



An evaluation of implementing long-term MSY in ecosystem-based fisheries management: Incorporating trophic interaction, bycatch and uncertainty



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ABSTRACT

Maximum sustainable yield (MSY), often defined in relation to a single species considered in isolation, has long been considered a cornerstone in fisheries management. It is difficult to expand the concept of MSY for the purpose of ecosystem-based fisheries management (EBFM). Here we consider MSY for a fishery in a multispecies fish community by addressing issues of trophic interaction and bycatch, along with parameter uncertainty. A size-spectrum model, which fully considers trophic interactions within the fish community, was used for simulating various fisheries scenarios including a single species fishery, a multispecies stow-net fishery, and a multispecies trawl fishery. Population biomasses, yields, and ecological indicators were used to assess the dynamics of the fishery and fish community status. The single species fishery with no bycatch resulted in a low impact on non-target stocks, but led to the collapse of the target stock at low fishing mortality rates. The stow-net and trawl fisheries had broader ecosystem impacts, but allowed target stocks to be fished at much higher fishing mortality rates with higher yields. Ecological indicators were related non-linearly to fishing mortality, possibly diminishing their effectiveness as management tools. Background resource carrying capacity was found to be a greater source of uncertainty than reproductive efficiency. This study demonstrates that bycatch mortality can play an important role in trophic interactions likely via predation release and depensation, and thus influence the resilience of fisheries to fishing pressure. The study indicates that the combination of mixed fisheries and multispecies effects lead to complex fish community dynamics that may present additional challenges for fisheries management.

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1. Introduction

Maximum sustainable yield (MSY) has long been used as the management goal for many fisheries around the world (Mace, 2001). The concept dates back to the 1930s (Russell, 1931; Hjort et al., 1933; Graham, 1935), and spread widely in the 1950s with the development of surplus production models (Schaefer, 1954). As commonly recognized, Ricker (1975) defined MSY as “the largest average catch or yield that can continuously be taken from a stock under existing environmental conditions”. MSY has served as a cornerstone for fisheries management (Mace, 2001), and was legally adopted in, for example, the 1982 United Nations Convention on the Law of the Sea, the EU Regulation 1380/2013 and the 2002 UN world

summit on sustainable development (A/CONF.199/20). It has also been the primary goal of many international fisheries organizations (Caddy, 1999; Mace, 2001; Andersen et al., 2015). However, the concept of MSY is based on a number of oversimplified assumptions and the application of MSY to fisheries management has long been questioned (Larkin, 1977; Sissenwine, 1978; Caddy, 1999; Legović et al., 2010; Mesnil, 2012). Implementation of MSY as a management objective has been scorned for leading to overexploitation of fisheries resources (Pauly et al., 2002; Hilborn, 2007), degradation of marine ecosystems as well as significant changes in community structure (Andersen et al., 2015).

In Larkin's well-known paper “An epitaph for the concept of maximum sustained yield”, this approach was criticized for neglecting the possible recruitment failure and the inability to achieve single-species MSY for all species in multispecies fisheries simultaneously (Larkin, 1977). Similar concerns were raised in the literature, along with criticism of the single-species management approach

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(e.g., Sissenwine, 1978; May et al., 1979; Caddy, 1999; Hilborn, 2007). Recent studies have further emphasized the shortcomings of the MSY approach, especially in related to species interactions, biodiversity, non-target species, habitat changes and long-term ecosystem functions and services (Pauly et al., 1998; Mace, 2001). It has been generally recognized that MSY provides “incomplete policy guidance” for ecosystem sustainability in a single-species framework (Gaichas, 2008).

Critics regarded MSY as a limit reference point within the context of the precautionary approach to fisheries management (Foster et al., 2000; Essington, 2001). However, the fundamental limitation of MSY in the single-species approach has not been well addressed, i.e., the lack of explicit consideration of species interactions (Goñi, 1998; Pikitch et al., 2004; Rice, 2011; Fogarty, 2014). Generally, fishing on one species will unavoidably influence the population dynamics of other species through processes such as bycatch, habitat change, predator-prey interaction, and competition (Gislason, 1999; Hilborn, 2011; Smith et al., 2015). The dynamics of species interactions are complex (McCann et al., 1998; Kéfi et al., 2015) since ecosystems involve interactions among all species and ecological components at different levels and scales, resulting in unresolvable complexity known as “complex adaptive system” (CAS) (Levin, 1998; Gaichas, 2008; Berkes, 2012). This inherent complexity makes the application of MSY in the traditional fisheries management framework challenging (Gaichas, 2008), leading to the inevitable conclusion that a more holistic ecosystem-based fisheries management approach is needed (EBFM) (FAO, 2001; Hall and Mainprize, 2004; Garcia and Cochrane, 2005).

Sustainability is one of the central concerns in fisheries (Pauly et al., 2002; Gaichas, 2008). There is increasing recognition that it is necessary to manage fisheries in a broader ecological context (Constable, 2001; Garcia et al., 2003; Sainsbury and Sumaila, 2003; Pikitch et al., 2004; Fulton et al., 2005; Fogarty, 2014). In this study we developed a simulation approach using a multispecies size-spectrum model (Scott et al., 2014a) to evaluate MSY from an ecosystem perspective. We integrated the critical, but generally ignored, components of trophic interactions, bycatch and uncertainty into the concept of MSY (Collie et al., 2014 in press), i.e., (1) trophic interactions, described by size-dependent predation and food competition emerging from the size-spectrum model; (2) bycatch, simulated using different catchability coefficients among species by fishing gear; and (3) uncertainty associated with the status of the fish community deviating from the deterministic model (Larkin, 1977; Essington, 2001; Pauly et al., 2002). The uncertainty was simulated as a stochastic process.

The objective of this study was to (1) evaluate the role of trophic interactions, bycatch and uncertainty in defining MSY within a fish community and (2) monitor the dynamics of fish community using multiple ecological indicators to relate the community dynamics to fisheries management. Although the size-spectrum modeling framework has been used to evaluate impacts of fishing on ecosystems (Blanchard et al., 2014; Andersen and Beyer, 2015), the combined effects of trophic interactions, bycatch and uncertainty have rarely been accounted for in fisheries management. This study intends to improve the general understanding of sustainability in the EBFM framework and the development of fisheries management strategies.

2. Materials and methods

2.1. The operational model

A multispecies size-spectrum model was used as the operational model for the simulations. The model was developed by Andersen and Beyer (2006) and Hartvig et al. (2011) based on the size spec-

trum theory, and assumes food-dependent and size-related trophic interaction among species (Andersen and Beyer, 2006; Hartvig et al., 2011). The size-spectrum model explicitly addresses trophic interactions in the fish community and allows dynamic growth, mortality and recruitment to emerge from food availability (Houle et al., 2013). It has been used for exploring community properties and fishing effects on ecosystems (Andersen and Pedersen, 2010; Hartvig et al., 2011; Blanchard et al., 2014; Andersen and Beyer, 2015). The size-structured community dynamics are described by the McKendrick–von Foerster conservation equation (McKendrick, 1925; Von Foerster, 1959),

$$\frac{\partial N_i(w)}{\partial t} + \frac{\partial g_i(w)N_i(w)}{\partial w} = -\mu_i(w)N_i(w),$$

where abundance $N_i(w)$, individual growth $g_i(w)$ and mortality $\mu_i(w)$ are specific for species i and body size w . Food preference is size-dependent and predation provides energy for other biological processes including growth and reproduction. The processes of food intake, metabolism, growth, reproduction and mortality are formulated using sub-models (see details in Supplementary materials, Table S1). The R package “mizer” is used for implementing this model (Scott et al., 2014b).

The model was parameterized based on a fish community survey in Haizhou Bay, China. Haizhou Bay serves as important spawning habitat for many fish species of commercial importance and used to be a productive fishing ground. However, commercial landings have decreased dramatically since the end of last century, which is associated with substantial changes in species composition (Tang et al., 2011). A stow-net fishery is currently the dominant fishery in the Bay. A stratified random designed bottom trawl survey was conducted in March, May, July, September and December 2011 in Haizhou Bay. The 23 most abundant species, accounting for over 90% of the total fish biomass in the survey, are included in the model. Each species is characterized by a set of parameters describing life-history traits obtained from FishBase (www.fishbase.org), previous studies and the bottom trawl survey data. Other parameters, including metabolic scaling, background resource capacity, maximum recruitment and fishing effort, were either derived from previous studies or calibrated from survey data (Blanchard et al., 2014; Jacobsen et al., 2014). Model parameterization is detailed in the Supplementary materials (Tables S2 and S3).

2.2. Simulation scenarios

Fishing mortality in the size-spectrum model is a product of three factors: fishing effort, size selectivity and catchability (Scott et al., 2014b). Fishing effort was defined by a wide range of values for the purpose of this study to explore the optimum effort for sustainable yields. Selectivity was assumed to have a “knife-edge” shape because of lack of selectivity information for each species (Blanchard et al., 2014; Scott et al., 2014b). The knife-edge size that indicates the availability of fish to be captured was estimated from the survey data (see Supplementary materials). Catchability was used to describe bycatch in multispecies fisheries with different levels of vulnerability for different fish species in simulated fisheries (see Supplementary materials, Model parameterization).

The simulations were focused on two species in Haizhou Bay, a predatory fish “yellow croaker” (*Pseudosciaena polyactis*) with economic importance in the stow-net fishery and a forage fish “Fang gunnel” (*Pholis fangi*) that is abundant in the survey but has a low catch in the stow-net fishery. Yellow croaker has a large asymptotic body size of 579 g and a relatively slow von Bertalanffy growth rate of 0.50. The Fang gunnel has a smaller asymptotic body size (30 g) and faster growth rate (0.65) (see Supplementary materials, Table S2). The other 21 species are non-target species, but may/may not sustain capture as bycatch in different fisheries. The following three

scenarios were simulated to address catchability and fishing effects on target and non-target species:

- (1) A single-species fishery simulated the “ideal” catchability of fishing gears of 1 for target species and 0 for non-target species. We simulated two exclusive gears fishing on two target fish species, and no bycatch in this scenario. Fishing effects on non-target species resulted completely from trophic interactions that emerged from predation and competition processes. Considering the potential “path-dependence” characteristics of CAS (i.e., the current status of system shapes its future, as a result of nonlinearity from local interactions such as hysteresis behavior) (Levin, 1998), fishing efforts were simulated with different timing in the following three sub-scenarios: (i) fishing was imposed simultaneously on two species; (ii) yellow croaker were subject to fishing for 50 years firstly and then both the species were subject to fishing afterwards; and (iii) fishing was applied to Fang gunnel for 50 years and then on both species. Fishing mortality (instead of fishing effort, for a direct comparison regarding catchability) was set from 0 to 0.5 year⁻¹ for yellow croaker (step = 0.02 year⁻¹) and 0 to 5 year⁻¹ for gunnel (step = 0.2 year⁻¹).
- (2) A multispecies stow-net fishery simulated the actual stow-net fishery in Haizhou Bay. Species-specific catchability was estimated from the survey data. The catchability of the target species was 0.15 and 1 for Fang gunnel and yellow croaker, respectively. The catchability coefficients of the other 21 species were listed in the Supplementary materials (Table S2). Fishing effort was constant across all species and varied in different simulation runs, ranging from 0 to 3 year⁻¹ to cover the estimated fishing mortality of 1.47 year⁻¹ in Haizhou Bay. Impacts of fishing on non-target species were attributed to both bycatch and trophic interactions.
- (3) A multispecies trawl fishery simulated constant catchability for all the species. The trawl fishery was used to illustrate the theoretical effects of constant catchability. This scenario assumed a catchability coefficient of 0.5 for all species for simulation purposes. However, catchability may vary substantially among species in trawl fisheries (Fraser et al., 2007). Fishing efforts were assumed to be the same across species, ranging from 0 to 3 year⁻¹, and fishing effects on non-target species were attributed to both bycatch and trophic interactions.

The stochasticity of the fish community was assumed to arise from two sources in the operational model, i.e., reproductive efficiency (efficiency of turning energy into offspring) (Hartvig et al., 2011) and carrying capacity of background resources (Shepherd and Cushing, 1980; Maury, 1996; MacKenzie et al., 2003; Houde, 2008). It is noteworthy that this approach intended to account for critical stochastic processes, whereas the environmental fluctuations that influence fish community dynamics could not be fully evaluated. The size-spectrum model does not explicitly include environmental variation, which influence multiple biological processes simultaneously. Stochasticity was simulated using a Monte Carlo approach (Houle et al., 2012). Reproductive efficiency was assigned a lognormal distribution with mean of 0.1 (consistent with the deterministic model) and standard deviation of 0.05. The carrying capacity was assumed to follow a lognormal distribution with mean from the deterministic model and standard deviation 0.5 of the mean (the value was used to match the CV of 0.5 for the variability of reproductive efficiency). Three sub-scenarios were considered, including separate simulations for the two individual sources of uncertainty and one combining both sources of uncertainty.

The settings of the simulation scenarios are summarized in Table 1. For each scenario, the models were run for 150 years to

simulate long-term fishing. Fish community dynamics over the last 30 years were used to evaluate the effect of fishing on the target species and the fish community.

2.3. Measurement of fisheries status

The projected population biomass and yield of the target species were recorded in each simulation run. The optimum fishing effort F_{MSY} was derived from the yield curve. We used the following ecological indicators to monitor the dynamics of fish community in abundance, species composition and size characteristics:

- (1) Total biomass of fish community, $B = \sum \text{Biomass}_i$, indicating the total biomass of individual fishes (Murawski, 2000; Fulton et al., 2005);
- (2) Shannon biodiversity index, $H' = -\sum p_i \ln(p_i)$, where p_i indicates the proportion of biomass of each species in the fish community (Shannon, 1948);
- (3) Mean body weight, $W = \frac{\sum W_i}{\sum N_i}$, denoting the mean weight of all individuals in the community (Rochet and Trenkel, 2003), where W_i and N_i indicated the total biomass and abundance of each species; and
- (4) The slope of community size spectrum γ , derived as the slope of linear regression between log-abundance and log-weight, $\log(N_w) = \alpha + \gamma \log(w)$; where N_w is the total abundance of all species in size-bin w (Rice and Gislason, 1996).

Only individuals larger than 0.1 g were included in the calculation of the ecological indicators. The effects of trophic interactions, bycatch and uncertainty were evaluated by comparing the dynamics of the fish community in different scenarios. The processes of model building, simulation, and MSY evaluation are summarized in Fig. 1.

3. Results

3.1. Single-species fishery

The single-species fishery imposed no direct influence on the non-target species. However, this scenario was different from traditional single-species assessment, since it explicitly accounted for trophic interactions (in this sense the simulated fishery could be referred to as ecosystem-based single-species fishery). The three fishing scenarios addressing potential path-dependent effects led to consistent results. Thus only the scenario with simultaneous fishing effort (scenario 1a) was shown (Fig. 2). The population biomass of Fang gunnel and yellow croaker decreased with increasing fishing mortality, and the croaker population collapsed (population biomass close to zero) when fishing mortality was higher than 0.3 year⁻¹. The yield of gunnel kept increasing to reach 150 t/year within the range of fishing mortality (0–5 year⁻¹), while croaker had a maximum yield around 3 t/year with a fishing mortality of 0.16 year⁻¹. The population size of croaker was 39% of unfished biomass when long-term MSY was achieved, while total community biomass decreased by 5% (Table 2). The harvest of croaker had a limited effect on gunnel biomass and yield, but increased fishing effort on gunnel increased the yield of croaker (Fig. 2, 4th panel). The four ecological indicators showed limited responses to the two fisheries (Table 2).

3.2. Stow-net fishery

The stow-net is the prevalent fishing gear in Haizhou Bay. The small mesh size results in the capture of various species with different efficiencies (Supplementary materials, Table S2). The yield

Table 1
Summary of fishery settings in the simulation scenarios. In scenario 1, fishing efforts were simulated with three timing, (1a) fishing imposed simultaneously on two species; (1b) fishing on yellow croaker for 50 years then on both species afterwards (1c) fishing on Fang gunnel for 50 years then on both species afterwards. In Scenario 4, a Monte Carlo simulation approach was used to examine the consequence of the uncertainty arising from (4a) reproductive efficiency (4b) carrying capacity of background resources, and (4c) a combined sources of uncertainty.

Scenario	Simulation	Fishing effort	Catchability	Selectivity	Uncertainty
1	Single-species fishery for croaker and gunnel, “ideal” catchability	0–0.5 year ⁻¹ for yellow croaker, 0–5 year ⁻¹ for gunnel with three schedules	1 for target species, and 0 non-target for species	Species-specific knife-edge selectivity	Deterministic
1a	–	Fishing simultaneously on two species	–	–	–
1b	–	Fishing croaker for 50 years then on two species	–	–	–
1c	–	Fishing gunnel for 50 years then on two species	–	–	–
2	Stow-net fisheries in Haizhou Bay, “realistic” catchability	0–3 year ⁻¹ for all species	Species-specific catchability estimated from stow-net fisheries	Knife-edge selectivity	Deterministic
3	Trawl fishery, “theoretical” catchability	0–3 year ⁻¹ for all species	0.5 for all species	Knife-edge selectivity	Deterministic
4	Stow-net fisheries with uncertainty	0–1.5 year ⁻¹ for all species	Species-specific catchability for stow-net fisheries	Knife-edge selectivity	Lognormal variation (CV = 0.5)
4a	–	–	–	–	Variation in reproductive efficiency
4b	–	–	–	–	Variation in carrying capacity of background resources
4c	–	–	–	–	Combined variation

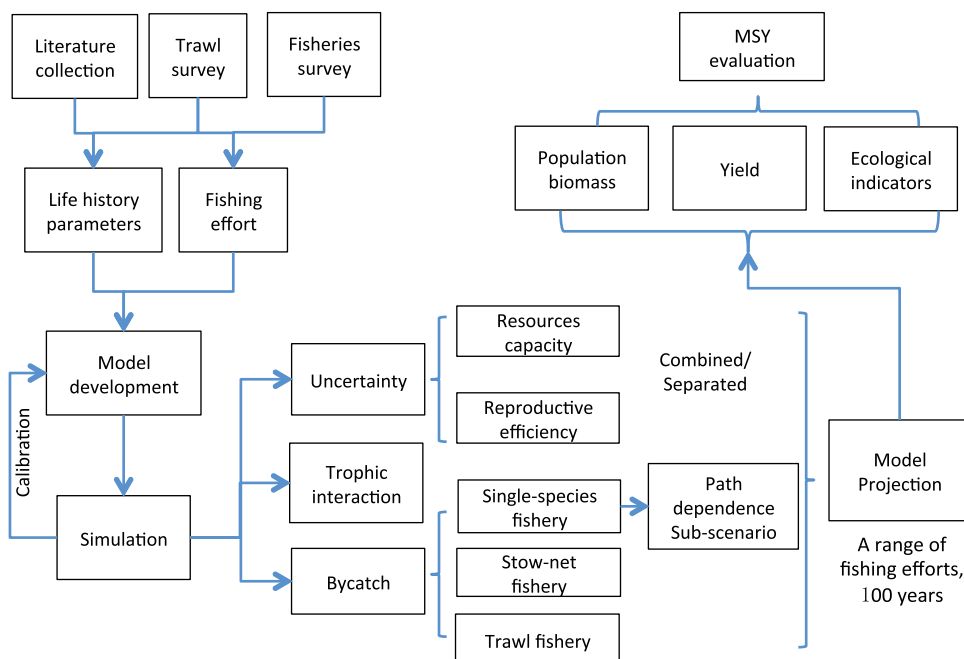


Fig. 1. Flow chart of the processes of model building, simulation design, and MSY evaluation.

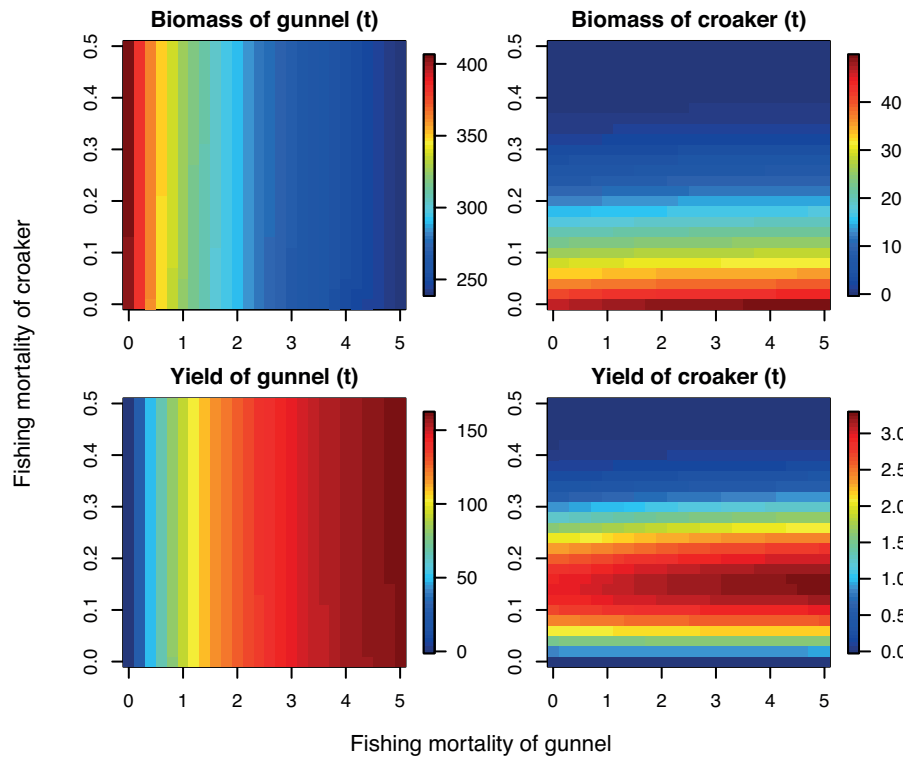


Fig. 2. Population biomass and yield of yellow croaker and Fang gunnel in a single-species fishery (Scenario 1). Biomass and yield are measured as the total weight of the whole marine area (t and t/year respectively). Results are for the scenario with fishing effort imposed simultaneously on two species.

Table 2

Summary of fishery status at MSY for yellow croaker in a single-species fishery, stow-net fishery and trawl fishery. $P_{MSY}\%$ of yellow croaker was the proportion of target species population biomass at MSY compared to the maximum population biomass, and $B_{MSY}\%$ was the proportion of community biomass at MSY compared to unfished community biomass. The values inside parentheses denote the minimum and maximum of ecological indicators resulted from the various simulation scenarios of fishing effort for each type of fisheries listed in Table 1. (The statistics for Fang Gunnel were not shown as its yield kept increasing beyond the simulation scope)

	Single-species fishery	Stow-net fishery	Trawl fishery
F_{msy} (year ⁻¹)	0.16	1.02	1.02
MSY (t)	3.27	661.4	2007.2
$P_{MSY}\%$	39%	77%	59%
$B_{MSY}\%$	95%	75%	80%
B (10 ³ t)	9.69 (9.67, 10.16)	8.07 (4.30, 10.78)	8.68 (5.82, 10.78)
H'	1.57 (1.56, 1.60)	2.70 (1.61, 2.86)	1.75 (1.33, 2.25)
mW (g)	2.36 (2.35, 2.43)	3.03 (2.50, 3.10)	4.39 (2.48, 5.88)
γ	-1.40 (-1.40, -1.40)	-1.37 (-1.56, -1.23)	-1.69 (-5.23, -1.26)

of Fang gunnel increased to 150 t/year within the range of simulated fishing effort (Fig. 3). The yield of yellow croaker showed a unimodal response to harvest with a maximum yield of 661 t/year at $F=1.02$ year⁻¹ (Fig. 3, panel D), which was substantially higher than that achieved for the single-species fishery (Table 2). The population biomass of the two species peaked at $F=1.62$ year⁻¹ and $F=0.62$ year⁻¹, respectively (Fig. 3, panels A and B). The population size of yellow croaker at MSY was 77% of the maximum population biomass (Table 2).

The total community biomass decreased monotonically as a result of harvest (Fig. 3, panel E). The biodiversity index H' increased with fishing effort (Fig. 3, panel F), and was maximized at $F=2.22$ year⁻¹. Mean body weight showed a zigzag response curve, with a peak at $F=0.66$ year⁻¹ and a local minimum value at $F=2.2$ year⁻¹ (Fig. 3, panel G). The slope of the community size spectrum showed a discrete pattern, with sharp changes around $F=0.3$ year⁻¹ and $F=1.3$ year⁻¹ (Fig. 3, panel H). No distinguishable pattern (i.e., minimum or maximum) in the curves of ecological indicators corresponded to F_{MSY} of the two target species.

3.3. Trawl fishery

The trawl fishery scenario assumed the same catchability for all the species to illustrate the “theoretical” effect of catchability on the ecosystem. The fishery status in the trawl fishery had some similar patterns to that in the stow-net fishery, but was more variable (Fig. 4). The yield of Fang gunnel increased to 800 t/year except for a local minimum at $F=0.5$ year⁻¹ (Fig. 4, panel C). Yellow croaker had the maximum yield of 2007 t/year at $F=1.02$ year⁻¹ (Fig. 4, panel D), much higher than for the previous scenarios (Table 2). The biomass of gunnel was strongly dependent on fishing mortality, and increased sharply as F increased beyond 0.5 year⁻¹ (Fig. 4, panel A). The population biomass of croaker had a steep unimodal distribution (Fig. 4, panel B), and the biomass at MSY was 59% of that stock size (Table 2).

The four ecological indicators showed a sharp transition in F around 0.5 year⁻¹, at which community biomass, mean body weight, and the slope of the community size spectrum had local maximum values, while biodiversity index was minimized. The maximum value of biodiversity index was achieved at

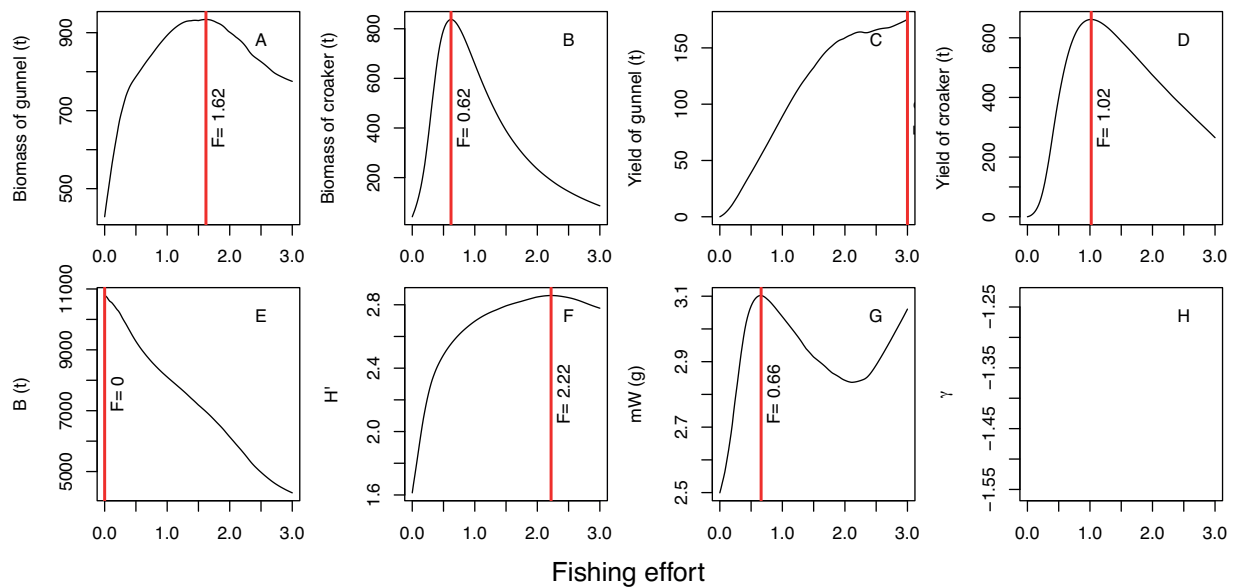


Fig. 3. The effects of the stow-net fishery on the fish community (Scenario 2). The top panel shows the population biomass and yield of yellow croaker and Fang gunnel, respectively, and the bottom panel shows the response of the ecological indicators to the long-term fishing. Vertical lines indicate the fishing effort at which each variable is maximized.

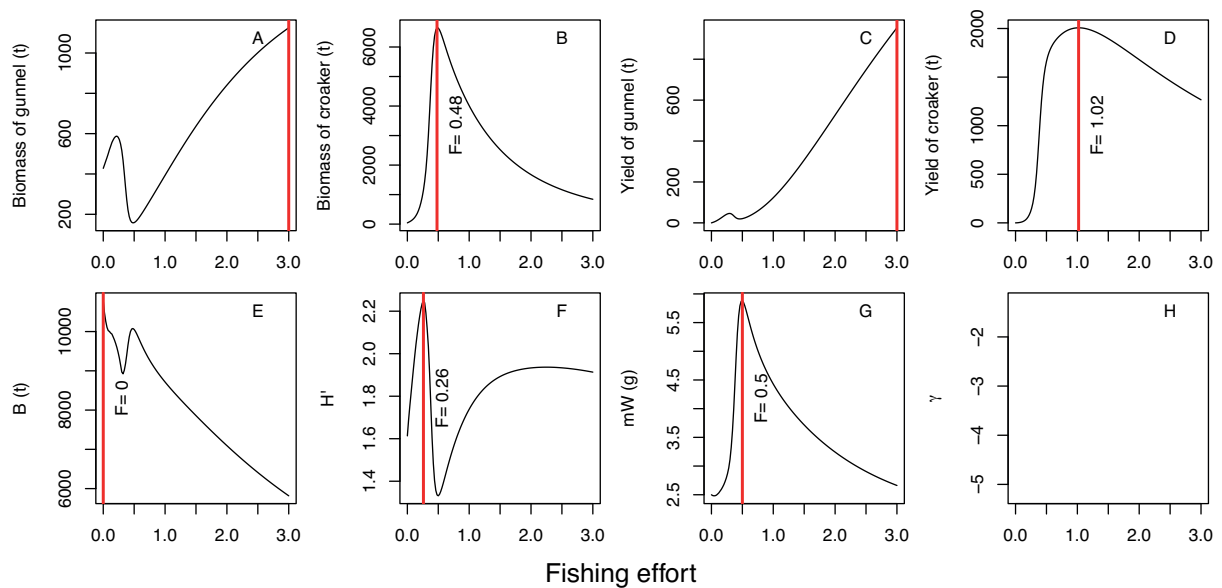


Fig. 4. The effect of the trawl fishery on the fish community (Scenario 3). The top panel shows the population biomass and yield of yellow croaker and Fang gunnel, respectively, and the bottom panel shows the response of the ecological indicators to the long-term fishing. Vertical lines indicated the optimum fishing efforts for the maximization of the measured variables.

$F = 0.26 \text{ year}^{-1}$ (Fig. 4, panel G), corresponding to the local minimum value of community biomass and the slope of size spectrum. The slope of the community size spectrum showed a discontinuous pattern (Fig. 4, panel H). No distinguishable pattern of ecological indicators corresponded to F_{MSY} of the two target species.

3.4. Uncertainty

Stochasticity in reproductive efficiency and the carrying capacity of background resources imposed different degrees of uncertainty on the stow-net fishery (Fig. 5). The dynamics of the carrying capacity dominated the variation of model outputs, while variation in reproductive efficiency had limited effect, given the same coefficient of variance (0.5 in all sub-scenarios). The projected population biomass and yield of the target species

showed similar patterns in the deterministic model. However, the stochastic carrying capacity slightly increased the stock biomass and yield, while reproductive efficiency led to the same values (Fig. 5).

The simulation in scenario 4a (i.e., stochastic reproductive efficiency) led to values for the ecological indicators that were similar to those for the deterministic model (Fig. 5, lower panel). Although the mean body weight in scenarios 4b (i.e., stochastic carrying capacity) and 4c (i.e., combined two stochastic sources) had a similar shape to that of the deterministic model, the expected values increased sharply. The slope of the community size-spectrum showed different trends among the scenarios. The variation of projected community biomass and mean body weight was remarkably large in scenarios 4b and c, and biodiversity showed low variability even in the presence of uncertainty of all sources.

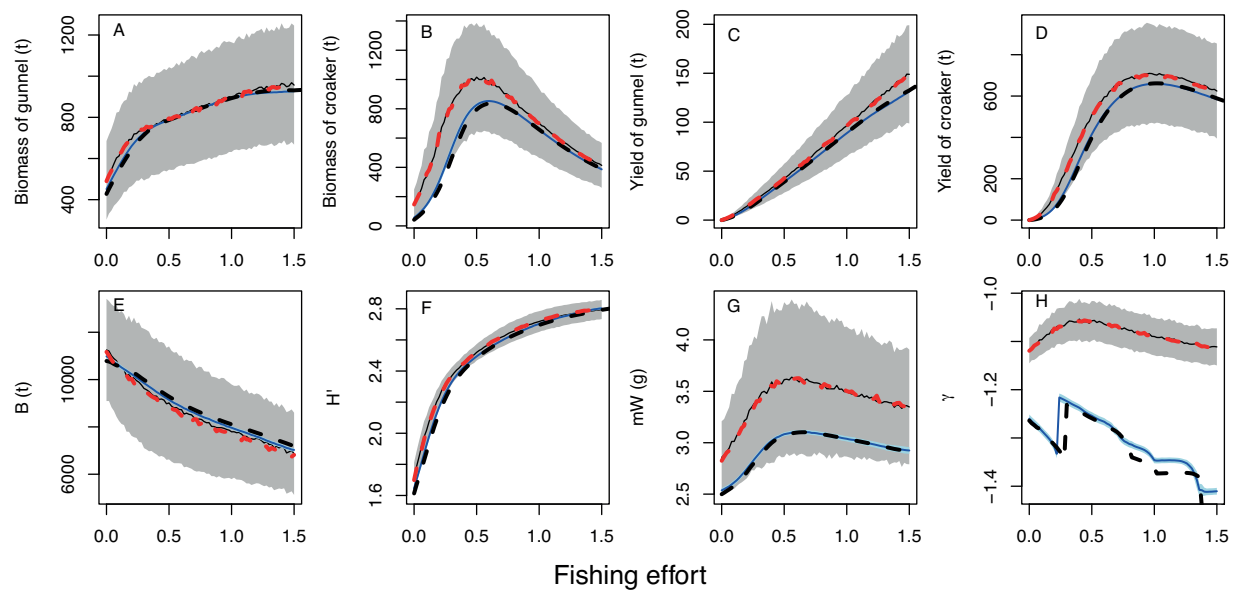


Fig. 5. The effects of the stow-net fishery on the fish community when there is uncertainty arising from dynamic carrying capacity of background resources and reproductive efficiency. The blue lines with shading represent the mean and standard deviation of measurement variables in the simulation with dynamic reproductive efficiency (Scenario 4a, the blue shade is narrow); the black lines with shading indicate the projection in the simulation with dynamic carrying capacity (Scenario 4b); the red dash lines show the model output with combined sources of uncertainty (Scenario 4c); and the black dash lines indicated the deterministic model output (Scenario 2). The shading in Scenario 4c is not shown as it mostly overlaps with the shading in Scenario 4b.

4. Discussion

Sustainability is an essential goal for fisheries management that should be achieved in an ecosystem context (Gaichas, 2008), although the concept is currently subject to much debate (Pauly et al., 2002). This study evaluated the application of MSY in an explicit ecological context with regard to trophic interactions, bycatch and uncertainty, and explored emergent dynamics of fish stocks subject to multispecies fisheries. The results illustrated the following fundamental effects of ecological processes in determining harvest and fish community structure: (1) the single-species fishery imposed heavy fishing pressure on target species and could easily lead to stock collapse, but had limited effects on non-target fishes; (2) the stow-net and trawl fisheries increased MSY for the target species and promoted their resistance to fishing pressure; (3) uncertainty associated with background carrying capacity greatly changed the size structure of the fish community and reduced predictability; and (4) the response of ecological indicators to fishing pressure was generally nonlinear, which suggests that the long-term MSY might be difficult to monitor. The results highlighted the ecological complexity of marine ecosystems and the associated challenges facing fisheries management (Levin, 1998; Gaichas, 2008).

4.1. Trophic interactions and catchability

The role of trophic interactions has long been recognized in regulating the structures of food webs (Sissenwine, 1984; Hunsicker et al., 2011), density-dependent mortality and food competition (Frank et al., 2005; Hixon and Jones, 2005). One advantage of the size-spectrum model is the explicit consideration of trophic interactions (Andersen and Beyer, 2006; Pope et al., 2006; Hartvig et al., 2011; Andersen et al., 2015), since a rapid increase of interactions with increasing numbers of stocks are difficult to address using traditional approaches (Link, 1999; Mace, 2001). This study simulated the trophic interactions by assuming that individual fish were exposed to predation by all other species (Scott et al., 2014a), which allowed the dynamics of fish populations to emerge from underly-

ing ecological processes. For example, in the single-species fishery, increasing fishing mortality led to a monotonic reduction in the biomass of the target fish species, but the fish stock dynamics were completely different when bycatch was included. MSY increased by an order of magnitude, and the biomasses of both target species increased substantially as a result of fishing within certain ranges, which has been observed by a study using a similar operational model (Houle et al., 2013). Although the low MSY in the single-species fishery (3t/year) and large MSY in the trawl fishery (2007 t/year) were theoretical yields that are difficult to achieve in an actual ecosystem, the result highlighted the role of bycatch in fisheries and the emergent dynamics of ecosystems, which are often counterintuitive. The increasing biomass in the stow-net and trawl fisheries could be attributed to a **release of predation**, i.e., improved survival rates as a result of removing predators (Daskalov, 2002; Law et al., 2014). It should be noted that this process does not hold for all ecosystems, as some studies suggested that this was not likely to happen since complex food webs could offset the effects of predation release, which means that the removed predators should be replaced with other species within “finely meshed” food webs (Pace et al., 1999; Pauly et al., 2002). In addition, predators could indirectly impose positive effects on their prey by consuming other predators and competitors of the prey (Ulanowicz and Puccia, 1990), thus fishing on predators does not necessarily lead to an increase in the abundances of their prey (Pauly et al., 2002).

The size-spectrum model that implicitly defines a “meshed” food web with trophic interactions confirmed that the removal of yellow croaker in single-species fishery had limited influence on the fish community, implying the offset of predation release. However, in the stow-net and trawl fishery, the predation-release effect was significant (Figs. 3 and 4), suggesting the failure of compensation when non-target species were substantially removed (Supplementary materials, Fig. S6). The result suggests that the effect of predation release depends on bycatch. A caveat is such a pattern may also depend on the life-history of target species, the functional redundancy of the community, the intensity of fishing (National Research Council, 2006), and the discarding and survival rate of bycaught individuals. Predation release and other emergent

behaviors of the model should also be examined with regard to the model assumptions and the emergent processes in future studies.

Yellow croaker collapsed in the single-species fishery scenario with a fishing mortality of 0.3 year^{-1} , but was more resistant to fishing in the other scenarios. A possible explanation is that the disproportionate removal of the target and non-target species resulted in the changes in ecological roles (Zhou et al., 2010). Specifically, the collapse in single-species fishery could be attributed to “depensatory effect” (Walters et al., 2005), in which fishing on one species might increase the abundance of other species and lead to further decreases of the target species. Walters et al. (2005) proposed three potential mechanisms for such a phenomenon, including (i) cultivation effect, in which adult individuals suppress the competitors and predators of their own juveniles; (ii) competition-predation trade-offs, where fishing pressure may break the balance of fish competition and avoiding predation; and (iii) predation of multiple trophic levels, where the target species have a predator that can feed on fishes of lower trophic levels, which benefit from “predation release” and enhance food supply of their predators, thus suppress more on the target species. The size-spectrum model included mechanisms (i) and (iii) given the assumption of size-dependent predation, including the early life stage (De Roos et al., 2003).

Fishing mortality led to a reduced competitive capacity of the target species compared to their non-target competitors that could occupy ecological resources used to be available to the target species (Crowder et al., 2008; Zhou, 2008). An example of such a replacement is the collapse of Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf, where alternative predators, such as dogfish shark (*Squalidae* spp.) took the ecological niche of cod populations (Bundy and Fanning, 2005). In contrast, more “balanced harvest” (Garcia et al., 2012) in the stow-net and trawl fishery removed the competitive species proportionally, kept the relative competitive capacity, and promoted the resistance of target species to fishing pressure. The concerns of fishery selectivity were addressed in several studies (Zhou et al., 2010; Garcia et al., 2012), which suggests the potential of non-selective fishery to stabilize food web and increase overall productivity (Benoît and Collie, 2009; Jacobsen et al., 2014; Law et al., 2014). Our study showed that the increased productivity could also be achieved for a target species if fishery selectivity was manipulated with ecological considerations. Although there are controversies in the concept and implementation of balanced harvest such as discard management and endangered species conservation (Burgess et al., 2015 in press; Dambacher et al., 2015; Froese et al., 2015 in press), the balanced harvest strategy may provide a promising approach for EBFM.

4.2. Ecological indicators and uncertainty

Implementing EBFM requires the quantification of fishing impacts on marine ecosystems (Garcia and Staples, 2000), and the clear definition of ecosystem-based decision criteria (Link, 2005), for which purpose, ecological indicators can be used to provide the input for decision rules and to monitor management performances (Sainsbury et al., 2000). This study demonstrates that the performance of ecological indicators in multispecies fisheries would be greatly influenced by trophic interaction, bycatch and uncertainty. For example, the dynamics of ecological indicators around F_{MSY} of yellow croaker highly depended on the catchability scenarios, and it is difficult to use ecological indicators to indicate F_{MSY} . This pattern might blur decision making in practice, especially when there was significant uncertainty as shown in Fig. 5. Some ecological indicators showed desirable performances in the simulation, such as the biodiversity index in the stow-net fishery, which responded monotonically to fishing with small variation. We highlight that the assessment of ecological indicators should be considered in specific temporal and spatial scales, and an empirical reference system is

needed to validate the implementation (Rochet and Trenkel, 2003). Integrating multiple indicators in a state space model may adjust the issue and improve the validation of management strategies (Caddy, 2004; Rice and Rochet, 2005).

Recruitment variability has been recognized as the main driver of marine stock abundance (Hjort, 1914; Sinclair, 1997; Archambault et al., 2014), and several studies suggest the high variability in recruitment is related to variation in the mortality of early life stages, which can be attributed to many processes associated with growth and survival including temperature variation, larval drift, predator-prey interactions (Houde, 2008). Our study focused on the influence of reproductive efficiency and environmental carrying capacity, and the results showed that reproductive efficiency had trivial effects on the long-term dynamics (small variation in Fig. 5), while carrying capacity contributed substantially to the variability of yield, population biomass and ecological indicators (Fig. 5). The limited effect of reproductive efficiency may be attributed to the interactive food web that provides replaceable food sources and forms omnivory and weak association within the fish community (Pimm and Rice, 1987; Hartvig and Andersen, 2013). The weak and omnivore linkages may promote community persistence and stability (McCann et al., 1998; Emmerson and Yearsley, 2004), offsetting fluctuations in reproductive efficiency. On the other hand, the carrying capacity imposes a bottom-up control on trophic interactions (Ware and Thomson, 2005; Field et al., 2006; Hunt and McKinnell, 2006). The dynamics of carrying capacity drive the ecosystem with food availability for planktivores and larvae and juveniles of piscivores. This result suggests the potential recruitment failure can be less attributed to reproductive efficiency, but more to food limitation and the associated larval survival (Matsuura, 1996; Hughes and Tanner, 2000; Ljunggren et al., 2010), given the model assumption of size-dependent trophic interactions.

Although high fishing effort led to considerable variation in the projected biomass and yield, there was no sign of population collapses when F constantly exceeded the ideal F_{MSY} (Fig. 5). The contrast of this result with the aforementioned collapse of yellow croaker suggested that bycatch might play a more important role than ecological stochasticity in fish's resistance to fisheries. However, there were some caveats to be noted for our simulation approach. Firstly, the simulation included the species covering 90% of the biomass of the fish community, and rare species and their potential collapses were not included, which implies regime shifts, e.g., the current rare species become abundant in the fish community (Levin and Mollmann, 2014) cannot occur. The simulation showed a limited influence of the single species fisheries on non-target species. However, this result may not necessarily be real if predatory preferences were species- rather than size-specific. In addition, the assumed sources of uncertainty, reproductive efficiency and carrying capacity are only one piece of the whole picture of recruitment variability and uncertainty (Walker et al., 2003; Refsgaard et al., 2007; Houde, 2008; Thorpe et al., 2015), and there are many other factors that might influence the dynamics of ecosystems (Froese et al., 2008; Zhang et al., 2015 in press). The fish community in Haizhou Bay is not a closed system, and the adjacent fish community may have a great influence on the ecosystem when seasonal migration and meta-populations exist (Ying et al., 2011; Zhang et al., 2014). In general, the model is not yet capable of supporting tactical management decisions, but rather a tool for evaluating management strategies (Collie et al., 2014 in press; Scott et al., 2014a).

4.3. Implications for fisheries studies and management

The effects of implementing conventional MSY in a multispecies context has been evaluated by several studies using various ecolog-

ical models including Ecopath with EcoSim, differential equations of multi-populations, Volterra-type model, OSMOSE, Atlantis, and eventual threat index (Walters et al., 2005; Matsuda and Abrams, 2006; Worm et al., 2009; Legović et al., 2010; Smith et al., 2011; Geček and Legović, 2012; Burgess et al., 2013), which illustrated the application of single-species derived MSY might cause fish stock depletion and the deterioration of ecosystem structure. The size-spectrum model assumes size-dependent predation which implies two critical processes that are previously not considered adequately in shaping community dynamics: (1) trophic ontogeny, i.e., individual fish change food preference with the body size (Werner and Gilliam, 1984; Pimm and Rice, 1987); and (2) early-life mortality, due to predation and starvation (Jennings et al., 2001). Including these processes in modeling has contributed to new insights in implementing MSY. For example, Walters et al. (2005) used the Ecosim model to fit a wide variety of ecosystems and suggested that severe population depletion could result from applying MSY policies for every species in the ecosystem, but the depletion would not occur when the non-target species were managed conservatively. The simulation of a single-species fishery in this study provides a qualitatively different result, in which the fishery for yellow croaker rapidly collapsed when fished in isolation, although the size-spectrum model assumed a Beverton–Holt type of egg production–recruitment relationship. This unexpected consequence highlighted a risk that should be considered in the management of predator species fisheries with high selectivity. In addition, the maximum biomass of a target species could occur whilst it was being fished to a significant degree, once bycatch effects were included (Figs. 3 and 4). An increasing population size with fishing pressure runs contrary to the usual paradigm, and challenges management policies based upon thresholds proportional to the “unfished” stock biomass (Worm et al., 2009). The yield of yellow croaker in a single-species fishery, stow-net and trawl fishery, might represent an oversimplified reality, but implies the possibility of promoting the fishery harvest with a careful control of bycatch.

Our study demonstrates the role of trophic interaction, bycatch and uncertainty in the context of ecological sustainability. We identify a possible risk of implementing MSY without integrated considerations of ecological processes (Skern-Mauritzen et al., 2015 in press). In particular we emphasize the importance of addressing bycatch mortality for future model building and target setting for fisheries management. In addition, other harvest control rules, targets and threshold for fisheries management need to be evaluated within broader ecological considerations, which include species interactions, climate change, habitat conservation and social-economic factors. Moreover, dynamic rather than static control rules, such as short-term adaptive MSY can also be evaluated in the ecological context for improving fisheries management (Fogarty, 2014; Collie et al., 2014 in press).

Supplementary material

In the Supplementary materials, we summarized the structure and parameterization of the multispecies size-spectrum model. We listed the sub-models in Table S1, the species-specific parameters in Table S2, and additional parameters in Table S3. The distribution of the studied area, Haizhou Bay was mapped in Fig. S1. A basic output of the calibrated model was shown in Fig. S2, and the predicted biomass and the observed survey data were compared in Fig. S3. The dynamics of species composition in the fish community caused by changing fishing efforts in stow-net and trawl fishery were shown in Figs. S4 and S5, respectively. The predation mortality of Fang gunnel and yellow croaker in stow-net and trawl fishery were shown in Fig. S6 to illustrate the “predation release” effect.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fishres.2015.10.007>.

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