Risks of ignoring fish population spatial structure in fisheries management

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Risks of ignoring fish population spatial structure in fisheries management

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Abstract: Ignorance of spatial structures in fisheries management may lead to unexpected risks of overexploitation. Based on the information about small yellow croaker (*Larimichthys polyactis*) off the coast of China, we simulated a fish population consisting of three subpopulations mixing at intermediate levels, which was considered in the "true" spatial structure of the population in this study. Three scenarios of population spatial structure were assumed in assessing and managing this simulated fishery: (*i*) metapopulation, which has the same structure as the "true" population; (*ii*) three independent subpopulations, which overlook the exchanges among the subpopulations; and (*iii*) unit population, which completely ignores the population spatial structure. Corresponding approaches were applied to assess and manage each of these assumed fish populations. The management time period was assumed to be 10 years with two harvesting levels (i.e., maximum sustainable yield (MSY) and $f_{0.1}$). Assessing and managing the metapopulation as several independent populations could lead to a high probability of overexploitation. Managing the metapopulation as a unit population could lead to local depletion. Use of MSY as a management target may be risk prone in the existence of a metapopulation, and use of a fishing mortality lower than $f_{0.1}$ as a management target is more desirable.

Résumé : Ne pas tenir compte des structures spatiales dans la gestion de la pêche peut mener à des risques imprévus de surexploitation. En utilisant des données sur la courbine jaune (*Larimichthys polyactis*) du large de la côte de Chine, nous avons simulé une population de poissons comprenant trois sous-populations qui se mélangent à des niveaux intermédiaires, ce qui est considéré la « véritable » structure spatiale de la population dans notre étude. Nous avons supposé trois scénarios de structure spatiale de la population dans l'évaluation et la gestion de cette pêche simulée, (*i*) une métapopulation qui a la même structure que la population « véritable », (*ii*) trois sous-populations indépendantes, ce qui néglige les échanges entre les sous-populations et (*iii*) une population unitaire qui ignore complètement la structure spatiale de la population. Nous avons utilisé des méthodes semblables pour évaluer et gérer chacune de ces populations hypothétiques de poissons. Nous avons déterminé une période de gestion de 10 ans avec deux niveaux de récolte (c.-à-d. le rendement maximum durable (MSY) et $f_{0,1}$). L'évaluation et la gestion de la métapopulation comme plusieurs populations indépendantes pourraient mener à une forte probabilité de surexploitation. La gestion de la métapopulation comme une population unitaire pourrait provoquer des déplétions locales. L'utilisation de MSY comme cible de gestion peut entraîner des risques, s'il existe une métapopulation; l'utilisation d'une mortalité due à la pêche inférieure à $f_{0,1}$ comme cible de gestion semble donc plus désirable.

[Traduit par la Rédaction]

Introduction

A metapopulation is defined as a group of subpopulations in which local subpopulation dynamics are driven in part by dispersal from other subpopulations in the group (Hanski 1999). Many studies suggest that metapopulations are common and their dynamics are strongly influenced by spatial attributes of habitat patches (Lindenmayer et al. 2001; Schtickzelle et al. 2005), life history patterns, and distances and dispersal rates among local subpopulations (Sawchik et al. 2002; Curtis and Naujokaitis-Lewis 2008).

In marine fisheries, two important factors should be considered when we evaluate impacts of exploitation on fish population dynamics: (*i*) population spatial structure resulting from dispersal and movement of fish in different life history stages (Dieckmann at al. 1999) and (*ii*) spatial dynamics of fishing efforts often resulting from spatial variability in population density (Botsford et al. 2009).

In most marine species, early life history is characterized by a planktonic larval stage. Because of the mainly passive nature of the larval stage, they are often carried over large distances by the dominant ocean currents (Shanks et al. 2003; Kinlan et al. 2005; Trakhtenbrot et al. 2005). When the adult stage is predominantly sessile, larval dispersal is

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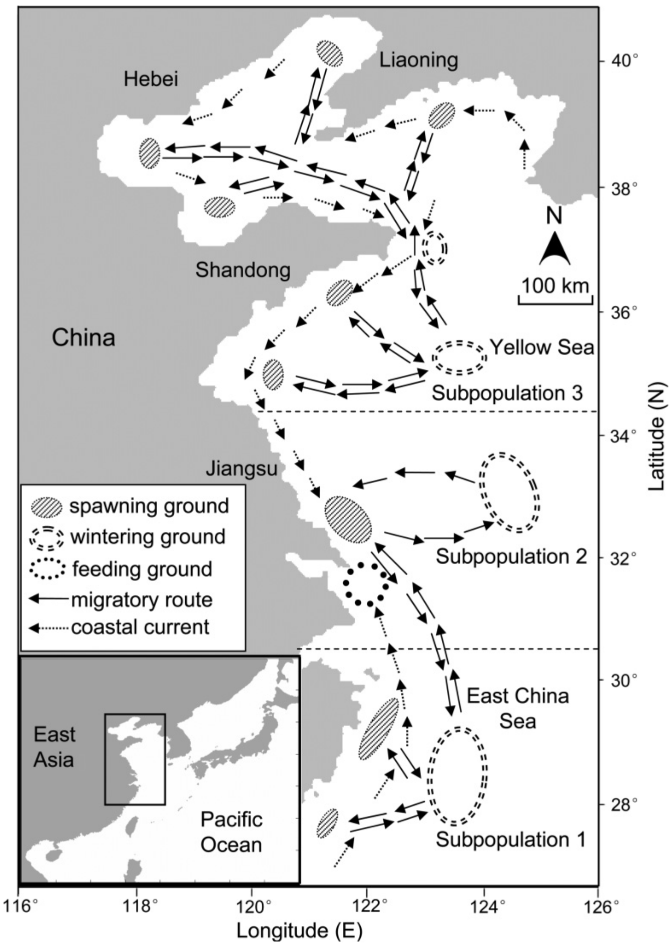
the main cause of spatial structure in marine populations. However, for many species the adult stage is actually more mobile than the larval stage. In such cases, this provides additional connectivity over a broad range of spatial scales, ranging from daily movement over metres to migrations over thousands of kilometres.

Many studies suggest that increasingly more marine fish populations should be considered as metapopulations, which are spatially structured and divided into several subpopulations mixing in intermediate levels (Kritzer and Sale 2004). This implies that it is necessary to control the repartition of the fleets on different fishing zones based on known spatial structures and interactions among subpopulations in fisheries management (Mchich et al. 2006). However, in many cases spatial structures are often ignored, and fish populations are considered as single and well-mixed populations or identical and independent populations in assessment and management (Botsford et al. 2009), often leading to over-exploitation (Stephenson 1999). The importance of considering spatial structure in the management of metapopulation fisheries was described in several studies (e.g., Hutchings 2000; Hutchinson 2008). Heifetz and Quinn (1998) showed that it is critical to consider movement and spatial structures in management. Hart and Cadrin (2004) developed a metapopulation approach to assess the yellowtail flounder (*Limanda ferruginea*) fishery. Heath et al. (2008) developed a metapopulation model in the case of North Sea cod (*Gadus morhua*) and showed the importance of considering population spatial structure in the management. More studies are still needed to improve our understanding of impacts of population spatial structure on fisheries stock assessment and management.

Based on the information about the small yellow croaker, *Larimichthys polyactis* in China, we simulated a metapopulation consisting of three subpopulations with migrations among the subpopulations. We then evaluated consequences of ignoring fish population spatial structure in metapopulation stock assessment and management.

Fig. 1. China Coastal Current and migration routes and three subpopulations of small yellow croaker. The two horizontal dashed line divides the small yellow croaker into three subpopulations, based on the migration routes.



Materials and methods

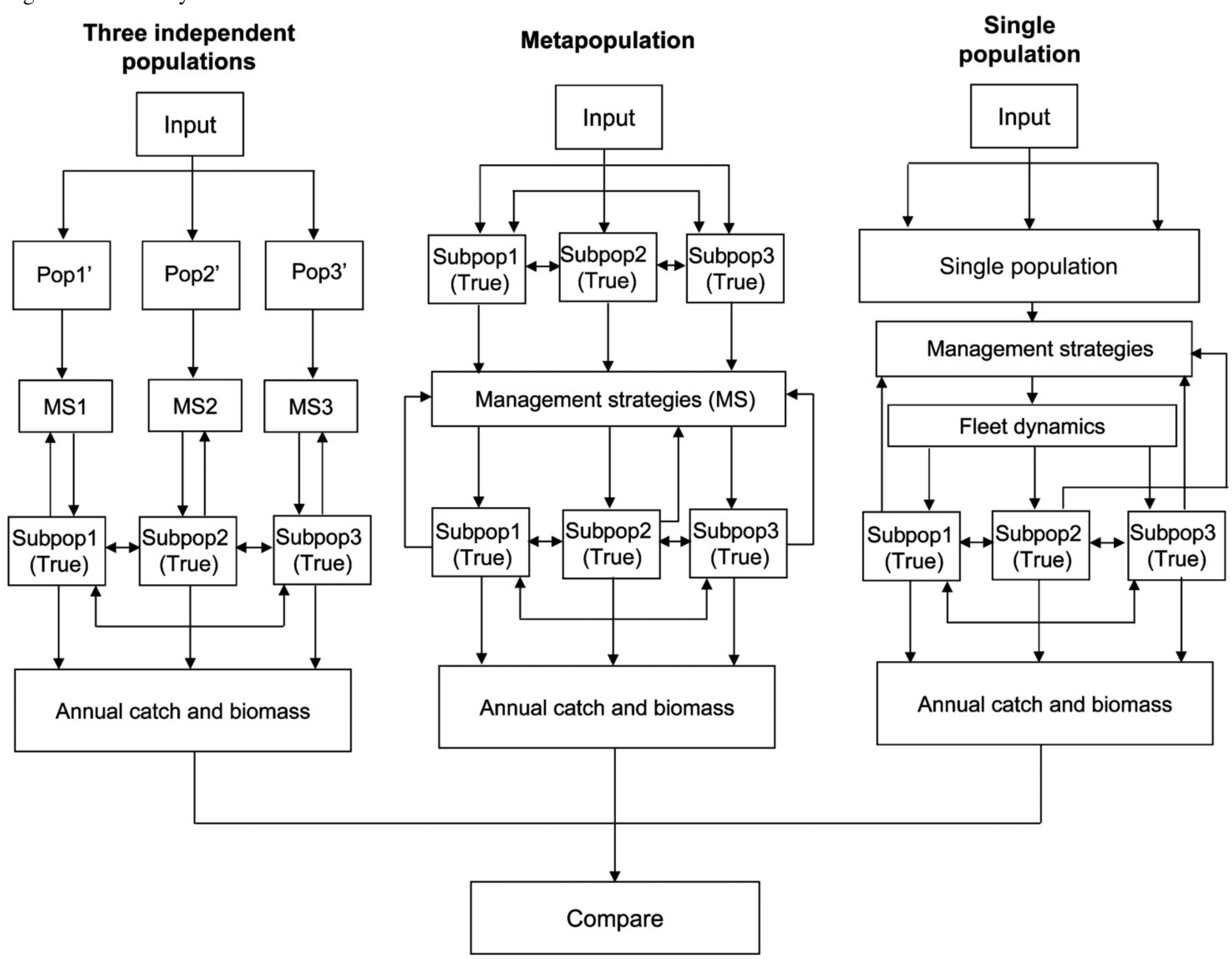
The small yellow croaker is a bentho-pelagic fish species of family Sciaenidae, inhabiting coastal waters and estuaries (Seikai National Fisheries Research Institute 2001). It supports important fisheries in Korea, Japan, and China. The species is widely distributed in the Bohai Bay and the Yellow and East China seas of the Northwest Pacific Ocean (Seikai National Fisheries Research Institute 2001). The small yellow croaker spawn pelagic eggs in spring, and its breeding grounds are located in the coastal area (Seikai National Fisheries Research Institute 2001). A long pelagic larval phase is observed in the small yellow croaker, which implies the high dispersal ability of this species. However, the small yellow croaker migrates back and forth regularly, between their spawning ground (also their feeding ground) in shallower water and three overwintering grounds (Fig. 1; Liu 1962). Based on the studies of its spawning migration patterns and morphological variables, Liu (1962) and Ikeda (1964) suggested that three groups existed throughout the range of small yellow croaker (Fig. 1). Molecular biology studies suggested weak but significant population genetic structures among the three subpopulations (Han et al. 2009; Lin et al. 2009). Weak genetic structures indicated the existence of gene flow but limited individual exchanges among the subpopulations. The early life history, migration routes, population spatial structure, and intermediate levels of individual exchanges among the subpopulations imply that the small yellow croaker population is a metapopulation. Thus, this species is a good candidate to evaluate the impacts of spatial structure on stock assessment and management.

For this study, it was assumed that the metapopulation of the small yellow croaker in China consisted of three subpopulations. The subpopulation in the East China Sea (subpopulation 1) was distributed in the area to the south of 30.5°N. The South Yellow Sea subpopulation (subpopulation 2) was located in the area between 30.5°N and 34.5°N. The North Yellow Sea and Gulf of Bohai subpopulation (subpopulation 3) was located in the area to the north of 34.5°N (Fig. 1). We collected the yield (Chinese Fishery Yearbook Publishing House 2000–2009) and scientific survey catch-per-unit-effort (CPUE) data (Lin et al. 2006; Lin 2009; Chinese Fishery Yearbook Publishing House 2000–2009) for the small yellow croaker of the three subpopulations from 1999 to 2008. Owing to lack of reliable estimates, a constant migration rate was assumed based on the coastal current direction and speed in spring (Table 1; Li et al.

Table 1. Exchange rates among different subpopulations assumed based on the coastal current orientation and velocity in spring seasons.

	From		
To	Subpopulation 1	Subpopulation 2	Subpopulation 3
Subpopulation 1	—	0.15	0.05
Subpopulation 2	0.18	—	0.15
Subpopulation 3	0.08	0.1	—

Fig. 2. The design of this study. Three spatial options were considered in the management: (*i*) metapopulation structure assuming that the spatial structure is correctly identified; (*ii*) three independent subpopulations ignoring the exchange among subpopulations; (*iii*) unit population ignoring the spatial structure. The parameters were estimated based on different spatial options and then used to estimate the harvest level. The harvest level was applied to the metapopulation (true population structure) to manage the fishery based on assumed spatial structures to generate annual yield and stock biomass data.



2000), because larval dispersal of this species with the China Coastal Current was considered to play a primary role in the formulation of their spatial structure (Han et al. 2009; Lin et al. 2009).

We simulated a metapopulation with three subpopulations and limited movements between the subpopulations. Although the fishery was simulated based on the information available on the small yellow croaker population, it should not be considered as exactly the same as the small yellow croaker fishery, because many key parameters had to be assumed. Nevertheless, such a simulated fishery with known spatial structure is sufficient for this study.

The "true" population structure assumed for the simulations was that of a metapopulation. Three spatial options were considered in the assessment and management: (*i*) metapopulation structure, which implies we "correctly" delineated the "true" spatial structure of the population; (*ii*) three independent subpopulations with no intersubpopulation mixing, which implies that we considered the separation of the three subpopulations, but ignored the migration among the three subpopulations; and (*iii*) unit population, which means we ignored the spatial structure existing in the "true" population. These three spatial options correspond to "correct", "partially correct", and "wrong" interpretation of the population spatial structure, respectively, in the assessment and management.

Four steps were taken in evaluating the risk of ignorance of the spatial structures in fisheries management (Fig. 2). First, an operating model was developed to define the "true" dynamics and spatial structure of a target metapopulation. The operating model was fitted to the data of Chinese small yellow croaker fishery to estimate parameters for simulating "correctly" defined metapopulation dynamics. Second, random variability was added to the data generated from the first step to generate simulated "observed" data for the metapopulation. The population parameters were estimated for the respective three spatial options considered in this study. Corresponding management harvest control rules were developed. Third, these harvest rules were applied to manage the simulated fishery to generate a set of annual yield and stock biomass data. Finally, we used yield, population biomass, and stock status to compare managements based on different population spatial structures assumed in the assessment.

In summary, we simulated a fishery with a defined spatial structure as a "true" fishery and tried to manage this fishery under the scenarios having perfect, partial, and wrong knowledge about the population structure. We compared the performance of management under these three scenarios to determine the importance of population spatial structure in fisheries assessment and management.

Operating model

The "true" population dynamics were simulated using a surplus production model with the consideration of migrations among the three subpopulations. The metapopulation structure likely results from larval transportation in their pelagic phase and adults in each subpopulation having migration routes that maintain isolation among subpopulations and result in limited mixing among adults of differing "home" populations. However, it is impossible to know the relative contributions of larval transportation and adult movements to the exchange of fish among the subpopulations. Thus, the ranges of exchange rates among subpopulations were assigned somewhat arbitrarily based on relative differences in coastal currents (Li et al. 2000). For lack of information, the exchange rates were assumed to be density-independent.

The population dynamics of the metapopulation were given by the equation

$$(1) \qquad B_{i,t+1} = B_{i,t} + r_i B_{i,t}\left(1 - \frac{B_{i,t}}{K_i}\right) - \sum_{j \neq i}^{R} \theta_{i \to j} B_{i,t} + \sum_{j \neq i}^{R} \theta_{j \to i} B_{j,t} - C_{i,t}$$

where $B_{i,t}$ is the biomass of subpopulation i in year t; r_i is the growth rate of subpopulation i; K_i is the carrying capacity of subpopulation i; $\theta_{i \to j}$ is the annual rate of movement from subpopulation i to j, describing the proportion of individuals moving out of subpopulation i to subpopulation j in a year; and $C_{i,t}$ is the catch of subpopulation i in year t.

The annual predicted CPUE of subpopulation i in year t, $\hat{U}_{i,t}$, is calculated as

$$(2) \qquad \widehat{U}_{i,t} = q_i B_{i,t} \mathrm{e}^{\varepsilon} \qquad \varepsilon \sim N(0, \sigma^2)$$

where q_i is the catchability of subpopulation i; ε is the normally distributed errors; σ is the standard deviation of ε; and $B_{i,t}$ is defined as above. We estimated the parameters of the metapopulation (r, K, q, and B_0) by minimizing the following objective function:

$$(3) \qquad \mathrm{RSS} = \sum_{i}^{R} \sum_{t}^{T} (\log \widehat{U}_{i,t} - \log U_{i,t})^2$$

where $\hat{U}_{i,t}$ is the predicted CPUE of subpopulation i in year t; $U_{i,t}$ is the observed CPUE of subpopulation i in year t; R is the total number of subpopulations; and T is the total number of years for which data were available.

Estimation model

For the metapopulation management option, we used the true parameters estimated using eqs. 1 to 3 to develop harvest control rules. For the three independent subpopulations management option, we estimated the parameters separately for each subpopulation as if they were the independent populations. The dynamics of each population can be described as

$$(4) \qquad B_{i,t+1} = B_{i,t} + r_i B_{i,t}\left(1 - \frac{B_{i,t}}{K_i}\right) - C_{i,t}$$

where K_i is the carrying capacity of "population" i; and $B_{i,t}$, r_i, and $C_{i,t}$ are defined as above. Parameters were then estimated using eqs. 4, 2, and 3 for each subpopulation separately.

For a unit population management option, we used the following equation to describe the population dynamics:

$$(5) \qquad B_{\mathrm{all},t+1} = B_{\mathrm{all},t} + r_{\mathrm{all}} B_{\mathrm{all},t}\left(1 - \frac{B_{\mathrm{all},t}}{K}\right) - C_{\mathrm{all},t}$$

where $B_{\mathrm{all},t}$ is the "current population biomass" for all the three subpopulations treated as if they were a unit population in year t. The population parameters were estimated using eqs. 5, 2, and 3.

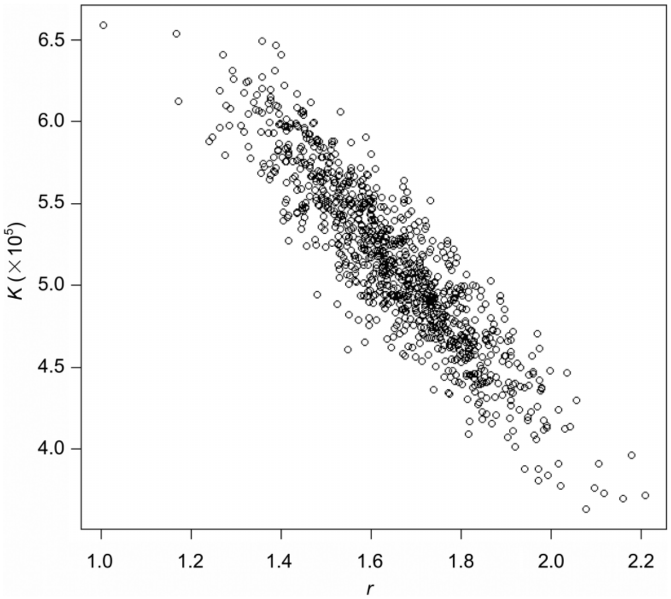
Uncertainty can be incorporated in a surplus production model in different ways. One approach is to simulate parameters r and K from a given multivariate normal distribution defined by a vector of means and variance–covariance matrix of the parameters (see Bard 1974, p. 316 for the algorithm). Many studies suggest a negative correlation between r and K (Bell 1990; Underwood 2007). We developed a variance–covariance matrix of r and K, with a correlation coefficient of –0.9 and the coefficient of variation (CV) of 10%. This is equivalent to the level of the correlation coefficient and CV in estimating r and K in the parameter estimation of this study when we fitted the production model to CPUE and catch data for the small yellow croaker. The variance–covariance matrix $\mathbf{\Sigma}$ was defined as

$$(6) \qquad \mathbf{\Sigma} = \begin{pmatrix} \sigma_r^2 & \rho\sigma_r\sigma_K \\ \rho\sigma_r\sigma_K & \sigma_K^2 \end{pmatrix}$$

where σ_r is standard deviation of parameter r; σ_K is standard deviation of parameter K; and ρ is the correlation coefficient. One thousand pairs of normally distributed r and K values were then simulated using the variance–covariance matrix (Fig. 3) as

$$(7) \qquad \begin{pmatrix} r_s \\ K_s \end{pmatrix} \sim N\left[\begin{pmatrix} r \\ K \end{pmatrix}, \mathbf{\Sigma}\right]$$

Fig. 3. The plot of 1000 pairs of r and K simulated from a multivariate normal distribution with correlation coefficient between r and K of –0.9 (based on the parameters of subpopulation 1).



where r_s and K_s are simulated r and K. This is similar to the approach used by Chen (1997).

Harvest control rule

We developed the following harvest control rule to determine annual catch using the parameters estimated for the three different spatial structure options in the management. We set the biomass limit to be $0.25B_{MSY}$ and the management target to be B_{MSY}, where MSY is maximum sustainable yield. When the current biomass was higher than the management target, we used the calculated annual catch. If the current biomass was less than the target biomass but more than the biomass limit, we determined the next year's catch level as follows:

$$(8)\qquad \text{(current biomass} - \text{biomass limit)} \times \text{(catch target level)/(biomass target} - \text{biomass limit)}$$

If the current biomass was less than the biomass limit, the fishery was closed with no catch for the next year.

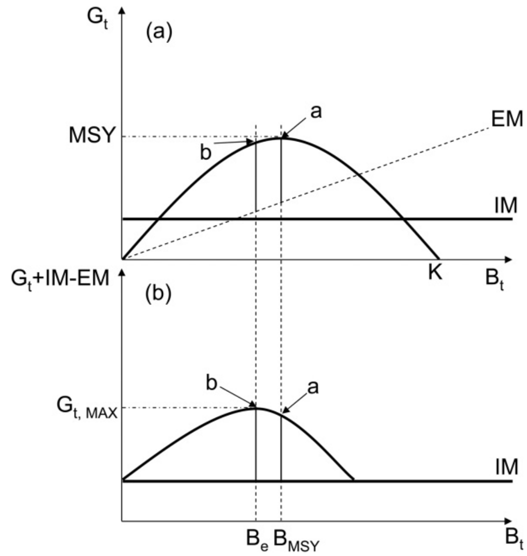
For the metapopulation management option, we had to consider the movement among subpopulations. Thus, we calculated a Y_t to describe the biomass used to decide the harvest level. Y_t is the biomass at the beginning of the year plus the net immigration:

$$(9)\qquad Y_{i,t} = B_{i,t} + \sum_{j\neq i}\theta_{j\rightarrow i}B_j - \sum_{i\neq j}\theta_{i\rightarrow j}B_i$$

The annual catch was then determined based on the harvest control rule defined above. For the other two spatial structure options, we used the biomass at the beginning of each year to determine the annual catch level based on the defined harvest control rule.

Many biological reference points can be used to determine total allowable catch (TAC) and catch level (Hilborn and Walters 1992; Quinn and Deriso 1999; Chen and Montgomery 1999). In this study, we used MSY and $f_{0.1}$ to determine TAC (Chen and Montgomery 1999; Quinn and Deriso 1999). For the three independent and unit population options, we used both to set target catch and compare their performance. In this case, MSY was calculated as $0.25r_iK_i$ (Hilborn and Walters 1992). The $f_{0.1}$ was defined by Chen and Montgomery (1999) as

Fig. 4. The two levels of total allowable catch used in the metapopulation management. The equilibrium catch level at B_{MSY} is the point "*a*". The catch level at maximum growth (equilibrium point at slope equal to 0) of a subpopulation is point "*b*". G_t (panel *a*) is the growth of the subpopulation in 1 year when the biomass of the subpopulation in the beginning of the year equals it in the end of the year. B_t is the biomass at the beginning of the year. The line labeled "EM" is the emigration of target subpopulation. The line labeled "IM" is the immigration from other subpopulations to the target subpopulation. G_t + IM – EM (panel *b*) is used to design the catch level for metapopulation management.



$$(10)\qquad \left.\frac{\partial C(E)}{\partial E}\right|_{E=f_{0.1}/q} = 0.1\left.\frac{\partial C(E)}{\partial E}\right|_{E=0}$$

where $C(E)$ is the equilibrium yield corresponding to effort E (Punt 1993). From the above equation and eq. 4, $f_{0.1}$ can be calculated as $f_{0.1} = 0.45r$ (Chen and Montgomery (1999).

However, determining TAC for the metapopulation option was more complicated because it needs to consider subpopulation mixing. The MSY of non-metapopulation management is the equilibrium yield at B_{MSY} ($B_{MSY} = 0.5K_i$; Hilborn and Walters 1992). The yield at B_{MSY} is defined as the catch level at biomass supporting the highest population growth (Hilborn and Walters 1992) and leading to the next year's biomass equal to the last year's biomass. However, the equilibrium yield at B_{MSY} in the metapopulation option is not the same as the maximum equilibrium yield (Fig. 4). This can be described as

$$(11)\qquad C_{i,t} = r_iB_{i,t}\left(1-\frac{B_{i,t}}{K_i}\right) - \sum_{j\neq i}^{R}\theta_{i\rightarrow j}B_{i,t} + \sum_{j\neq i}^{R}\theta_{j\rightarrow i}B_{j,t}$$

When B_{MSY} of $0.5K_i$ is input into the above equation, the yield at B_{MSY} becomes

Table 2. Simulation scenarios considered in this study.

Scenario	Management option	Total allowable catch	Uncertainty	CV (%)	Exchange rate
1	Metapopulation	Point at B_{MSY}	Without	10	1×
2	Metapopulation	Equilibrium point at slope equal to 0	Without	10	1×
3	Metapopulation	Point at B_{MSY}	With	10	1×
4	Metapopulation	Equilibrium point at slope equal to 0	With	10	1×
5	Three populations	MSY	With	10	1×
6	Unit population	MSY	With	10	1×
7	Metapopulation	Point at B_{MSY}	With	5	1×
8	Three populations	MSY	With	5	1×
9	Unit population	MSY	With	5	1×
10	Metapopulation	Point at B_{MSY}	With	20	1×
11	Three populations	MSY	With	20	1×
12	Unit population	MSY	With	20	1×
13	Metapopulation	Point at B_{MSY}	With	10	0.5×
14	Three populations	MSY	With	10	0.5×
15	Unit population	MSY	With	10	0.5×
16	Metapopulation	Point at B_{MSY}	With	10	1.5×
17	Three populations	MSY	With	10	1.5×
18	Unit population	MSY	With	10	1.5×
19	Metapopulation	90% of fishing effort at B_{MSY}	With	10	1×
20	Three populations	$f_{0.1}$	With	10	1×
21	Unit population	$f_{0.1}$	With	10	1×
22	Metapopulation	0.5 × point at B_{MSY}	With	10	1×
23	Three populations	0.5 × MSY	With	10	1×
24	Unit population	0.5 × MSY	With	10	1×
25	Metapopulation	1.5 × point at B_{MSY}	With	10	1×
26	Three populations	1.5 × MSY	With	10	1×
27	Unit population	1.5 × MSY	With	10	1×

Note: B_{MSY} is the management target for annual biomass catch, where MSY is maximum sustainable yield (see Fig. 4); CV is coefficient of variation. Exchange rate is compared with the base case rate defined in Table 1.

$$(12)\qquad C_{i,t} = \frac{r_i K_i}{4} - \frac{K_i}{2}\sum_{i\neq j}\theta_{i\to j} + \sum_{j\neq i}\theta_{j\to i}B_{j,t}$$

The maximum equilibrium yield (Fig. 4) can be defined as

$$(13)\qquad \frac{\partial C_{e,i}}{\partial B_i} = \left(r_i - \sum_{i\neq j}\theta_{i\to j}\right) - \frac{2B_i r_i}{K_i} = 0$$

where $C_{e,i}$ is the yield leading to the next year's biomass equal to the last year's biomass, which is the same as eq. 11.

From eqs. 8 and 10, the equilibrium can be determined as

$$(14)\qquad C_{i,t} = \frac{K_i\left(r_i - \sum_{i\neq j}\theta_{i\to j}\right)^2}{4r_i} + \sum_{j\neq i}\theta_{j\to i}B_{j,t}$$

The estimation of $f_{0.1}$ for the metapopulation option is also complicated and could not be simply determined as $0.45r$. Because the fishing mortality at MSY level is $0.5r$ (Quinn and Deriso 1999; Chen and Montgomery 1999), we used 90% of the harvest level at B_{MSY} as the catch level for the metapopulation option using $f_{0.1}$ as biological reference point (Chen and Montgomery 1999).

Simulation of the management

The harvest rules, derived above, were applied to manage the simulated fishery. For the metapopulation and three independent subpopulation options, the harvest level of each year and dynamics of subpopulations were estimated with the harvest control rules. For the unit population option, the fleet dynamics were also considered, with the allocation of fishing effort and TAC among the three subpopulations being determined based on the relative difference in CPUE among the three fishing areas targeting the three subpopulations. The proportion of TAC of subpopulation i in year t was determined as

$$(15)\qquad \text{TAC proportion of subpopulation } i = \frac{U_{i,t}}{\sum_{j=1}^{R} U_{j,t}}$$

where $U_{i,t}$ is the observed CPUE of subpopulation i in year t; and R is the total number of the subpopulations. This implies that fishermen are mobile and have knowledge about the performance of other fishermen and where the fish are located (Hilborn and Walters 1992; Wilson et al. 1999). We used 10 years as management time period in this study, which is long enough to address the objective of this study.

Simulation scenarios

To evaluate risks of ignoring fish population spatial structure, we developed various simulation scenarios in this study (Table 2). Scenarios 1, 2, 3, 4, 7, 10, 13, 16, 19, 22, and 25 were based on the assumption that the population was managed under the metapopulation option (i.e., assumed spatial structure in the assessment is correct); Scenarios 5, 8, 11, 14, 17, 20, 23, and 26 assumed that the population was managed under the three independent subpopulations option (i.e., assumed spatial structure does not consider movement among the subpopulations); and Scenarios 6, 9, 12, 15, 18, 21, 24, and 27 assumed that the population was managed under the unit population option (i.e., no spatial structure was assumed in the assessment; Table 2).

Scenarios 1 to 6 were used to test the TAC-based management with catch being set at MSY. Different biological references in the simulation were assumed as the MSY in the metapopulation management. MSY was calculated based on B_{MSY} for Scenarios 1 and 3 (Fig. 4), and MSY was calculated at equilibrium point with the slope of 0 for Scenarios 2 and 4 (Fig. 4). For the other scenarios (i.e., 5 and 6), MSY was calculated based on B_{MSY}. Scenarios 1 and 2 were the control scenarios without consideration of uncertainty (Table 2).

Scenarios 7 to 12 were used to evaluate different levels of uncertainty. Scenarios 7 to 9 used 5% of CV and Scenarios 10 to 12 used 20% of CV for parameters r and K to simulate the uncertainty (Table 2).

Scenarios 13 to 18 were used to evaluate different levels of exchange rate. Scenarios 13 to 15 used 0.5 times the exchange rates for the base case described (Table 2), and Scenarios 16 to 18 used 1.5 times the exchange rates for the base case (Table 2).

Scenarios 19 to 27 were used to test different catch levels. Scenarios 19 to 21 used a relative robust fishing mortality level $f_{0.1}$ (Chen and Montgomery1999). Scenarios 22 to 24 used a low catch level (0.5 × MSY), and Scenarios 25 to 27 used a higher catch level (1.5 × MSY).

Results

The mean values of parameters for the three spatial structure options were summarized (Table 3). The B_0 and K values in subpopulations 1 and 3 and the growth rate r of subpopulation 2 were higher than those for the "true" population when the migration was not considered (Table 3). The value of growth rate r of each subpopulation estimated in this study was common in family Sciaenidae (http://www.fishbase.org/Nomenclature/NominalSpeciesList.cfm?family=Sciaenidae), suggesting that the simulated population is biologically reasonable.

Boxplots of stock biomass and annual catch are presented for each simulated scenario (Figs. 5–13). The box depicts the interquartile range; the horizontal line through the box represents the median score; and the whiskers represent 95% confidence intervals.

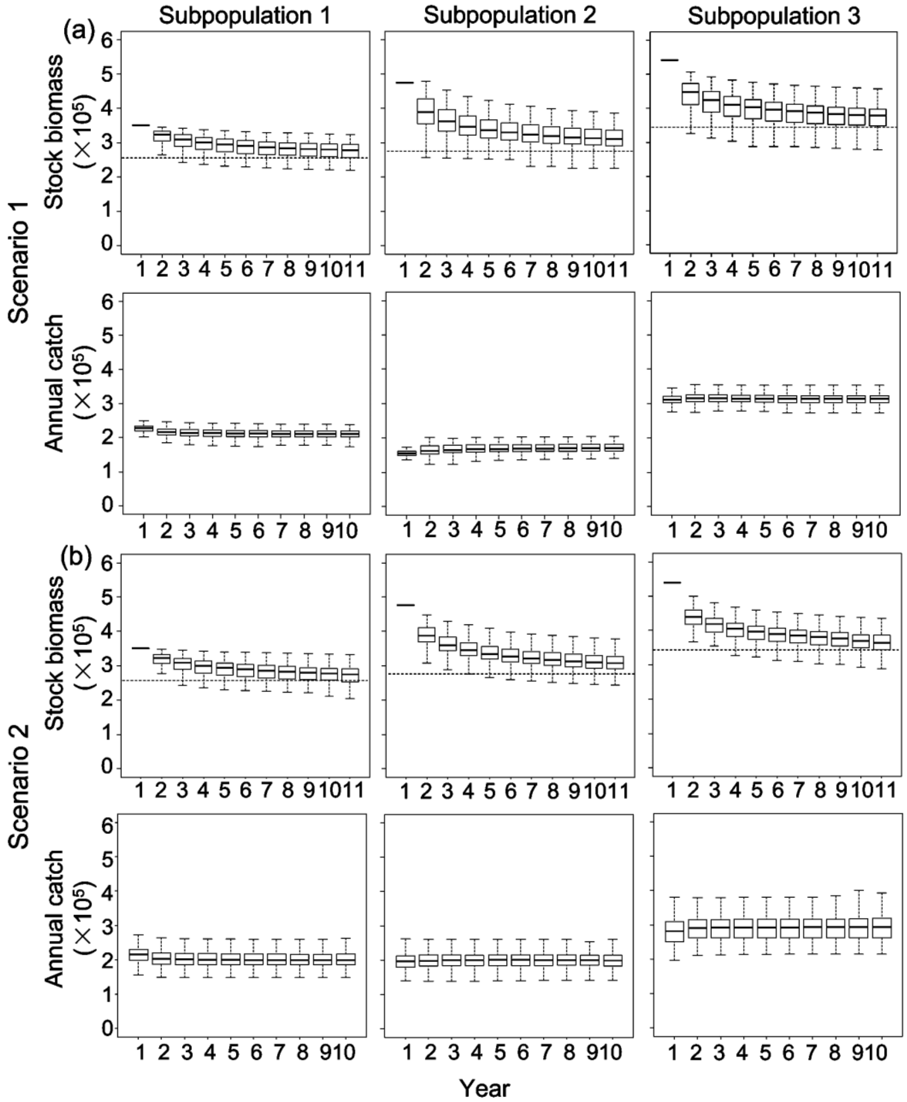
For the control cases without uncertainty (i.e., Scenarios 1 and 2; Table 2), all subpopulations had stable stock biomass over the simulation time period (Fig. 5). The annual biomass was kept above the mean value of the biomass management target, and the annual yields of each subpopulation were stable (Fig. 5). For Scenarios 3 and 4 considering the uncertainty of parameter estimates, over-exploitation of the subpopulations occurred in some of the simulation runs, indicating the possibility that over-exploitation existed (Fig. 6), although the annual yield was stable for each subpopulation. The median values of population biomass were higher than the management target for Scenario 3, but lower than the

Table 3. The average population parameters and biomass management targets estimated for the three spatial options considered in the management.

			r			K ($\times 10^5$)				Biomass targets ($\times 10^5$)		
Management strategy	Area	B_0 ($\times 10^5$)	$1 \times \theta$	$0.5 \times \theta$	$1.5 \times \theta$	$1 \times \theta$	$0.5 \times \theta$	$1.5 \times \theta$	q ($\times 10^{-8}$)	$1 \times \theta$	$0.5 \times \theta$	$1.5 \times \theta$
Metapopulation (true)	Subpopulation 1	3.59	1.64	1.52	1.52	5.15	5.16	5.16	4.47	2.57	2.58	2.58
	Subpopulation 2	4.61	1.24	1.61	1.39	5.57	5.43	5.49	6.54	2.78	2.72	2.75
	Subpopulation 3	5.11	1.8	1.62	1.99	6.99	6.92	7.03	6.03	3.49	3.46	3.51
Three independent populations	Population 1	3.75		1.41				5.16	4.53		2.58	
	Population 2	4.33		1.94			5.36		6.59		2.68	
	Population 3	5.22		1.8			6.99		5.73		3.5	
Unit population	Whole population	13.02		1.79			19.11		1.12		9.55	

Note: θ is the exchange rate shown in Table 1.

Fig. 5. Boxplots of stock biomass at the beginning of the years and annual catch of simulation Scenarios 1 (*a*) and 2 (*b*) defined in Table 2 (metapopulation management at MSY without uncertainties). The mean values of biomass management targets in the 1000 simulation runs are shown by horizontal dotted lines.



management target for subpopulation 2 in Scenario 4 (Fig. 6). For Scenario 5, which ignored the migration among subpopulations, over-exploitation was detected for all the three subpopulations (Fig. 6). The biomasses of subpopulations 2 and 3 were depleted, respectively, in the fourth and sixth years (Fig. 6). The yield of the two subpopulations continuously declined. Under a constant catch management regime, the biomass of subpopulation 1 declined substantially, leading to high probability of over-exploitation (Fig. 6). For Scenario 6, which ignored all of the spatial information of the metapopulation, the stock biomasses of all the three subpopulations were severely depleted early in the simulation and maintained very low levels of biomass (Fig. 6). The annual yields fluctuated greatly among years for all the subpopulations (Fig. 6).

For Scenarios 7, 8, and 9, 5% of CV was employed to simulate low uncertainty. The biomass under the metapopulation management option (Scenario 7; Fig. 7) remained stable and was close to the target. Under the independent population management option (Scenario 8; Fig. 7), the stock biomass of subpopulations 2 and 3 was stable at the level slightly lower than the management target. The stock biomass of all subpopulations under the unit population management option (Scenario 9; Fig. 7) was severely depleted early in the simulation. In contrast, for Scenarios 10, 11, and 12, 20% of CV was employed to simulate high uncertainty. Large variability could be seen in the simulation results, but the median catch and biomass values were similar to those for scenarios having 5% of CV, except the independent population management option, which maintained a stock biomass lower than that for the scenario with 5% of CV (Fig. 8).

For Scenarios 13 to 18, low and high exchange rates were employed. Half of exchange rate values shown in Table 2 were used in Scenarios 13, 14, and 15 (Fig. 9). Stock biomasses and catches under the single population management option were similar with the values under the metapopulation management scenarios, but severe depletion was still observed for the unit population management option.

In contrast, for Scenarios 16, 17, and 18, 1.5 times the exchange rate value shown in Table 3 were used. Biomasses under the single population management option (Scenario 17) were over-exploited to a level much lower than those for the metapopulation management option (Scenario 16). The subpopulations under the unit population management option (Scenario 18) declined moderately, though over-exploitation was observed (Fig. 10).

For Scenarios 20 and 21, which used $f_{0.1}$ instead of MSY to determine TAC, the annual stock biomass levels were higher and more stable than those for Scenarios 5 and 6 (Fig. 11). For Scenario 20, only light over-exploitation was detected, and both stock biomasses and yields were stable (Fig. 11). For Scenario 21 (Table 2), although a severe depletion happened in the beginning of the simulation, the stock biomass recovered and remained low but stable in the next several years (Fig. 11).

For Scenarios 22 to 27, different catch levels were assumed in management. For Scenarios 22, 23, and 24, TAC was set at 50% of MSY (Fig. 12). Stock biomasses were higher than the management target for all of the three scenarios (Fig. 12). For Scenarios 25, 26, and 27, TAC was set at 1.5 times of MSY (Fig. 13). Over-exploitation was detected for all of the three management scenarios. The stock biomasses were reduced, but maintained at a low level for Scenarios 25 and 26, but all the three subpopulations were close to extinction for Scenario 27, which ignored the population spatial structure (Fig. 13).

Discussion

Mixing among the subpopulations of a metapopulation, resulting from dispersal and migrations (Hansson 1991), has profound consequences to the persistence of populations, the distribution and abundance of species, and community structure (Dieckmann at el. 1999), and subsequently to fisheries assessment and management. Curtis and Naujokaitis-Lewis (2008) suggested that the dynamics of a metapopulation could be influenced by dispersal rates among populations. Failure to recognize complex population structure in management may lead to erosion of local subunits with unknown ecological consequences (Stephenson 1999). This study suggests that managing a metapopulation as several independent populations could lead to reduced stock biomass and high probability of over-exploitation. Ignorance of the exchange among the subpopulations might be responsible for the biases in estimating population parameters and subsequent determination of harvest level.

Age at sexual maturity becomes younger and the number of age groups is reduced as a result of over-exploitation for small yellow croakers (Lin 2009). The dominant age groups were 3–6 years old in 1963, 1–2 years in 1983, and 0–1 year in 2001; and the 0–1 age group consisted of 98.8% of the total population in 2001 (Lin 2009). From the 1990s, the spawning stock of small yellow croakers was mainly composed of the young of the year (Lin 2009). Recently, small yellow croaker was considered as a short-lived and fast-growing species. For such a stock with simple age structure, a production model is a good candidate for quantifying its population dynamics. Use of production model also does not require information such as recruitment, natural mortality, and selectivity, which is often not available. Thus we used surplus production model in this study.

This study shows that managing a metapopulation as a unit population could lead to local depletion. Botsford et al. (2009) suggested that the movement of fishermen had a significant effect on the dynamics of exploited, spatially structured marine populations. This study suggests that the depletion might be caused by the fishing fleet concentrating in areas of higher abundance.

For a metapopulation, two MSYs could be estimated: one estimated based on B_{MSY} and the other estimated by setting the slope of the equilibrium catch–effort curve equal to 0 (i.e., maximum rate). The catch level at B_{MSY} tended to be lower than the catch level at the maximum rate. Thus, the catch level at B_{MSY} tends to be a more conservative management reference point.

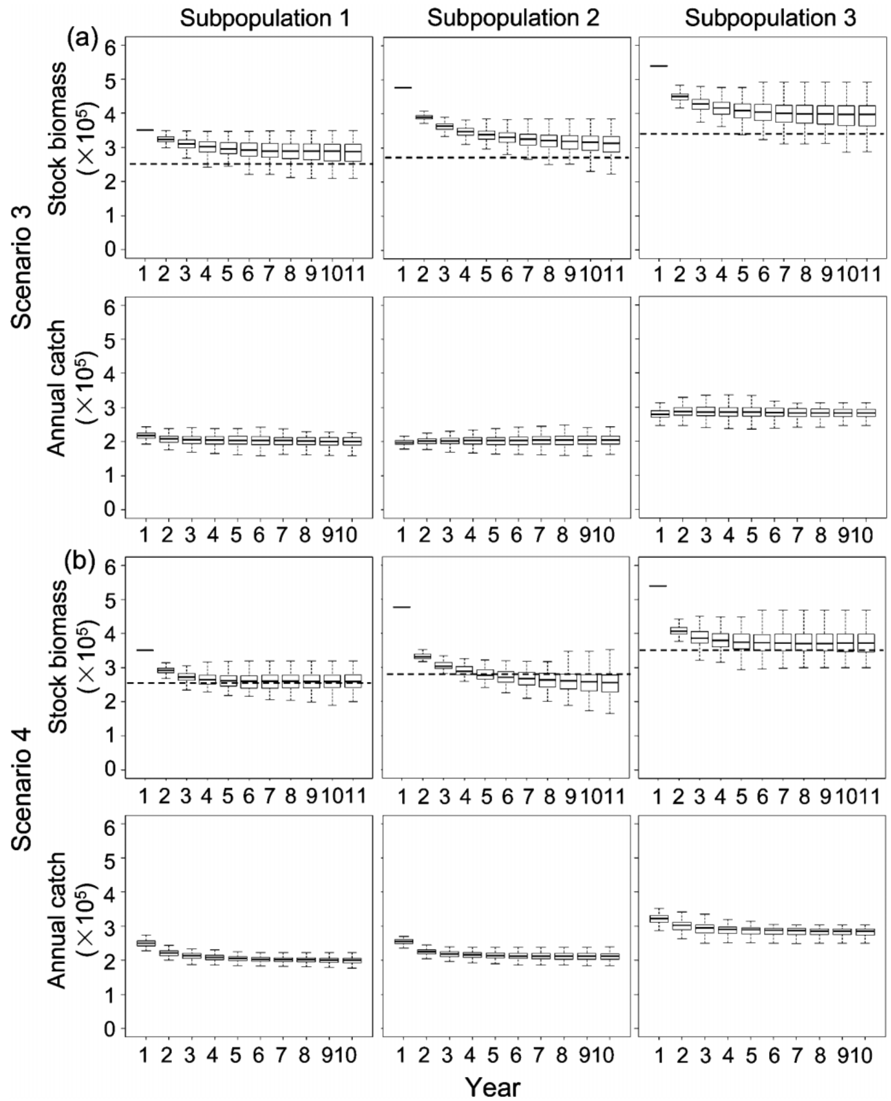
The quality of fisheries data has great impacts on the quality of stock assessment (Chen 2003). This study shows that uncertainties in estimating population parameters in metapopulation fisheries management can affect the management of a metapopulation. Over-exploitation of subpopulations occurred in some simulation runs for the scenarios with uncertainty, even when the spatial structure was correctly defined in the assessment. For the scenarios with lower levels of uncertainty, the variability was smaller and the stock biomass under the independent population option was stable at a higher biomass than that under the scenario with a higher uncertainty level. This suggests that reducing uncertainty associated with key population parameters such as K and r in stock assessment is important in metapopulation fisheries management.

The management of metapopulations is considered to be sensitive to the exchange rate (Curtis and Naujokaitis-Lewis 2008). In general, we expect that a high level of exchange among subpopulations makes the population similar to a unit population; but a low level of exchange makes the population similar to several independent populations. The results of this study are consistent with such an expectation. For the scenarios with low exchange rates, the independent population management option seemed to perform well; but for the scenarios with high exchange rates, the metapopulation managed under the unit population assumption performed better than it did with lower exchange rates. The sensitivity of the results to the exchange rates indicates the importance of knowing movement information for the assessment and management of a metapopulation.

We compared differences in management using $f_{0.1}$ and MSY-based reference points. We found that the annual stock biomass levels with $f_{0.1}$ as the management target were higher and more stable for the same spatial structure scenarios assumed in the management than those with the MSY as the management target. Therefore, exploitation based on MSY is risk-prone because the ability of the population to recover from exploitation might be impaired in the presence of uncertainties. Use of $f_{0.1}$ as management target is more desirable. The $f_{0.1}$ is often considered as a more conservative biological reference point (Chen and Montgomery 1999). Chen and Montgomery (1999) proposed to use $f_{0.1}$ as a biological reference point in a surplus production model and suggested it is more robust than the F_{MSY} regarding uncertainty.

For the scenarios with TAC being set at 1.5 times MSY, the high catch level led to high risks of over-exploitation in

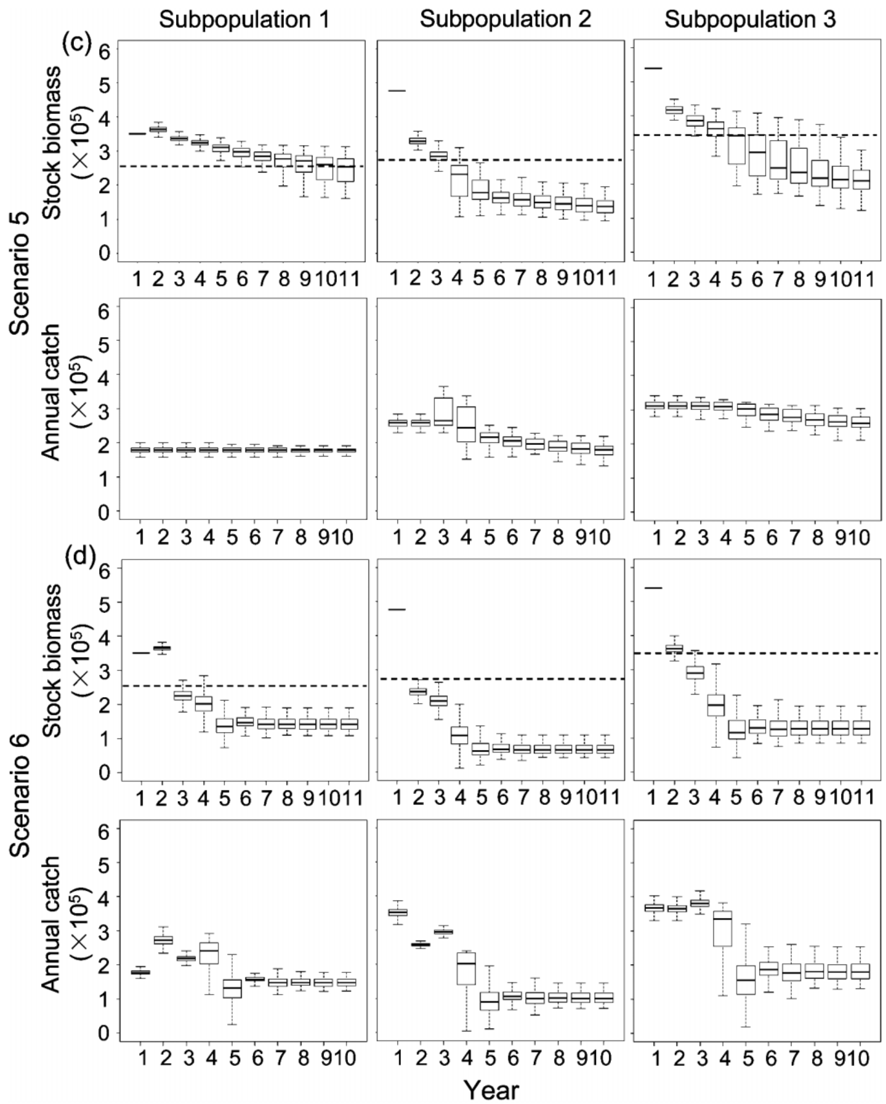
Fig. 6. Boxplots of stock biomass at the beginning of the years and annual catch for Scenarios 3 (*a*), 4 (*b*), 5 (*c*), and 6 (*d*) defined in Table 2 (managements with catch level at MSY for three spatial options). Scenario 3 (*a*) used the catch at B_{MSY} as MSY, and Scenario 4 (*b*) used the catch at equilibrium point at slope equal to 0. The biomass management targets of the "true" population are shown by horizontal dotted lines.



all the three management options. However, TAC of 50% MSY led to no over-exploitation being found in all management options, and stock biomass remained stable in the unit population option. Clearly reducing catch level can reduce the risks of over-exploitation in the management of metapopulations even though spatial structure of the population is wrongly assumed in the assessment and management.

Several studies suggest dangers of ignoring the spatial structure of fish populations in fisheries assessment and management (e.g., Hutchings 1996, 2000; Frank and Brickman 2000). Frank and Brickman (2000) developed a model based on the stock–recruitment (S–R) relationship with the Allee effect and suggested that biological reference points developed from the models ignoring multiple subpopulations and used in conventional fisheries assessment are likely to be inaccurate and possibly nonconservative. Hutchings (1996, 2000) shows the importance of subpopulation structure in the management of Atlantic cod (*Gadus morhua*) fisheries in Canada. Numerous studies suggested that ignorance of spatial structure in cod fisheries management might be responsible for the collapse of the cod populations (e.g., Hutchings 1996, 2000; Frank and Brickman 2000). Decrease in the Atlantic herring (*Clupea harengus*) population was also thought to be caused by failure to recognize the complex spatial structure (Stephenson 1999). The crustacean fisheries of Alaska (e.g., red king crab, *Paralithodes camtschaticus*) provide notable examples of fishery collapses (Wooster 1992), and ignorance of spatial structure in the management was considered one of the major reasons for the collapse (Orensanz et al. 1998). While the small yellow croaker is a short-lived and fast-growing species, the Atlantic cod and red king crab are considered long-lived species. Although different in their life history, the role of spatial structure and consequence of ignoring of population spatial structure in the management might be the same as long as they have metapopulation structure. Previous studies suggest the importance of spatial structure for long-lived species (e.g., Atlantic cod and red king crab), but limited work was done for short-lived species, which might be less likely to be affected by their spatial structure because of their high growth rates and small num-

Fig. 6. (*concluded*).



ber of age classes. Thus, this study complements the studies done previously for long-lived species.

Many short-lived species were considered to exhibit large variability in recruitment (e.g., Milton et al. 1996; Dichmont et al. 2006). As a short-lived species, the small yellow croaker also exhibit high variability in recruitment. Further, recent research observed an increasing trend in the recruitment rate of small yellow croaker (Lin 2009). However, in the simulation of this study, we did not explicitly incorporate temporal variability in recruitment because the surplus production model only considers intrinsic population growth, which combines recruitment, somatic growth, and natural mortality. The intrinsic growth, which includes recruitment, is dependent and varies with stock biomass. Thus, although we did not explicitly consider recruitment dynamics, we did implicitly consider temporal variability in recruitment.

The fishery was simulated based on the life history traits of small yellow croaker that spawn pelagic eggs in spring in the coastal area. However, recent studies showed that the spawning grounds of small yellow croaker had expanded offshore (Lin et al. 2008). Changing of spawning grounds might influence the migration routes and relative strength of three subpopulations. Its management implications thus need to be evaluated. The monitoring of the spatial distribution and movement of the population of small yellow croaker should be continued.

The assumptions used in this study are typical, and some values (e.g., exchange rates among the subpopulations) used were determined somewhat arbitrarily. The impacts of the assumptions and choices of the population parameters may influence the dynamics of fisheries population and should be evaluated more carefully. The harvest control rules considered in this study were limited. More harvest control rules and other management strategies such as marine reserves can be considered in management of metapopulations.

In summary, this study suggests that ignoring spatial structures in fisheries assessment and management may result in (*i*) biases in estimating population parameters; (*ii*) biases in estimating stock status; (*iii*) developing inappropriate management targets; (*iv*) recommending inappropriate harvest levels; and (*v*) depleting local populations. All of these might lead to higher risks of depleting fisheries populations. Thus,

Fig. 7. Boxplots of stock biomass at the beginning of years and annual catch of simulation Scenarios 7 (*a*), 8 (*b*), and 9 (*c*) defined in Table 2 (with 5% CV of uncertainties for the three spatial options). The biomass management targets of the “true” population are shown by horizontal dotted lines.

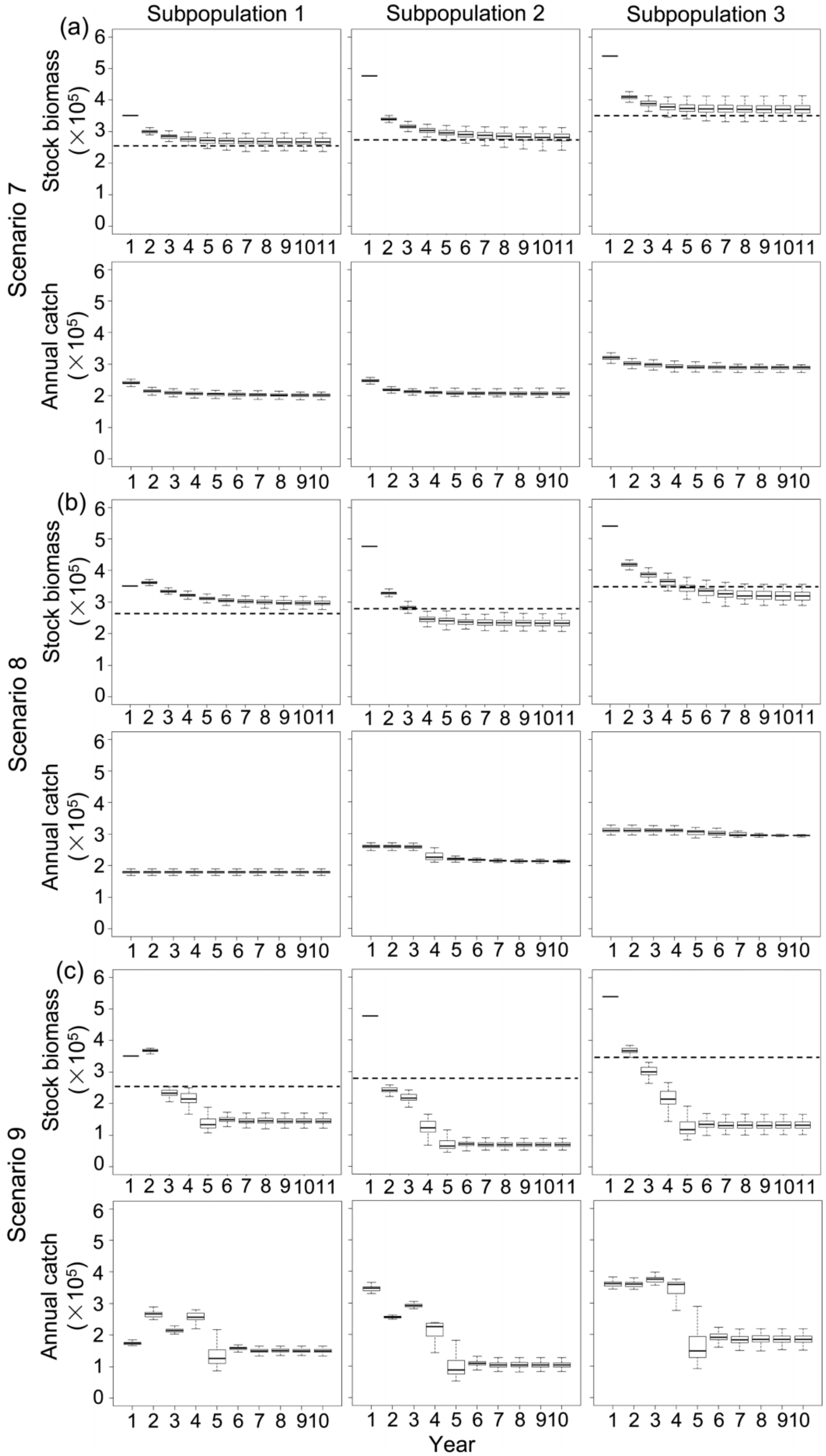


Fig. 8. Boxplots of stock biomass at the beginning of years and annual catch for Scenarios 10 (*a*), 11 (*b*), and 12 (*c*) defined in Table 2 (with 20% CV of uncertainties for the three spatial options). The biomass management targets of the "true" population are shown by horizontal dotted lines.

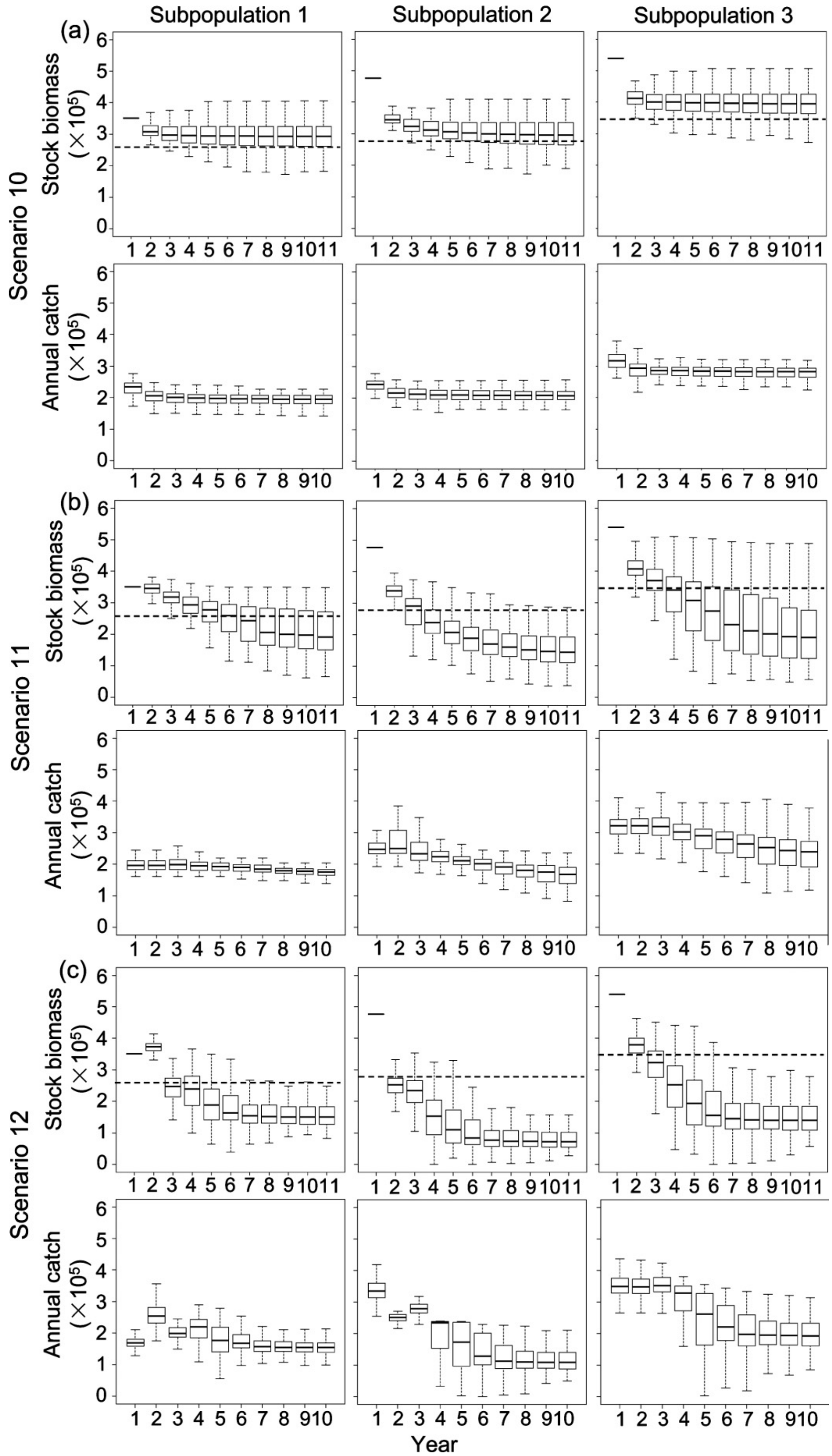


Fig. 9. Boxplots of annual biomass at the beginning of years and annual catch for Scenarios 13 (*a*), 14 (*b*), and 15 (*c*) defined in Table 2 (with 0.5 times the exchange rates for the three spatial options). The biomass management targets of the "true" population are shown by horizontal dotted lines.

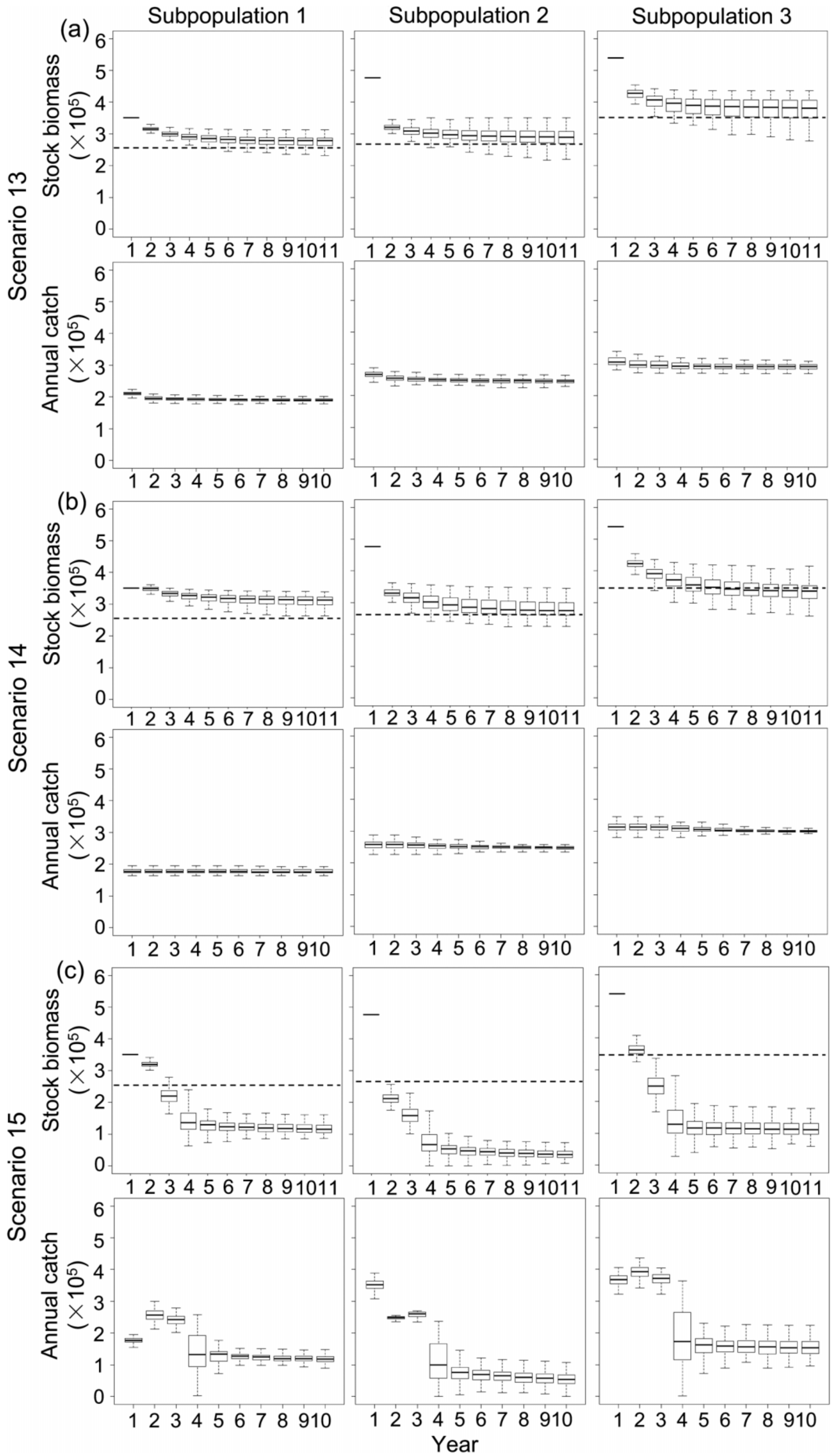


Fig. 10. Boxplots of stock biomass at the beginning of the years and annual catch for Scenarios 16 (*a*), 17 (*b*), and 18 (*c*) defined in Table 2 (with 1.5 times the exchange rates for the three spatial options). The biomass management targets of the "true" population are shown by horizontal dotted lines.

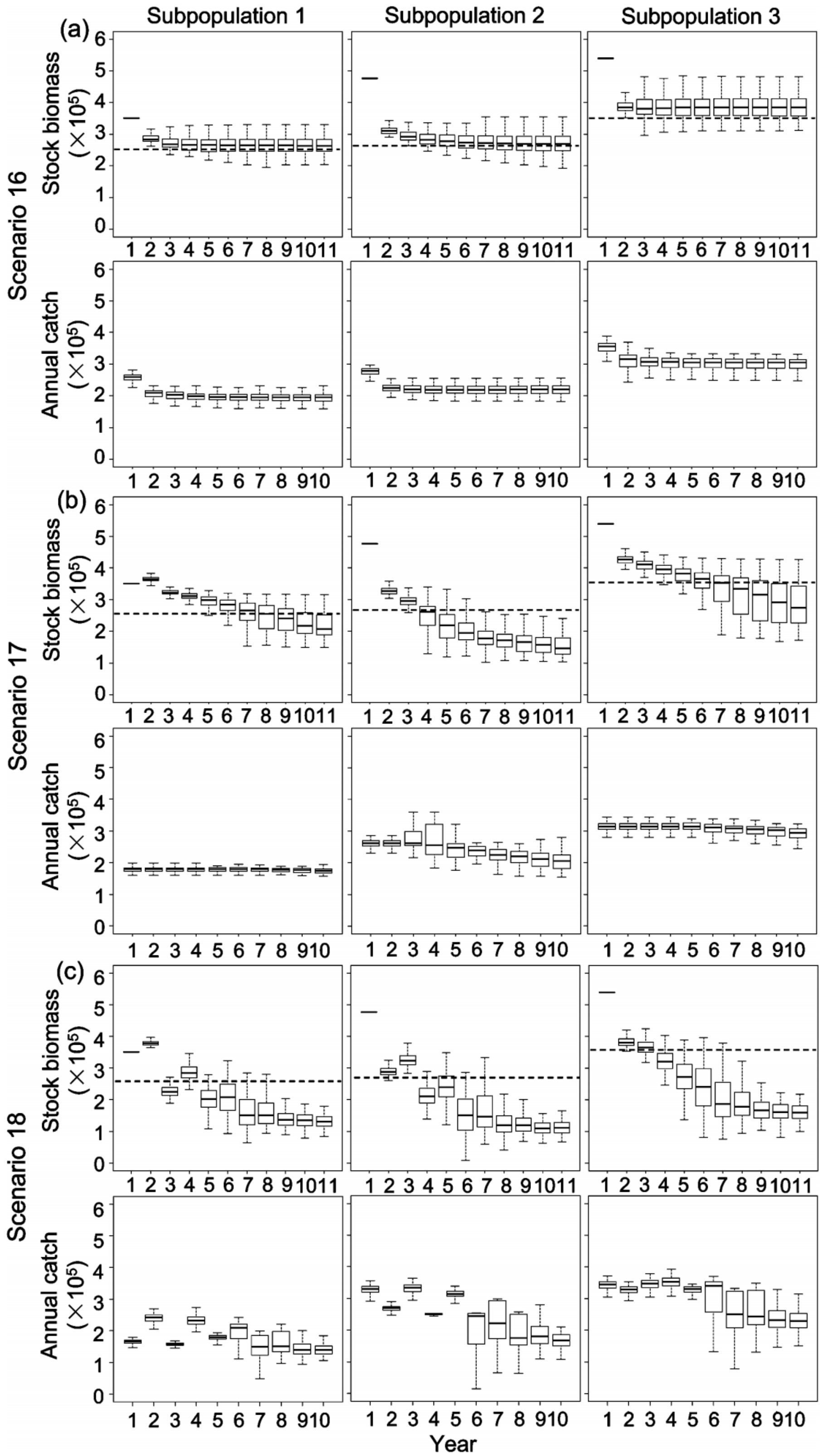


Fig. 11. Boxplot of stock biomass at the beginning of the years and annual catch for Scenarios 19 (*a*), 20 (*b*), and 21 (*c*) defined in Table 1 (scenarios under $f_{0.1}$ management for the three spatial options). The biomass management targets of the "true" population are shown by horizontal dotted lines.

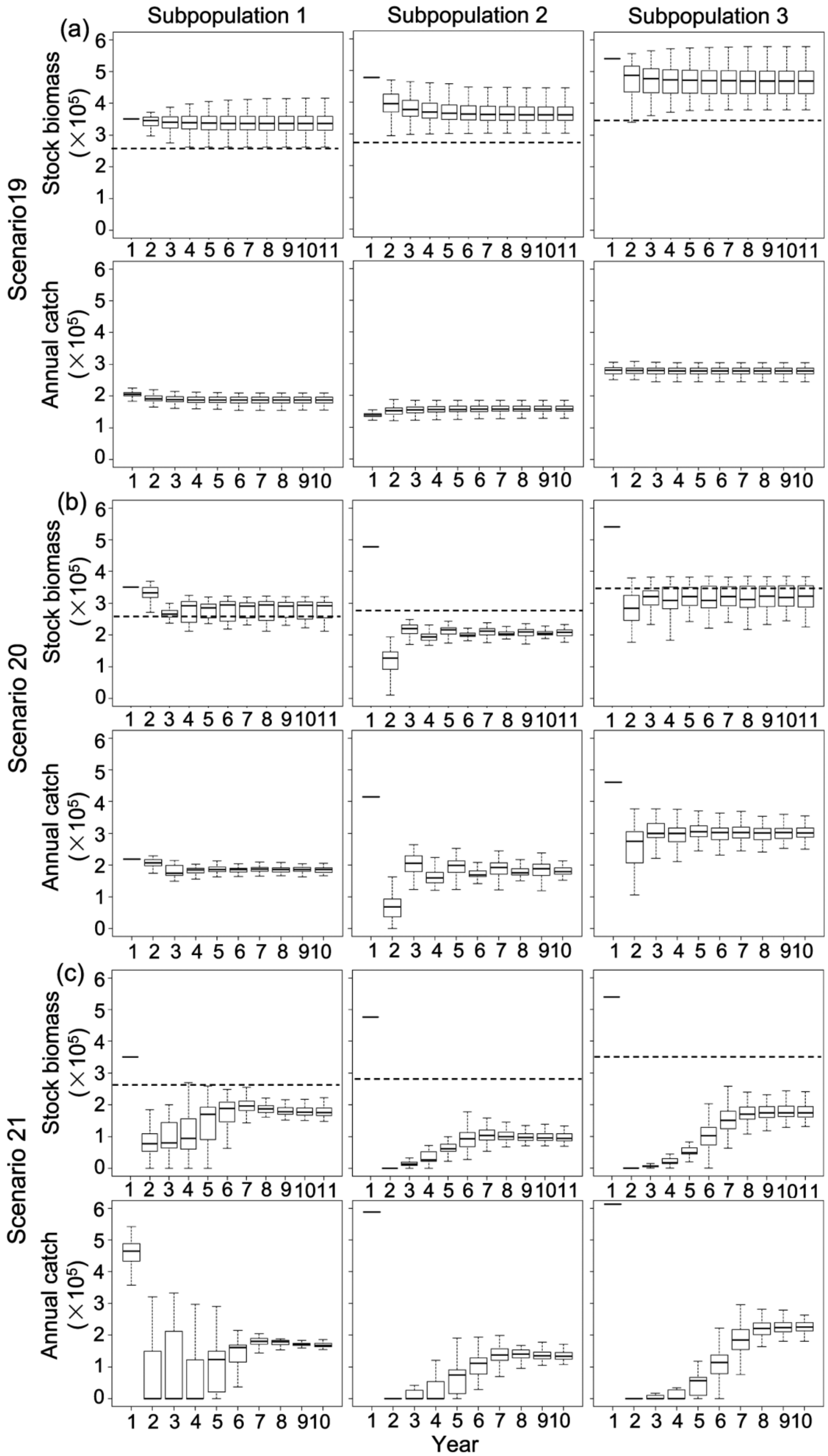


Fig. 12. Boxplots of stock biomass at the beginning of the years and annual catch for Scenarios 22 (*a*), 23 (*b*), and 24 (*c*) defined in Table 2 (scenarios with catch level at 0.5MSY for the three spatial options). The biomass management targets of the "true" population are shown by horizontal dotted lines.

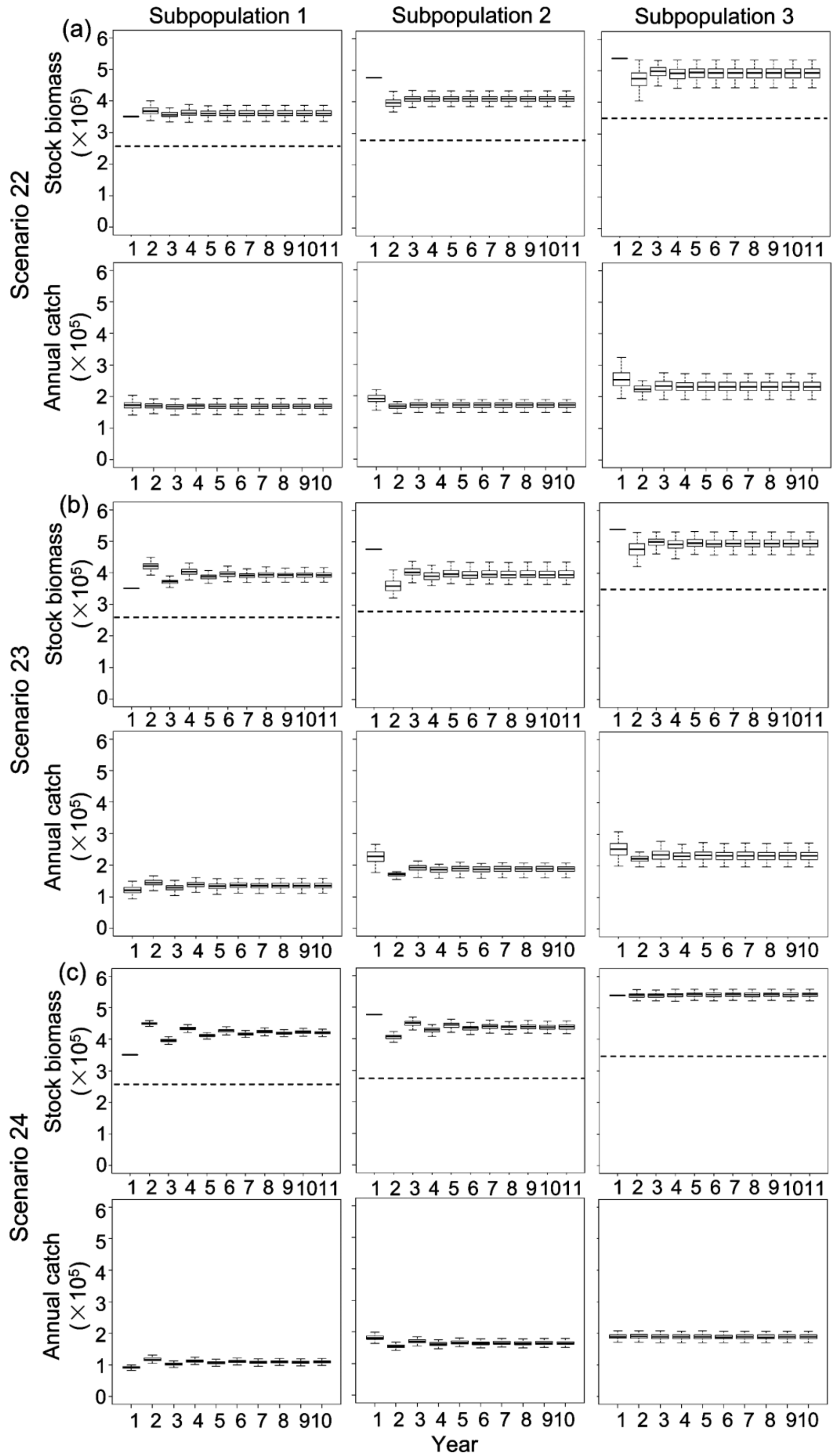
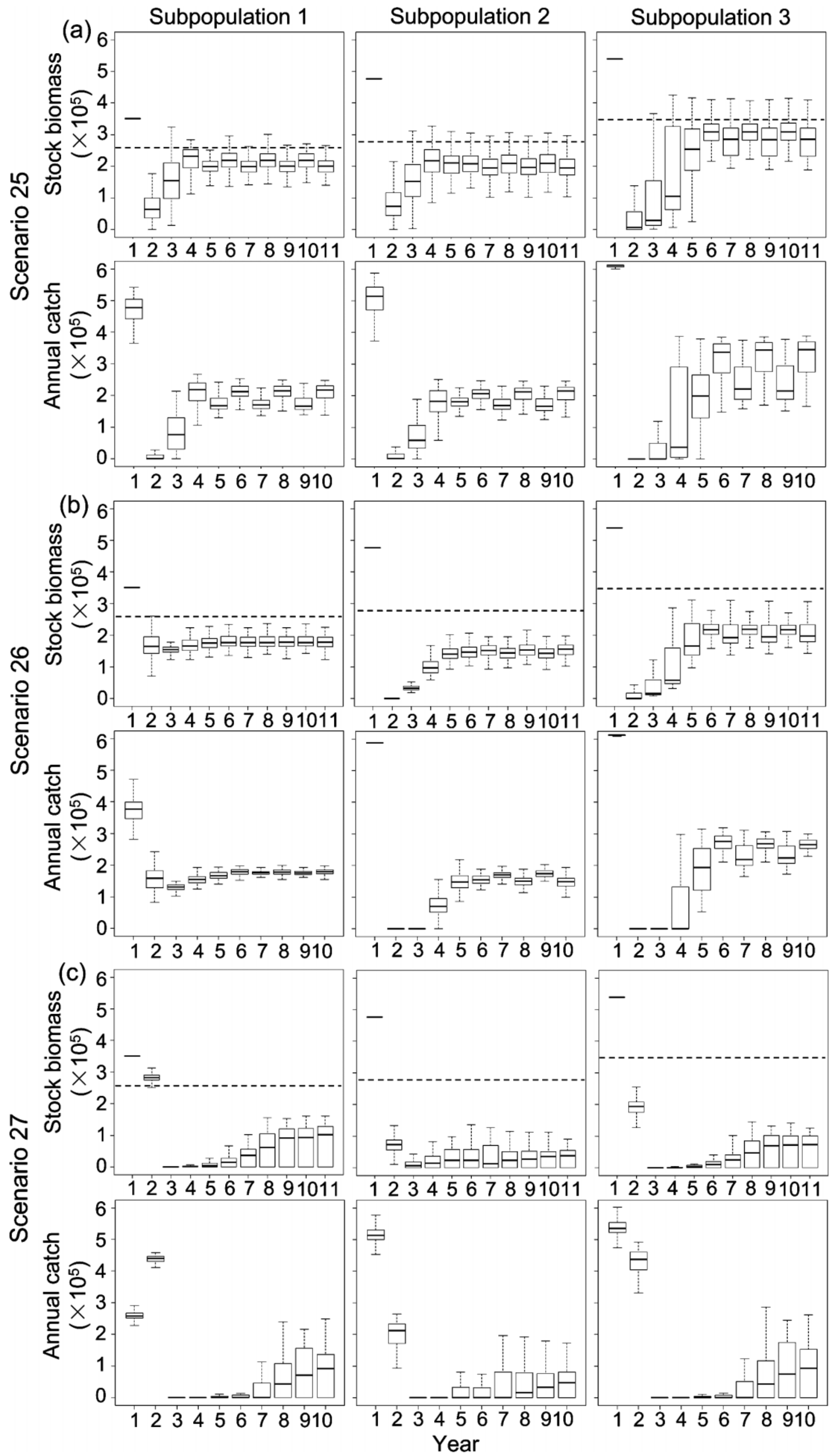


Fig. 13. Boxplots of stock biomass at the beginning of the years and annual catch Scenarios 25 (*a*), 26 (*b*), and 27 (*c*) defined in Table 2 (scenarios with catch level at 1.5MSY for the three spatial options). The biomass management targets of the “true” population are shown by horizontal dotted lines.



a delineation of the population spatial structure and interactions among the subpopulations is critical in developing a sustainable fishery.

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References

Bard, Y. 1974. Nonlinear parameter estimation. Academic Press, New York.

Bell, G. 1990. The ecology and genetics of fitness in *Chlamydomonas*. I. Genotype-by-environment interaction among pure strains. Proc. R. Soc. B Biol. Sci. **240**(1298): 295–321. doi:10.1098/rspb.1990.0039.

Botsford, L.W., Brumbaugh, D.R., Grimes, C., Kellner, J., Largier, J., O'Farrell, M.R., Ralston, S., Soulanille, E., and Wespestad, V. 2009. Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. Rev. Fish Biol. Fish. **19**(1): 69–95. doi:10.1007/s11160-008-9092-z.

Chen, Y. 1997. A comparison study of age- and length-structured yield-per-recruit models. Aquat. Living Resour. **10**(5): 271–280. doi:10.1051/alr:1997030.

Chen, Y. 2003. Quality of fisheries data and uncertainty in stock assessment. Sci. Mar. **67**(Suppl. 1): 75–87.

Chen, Y., and Montgomery, S.S. 1999. Modeling the dynamics of eastern rock lobster, *Jasus verreauxi*, stock in New South Wales, Austrilia. Fish Bull. **97**: 25–38.

Chinese Fishery Yearbook Publishing House. 2000–2009. China Fishery Yearbook (2000–2009). China Agriculture Press, Beijing. [In Chinese.]

Curtis, J.M.R., and Naujokaitis-Lewis, I. 2008. Sensitivity of population viability to spatial and nonspatial parameters using GRIP. Ecol. Appl. **18**(4): 1002–1013. doi:10.1890/07-1306.1. PMID:18536258.

Dichmont, C.M., Deng, A., Punt, A.E., Venables, W., and Haddon, M. 2006. Management strategies for short-lived species: the case of Australia's northern prawn fishery: 1. Accounting for multiple species, spatial structure and implementation uncertainty when evaluating risk. Fish. Res. **82**(1–3): 204–220. doi:10.1016/j.fishres.2006.06.010.

Dieckmann, U., O'Hara, B., and Weisser, W. 1999. The evolutionary ecology of dispersal. Trends Ecol. Evol. **14**(3): 88–90. doi:10.1016/S0169-5347(98)01571-7.

Frank, K.T., and Brickman, D. 2000. Allee effects and compensatory population dynamics within a stock complex. Can. J. Fish. Aquat. Sci. **57**(3): 513–517. doi:10.1139/f00-024.

Han, Z., Lin, L., Shui, B., and Gao, T. 2009. Genetic diversity of small yellow croaker *Larimichthys polyactis* revealed by AFLP markers. Afr. J. Agr. Res. **4**(7): 605–610.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, UK.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biol. J. Linn. Soc. **42**(1-2): 89–103. doi:10.1111/j.1095-8312.1991.tb00553.x.

Hart, D.R., and Cadrin, S. 2004. Yellowtail flounder (*Limanda ferruginea*) off the northeastern United States: implications of movement among stocks. *In* Species conservation and management: case studies. *Edited by* H.R. Akçakaya, M. Burgman, O. Kindvall, C.C. Wood, P. Sjögren-Gulve, J.S. Hatfield, and M.A. McCarthy. Oxford University Press, New York. pp. 230–243.

Heath, M.R., Kunzlik, P.A., Gallego, A., Holmes, S.J., and Wright, P.J. 2008. A model of meta-population dynamics for North Sea and West of Scotland cod — the dynamic consequences of natal fidelity. Fish. Res. **93**(1–2): 92–116. doi:10.1016/j.fishres.2008.02.014.

Heifetz, J., and Quinn, T.J., II. 1998. Dynamics of an age by region fish population model. *In* Proceedings of the Symposium on Fishery Stock Assessment Models in the 21st Century, Anchorage, Alaska, 8–11 October 1997. Alaska Sea Grant College Program, Fairbanks, Alaska. pp. 219–244.

Hilborn, R., and Walters, C. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

Hutchings, J. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can. J. Fish. Aquat. Sci. **53**(5): 943–962. doi:10.1139/f96-097.

Hutchings, J.A. 2000. Collapse and recovery of marine fishes. Nature, **406**(6798): 882–885. doi:10.1038/35022565. PMID:10972288.

Hutchinson, W.F. 2008. The dangers of ignoring stock complexity in fishery management: the case of the North Sea cod. Biol. Lett. **4**(6): 693–695. doi:10.1098/rsbl.2008.0443. PMID:18782730.

Ikeda, I. 1964. Studies on the fisheries biology of the yellow croaker in the East China and the Yellow Seas. Bull. Seikai Reg. Fish. Res. Lab. **31**: 1–81.

Kinlan, B.P., Gaines, S.D., and Lester, S.E. 2005. Propagule dispersal and the scales of marine community process. Divers. Distrib. **11**(2): 139–148. doi:10.1111/j.1366-9516.2005.00158.x.

Kritzer, J.P., and Sale, P.F. 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. Fish Fish. **5**: 131–140.

Li, N., Zhao, S., and Wasiliev, B. 2000. Geology of Marginal Sea in the Northwest Pacific. Heilongjiang Education Press, Harbin, China. [In Chinese.]

Lin, L. 2009. Study on the fishery biology and management strategy of *Larimichthys polyactis* in the southern Yellow Sea and the East China Sea. Ph.D. dissertation, Fisheries College, Ocean University of China, Qingdao, China. [In Chinese with abstract in English.]

Lin, L., Wang, X., and Ma, C. 2006. A preliminary study on total allowable catch (TAC) of *Pseudosciaena polyactis* in the East China Sea Region. Mar. Environ. Sci. **25**: 30–32. [In Chinese with abstract in English.]

Lin, L., Cheng, J., Jiang, Y., Yuan, X., Li, J., and Gao, T. 2008. Spatial distribution and environmental characteristics of the spawning grounds of small yellow croaker in the southern Yellow Sea and the East China Sea. Acta Ecol. Sin. **28**: 3485–3494. [In Chinese with abstract in English.]

Lin, L., Ying, Y., Han, Z., Xiao, Y., and Gao, T. 2009. AFLP analysis on genetic diversity and population structure of small yellow croaker *Larimichthys polyactis*. Afr. J. Biotechnol. **8**: 2700–2706.

Lindenmayer, D.B., Ball, I., Possingham, H.P., McCarthy, M.A., and Pope, M.L. 2001. A landscape-scale test of the predictive ability of a spatially explicit model for population viability analysis. J. Appl. Ecol. **38**(1): 36–48 . doi:10.1046/j.1365-2664.2001.00558.x.

Liu, X. 1962. The research of small yellow croaker (*Larimichthys polyactis*) geographic race and gonad. Science Press, Beijing, China. [In Chinese.]

Mchich, R., Charouki, N., Auger, P., Raissi, N., and Ettahiri, O. 2006. Optimal spatial distribution of the fishing effort in a multi fishing zone model. Ecol. Model. **197**(3–4): 274–280. doi:10.1016/j.ecolmodel.2006.03.026.

Milton, D.A., Rawlinson, N.J.F., and Blaber, S.J.M. 1996. Recruitment patterns and factors affecting recruitment of five species of short-lived clupeoids in the tropical South Pacific. Fish. Res. **26**(3–4): 239–255. doi:10.1016/0165-7836(95)00434-3.

Orensanz, J.M., Armstrong, J., Armstrong, D., and Hilborn, R. 1998. Crustacean resources are vulnerable to serial depletion — the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. Rev. Fish Biol. Fish. **8**(2): 117–176. doi:10.1023/A:1008891412756.

Punt, A.E. 1993. The comparative performance of production-model and ad hoc tuned VPA based feedback-control management procedures for the stock of Cape hake off west coast of South Africa. *In* Risk evaluation and biological reference points for fisheries management. *Edited by* S.J. Smith, J.J. Hunt, and D. Rivard. Can. J. Fish. Aquat. Sci. Spec. Publ. 120. pp. 283–299.

Quinn, T.J., II, and Deriso, R.B. 1999. Quantitative fishery dynamics. Oxford University Press, New York.

Sawchik, J., Dufrene, M., Lebrun, P., Schtickzelle, N., and Baguette, M. 2002. Metapopulation dynamics of the bog fritillary butterfly: modeling the effect of habitat fragmentation. Acta Oecol. **23**(5): 287–296. doi:10.1016/S1146-609X(02)01157-8.

Schtickzelle, N., Choutt, J., Goffart, P., Fichefet, V., and Baguette, M. 2005. Metapopulation dynamics and conservation of the marsh fritillary butterfly: population viability analysis and management options for a critical endangered species in Western Europe. Biol. Conserv. **126**(4): 569–581. doi:10.1016/j.biocon.2005.06.030.

Seikai National Fisheries Research Institute. 2001. Biological and ecological characteristics of valuable fisheries resources from the East China Sea and the Yellow Sea — comparison between the Chinese and Japanese knowledges. Seikai National Fisheries Research Institute, Nagasaki, Japan. [In Japanese.]

Shanks, A.L., Grantham, B.A., and Carr, M.H. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecol. Appl. **13**(Suppl. 1): S159–S169. doi:10.1890/1051-0761(2003)013[0159:PDDATS]2.0.CO;2.

Stephenson, R.L. 1999. Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. Fish. Res. **43**(1–3): 247–249. doi:10.1016/S0165-7836(99)00076-4.

Trakhtenbrot, A., Nathan, R., Perry, G., and Richardson, D.M. 2005. The importance of long-distance dispersal in biodiversity conservation. Divers. Distrib. **11**(2): 173–181. doi:10.1111/j.1366-9516.2005.00156.x.

Underwood, N. 2007. Variation in and correlation between intrinsic rate of increase and carrying capacity. Am. Nat. **169**(1): 136–141. doi:10.1086/509942. PMID:17206592.

Wilson, J., Ostrom, E., Low, B., and Costanza, R. 1999. Scale misperceptions: and the spatial dynamics of a social–ecological system. Ecol. Econ. **31**(2): 243–257. doi:10.1016/S0921-8009(99)00082-8.

Wooster, W.S. 1992. King crab dethroned. *In* Climate, variability, climate change and fisheries. *Edited by* M.H. Glantz. Cambridge University Press, New York. pp. 14–30.