Walters et al., 2008; Yemane et al., 2009; Andersen and Rice, 2010; Collie et al., 2013). Generally, modeling species interactions among fishes is difficult because fishes are commonly opportunistic predator and individual fish may change food preference with the growth of body size, namely "ontogenetic niche shifts" and "life-history omnivory" (Werner and Gilliam, 1984). Therefore, most predator–prey relationships in marine ecosystems are weakly linked (McCann et al., 1998; Berlow et al., 2004). Moreover, species are adaptable to abiotic/biotic environment (Hunsicker et al., 2011; Kéfi et al., 2015) and there is emergent nature of "complex adaptive system" (Levin, 1998; Gaichas, 2008). These characteristics are difficult to deal with in the traditional stock assessment framework, and associated management plans including stock rebuilding are debatable.

This study focuses on the effects of trophic interactions in mitigating the effectiveness of depleted fish stock rebuilding using closures. We systematically explore the potential of stock recovery in a wide range of biological/ecological and management scenarios. The overall objective of this study is to evaluate potential factors influencing the recovery process of depleted fish stocks. A multispecies size-spectrum model (Andersen and Beyer, 2006; Hartvig et al., 2011) is implemented to explicitly capture the dynamical trophic interactions in simulated fishery closure. We simulate heavy fishing intensity that leads to stock depletion, followed by fishery moratorium to allow stock recovery. We found that community complexity, life-history characteristics, and fisheries practice had substantial influence on the effectiveness of fisheries closure. Based on these results, we also designed and tested an external interruption of fishing to modify adverse community size structure in simulation to promote stock recovery (Bakun and Weeks, 2006). This study contributes to the improvement of our understanding of the rationality of fishery closure and the efficacy of fisheries management for a wide range of degraded ecosystems.

2. Materials and methods

2.1. Size-spectrum model

Various mechanistic models have been used to simulate ecosystem dynamics, such as the EwE model (Pauly et al., 2000; Christensen and Walters, 2004), the Atlantis model (Fulton et al., 2004), the LeMANS model (Hall et al., 2006) and the OSMOSE model (Shin and Cury, 2004). This study simulates multispecies trophic interactions using a size-spectrum model (Andersen and Beyer, 2006; Hartvig et al., 2011) for its capability and flexibility in capturing and generalizing fish community trophodynamics. This model is physiologically structured with sub-models that describe the processes of feeding, growth, mortality and reproduction at the individual level (Supplementary materials, Table S1). The size-spectrum model is characterized by three fundamental assumptions (Andersen et al., 2009): (1) individual feeding preference is determined by body size ratio between predator and prey; (2) energy obtained from food consumption is used to fuel metabolism, growth and reproduction; and (3) biological process rates are related to individual body size, namely allometric scaling law (more details can be found in Supplementary material). These assumptions address opportunistic prediction, omnivory, cannibalism, and ontogenetic niche shifts (Andersen et al., 2009). Every individual is replaceable and forage for all others, which implies weak species association and allow the emerging dynamics of fish community (Andersen and Rice, 2010). The model is implemented with R package "mizer" (Scott et al., 2014a), which uses a semi-implicit upwind finite-difference scheme to numerically solve the coupled partial integral-differential equations (Hartvig et al., 2011).

2.2. Model parametrization

We parameterized the size-spectrum model using a trait-based approach to generalize community structure (Jacobsen et al., 2014; Scott et al., 2014a), in which each species is characterized by an asymptotic body weight distributed in an even log scale. The other parameters of feeding, growth, mortality and reproduction are assumed equal for all species followed relevant studies (Jacobsen et al., 2014; Scott et al., 2014a) and are summarized in Supplementary material (Table S2). It should be noted that the generalization comes with the cost of ecological realism: (1) species-specific characteristics are ignored in the trait-based model; (2) fishes are assumed to be well-mixed but closed from external meta-populations or regional migrations; and (3) environmental conditions are assumed constant without the fluctuations such as habitat loss and changing climate.

2.3. Simulation scenarios

It is well acknowledged that the resilience of fish to fishing pressure differs among species, and generally large species recover slower than small ones as large fish tend to have slower growth and reproduction rates. This study focuses on a target species with large body size. The asymptotic body weight of the species is around 40 kg, simulating a cod-type predator species. We simulate the process of stock depletion and recovery using the trait-based model. The model is run for 200 years without fishing to simulate a pristine ecosystem, then heavy fishing effort is implemented to drive the target species stock to depletion. When spawning stock biomass (the biomass of individuals beyond maturation size, referred to as **SSB**) drop to 10% of the pristine SSB (SSB_0), the fishery is closed for all species for 100 years to recover the target species stock.

Fishery stock rebuilding could be impacted by a variety of environmental, ecological and anthropogenic processes. This study focuses on three factors considered to be critical for ecosystem dynamics (Caddy and Agnew, 2004; Murawski, 2010; Collie et al., 2013), i.e., community structure, life-history traits, and fishing regime. Following simulation scenarios were designed accordingly to evaluate the effect of these three factors (Table 1):

(1) Community structure: The complexity of community structure is primarily determined by the number of species in model, as species interactions depend on size selection in a well-mixed community. Therefore, a continuum of number of species is simulated in fish communities, ranging from 2 to 30 species. The asymptotic body sizes of these fishes are arranged in an even log-scale from 10 g to 30 kg (Hartvig et al., 2011).
(2) Life-history traits: The trait-based model generalizes species characteristics using the allometic scaling law, therefore, asymptotic body weight ($\boldsymbol{W}$) is the most important life-history trait. Besides, trophic interaction in the model is primarily determined by predation selection, which is described using a lognormal equation (Scott et al., 2014a),

$$\phi\left(\frac{w_p}{w}\right) = \exp\left[\frac{-(\ln(w/(w_p\beta)))^2}{2\sigma^2}\right]$$

where ϕ is a selection coefficient that describes the selectivity of a predator on the size of its prey, ranging from 0 to 1. w is the body size of the predator and w_p is the body size of the prey. β is the predator–prey size preference coefficient, and σ