Maximum sustainable yield estimation of enhancement species with the characteristics of movement inside and outside marine ranching*

Yingbin WANG**, Wei ZHANG

School of Fisheries, Zhejiang Ocean University, Zhoushan 316022, China

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Abstract Marine ranching can be regarded as a type of artificial fishery, and its construction aims at the sustainable utilisation of fishery resources. Therefore, the sustainable yield level of target species in marine ranching has become one of the concerns of stakeholders. The enhancement surplus production model proposed by Wang (2021) based on the traditional surplus production model can be used to assess the sustainable utilisation of settled species in marine ranches. However, when the target species has the characteristics of migration inside and outside marine ranches, its sustainability assessment will be affected. Based on the movement range and resource density levels of enhancement species inside and outside marine ranches, we built a biomass change model that is suitable for enhancement species with migration characteristics inside and outside marine ranches (migration enhancement biomass model). Moreover, we simulated the effects of factors, such as the ratio of the movement range and the ratio of resource density within and outside marine ranches and the fishing strategy for the enhancement species in marine ranches, on the estimation of maximum sustainable yield (MSY). Results show that the large movement range of enhancement species outside marine ranches was associated with the obvious advantage of the proposed migration enhancement model over the traditional enhancement production model. A small difference in the densities of enhancement species inside and outside marine ranches was highly beneficial for improving the accuracy of MSY estimation. The migration enhancement biomass model proposed in this study provides an idea for estimating the MSY of an enhancement species that migrates inside and outside marine ranches. Researchers can adjust the parameters of the model in accordance with the actual situation of resource distribution and changes to improve the scientificity of fishery stock assessment.

Keyword: marine ranching; stock enhancement and releasing; migration; production model; maximum sustainable yield (MSY)

1 INTRODUCTION

In the second half of the 20th century, China's offshore capture fisheries developed rapidly. As a result, China has become the largest fishery producer and aquatic product trading country in the world. At the same time, overfishing and the deterioration of the fishing ground environment have resulted in the degradation of the offshore fishery resources in China (Zhang et al., 2003). Following some countries and regions with developed fisheries, in recent years, China has also started the research and development of technologies for artificial habitat construction, aquatic biology behavioral control, and environmental

monitoring, and has established a stock enhancement and aquaculture industry that can sustainably supply high-quality aquatic products. One of the successful forms of such a technology is the construction of marine ranches (Zhang et al., 2003).

Marine ranching refers to the fishery mode that can increase the conservation of fishery resources,

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^{**} Corresponding author: yingbinwang@126.com

improve the marine ecological environment, and achieve the sustainable utilisation of fishery resources. These can be achieved by constructing or repairing sites required for reproduction, growth or feeding in specific sea areas through placing artificial reefs and releasing based on the principles of the marine ecosystem (General Office of Shandong Provincial People's Government, 2019). Through human intervention, fishery resources in marine ranches can be concentrated and utilised sustainably, which is one of the goals of marine ranch construction and management and is a concern of managers and resource scientists.

Marine ranching activities can be traced back to more than a century ago (Liao, 1997; Liao et al., 2003). Ever since, stock enhancement has been attempted at some level in over 25 countries worldwide (Bartley, 1999) with more than 100 species (fish, crustaceans, molluscs, and other invertebrates) (Liao, 1999; Fushimi, 2001). In-depth studies on marine ranching were conducted in the early 21st century and focused on juvenile releasing techniques (Fushimi, 2001; Junio-Meñez et al., 2002; Yamamoto Morioka, 2002), released species health management (Buchmann et al., 2001), tagging methods (Brennan et al., 2002a, b), and ecological and genetic diversity (Tseng et al., 2001; Miller and Walters, 2004). Scholars in China have also carried out considerable research on the assessment of the conservation and enhancement effects of marine ranching resources. In Zhangzi Island, investigation and evaluation of fishery resources in marine ranches and the comparison of species within and outside reef areas have shown that artificial reefs have a good conservation effect on fishery resources (Wang et al., 2018). The evaluation of the conservation effect on fishery resources in marine ranches in Xiangshan Port illustrates that the species richness, total biomass, and abundance increased after artificial reefs were installed (Wang et al., 2019b). The results of the assessment of the fishery resource enhancement effect of marine ranching in Zhelin Bay in the eastern Guangdong Province depict that fishery habitats have improved and the catch per unit of effort (CPUE) has increased (Wang et al., 2019a). Recent reports have proposed strategies for the principles and techniques of the conservation of resources in marine ranches in China (Zhang et al., 2020). Although these studies have focused on the sustainable utilisation of fishery resources in marine ranching, they do not involve the quantitative analysis of the development and management of important species, which is one of the issues of concern of the experts in this field.

The surplus production model (SPM) is one of the most important fishery stock assessment models used for estimating the annual sustainable catch of the objective species (Punt, 2003). When both the habitat water and fishing water for the target species are limited to the marine ranch, the traditional SPM can be used to estimate the maximum sustainable yield (MSY) of the species in it. However, after the implementation of stock enhancement, the MSY of the enhancement species cannot be effectively estimated using the traditional SPM. Wang (2021) proposed an enhancement SPM for the estimation of the MSY for enhancement species settled in marine ranches. However, this enhancement SPM is unsuitable for species that migrate inside and outside marine ranches; such migratory behaviour is highly common for fish living in the sea areas of marine ranches. The migration of fish inside and outside marine ranches will affect the assessment results of MSY, especially when the living area outside a marine ranch is large. At the same time, the implementation of stock enhancement also increases the complexity of the stock assessment. In this research, a new model for describing the biomass change of the enhancement species migrating inside and outside marine ranches was proposed based on the enhancement SPM, which can be used to estimate the MSY of the species that is released to marine ranch but migrate inside and outside of it. The comparison between the proposed model and the enhancement SPM were also made.

2 MATERIAL AND METHOD

2.1 Model

Wang (2021) established a discrete nonequilibrium SPM for enhancement species based on the logistic biomass growth model (here, we call this model the enhancement model). The general form of biomass changes, which is the theoretical basis of the model, is

$$B_{t+1} = B_t + (rB_t + eS_t) \left(1 - \frac{B_t}{K} \right) - C_t, \tag{1}$$

where B_t is the biomass in year t, r is the intrinsic rate of growth, e is the effective enhancement rate, S_t is the enhancement biomass in year t, K is the carrying capacity and C_t represents the catch in year t. This model can be used to estimate the MSY of the species settled in a marine ranch under the influence of stock enhancement. Given that, the movement range of this

species usually does not exceed the boundary of the marine ranch, and the living area of the species is consistent with their fishing seas. In this way, the estimated MSY for such a species will be highly accurate. However, in addition to settled species, species with strong swimming capability will be released into the marine ranch. The movement range of these species is not limited within the marine ranch. For example, the movement range of some fish may exceed several times the area of the ranch. Equation 1 will not be a good choice for the estimation of the MSY of such a species.

When the movement range of the enhancement species exceeds the boundary of a marine ranch, the individuals inside and outside the marine ranch can be treated separately. Suppose that the movement ranges inside and outside the marine ranch are $A_{\rm in}$ and $A_{\rm out}$, respectively, and the ratio of the resource density inside and outside the marine ranch is equal to τ (usually τ >1 considering the effect of fish collection due to the construction of artificial habitats in the marine ranch). Based on Eq.1, the changes in the biomass inside and outside the marine ranch can be expressed by using the following equations:

$$B_{(\text{in})t+1} = B_{(\text{in})t} + (rB_{(\text{in})t} + eS_t \frac{\tau A_{\text{in}}}{\tau A_{\text{in}} + A_{\text{out}}})$$

$$\left(1 - \frac{B_{(\text{in})t}}{K \frac{\tau A_{\text{in}}}{\tau A_{\text{in}} + A_{\text{out}}}}\right) - C_t + B_{(\text{supp})t}, \qquad (2)$$

$$B_{(\text{out})t+1} = B_{(\text{out})t} + (rB_{(\text{out})t} + eS_t \frac{A_{\text{out}}}{\tau A_{\text{in}} + A_{\text{out}}})$$

$$\left(1 - \frac{B_{(\text{out})t}}{K \frac{A_{\text{out}}}{\tau A_{\text{in}} + A_{\text{out}}}}\right) - B_{(\text{supp})t}, \tag{3}$$

where
$$\frac{\tau A_{\rm in}}{\tau A_{\rm in} + A_{\rm out}}$$
 and $\frac{A_{\rm out}}{\tau A_{\rm in} + A_{\rm out}}$ represent the

proportion of the biomasses inside and outside the marine ranch to the total biomass and are used as the ratios of the enhancement species biomasses inside and outside the marine ranch and as the indexes of the total carrying capacity allocated inside and outside the marine ranch. $B_{(\text{in})t}$ and $B_{(\text{out})t}$ represent the biomasses of the enhancement species inside and outside the marine ranch in year t, respectively. B_{supp} represents the biomass recruited into the marine ranch from the outside after the catch of C_t has been removed

from the ranch. The value of B_{supp} is determined by the ratio of the resource density of the species inside and outside the marine ranch, i.e. τ , and its calculation formula is

$$B_{\text{supp}} = \frac{\tau A_{\text{in}} B_{\text{out}} - A_{\text{out}} (B_{\text{in}} - C_t)}{\tau A_{\text{in}} + A_{\text{out}}}.$$
 (4)

By adding Eqs.2 & 3 together, we can obtain Eq.5, which is suitable for the biomass change of enhancement species with the characteristics of migration inside and outside marine ranches (migration enhancement biomass model):

$$B_{t+1} = B_{t}(1+r) + eS_{t} - \left[\frac{r(\tau A_{\text{in}} + A_{\text{out}})}{K} \left(\frac{B_{\text{in}}^{2}}{\tau A_{\text{in}}} + \frac{B_{\text{out}}^{2}}{A_{\text{out}}} \right) + \frac{eS_{t}}{K} B_{t} \right] - C_{t}.$$
 (5)

The parameters r, q, K, B_t (when t is the initial year) and e are estimated by using the observation error method, and then MSY can be calculated.

$$CPUE_{t} = \frac{C_{t}}{E_{t}} + \varepsilon_{t}$$

$$\sum_{t} (CPUE_{t} - qB_{t}),$$

where CPUE_t is the catch per unit of effort in year t; E_t is the fishing effort in year t; q is catchability; ε_t represents the error and follows a normal distribution $N(0, \sigma^2)$, the parameter σ came from the actual observations data in the past few years, and was equal to 10%. After obtaining the parameter values, the MSY of the enhancement species in a marine ranch can be calculated by using the following equation:

$$MSY = \frac{rK}{4} + \frac{eS_t}{2} + \frac{e^2S_t^2}{4rK}.$$
 (6)

The specific derivation of Eq.6 can be found in Wang (2021).

2.2 Simulation analyses

In the simulation analyses, 20 scenarios were assumed to compare the impacts of different factors on the enhancement model and migration model (Table 1). Three impact factors were considered, including (1) the living area of the enhancement species, (2) the difference of resource densities inside and outside marine ranch, and (3) the fishing strategy in marine ranch. For the first factor, the living area of enhancement species excluding the marine ranch (A_{out}) was used; for the second factor, the ratio of resource density inside and outside marine ranch ($D_{\text{in}}/D_{\text{out}}$) was used; for the third factor, we assumed four change

Table 1 Simulation scenarios of the enhancement species and fishing strategy

No.	$A_{\rm out}({\rm km^2})$	$D_{ m in}\!/\!D_{ m out}$	Fishing strategy in marine ranch			
1	0	-	Continuously decreases			
2	0	-	Continuously increases			
3	0	-	Increases first and then decreases			
4	0	-	Decreases first and then increases			
5	3	2	Continuously decreases			
6	3	2	Continuously increases			
7	3	2	Increases first and then decreases			
8	3	2	Decreases first and then increases			
9	6	2	Continuously decreases			
10	6	2	Continuously increases			
11	6	2	Increases first and then decreases			
12	27	2	Decreases first and then increases			
13	27	2	Continuously decreases			
14	27	2	Continuously increases			
15	27	2	Increases first and then decreases			
16	27	2	Decreases first and then increases			
17	27	3	Continuously decreases			
18	27	3	Continuously increases			
19	27	3	Increases first and then decreases			
20	27	3	Decreases first and then increases			

For each scenario, the enhancement number is 240 000, and the area of the marine ranch is $3~{\rm km^2}$. $A_{\rm out}$ represents the living area of enhancement species excluding the marine ranch; $D_{\rm ini}/D_{\rm out}$ represents the ratio of resource density inside and outside marine ranch. – means no data.

trends of catch in the marine ranch, namely annual catch continuously decrease, annual catch continuously increase, annual catch increase first then decrease, and annual catch decrease first then increase (Table 1). For each scenario, Eq.1 (enhancement model) and Eq.5 (representing the new model, which we call the migration model) were used to estimate MSY to analyse the differences between the two models. The MSY estimation was repeated 1 000 times.

3 RESULT

3.1 Models and curves

Compared with the enhancement model (Eq.1), the migration model (Eq.5) proposed in this research has two more variables, i.e., the movement ranges inside and outside the marine ranch ($A_{\rm in}$ and $A_{\rm out}$). At the same time, the original initial biomass B_0 is replaced by the initial biomass inside and outside the marine ranch, i.e. $B_{\rm (in)0}$, $B_{\rm (out)0}$ and $B_0 = B_{\rm (in)0} + B_{\rm (out)0}$.

The curves of the migration model are similar to

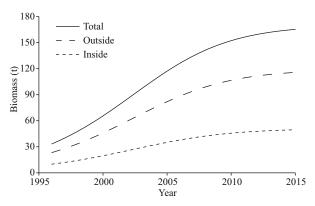


Fig.1 Schematic of the biomass change trend for the migration enhancement biomass model

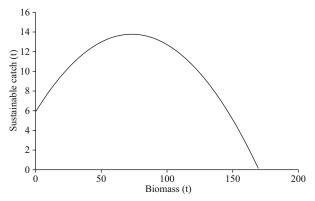


Fig.2 Schematic of the sustainable yield for the migration enhancement biomass model

those of the enhancement model. The growth curves for the total biomass and the biomass inside and outside the marine ranch are all S-shaped (Fig.1). The relationship between continuous yield and biomass is parabolic and is affected by stock enhancement. Consistent with the report by Wang (2021), yield is still present even when the biomass is zero (Fig.2).

3.2 Simulation analyses

Under different simulation scenarios, the MSY is underestimated by the enhancement model (Table 2). The size of the movement range outside the marine ranch has great effect on the enhancement model. As the movement range outside the marine ranch increases, the absolute value of the relative estimation error (REE) of the estimated MSY also increases. For the migration model, it is not sensitive to the movement range outside the marine. Different fishing strategies have different effects on the MSY estimation. Generally, when the catch continuously increases, the MSYs are underestimated, and for other three fishing strategies the MSYs are overestimated. When the catch decreases first and then increases, the

Table 2 REE of MSY under different movement ranges of enhancement species and fishing strategies in marine ranches

$A_{\rm out}({\rm km^2})$	Measurement _ index	Catch-D		Catch-I		Catch-I-D		Catch-D-I	
		EM	MM	EM	MM	EM	MM	EM	MM
0	Mean	-0.45	-0.45	-5.49	-5.49	-5.06	-5.06	-2.14	-2.14
	Median	0.17	0.17	-5.87	-5.87	-5.11	-5.11	-4.05	-4.05
3	Mean	-68.11	15.90	-77.05	-15.70	-74.92	15.09	-72.79	6.72
	Median	-71.52	14.51	-77.89	-22.24	-76.19	15.07	-74.08	4.63
6	Mean	-99.14	15.85	-119.15	-11.98	-117.14	15.01	-112.89	5.57
	Median	-95.33	14.40	-120.81	-12.93	-118.41	15.08	-115.63	4.78
27	Mean	-288.48	18.26	-315.22	-39.71	-313.77	13.09	-305.02	4.07
	Median	-304.59	16.41	-323.69	-48.50	-323.34	13.08	-304.67	3.48

The ratio of the biomass density of enhancement species inside and outside marine ranches is 2:1, and the area of a marine ranch is 3 km². A_{out} represents sea area outside the marine ranch; Catch-D, Catch-I, Catch-I-D, and Catch-D-I represent the catch continuous decrease, catch continuous increase, catch increase first then decrease, and catch decrease first then increase, respectively; mean and median represent the arithmetic mean and median of 1 000 REE, respectively; EM and MM represent enhancement model and migration model, respectively.

error of the estimated MSY is relatively small. When the catch continuously increases, the estimated MSY differs greatly from the true value. When the proportion of movement range outside the marine ranch increases, the MSY estimated by using the migration model is more accurate than that estimated by using the enhancement model.

Given the construction of marine ranches, the density of the enhancement species inside marine ranches will be higher than that outside. When the biomass density ratio of the enhancement species inside a marine ranch to that outside increases from 2:1 to 3:1, the error of the estimated MSY increases (Tables 2 & 3). The distribution of 1 000 MSY values of the enhancement species estimated using the migration model indicates its advantages when the resource density of the target sepcies in the marine ranch is high and the living area outside the ranch is large (Supplementary Figs.S1 & S2).

4 DISCUSSION

The structure of the migration model proposed in this study is similar to that of the enhancement model. However, because it is not only affected by stock enhancement but also by the biomass and migration of the enhancement species inside and outside marine ranches, the migration model is more complex than the enhancement model. The enhancement model contains five parameters $(r, K, B_t, q, \text{ and } e)$, whereas the migration model contains one more parameter than the enhancement model (that is, B_t is divided into $B_{[in]t}$ and $B_{[out]t}$) because it treats the inside and outside areas of marine ranches as independent sea areas. In addition, when using the migration model, we should provide

Table 3 REE of MSY for different fishing strategies obtained by using the migration model when the ratio of biomass density of enhancement species inside and outside marine ranches is 3:1

$A_{\rm out}$ (km ²)	Measurement index	Catch-D	Catch-I	Catch-I-D	Catch-D-I
27	Mean	36.61	19.36	28.56	31.26
21	Median	34.85	16.34	8.32	27.67

The area of the marine ranch is 3 km². $A_{\rm out}$ represents sea area outside the marine ranch; Catch-D, Catch-I, Catch-I-D, and Catch-D-I represent the catch continuous decrease, catch continuous increase, catch increase first then decrease, and catch decrease first then increase, respectively; Mean and Median represent the arithmetic mean and median of 1 000 REE, respectively.

the preliminary estimate of the movement range of the enhancement species and the area of the marine ranch. Although its parameters have been increased, the migration model can address the changes in the biomass inside and outside marine ranches separately in one model. If the enhancement species move inside and outside marine ranches, a recruitment mechanism will form between these two areas. When fishing occurs within a marine ranch, the unfished stock outside the marine ranch will be recruited into the marine ranch; this trend maintains the ratio of resource densities inside and outside the marine ranch at the initial level. Although a recruitment trend for the enhancement species inside and outside the marine ranch is observed, it is not as regular as the trend described above because the movement of the enhancement species exhibits randomness. Equation 5 provides a way to estimate the MSY of the enhancement species that migrates inside and outside marine ranches.

In fact, the ratio of the biomasses of the enhancement species and the ratio of the carrying capacity (K) inside

and outside marine ranches in Eqs.2, 3, & 5 can be set in accordance with the specific situation. In this study, the ratio is set based on the movement range areas of the enhancement species inside and outside marine ranches, whose resource densities are used as the weight coefficients. In practical applications, the researcher should provide initial estimates of the ratios of the area and resource density of the enhancement species inside and outside marine ranches in line with actual conditions through surveys or historical data.

As inferred from the simulation analysis results of the enhancement model and migration model, when fishing only occurs within the marine ranch, and the living area of the enhancement species does not exceed the boundaries of the marine ranch, the enhancement model and migration model are exactly the same. Thus, both models can be used to estimate the MSY of the enhancement species. As the movement range of enhancement species outside the marine ranch increases, the advantages of the migration model become increasingly obvious (Table 2 and Supplementary Fig.S1).

There are few reports on the estimation of MSY of enhancement species in marine ranch, and only Wang (2021) proposed an enhancement SPM for the estimation of the MSY for enhancement species settled in marine ranches. In the current study, we compared the results of enhancement model and migration model when dealing with the situation that enhancement species can migrate inside and outside the marine ranch. The results showed that the migration model is more suitable for the enhancement species that migrate inside and outside the marine ranch than the enhancement model. When the $A_{out}=0$, the estimated MSY of the two models are exactly the same. When $A_{\text{out}} > 0$, the enhancement model only considers the enhancement individuals inside the marine ranch, and does not deal with those outside the marine ranch. When the movement range of the enhancement species outside marine ranch becomes large, the consistency between the fishing area inside the marine ranch and the living area of the enhancement species becomes poor. Using the enhancement model is equivalent to estimating the biomass in the entire movement range based on only the catch data in the marine ranch, indicating that the representativeness of the fishing information is very low. Thus, it may underestimate the MSY. The improvement of the proposed migration model over the enhancement model is that it extends the scope of application beyond marine ranch by introducing the ratio of the

resource density (τ) and treating the individuals inside and outside the marine ranch separately (Eqs.2, 3, & 5). Therefore, the estimated MSYs of migration model are better than those of enhancement model when the proportion of movement range outside the marine ranch increases (Table 2).

Although the migration model is appropriate to the migration characteristics of the enhancement species inside and outside marine ranch, it has a tendency to overestimate the results, especially when the movement range of enhancement species outside the marine ranch increases. There may be many reasons for the overestimation. First, given that the enhancement species can move freely inside and outside marine ranches, the MSY of the enhancement species in a marine ranch and the MSY in the entire living area should be similar, i.e., the resources that are reduced because of capture in the marine ranch can be recruited from outside the ranch. Therefore, the catchability coefficient (q) is the critical parameter for stock assessment for a large-scale sea area based on the catch data in marine ranches. q represents the proportion of the biomass of the target species to the total biomass in a certain sea area caught by one unit of effort. In theory, as long as the value of q can be accurately determined, a viable MSY can be estimated. However, when fishing only occurs in marine ranch, and at the same time the resource density in the marine ranch is higher than that outside, q is prone to be overestimated, which will lead to the overestimation of MSY. Second, the parameter value of e may also be overestimated since the survival rate of the enhancement species maybe high benefit from the recruitment from outside the marine ranch and the protective effects of artificial reefs, etc. Third, the division of carrying capacity (K) and enhancement biomass (S) inside and outside marine ranch is based on the resource density and area (Eqs. 2 & 3), which is a mathematical approach we had to use since the field monitoring data was unavailable. Fourth, the recruitment biomass (B_{supp}) lacks a specific calculation formula, which may also be a source of error in overestimating MSY. All of the above issues are needed to be studied in depth in future research.

The difference in the resource density of the enhancement species inside and outside marine ranches can also affect the MSY estimation results. Great differences provide poor estimation results. A large difference in density means that the homogeneity of resource distribution inside and outside a marine ranch is poor, which inevitably affects the randomness

of the migration of the enhancement species inside and outside the marine ranch. When fishing occurs in the marine ranch, ensuring that the ratio of resource densities inside and outside the marine ranch remains at the original level becomes difficult even though resources may be recruited into the marine ranch from the outside. If the resource densities inside and outside the marine ranch are similar, maintaining the consistency of the resource density through resource migration, which can also improve the accuracy of the estimation of MSY, is easy.

In 1998, Hannesson proposed a biomass variation model based on the migration characteristics of fish inside and outside marine reserves (Hannesson, 1998). A parameter of the migration rate of the stock in the marine reserve is introduced into this model. Subsequently, some scholars applied the concept of migration rate in the study of the sustainable yield of fishery resources in protected marine areas (and sea areas where fishing operations cannot be performed due to special reasons) (Pincin and Wilberg, 2012; Shibata et al., 2015; Paul et al., 2018). In contrast to marine protected areas, marine ranches are artificial fishing grounds (Shandong Provincial Oceanic and Fishery Department, 2017) and are a service provided for the sustainable utilisation of fishery resources. Therefore, fishing operations occur within marine ranches. However, fishing behaviour is usually restricted in marine ranches and is forbidden in surrounding sea areas to protect resources from being overexploited. The concept of migration rate can also be applied in the study of the dynamics of fishery resources inside and outside marine ranches. However, determining the actual migration rate of the target species is difficult. Techniques, such as marking or underwater observation, can be used for the estimation of migration rate, and their results are usually subject to large errors. Therefore, we did not use the parameter of migration rate in the current study but instead added variables representing the areas and the original biomasses inside and outside a marine ranch to the model. These variables can be obtained through routine surveys and are easy to acquire.

In the current study, a migration enhancement biomass model for an enhancement species is proposed based on the movement ranges and density ratios of the target species inside and outside marine ranches. It provides an idea of estimating the MSY of the target species for similar situations. The application of this model is not limited to marine ranch. The model can be used to estimate the MSY of an enhancement species

when the sea area for its fishing operation is inconsistent with its living area. Moreover, the accuracy of the results estimated by this model is higher than that of the results estimated by the enhancement model. The parameters in the model can be adjusted in accordance with the actual situation to meet the characteristics of resource migration and distribution, thereby improving the accuracy of stock assessment.

5 CONCLUSION

The migration enhancement biomass model proposed in this study can be used to estimate the MSY of the enhancement species with migration characteristics inside and outside marine ranches. The MSY is prone to be overestimated, and movement range ratios and biomass density inside and outside marine ranches are two important parameters that can affect the accuracy of the estimation results. The proposed model also provides an idea for estimating the MSY of species with inconsistent living and fishing areas.

6 DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

7 ACKNOWLEDGMENT

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Electronic supplementary material

Supplementary material (Supplementary Figs.S1–S2) is available in the online version of this article at https://doi.org/10.1007/s00343-020-0288-y.