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Dynamic simulation of tropical coral reef ecosystem being disturbed by multiple situations

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Abstract

In consideration of the rapid degradation of coral reef ecosystems, the establishment of models is helpful to comprehend the degradation mechanism of coral reef ecosystems and predict the development process of coral reef communities. According to the characteristics of complex ecosystem of tropical coral reefs in China, the coral reef functional group is the core level variable; combined with the multiple feedback effects of coral reef functional groups and environmental changes, the study presents a coral reef ecosystem dynamics model with hermatypic corals as the core. Based on the simulation of the assumed initial value and the internal feedback of the system, the results show that in the basic simulation (relative health conditions), the coverage area of live corals and coral reefs generally decreased first and then increased, and increased by 4.67% and 6.38% between 2010 and 2050, respectively. Based on the calibration model and the current situation of the studied area, the multi-factor disturbance effects of coral reef communities were simulated and explored by setting up three scenarios involving fishing policy, terrestrial deposition, and inorganic nitrogen emissions. Among them, in the single factor disturbance, the fishing policy exerts the most direct impact on the community decline; and the succession phenomenon is obvious; the terrestrial sedimentation has a faster and more integrated effect on the community decline; the effect of inorganic nitrogen emission on the community decline is relatively slow. In the double/multi-factor disturbance, the superimposed disturbance will aggravate the multi-source feedback effect of the coral reef communities development, accelerate the community decay rate, and make its development trajectory more complicated and diverse. This method provides a scientific and feasible method for simulating the damage of long-term coral reef community and exploring the development law and adaptive management of coral reef ecosystems. In the future, it can be further studied in the ecological restoration process and decision-making direction of coral reefs.

Key words: coral reef ecosystem, system dynamics, situational disturbance, simulation

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1 Introduction

In recent years, with the impact of global climate change and increased human activities, coral reefs, known as "submarine rainforests" (Zhou et al., 2014), have been endangered and are experiencing rapid decline world-wide. In 2004, the World Coral Reef Survey pointed out that more than 20% of coral reefs in the world had been completely destroyed (Wilkinson, 2004), and in 2008, research showed that more than one-third of the world-wide coral reefs have been seriously degraded (Carpenter et al., 2008). Furthermore, seventy-two percent of world heritage reef properties (21 of 29) have been exposed to severe and/or repeated heat stress (Heron et al., 2017). Therefore, the degradation of coral reefs and their ecological protection and restoration have become a major issue for the world to face.

Although domestic and foreign research and the implementation of coral reef protection and restoration schemes have made some progress, they are still in the exploratory stage. Coral reef restoration research in the United States, Australia, Singapore and other countries has mainly focused on habitat restoration, biological resource conservation, and monitoring management. Rinkevich (2005) reviewed the methods and progress of coral reef restoration over the past decade, demonstrating that active conservation measures and appropriate human intervention can accelerate the ecological restoration process of coral reefs. Bongiorni et al. (2011) used *in situ* intensive coral farming as an active restoration strategy for coral reefs, supporting the idea of *in-situ* coral mariculture in an integrated coastal management program. Ramos-Scharrón et al. (2015) analyzed the potential impacts of the Puerto Rico basin and changes in land cover on coral reef ecosystems, where they inferred that coral reef restoration activities must address concurrently numerous stressors. Branchin et al. (2015) described employing citizen science programs to monitor the biodiversity of coral reefs, while Shlesinger and Loya (2016) demonstrated that understanding coral recruitment and the dynamics of coral settlements are important for coral reef management.

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Coral reef protection and restoration research in China started late. Zhao et al. (2006) studied the biodiversity of coral reefs and their ecological functions, and reviewed the development trend of coral reef biodiversity research and the significance of coral reef protection. Li et al. (2008) put forward a strategy suitable for the protection and restoration of coral reef resources in China based on the causes of coral reef destruction and ecological restoration methods. Wang et al. (2011) examined the problem of the source of corals in China based on the study of the diffusion pathway of coral recruits, and proposed a new concept where recruit sources and diffusion corridors should be protected for the management of protected coral reef areas. Qin et al. (2016) studied the theoretical feasibility of coral reef ecological restoration and discussed its technical methods, while Zhao et al. (2016) presented the concepts and patterns behind the sustainable development of coral reefs, and proposed such pathways for coral reefs in the South China Sea islands. In general, coral reef related research has gradually evolved from static, single-scale and structural studies to dynamic, system-scale and functional programs.

As a complex ecosystem, coral reefs are affected by multiple correlated factors. Conventional experimental methods are extremely complicated and expensive for finding the specific processes that affect the overall state of a coral reef and the feedback loops within ecosystem (Kubicek and Reuter, 2016). As a simplification of the structure and process of the ecosystem, models are especially suitable for operations that are difficult to test on site (Precht, 2006), while contributing to understanding the degradation and development mechanisms of coral reefs from the perspective of ecosystem integrity. Therefore, modeling can be a powerful tool for applying ecological protection measures and the restoration of coral reefs.

There are vast coral reefs in the tropical waters of China, (Huang et al., 2008), and they are extremely important in terms of their ecology and environment. In recent years, due to rising water temperatures, starfish outbreaks, destructive fishing practices, and other reasons, the degradation of coral reefs in these areas has become increasingly severe, with the coverage of living hermatypic corals reduced sharply (Li et al., 2018). Therefore, this study took the characteristics of regional degradation as a reference, constructed a dynamic model of the coral reef ecosystem based on system theory and restoration ecology, designed the dynamic development analysis of the coral reef communities disturbed by three kinds of human influence at difference levels, namely fishing policy, terrestrial deposition, and total inorganic nitrogen emission. Then this study elaborated upon the general principles of coral reef development from the perspective of system integrity, which is potentially of great significance to the ecological protection and sustainable development of coral reefs in China.

2 Methodology

System dynamics (SD) as a non-phenomenological "physical" method has the two distinct characteristics of endogenesis and feedback. Since the degradation process of coral reefs is highly consistent with the development of complex systems, it is a good means to study the integrity of coral reef ecosystems from a systematic perspective, although there have been few successful applications of SD models for the simulated study of coral reef ecosystem (Chang et al., 2008; Holmes and Johnstone, 2010; Bartelet, 2017).

2.1 *System boundary and structure*

This study considered hermatypic corals as the main subject. Considering efforts to improve the structure and function of degraded coral reef ecosystems (Li et al., 2015), the relevant variables are classified into endogenous and exogenous types, which both affect the development of coral reef ecosystems. The endogenous variables of the system are composed of the biota living on coral reefs, which can be classified into plankton, swimming biota, and benthic organisms, according to their habitual nature. This study focused on the simulation of system-level dynamics rather than individual nutrient dynamics (Liu et al., 2006). Therefore, the concept of a functional group is used to represent a collection of species that play a similar ecological role and occupy similar positions within the ecosystem. Based on ecosystem integrity and goal orientation, coral reef ecosystems can be divided into reef-building functional groups, macroalgae functional groups, herbivorous fish functional groups, predatory biological functional groups, and others (Table 1). In order to better understand the coral reef system, the subsequent construction of the model is based on representative organisms, and the individual differences should be balanced as much as possible when setting up the relevant parameters of the species. Among them, hermatypic corals, as the main contributor to the coral reef system (Zhao et al., 2006), not only provide habitats for most reef creatures, but they are also the main species involved in reef construction. Therefore, the protection and restoration of coral reef ecosystems should focus on these corals.

The exogenous variables of the system are composed of environmental factors that affect coral reef organisms, including global climate change and human activities. The rise of sea surface temperature (SST) caused by global warming is often considered to be the main cause of the large-scale bleaching of corals (Bellwood et al., 2006; Baker et al., 2008), but the specific reason is still unclear. Ocean acidification is the direct cause of the reduction of the calcification rate of reef-building organisms such as hermatypic corals, which aggravates the dissolution of coral reefs and increases the risk of damage (Wilkinson, 2008). As a result of global climate change, the frequency and intensity of natural disasters such as typhoons and storm surges are also increasing (Zhao et al., 2017), which also cause significant damage to the integrity and stability of coral reef systems. In addition, the adverse effects of human activities such as tourism, sewage disposal, engineering construction, and unsustainable fishing on coral reefs have become more apparent. Studies have shown that hermatyp-

Table 1. Functional groups and major organisms of coral reef ecosystems

Functional groups	Interpretation	Representative creature
Reef-building organisms	the main builder of coral reefs, organisms which have the ability to build reefs	hermatypic corals and other reef-building organisms
Macroalgae	an important part of the coral reef which competes with corals, especially in space	large fleshy seaweed, such as leafy seaweed, cortical large seaweed
Herbivorous fish	predators of macroalgae	parrotfish
Enemy organisms	predators of hermatypic corals	crown-of-thorns starfish
Balanced organisms	predators of the enemies of hermatypic corals	charonia tritonis

ic corals are particularly sensitive to the deterioration of environmental factors. This is very detrimental to coral recruitment, maturing and calcification (Fabricius, 2005), while it is promoting the growth of macroalgae and crown-of-thorns starfish (e.g., increase in seawater nutrients), and thus further endangering the development state of coral reef ecosystems within the relevant food chain (Hughes et al., 2010).

Considering the complexity of the coral reef ecosystem, the model is not constructed to describe all the structures and processes involved, but to analyze hermatypic corals and their related variables according to the research objectives and needs. Therefore, combined with field research and literature research, the coral reef food network relationship in the model and its interaction with the environment are appropriately simplified (Fig. 1). Among them, the internal feedback effects of the system mainly include the competition between reef-building biological functional groups and macroalgae, the predation of predatory organisms, and the regulation of herbivorous fish and balanced organisms. The feedback effect between the system and the external environment is generated by the complex energy logistics exchange process between the internal and external variables, which has a comprehensive impact on the system as a whole. According to the analysis of the causes of the degradation of coral reefs in the tropical waters of China in recent years, human activities is the primary impact (Li et al., 2018). Therefore, the model will enhance the general dynamic comprehension of the main causes of the main degradation of coral reef from a system perspective, mainly focusing on three typical artificial models of fishing activities, coastal engineering construction, and emission of inorganic nitrogen.

2.2 *Model variables and equations*

Based on the boundaries and structure of the coral reef ecosystem, the coral reef SD model system was simplified as much as possible. A total of 126 variables including 13 level variables, 34 rate variables, 32 auxiliary variables and 47 constants were selected. Due to the limited space, the main variables and expressions in the model are displayed according to the relationship of the functional group variables (Table 2).

2.3 *Model main parameter source*

Given the lack of a large amount of observational data and the difficulties in quantifying the related parameters, the following methods were used to determine the model parameters (Table 3).

2.4 *Model related assumptions and explanations*

In order to better understand the model to some extent, on the basis of not significantly affecting the objectivity of the simulation results, several assumptions are made on the model. The following are the main hypotheses and explanations:

(1) In order to reflect the natural mortality of corals and other causes of their death, the reasons are classified as natural and unnatural, and the model assumes that both are responsible for the death of corals.

(2) Since coral reefs belong to a three-dimensional geotechnical sedimentary construction, it is currently impossible to directly calculate the area of a coral reef by using calcification rates. The model assumes that the carbonate productivity coupled with the reef accretion factor equals the coral reef ind formation area.

(3) The model assumes that macroalgae and living corals mainly compete for coral reef living space. Although there are other physical, chemical and microbial processes, the impact of space competition on living corals is more direct (Liao et al., 2016).

(4) The model assumes that the change of inorganic nitrogen mainly affects the growth and development of macroalgae, and temporarily excludes the effects on the living coral tissue and its cycling process. Because compared to live corals, macroalgae are more sensitive to increased nutrients in the sea (Talbot and Wilkinson, 2001), and different corals respond differently to changes in nutrient salts.

(5) Considering the potential role of mature coral and coral reef development in improving fish spawning efficiency and reducing larval mortality, the model assumes a correlation between them in the form of a table function.

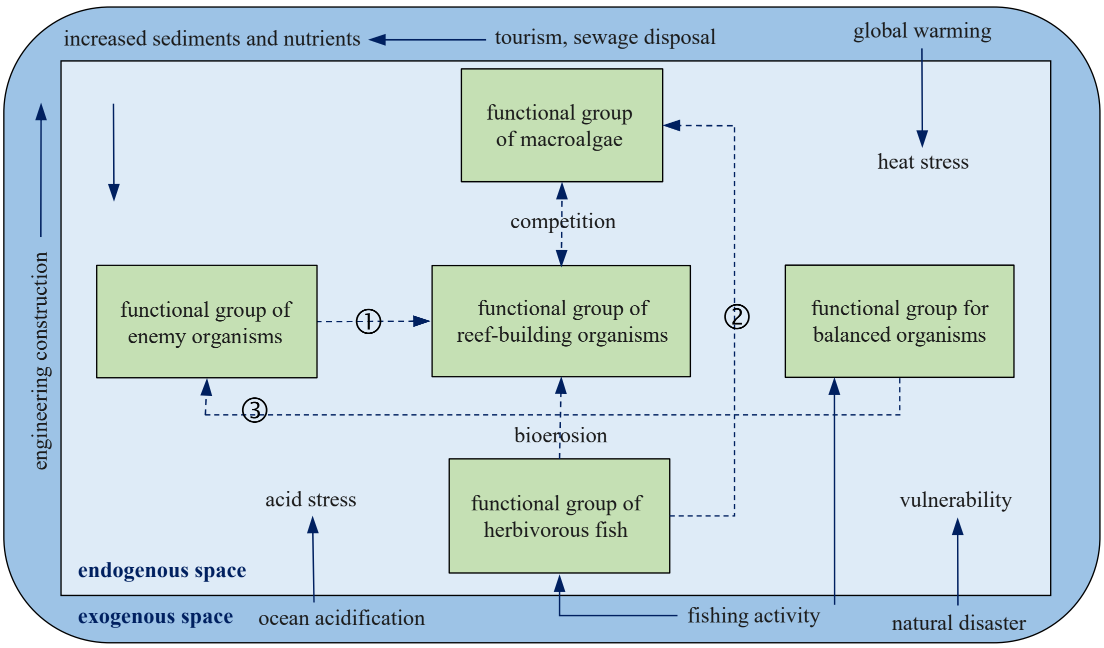

Fig. 1. Block diagram of a coral reef ecosystem. ①②③ all mean predation.

Table 2. Main variables and expressions of the coral reef SD model

Module	Variable name	Type	Equation expression
I	coral recruitment area/(10^4 m^2)	RV	=MIN (potential new coral recruitment, available space for coral reef)
	coral grazing area/(10^4 m^2)	RV	=MAX (crown-of-thorns starfish stock×average crown-of-thorns starfish predation coefficient, 0)
	coral carbonate productivity/(kg·a^{-1}·m^{-2})	AV	=living coral coverage rate×coral average calcification rate
	coral reef decline/(10^4 m^2)	RV	=coral reef stock/coral reef decay time+coral reef stock×(erosion rate by human activities+natural erosion rate)+parrotfish stock×3×10^{-7}
	sediment/(10^4 m^2)	LV	=INTEG (sediment input+coral reef decline stock–sediment dissipation, 10)
	available space for coral reef/(10^4 m^2)	AV	=coral reef stock-(coral recruitment+mature coral stock+macroalgae stock)
	effect of sediment on carbonate productivity of coral reefs	AV	=WITH LOOKUP {sediment, ([(0, 0)–(40, 1)], (0, 1),(5, 0.8), (10, 0.6), (15, 0.4), (20, 0.1), (30, 0), (40, 0)}
II	inorganic nitrogen content of coral reef/(mg·L^{-1})	LV	=INTEG (inorganic nitrogen dissolution–inorganic nitrogen dissipation, 0.02)
	potential new recruits macroalgae/(10^4 m^2)	AV	=mature macroalgae stock×annual average spawning efficiency of macroalgae×annual average spawning frequency of macroalgae
	macroalgae recruitment/(10^4 m^2)	RV	=MIN (available space for coral reef, potential new macroalgae recruitment)
	macroalgae time to mature/a	AV	=normal macroalgae time to mature×effect of nutrients on macroalgae time to mature×effect of sediment on macroalgae time to mature
	effect of nutrients on macroalgae time to mature	AV	=WITH LOOKUP (inorganic nitrogen content of coral reef, {[(0, 0)–(5, 1)], (0, 1), (1, 0.5), (2, 0.4), (15, 0.4), (3, 0.3), (4, 0.2), (5, 0.1)}
III	parrotfish overcrowding/ind.	AV	=MAX(0, parrotfish stock–parrotfish environmental capacity)
	spawning efficiency of parrotfish	AV	=WITH LOOKUP (mature coral stock, ([(0, 0)–(350, 0.8)], (0, 0.1),(100, 0.4), (150, 0.45), (200, 0.5), (250, 0.55), (300, 0.6), (350, 0.65))
	parrotfish recruits mortality	AV	=WITH LOOKUP(coral reef stock, ([(0, 0.6)–(1 000, 1)], (0, 0.9), (200, 0.85), (400, 0.8), (600, 0.75), (800, 0.7), (1 000, 0.65))
	crown-of-thorns starfish time to mature/a	AV	=nomal crown-of-thorns starfish time to mature×effect of phytoplankton increase on crown-of-thorns starfish time to mature

Note: The first column indicates the submodule to which the variable belongs, where I is a coral submodule, II is a macroalgae submodule, III is another biological submodule; and the third column represents the variable type, where LV is the level variable, RV is the rate variable, and AV is the auxiliary variable. INTEG, WITH LOOKUP are functional expressions in System Dynamics Vensim software.

Table 3. Main parameters and sources of the model

No.	Method	Main parameter	Value	Reference
1	Relevant literature determination or estimation	average annual spawning frequency of corals/(ind.·a^{-1})	1	Zhang et al. (2013)
		annual natural mortality of living corals/ind.	0.1	Huang et al. (2012); Zhou et al. (2017)
		average annual disease rate of corals/ind.	0.1	Huang et al. (2012); Zhu et al. (2012)
		normal time for corals to mature/a	1	Huang et al. (2011); Shen et al. (2014)
		average predation coefficient of crown-of-thorns starfish/(10^4 m^2·ind.$^{-1}$)	0.001 825	Bartelet (2017)
		average coral calcification rate/(g·cm^{-2}·a^{-1})	–	Shi et al. (2009); Zhang and Chen (2006)
2	Statistical yearbook and bulletin of the state of the marine environment	live coral coverage rate/ind.	–	National Bureau of Statistics of the People's Republic of China (2010–2016); South China Sea Bureau of Natural Resources Ministry (2013–2017)
		frequency of disasters/ind.	–	
		inorganic nitrogen content of coral reefs/(mg·L^{-1})	–	
3	Table function determination	the effects of sediments on the carbonate productivity of coral reefs, the influence of sediments on the time corals and macroalgae need to mature, the effects of nutrients on the time macroalgae need to mature, et cetera/ind.	–	Szmant (2002); Fabricius et al. (2003); Zou and Xia (2011)
4	Delphi method, trend extrapolation method	decay time of the coral reef/a	500	–
		average dissipation factor/ind.	0.25	–
		inorganic nitrogen dissolution factor/ind.	15	–
		inorganic nitrogen diffusion factor/ind.	10	–
5	Simulation trial method	reef accretion factor/ind.	0.001 8	the result of multiple simulation based on the model
		natural recovery rate of coral/ind.	0.03	–
		intensity of human activities/ind.	0.1	–

(6) The model defines the total amount of fishing as the sum of the numbers of parrotfish and charonia tritonis that are captured, and both are directly affected by the fishing policy.

2.5 *Model flow graph construction*

Using the Vensim platform software, the dynamics flow diagram of the coral reef ecosystem was obtained, as shown in Fig. 2. According to the relationship between coral reef functional groups, the model is divided into three sub-modules, namely coral sub-module (I), macroalgae sub-module (II) and other biological sub-modules (III).

2.6 *Testing of the model*

After the model was established, there are a variety of methods for testing it that can be employed, including dimensional tests, extreme condition tests, model limit tests, parameter evalu-

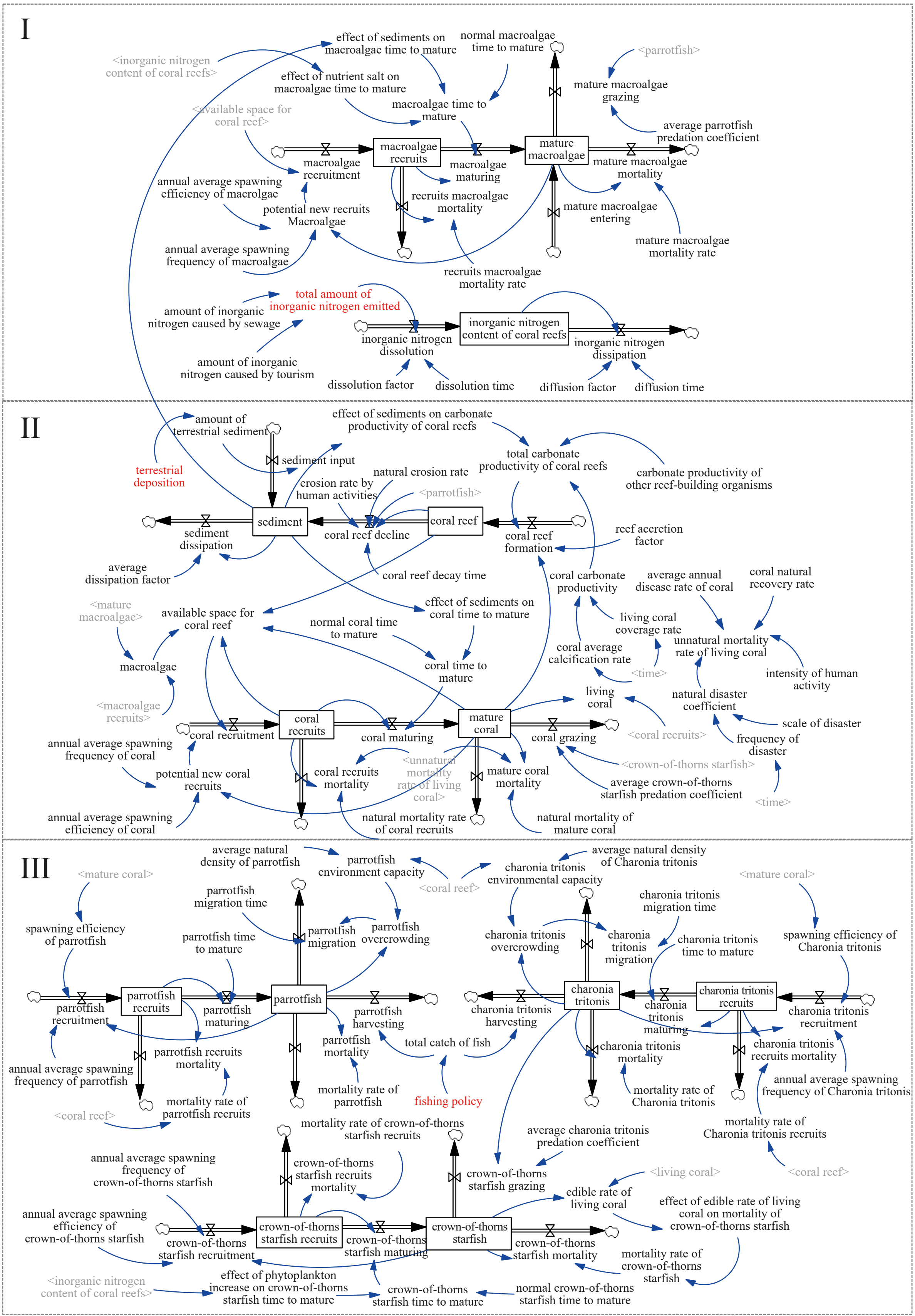

Fig. 2. Dynamics process of coral reef systems. The gray "< >" variables in the figure are shadow variables in system dynamics vensim.

ation tests, sensitivity tests, and so on. The purpose of this model is not aimed to accurately predict in the short term, but to understand the general dynamic mechanism of coral reef degradation from a systematic perspective, so as to provide theoretical references for coral reef restoration and management. Therefore, based on the validity of the purpose (Sterman, 2000), the model test is mainly focus on the structure and behavior tests of the model. To this end, this study repeated the "simulation-correction-simulation" process and consulted experts, and then passed the following test contents.

The first is a structural inspection. Through the rationality test of the model boundaries, variables and logical relationships, it is found that the generalization of model boundaries and variables is more reasonable, and the logical feedback is essentially consistent with human realistic cognition, and follows the basic laws of nature (this is also reflected in the subsequent analysis and discussion). The second is the behavioral test. After testing by behavioral modes, such as the direct running of the model, extreme condition testing, and sensitivity testing, the model basically shows the behavior patterns (including qualitative and quantitative) observed in the real system, and found that the expected behavior patterns of the system affected by the functional groups and human activities are similar. The third is the reality test (Fig. 3). Since the model's development involves some historical data from the studied area, comparing the trends inferred from the simulated values and observations allows a further understanding of the rationality behind the simulations and their effectiveness.

3 Simulation of coral reef ecosystem model

3.1 *Simulation setup and results analysis*

The period simulated in the model is from 2010 to 2050, with a time step of 0.25 a. The main initial value settings for the model: the area corals initially covered is 110×10^4 m^2 (including 10×10^4 m^2 of coral recruits and 100×10^4 m^2 of mature coral), the area that the coral reef initially coverd is 300×10^4 m^2, the area initially covered by macroalgae is 40×10^4 m^2, and there are initially 2×10^5 parrotfish, 2×10^5 charonia tritonis, and 2×10^3 crown-of-thorns starfish[①] (Grossman, 2014; Zhang et al., 2018). The initial sediment is 10×10^4 m^2 and the initial coral reef has an inorganic nitrogen content of 0.02 mg/L. This initial setting, assuming no additional factors interfere, also serves as a criterion for comparing subsequent work with various management strategies.

The basic simulation results are shown in Fig. 4: the coverage of living corals and coral reefs generally declines first and then rises. It will reach 115.14×10^4 m^2 and 319.15×10^4 m^2 by 2050, with an average annual growth rate of 0.12% and 0.16%, respectively. The number of parrotfish and charonia tritonis will also increase year by year, but due to the limitations of environmental capacity, both numbers will eventually remain at around 500 000. On the other hand, due to the increased number of parrotfish and charonia tritonis, macroalgae will disappear in less than a year, while the number of crown-of-thorns starfish will also decline and will disappear by 2044. According to the increasing and decreasing trends of each curve, there is a strong positive correlation between the area of living corals or coral reefs and the number of parrotfish or charonia tritonis, but they are negatively correlated with the growth of numbers of macroalgae and crown-of-thorns starfish, with the coral reef system developing sustainably. Overall, the coral reef community as a whole maintained developing in a low level, the average growth rate of live corals and coral reefs was too slow, and the predictions were based on the above-mentioned optimistic expectations (without the impact of large-scale bleaching events). This indicates that the coral reef ecosystem is basically unsustainable.

3.2 *Disturbance under different situations*

Numerous studies have shown that coral reef degradation is caused by global changes and increased human activities (Li et al., 2007; Yu, 2012). Human activities, as active behaviors, exert a more direct and complex impact on the development of coral reef communities. To further analyze the disturbance effects of the exogenous variables on coral reef systems, a multi-scenario simulation experiment was conducted on three types of adjustable factors (i.e., fishing policy, terrigenous deposition and total amount of inorganic nitrogen discharged) developed in the model, which are closely related to the management and practice of regional coral reef (Table 4). Firstly, by adjusting a certain regulatory factor several times, until the extinction of the reef coral or the succession of the dominant species in the time boundary is the regulation node, the sensitive threshold of the variable to the system change is identified (Liu et al., 2018). Among them,

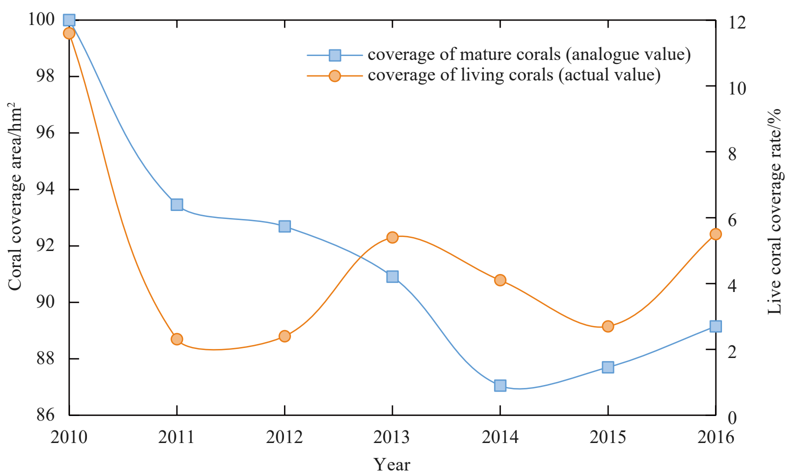

Fig. 3. Coral coverage area fitting comparison.

① Estimated by existing research, 300 hm^2 of coral reefs can support about 2 000 ind. crown-of-thorns starfish with an initial living coral coverage of 11.6%.

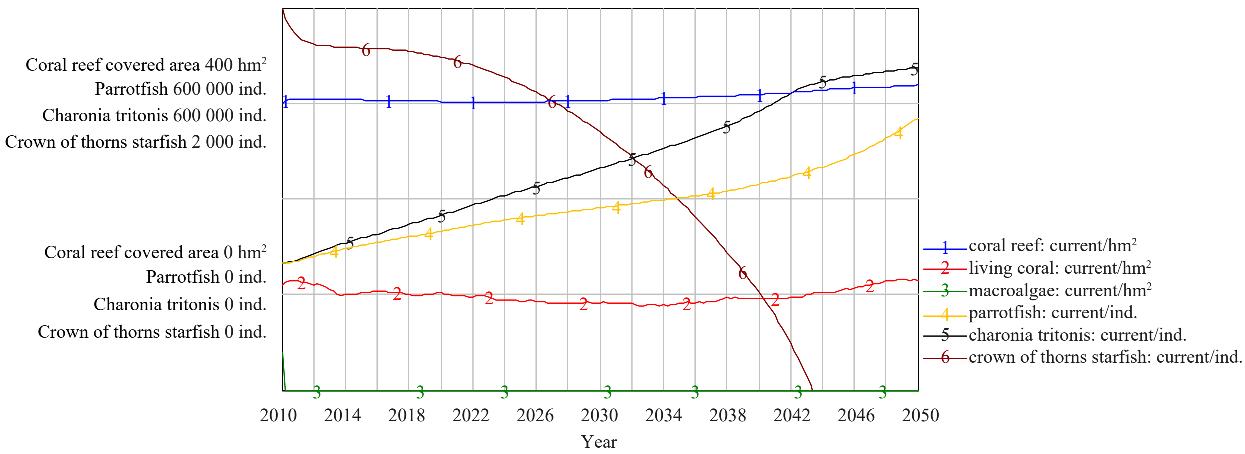

Fig. 4. Simulation results of the functional group number of coral reef SD model.

Table 4. Scenario design parameter settings

No.	Variables	Current value	Adjusted value		Relevant equations	Interpretation of the variable
			Threshold *A*	Threshold *B*		
1	Fishing policy ontrol variable	1	2	3	total number of captured fish=RANDOM UNIFORM (8 000, 12 000, 1)×fishing policy control variable	an indicator of the fishing intensity; the larger value, the more average annual catch
2	Terrestrial deposition	1	1.5	2.5	amount of terrestrial deposition =RANDOM UNIFORM (0, 5, 1)× amount of terrestrial deposition	represents sediments discharged from land to sea; the greater the value, the more sediments are inputted
3	Total amount of inorganic nitrogen emissions/(mg·L^{-1})	0.2	2	4.5	amount of inorganic nitrogen emissions=inorganic nitrogen caused by emissions + inorganic nitrogen caused by tourism	the inorganic nitrogen emissions by human activities; the greater the value, the more inorganic nitrogen is dissolved into the coral reef

the thresholds of the regulatory variables for the extinction of live hermatypic corals are listed as follows: fishing policy (2.8 mg/L), terrestrial deposition (2 mg/L), and total inorganic nitrogen emission (2.3 mg/L). The succession thresholds of the dominant species in the community are as follows: fishing policy (2.1 mg/L), terrestrial deposition (2.1 mg/L), and total inorganic nitrogen emission (4.2 mg/L).

Then, combination settings based on the thresholds of the variables, rather than simply combining them, enables an adaptive scenario that is more representative of the dynamic trends and developmental rules of coral reef communities to be constructed. In addition, this study considered the relevant investigations and research in the region, the visibility of the simulation, and summarized the control values of the two groups of policy variables as being below the threshold (*A*) and above the threshold (*B*), the final screening of twenty representative scenarios (Figs 5–7) are used to indicate the evolutionary characteristics of the system under different regulatory strategies.

3.2.1 *Disturbance by a single factor*

The effects of varying individually the above factors (Table 4) may be described as follows (Fig. 5):

(1) It can be seen from the fishing policy variables A_1 and B_1 (scenarios F1) that they directly affect the number of parrotfish and charonia tritonis. When the variable fishing policy is doubled, living corals are degraded year after year. When it continues to increase to 3 times, the number of parrotfish and charonia tritonis rapidly decreases until they go extinct at around 2034. Affected by this, macroalgae reappeared and began to grow after 2 a following the disappearance of the parrotfish. The number of crown-of-thorns starfish also increases year by year due to the decrease in the numbers of charonia tritonis and peaks in 2041. The increase in natural enemies of corals leads to a gradual reduction in living corals. In the later stage of the system's development, the dominant species of the coral reef community changes and the system is gradually dominated by macroalgae.

(2) It can be seen from the terrestrial deposition variables A_2 and B_2 (scenarios F2) that the input of terrestrial deposits leads to the overall decline of the coral reef community. When terrestrial depositions are gradually increased by 1.5–2.5 times from the current value, the area covered by living corals and coral reefs rapidly decreases. As the area of habitats and shelters gradually shrinks, the number of parrotfish and charonia tritonis will first rise, and then decrease continuously. At the end of the system's development, although the number of crown-of-thorns starfish has increased due to the decrease of charonia tritonis, it also decreases as with other creatures, which are affected by the feedback effect of the reduction of living corals that can be grazed.

(3) It can be seen from the values of total inorganic nitrogen emissions, A_3 and B_3 (scenarios F3), that with their increase, the phytoplankton in the seawater will obtain a large number of nutrients for growth. This indirectly shortens the development cycle of juvenile crown-of-thorns starfish which are predators of corals, so their numbers increase significantly. When inorganic nitrogen emissions increase to 4.5 mg/L, the proliferation of crown-of-thorns starfish will cause the rapid decline of living corals and they will die out at around 2035. At the end of the system's development, the number of crown-of-thorns starfish, parrotfish and charonia tritonis will decrease as a result of the reduced area of living corals, and macroalgae will begin to appear after the par-

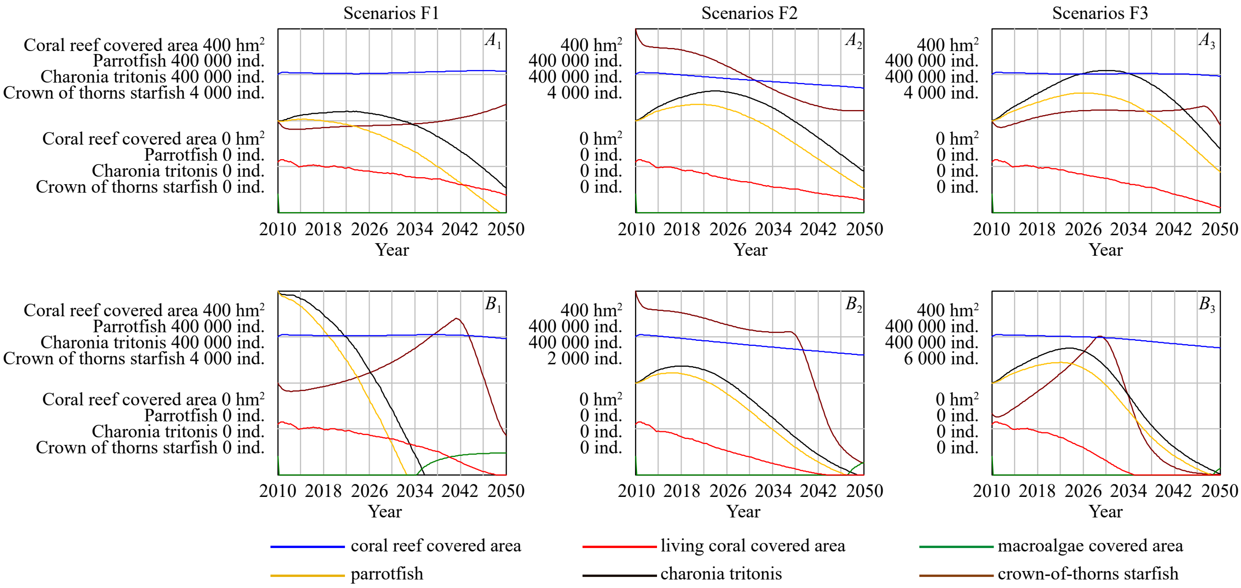

Fig. 5. Impact of single factor disturbance on the functional groups of coral reef ecosystem, the factors are fishing policy (scenarios F1), terrestrial deposition (scenarios F2) and total amount of inorganic nitrogen emissions (scenarios F3).

rotfish disappear.

By comparing and analyzing the results of altering these three factors, the following conclusions can be obtained. Affected by fishing policies, the decline of the coral reef community is the most direct response, and the evolution of the system's changes and development is obvious. For example, the crown-of-thorns starfish numbers increase sharply, with the macroalgae increasing prior to this, which leads to the accelerated succession of dominant species. Under the influence of terrestrial depositions, community decline tends to be integrated and more rapid. Due to the emissions of inorganic nitrogen, the community decline is malleable and hysteretic.

3.2.2 *Disturbance by double factors*

By combining variations in two of these factors at the same time, the following effects are noted (Fig. 6):

(1) It can be seen from the two-factor combination of fishing policy and terrestrial deposition (scenarios F4) that with the increase in their values, the living corals will die out around 2037-2047, with the parrotfish and charonia tritonis dying out earlier due to increased fishing intensity. The demise of these two promotes the emergence of macroalgae and the growth in the number of crown-of-thorns starfish. However, due to the combined disturbance of terrestrial depositions, the whole community declines, and the biomass growth of macroalgae and crown-of-thorns starfish is limited.

(2) The two-factor combination of fishing policy and inorganic nitrogen emissions sees (scenarios F5) that with the increase of the two values, the acquisition of nutrients and the reduction of predators have greatly promoted the increase in the numbers of crown-of-thorns starfish and extent of macroalgae. In scenario B_1B_3 (i.e., the higher values for these two factors), the peak density of the crown-of-thorns starfish will be about 1 684 ind./km² in 2027 (estimated for the case of 300 hm² of coral reefs), which is greater than the lowest value of the possible burst of proliferation of the crown-of-thorns starfish (1 500 ind./km²) previously found in the Great Barrier Reef, Australia (Moran and De'ath, 1992). At this time, there's an obvious contrast between the extinction curve of the parrotfish or charonia tritonis and the growth curve of the crown-of-thorns starfish or the macroalgae, and there is an intense succession within the coral reef community.

(3) From the two-factor combination of terrestrial deposition and inorganic nitrogen emissions (scenarios F6), it can be seen that living corals and coral reefs are rapidly degraded due to the direct impact of terrestrial deposition, while the number of parrotfish and charonia tritonis are also reduced due to the resulting positive feedback associated with the living coral and coral reefs. Because of the increase in inorganic nitrogen emissions and the decrease in the number of charonia tritonis, the number of crown-of-thorns starfish increased and reached a peak at some point. In the end, the three curves of parrotfish, charonia tritonis and crown-of-thorns starfish tend to be consistent, and their extinction time is later than that of the living coral.

By comparing and analyzing the results of these three combinations of varying two factors, the following conclusions can be drawn. On the basis of the original single-factor disturbance, the two-factor disturbance not only combines the variations associated with each single-factor, but also accelerates the decay rate of the living corals and coral reefs, and makes the development and change of coral reef communities more diversified and complicated. From the perspective of the early stage of system development, this difference is not obvious.

3.2.3 *Disturbance by multiple factors*

The next tests involve combining the fishing policy, terrestrial deposition, and inorganic nitrogen emissions as one factor (Fig. 7). Comparing this with the single-factor and two-factor disturbance conditions above, it is obvious that the coral reef community declines faster with a larger scale of change in these factors. In scenario F7, the living corals will disappear by around 2039, with an extinction time earlier than that in the scenario with single factor *A* and two factors *AA*, and showed a decay rate that even exceeded the other scenarios. In scenario F8, the degradation rate of living corals and coral reefs also reaches a maximum among all the scenarios considered. In general, with the change of type and intensity of the disturbance factor, the mul-

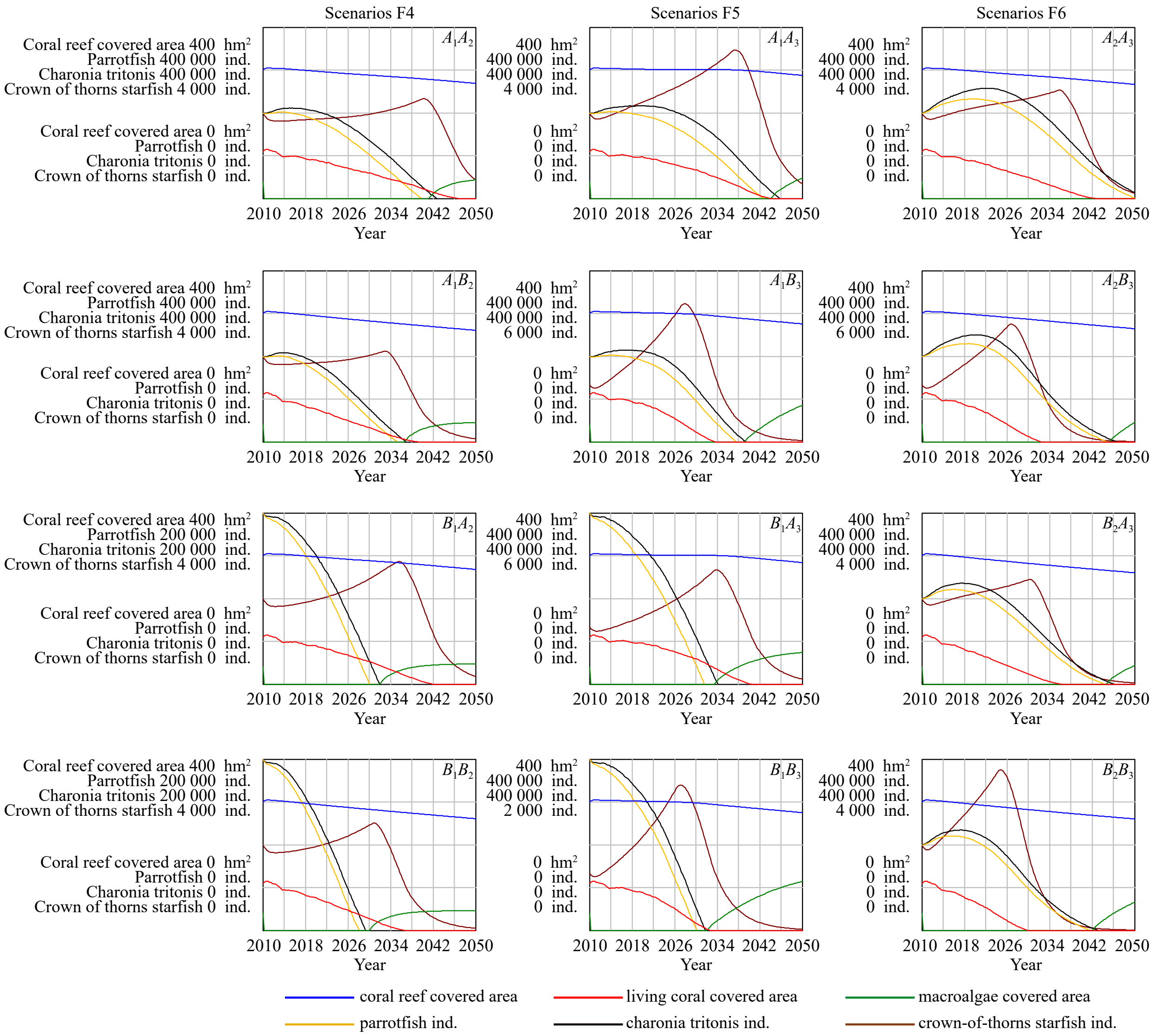

Fig. 6. Impact of double factors disturbance on the functional groups of coral reef ecosystem, the combination of factors are fishing policy and terrestrial deposition (scenarios F4), fishing policy and total amount of inorganic nitrogen emissions (scenarios F5), terrestrial deposition and total amount of inorganic nitrogen emissions (scenarios F6).

tiple feedback relationship within the coral reef community also increases, further promoting the development of the coral reef ecosystem through the effects of quantitative and qualitative changes.

The above scenario design is a relatively straightforward expression of the dynamic development of coral reef communities under the combined effects of three types of human activities. In summary, the following conclusions are drawn:

(1) From the perspective of coral reef ecosystems, although different species display differing degrees of diversity and substitutability, the loss of specific functional groups will destroy the future development of coral reef communities, which is consistent with most previous research. (2) Macroalgae can hardly survive when there is ample parrotfish, which indicates that herbivorous fish play a vital role in controlling the extent of macroalgae and maintaining the dominant position of living corals. (3) Regulatory organisms such as charonia tritonis have a more direct impact on the reduction of crown-of-thorns starfish and the sustainable development of coral reefs. (4) For human interference factor, when a single factor does not reach the sensitive threshold of the system, the system will maintain resilient. However, superimposed disturbances will exacerbate the demise of the already damaged or healthy coral reef community and move it towards another state, with the effect being enduring.

4 Discussion

This study takes the ecosystem as a starting point and builds a model that involves the multiple feedback effects of coral reef functional groups and environmental changes. After the structure, behavior, and authenticity tests, the results obtained from the model are believed to be objective, and the purpose of studying the degradation and development mechanisms of tropical coral reefs in China is achieved. However, due to the complexity of the actual coral reef and the lack of observational data, the current simulation is still macroscopic and remains at the exploratory stage.

(1) About model variables

The model takes crown-of-thorns starfish, hermatypic coral,

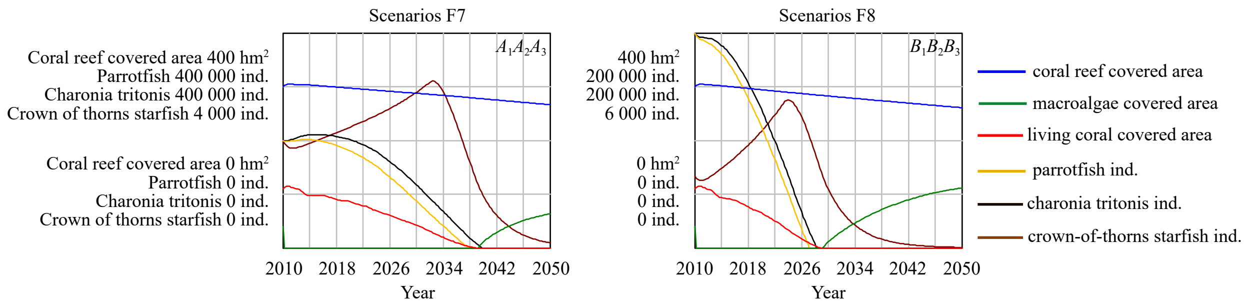

Fig. 7. Impact of multiple factors disturbance on the functional groups of coral reef ecosystem, the combination of factors are fishing policy, terrestrial deposition and total amount of inorganic nitrogen emissions.

parrotfish, macroalgae and charonia tritonis as five functional groups in the coral reef's food network, and uses this as the main connection variable to construct the causal relationship of system development as a whole. Although there are species and individual differences in the functional groups, the aggregation of functional species is effective for simulation at the system level, while the further classification of functional groups does not significantly change the model's results and suggestions. At present, in terms of variable settings and related interpretations, the model is still based on the number of functional groups. The understanding of the coral reef ecosystem is still very limited. In the future, the ecological process of coral reefs will be further analyzed by incorporating the theory of energy flow.

(2) About model boundaries

The higher predator did not be added into the model, mainly due to two considerations. First of all, charonia tritonis is the main natural enemy of the crown-of-thorns starfish. Due to the overfishing in recent years, the number of wild charonia tritonis in China has been rapidly attenuated, and the regional crown-of-thorns starfish outbreak is also considered to be closely related (Tu, 2007). Therefore, human beings may be the largest "predator" relative to natural predation activities. Moreover, due to the effects of overfishing, most of the advanced predators will also be gradually disappear by the up and down control of the fish caught. At present, the model behavior is applicable to the southern seas of China or other general tropical coral reef areas. If the model is used in the future, it is recommended to select functional species in terms of the causes of local coral reef degradation, to appropriately expand the model boundaries, and to consider the three types of shallow sea ecosystems, namely coral reefs, mangroves and seagrass beds, as a whole (Wang et al., 2018).

(3) About climate change

The climate change factor was not introduced in this study, but it does not mean that its impact is not important. On the contrary, a series of problems such as climate warming, ocean acidification and sea level rise have become common challenges for coral reefs around the world. First of all, it is still impossible to accurately predict the long-term development of climate change, and the various impacts and response mechanisms have not been clarified. Second, as an uncontrollable factor, even if human activities are reduced, climate change will still continue. Adding it or not may not significantly change the model's behavior, but will only accelerate the decline of coral reefs. Although the method to validate the impact of natural disasters is similar to that of climate change, their frequency and scale are easier to monitor, since tropical coral reefs in China are devastated by tropical cyclones all the year round. Therefore, adding this factor to the model can better reflect any sudden changes inflicted upon the system, and it is also in line with the local situation. The frequency of disastrous occurrences in the model is only quantified for storm surges and tropical cyclones that exceed the local warning level. This variable could therefore be more realistically defined with other models in the future.

(4) About human activities

The adverse effects of increased human activities on coral reefs are becoming more evident. For tropical waters in China, fisheries, coastal engineering, and seawater pollution have been one of the main causes of the degradation of the reefs over the past few years (Wu et al., 2011). In fact, the destructiveness of human disturbances may be more complex and more deserving of attention than climate change. In particular, in situations where disturbances arise from multiple superimposed factors, it is found that the coral reefs show degradation, but after exploring the source of the disturbance, it is found that the feedback mechanisms are completely different, and this difference is gradually amplified over time. At the same time, the coral reef system should have a multi-stable state during the development process, and there are thresholds for its transformation to different states. At present, it is still quite difficult to find these "threshold values", and the transformation mechanisms of various creatures residing in coral reefs in the phase shift process needs to be further studied.

(5) About model applications

As a "metaphorical" expression of the coral reef ecosystem, the application of system dynamics helps to understand the developmental characteristics and mechanisms of coral reef ecosystems from a more comprehensive perspective, providing a scientific and feasible method for assessing the "elasticity" of coral reef ecosystems and simulating coral reef damage and ecological restoration processes. In the future, based on this, the uncertainties associated with the model could be further analyzed, and by combining specific restoration measures in the studied area, a dynamic model of coral reef ecological restoration based on management objectives could be developed, so as to provide a reference for decision-making within the context of coral reef ecological restoration and management in China.

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