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Research Paper

# Ecological characteristics and carrying capacity analysis of marine ranching ecosystem in Beibu Gulf based on Ecopath model*

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**Abstract** Marine pollution and overfishing induced the biodiversity loss and ecological degradation of the Beibu Gulf ecosystem in Guangxi, SE China. In an effort to restore the ecosystem and fishery resources, artificial reefs were deployed in the Beibu Gulf as the marine ranching area and their ecological performance need to be investigated. We constructed Ecopath ecological trophic models for the marine ranching area and a nearby control area to compare their ecosystem throughput and food web structure difference, and to calculate the ecological carrying capacity of various functional groups. Results indicate that the total system throughput of the marine ranching area was significantly higher than the control area, and the majority of system throughput occurred at trophic levels I and II in both ecosystems. The system connectance indices for the marine ranching and control areas were 0.27 and 0.32, and the omnivory indices were 0.16 and 0.19, indicating simple food web structures; both areas are in a developmental stage with TPP/TR ratios of 2.69 and 9.36, respectively. Compared to the control area, marine ranching area exhibited a higher system maturity, and the ecological carrying capacity of "large and medium-sized demersal fish" and "other bivalves" functional groups in the marine ranching area increased by 43.83% and 233.62%, respectively, allowing for more high-trophic-level predators and large benthic animals. This study provided a reference for the formulation of fishery management policies in the Beibu Gulf, to maintain ecosystem stability and biodiversity.

**Keyword**: marine ranching; Ecopath; ecosystem maturity; trophic structure

## 1 INTRODUCTION

Marine ranching, as an important tool for resource enhancement and ecological sustainability, achieves the reproduction and protection of fishery resources as well as the improvement of the marine ecological environment through the establishment of seaweed beds, aquaculture cages, and artificial reefs (Zhou et al., 2019). Seaweed beds are capable of enhancing primary productivity, providing shelter for certain fish species, and absorbing atmospheric carbon dioxide (Jung et al., 2022). Aquaculture cages offer an efficient method for resource utilization in aquaculture (Lee et al., 2022).

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Artificial reef construction is an effective approach for coastal ecological restoration (Dupont, 2008). The deployment of artificial reefs not only provides shelter for various fish species to escape predators but also offers attachment substrates for algae and benthic animals, resulting in aggregation effects on marine life (Raj et al., 2020). The upwelling and back-eddy currents generated by artificial reefs accelerate the exchange between bottom and mid-upper water layers, replenishing and promoting nutrient cycling, thereby providing suitable nutrient conditions and flow field environments for various benthic organisms (Baynes and Szmant, 1989; Champion et al., 2015). There are many representative successful artificial reef deployment cases around the world to optimize food web structure, increase ecosystem maturity (e.g., in French Atlantic and English Channel coasts (Raoux et al., 2022), provide habitats for juvenile and adult fish (e.g., in Sydney Harbour, Australia (Becker et al., 2017), and enhance ecological connectivity between natural and artificial habitats (e.g., in Lidao Island, China (Wu et al., 2019)).

The Beibu Gulf, located in the northwestern part of the South China Sea, is a naturally semi-enclosed shallow bay with a water area of approximately $13\times10^4$ km$^2$, a maximum width of 180 nautical miles, an average depth of about 50 m, and a maximum depth of 100 m (Gao et al., 2017). In recent twenty years, with the extreme exploitation of fishery resources, overfishing of economically important species has led to a significant decline (Hong et al., 2023). Moreover, due to the reduction of high-trophic predators, the average trophic level has been decreased by 0.04 trophic levels per decade in the Beibu Gulf (Su et al., 2021). Therefore, constructing marine ranching with the deployment of artificial reefs is one of the important ways to restore the ecosystem and fishery resources (Pan et al., 2022). With considering the flow of energy and materials, reef affects the entire coastal ecosystem including both the physical and biological aspects from low-trophic plankton, pelagic, and attached organisms to high-trophic predators (Ramm et al., 2021). Meanwhile, carrying capacity, an essential indicator of system cycling and maximum development potential, has been widely used in coastal ecosystems and provides valuable insights for fishery management and resource restoration decisions (Lorenzen et al., 2010). However, evaluating ecological performance of the artificial reef deployment remains a challenge in terms of ecosystem. The lack of comprehensive data across trophic levels, a narrow focus on a few representative reef-dependent species or benthic habitats, and the careless application of complex ecosystem models without sufficient expertise may reduce the accuracy and completeness of reef area ecological assessments (Sambrook et al., 2019).

Ecopath with Ecosim (EwE), an ecological trophic model, has been widely applied in ecosystem modeling and management decision-making worldwide (Colléter et al., 2015). In China, Ecopath has been widely applied to the analysis of the structure and function of marine ranching ecosystems. For instance, Li et al. (2023) assessed the carbon sequestration capacity of bivalves in the Bohai Bay marine ranch and explained the limiting factors of bivalve biomass growth. Zhang et al. (2022) compared the differences between artificial reefs and natural reefs in the Yellow Sea ecosystem, elaborating on the variations in energy transfer efficiency. Suo et al. (2023) evaluated the ecological carrying capacity of small fish in the Zhujiang River estuary marine ranch and analyzed their role in the food chain. The basic assumption of the Ecopath model is that the ecosystem consists of a series of ecologically interconnected functional groups, encompassing all material or energy flow processes within the ecosystem (Christensen and Pauly, 1992). The output parameters allow us to describe the flow of materials and energy in the ecosystem, analyze interactions between functional groups, identify key species, assess ecosystem maturity, and calculate the ecological carrying capacity of each group.

To assess the ecosystem maturity status and the ecological carrying capacity of the Beibu Gulf, we established two Ecopath models for one of the representative marine ranching areas with reef deployment and a neighbor control area based on resource and environmental surveys conducted from 2022 to 2023. The main objectives of this study are: 1) to assess the differences in food web structure and ecosystem status between the marine ranching and control ecosystems; and 2) to calculate the ecological carrying capacity of various functional groups in these areas. This research aims to provide theoretical and data support for fishery resource management in the Beibu Gulf artificial reef areas. This study provides a basis for stock enhancement practices in marine ranching in the Beibu Gulf, grounded in the ecological carrying capacity.

# 2 MATERIAL AND METHOD

## 2.1 Study area

Marine ranching area is located between 108°11′E to 108°14′E and 21°24′N to 21°27′N, covering an area of approximately 36.35 km$^2$, with the artificial reef area encompassing 7.63 km$^2$. A total of 1 213 YJ1-type artificial reef monomers and 1 403 YJ2-type monomers have been deployed (Fig.1), amounting to a total volume of 176 500 m$^3$. The currents in the marine ranching area predominantly flow in an east-west reciprocating pattern. A control area, with a flat muddy bottom, was selected 3.59 km east of the marine ranching area's center point, in alignment with the incoming current direction, and covers an area of approximately 4.82 km$^2$ (Fig.2).

Two research cruises were conducted in November 2022 and April 2023 to perform comprehensive environmental and biological surveys. We selected the marine area adjacent to artificial reefs as the marine ranching zone to investigate the effects of artificial reefs. During each cruise, nine environmental stations, three trawl stations, two trap net stations, and three diving stations were established within the marine ranching area. Additionally, three environmental stations and one trawl station were set up in the control area (Fig.2).

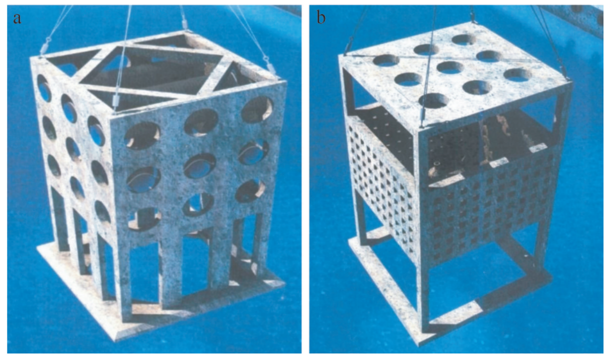



**Fig. 1 Artificial reef structure diagram**

a. YJ1-type artificial reef (3.6 m×3.6 m×5.5 m); b. YJ2-type artificial reef (4.0 m×4.0 m×6.0 m).

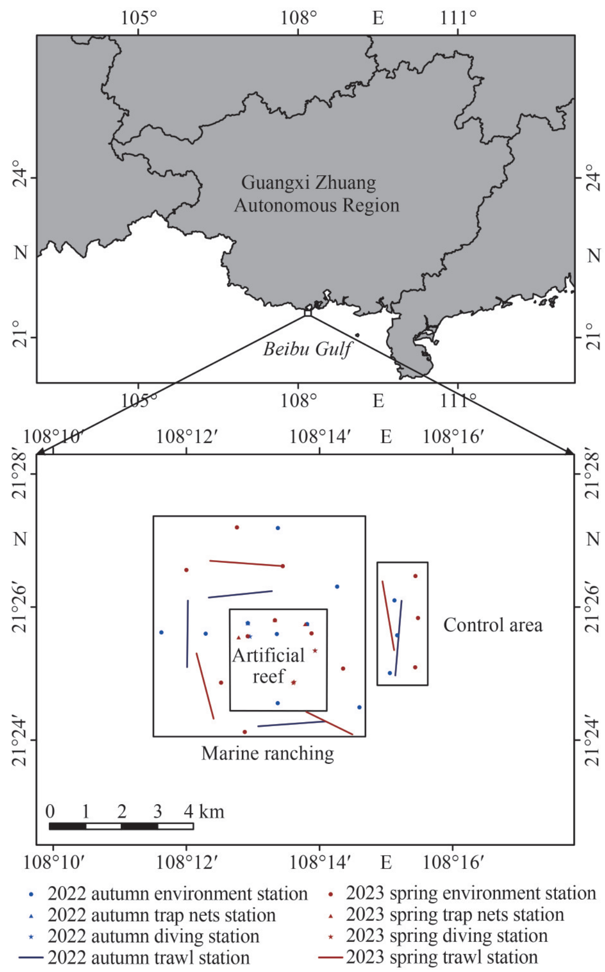



**Fig.2 Geographic location and sampling sites of marine ranching and control ecosystems**

## 2.2 Ecopath model construction

Ecopath models were constructed using the Ecopath with Ecosim software (Version 6.6.8). According to the laws of thermodynamics, when the diet composition of each organism remains constant, the production of each functional group equals the sum of predation mortality, biomass accumulation, fishing mortality, migration, and other mortalities (Christensen and Walters, 2004). The mass-balance equation is:

$$B_i\times\left(\frac{P}{B}\right)_i\times \mathrm{EE}_i-\sum_{j=1}^{n}B_j\times\left(\frac{Q}{B}\right)_j\times \mathrm{DC}_{ji}-Y_i-\mathrm{BA}_i-E_i=0,$$

where $B_i$, the biomass of prey $i$, $B_j$, the biomass of predator $j$, $(P/B)_i$, the ratio of production to biomass of prey $i$, $\mathrm{EE}_i$, ecotrophic efficiency, $Y_i$, the biomass captured, $(Q/B)_j$, the ratio of food consumption to biomass of predator $j$; $\mathrm{DC}_{ji}$, the fraction of prey $i$ in the average diet of predator $j$, $\mathrm{BA}_i$, the biomass accumulation rate of prey $i$, and $E_i$, the margin between immigration and emigration of prey $i$.

Additionally, energy balance must be satisfied with the consumption for each functional group equals the sum of its production, respiration, and unassimilated food. The energy balance equation is:

$$B_i\times\left(\frac{Q}{B}\right)_i=B_i\times\left(\frac{P}{B}\right)_i+R_i+U_i,$$

where $R_i$, the respiration and $U_i$, the food that is not assimilated.

The basic parameters required for constructing an Ecopath model are the biomass ($B$), production to biomass ratio ($P/B$), consumption to biomass ratio ($Q/B$), and ecotrophic efficiency (EE) for each functional group. Any three of these four parameters must be inputted, with the fourth parameter being calculated by the model. A diet composition matrix (DC) and fishing data are essential (Coll et al., 2009).

2.2.1 Data source

In this study, organisms from both the marine ranching and control areas were classified into functional groups based on dietary similarities (Christensen et al., 2005), with the species composition of each group provided in Supplementary Table S1. Biomass estimates for each functional group were obtained from two research cruises, using data collected from bottom trawling, traps, underwater videography, and diver sampling. Zooplankton and phytoplankton biomasses were evaluated using Shallow Water II and III plankton nets and transported to the laboratory for further biological analysis (Gorbatenko and Dolganova, 2007). Detritus biomass was measured by filtering 1 L of surface and bottom seawater with a 77-μm filter (Xu et al., 2021). Specific catch and calculation methods for each functional group are detailed in Supplementary Table S2.

The $P/B$ and $Q/B$ ratios for fish were calculated using empirical formulas from Christensen et al. (2005) and Palomares and Pauly (1998). For invertebrates, $P/B$ and $Q/B$ ratios were calculated using empirical formulas from Brey (1999) and Pauly (1990). The diet composition matrix for functional groups was derived from literature on nearby sea areas (Leitão et al., 2007; Yan et al., 2013; Lin et al., 2014; Yan et al., 2015) and the FishBase database (https://fishbase.se/) (Supplementary Tables S3 & S4).

Based on the studies of Li et al. (2023), the unassimilated consumption (UC) for oysters, mussels, other bivalves, and zooplankton were set to 0.4, and setting 0.35 for other benthic animals and 0.2 for all other functional groups.

2.2.2 Model balance and validation

The EE value of each functional group was first adjusted to fall between 0 and 1, indicating the proportion of a functional group's production that is utilized (Heymans and Tomczak, 2016). The $P/R$ ratio, representing food assimilation efficiency, must be less than or equal to 1. The $P/Q$ ratio, representing food conversion efficiency, generally ranges from 0.1 to 0.3 for most functional groups, with higher $P/Q$ values for some fast-growing species (Heymans et al., 2016).

Stable isotopes were used to calculate the trophic levels of organisms, and trophic levels for each functional group were obtained by biomass weighting. These were then compared with the trophic levels derived from the Ecopath model to validate its representation of the trophic interactions in the marine ranch ecosystem. Following the method outlined by Xu et al. (2024), $\delta^{15}N$ of all samples was measured using an isotope ratio mass spectrometer (Delta V Advantage). The isotope trophic level (TL) was calculated using the following formula (Pasquaud et al., 2010):

$$\mathrm{TL}=\left[\frac{\left(\delta^{15}\mathrm{N}_{\mathrm{pred}}-\delta^{15}\mathrm{N}_{\mathrm{base}}\right)}{\Delta\delta^{15}\mathrm{N}}+\mathrm{TL}_{\mathrm{base}}\right],$$

where $\delta^{15}N_{pred}$ is the $\delta^{15}N$ signature of the predator in question, $\delta^{15}N_{base}$ is the $\delta^{15}N$ signature of a representative baseline for the predator and $TL_{base}$ is the trophic level of that baseline. Primary consumers (*Mytilus edulis*) were used for that baseline. Therefore, $TL_{base}$ is equal to 2. $\Delta\delta^{15}N$ represents the trophic fractionation of $\delta^{15}N$ (3.4‰ (Post, 2002)).

2.2.3 Ecological index

The Mixed Trophic Impact (MTI) index quantitatively evaluates the predatory and competitive interactions among different functional groups within an ecosystem (Ulanowicz and Puccia, 1990). The negative and positive elements of MTI can be used to assess the impact of top-down and bottom-up effects, respectively (Libralato et al., 2006). The mixed trophic impact index for a biological group $MTI_{i,j}$ is calculated by constructing a matrix, with the formula:

$$MTI_{i,j}=DC_{i,j}-FC_{j,i},$$

where $FC_{j,i}$ is a host composition term giving the proportion of the predation on $j$ that is due to $i$ as a predator.

Keystone species (KS) are functional groups with relatively low biomass but significantly impacting the food web structure (Hale and Koprowski, 2018). Three indices, $KS_{1i}$, $KS_{2i}$, and $KS_{3i}$, were selected to evaluate keystone species in the ecosystem (Power et al., 1996; Latham II, 2006; Valls et al., 2015). The formulas are as follows:

$KS_{1i}=\log[\varepsilon_i\times(1-p_i)]$,
$KS_{2i}=\log[\varepsilon_i\times(1/p_i)]$,
$KS_{3i}=\log[\varepsilon_i\times\text{d-rank}(B_i)]$,

where $\varepsilon_i$, the overall impact of group $i$ on the other groups (excluding itself); $p_i$, the biomass proportion of group $i$; d-rank($B_i$), the rank (in descending order) of the biomass of group $i$.

Ecological network analysis was conducted directly using the network analysis plugin in the Ecopath with Ecosim software (Christensen and Walters, 2004). A suite of ecological indicators was employed to describe the structure and function of the ecosystem, including total system throughput (TST), total production (TP), total biomass (TB), Finn's cycling index (FCI), Finn's mean path length (FMPL), connectivity index (CI), and system omnivory index (SOI). These indicators characterize the overall activity level and scale of the ecosystem (Latham II, 2006).

2.2.4 Carrying capacity and potential stock enhancement estimation

Ecopath model allows the biomass of a functional group to gradually increase to perturb the model. The point at which the system can no longer compensate for any additional biomass, indicated by the EE value of any other functional group reaching 1, defines the carrying capacity of that functional group (Jiang and Gibbs, 2005). The potential for potential stock enhancement of that functional group was estimated by the difference between the carrying capacity and the current biomass (Outeiro et al., 2018). We calculated the ecological carrying capacity and estimated potential stock enhancement for functional groups other than detritus, phytoplankton and zooplankton.

## 3 RESULT

### 3.1 Model validation

The Ecopath and isotope-derived trophic levels of the marine ranching zone and the control area are shown in Table 1. The Pearson correlation coefficients between the Ecopath trophic levels and the stable isotope trophic levels for the marine ranching and the control area were 0.85 and 0.80, respectively. The Ecopath model effectively reflected the trophic relationships within the ecosystems of the marine ranching and the control area.

**Table 1 The trophic levels measurement using Ecopath and stable isotope analysis**

| Functional group | Marine ranching | | Control area | |
|---|---|---|---|---|
| | Ecopath trophic level | Stable isotopes trophic level | Ecopath trophic level | Stable isotopes trophic level |
| Pelagic fish | 2.70 | 2.67 | 2.71 | 2.67 |
| Large and medium benthic fish | 3.54 | 3.15 | 3.52 | 3.20 |
| Seabream | 3.51 | 3.16 | 3.51 | 3.28 |
| Leiognathidae | 2.85 | 3.24 | 2.81 | 3.21 |
| Small benthic fish | 3.22 | 3.15 | 3.11 | 3.30 |
| Scorpaenidae | 3.24 | 2.73 | 3.30 | 2.73 |
| Gobiidae | 3.15 | 3.00 | 3.14 | 2.81 |
| *Oratosquilla oratoria* | 3.08 | 3.18 | 3.07 | 3.18 |
| Large crab | 2.95 | 2.64 | 2.79 | 2.61 |
| Other crab | 2.86 | 2.73 | 2.71 | 2.66 |
| *Metapenaeopsis barbata* | 2.32 | 2.58 | 2.30 | 2.58 |
| Other shrimp | 2.38 | 2.47 | 2.35 | 2.44 |
| Cephalopod | 2.92 | 3.33 | 3.33 | 3.43 |
| Starfish | 2.45 | 2.22 | | |
| *Turritella terebra bacillum* | 2.20 | 1.88 | 2.20 | 1.88 |
| Oyster | 2.02 | 1.98 | | |
| Mytilus | 2.02 | 2.00 | | |

### 3.2 Biomass and ecotrophic efficiency

The marine ranching area contained 25 functional groups, while the control area comprised 20 functional groups. The values of *B*, *P*/*B*, *Q*/*B*, *P*/*Q*, UC, and EE indicators for each functional group are shown in Tables 2 and 3. In the marine ranching ecosystem excluding the functional group of detritus, the highest biomass was observed for phytoplankton at 32.780 t/km$^2$, followed by sea urchins at 30.000 t/km$^2$, with the lowest biomass recorded for leiognathidaes at 0.014 t/km$^2$. In the control area ecosystem excluding detritus, the highest biomass was also for phytoplankton at 31.330 t/km$^2$, followed by other bivalves at 3.987 t/km$^2$, with the lowest biomass for seabreams at 0.012 t/km$^2$. The highest EE value in the marine ranching ecosystem was for other crabs at 0.987, followed by large crabs at 0.965. In the control area, the highest EE value was for other shrimps at 0.984, followed by *Metapenaeopsis barbata* at 0.983.

### 3.3 Trophic level and energy flow

In both the marine ranching and control areas, phytoplankton, as primary producers, occupied the lowest trophic level, while large and medium benthic fishes held the highest trophic levels at 3.54 and 3.52, respectively (Fig.3). At trophic level I, the largest flow of materials in both ecosystems was from phytoplankton, followed by detritus (Tables 4 & 5). At trophic level II, the largest material flow in the marine ranching ecosystem was from zooplankton at 835.5 t/(km$^2$·a), followed by barnacles at 794.4 t/(km$^2$·a) (Table 4). Similar to the control area, the largest

**Table 2 Biomass, *P*/*B*, *Q*/*B*, *P*/*Q*, and EE values of each functional group in marine ranching**

| No. | Functional group | Biomass (t/km$^2$) | Production/ biomass (/a) | Consumption/ biomass (/a) | Production/ consumption (/a) | Unassimilated consumption | EE |
|---|---|---|---|---|---|---|---|
| 1 | Pelagic fish | 0.022 | 0.808 | 14.688 | 0.055 | 0.200 | 0.000 |
| 2 | Large and medium benthic fish | 0.214 | 1.073 | 11.224 | 0.096 | 0.200 | 0.845 |
| 3 | Seabream | 0.057 | 0.824 | 9.585 | 0.086 | 0.200 | 0.919 |
| 4 | Leiognathidae | 0.014 | 2.429 | 12.737 | 0.191 | 0.200 | 0.938 |
| 5 | Small benthic fish | 0.059 | 1.834 | 12.010 | 0.153 | 0.200 | 0.806 |
| 6 | Scorpaenidae | 0.070 | 1.093 | 19.625 | 0.056 | 0.200 | 0.821 |
| 7 | Gobiidae | 0.026 | 2.149 | 13.070 | 0.164 | 0.200 | 0.821 |
| 8 | *Oratosquilla oratoria* | 0.343 | 5.725 | 30.018 | 0.191 | 0.200 | 0.050 |
| 9 | Large crab | 0.370 | 5.129 | 28.439 | 0.180 | 0.200 | 0.965 |
| 10 | Other crab | 0.287 | 5.916 | 30.066 | 0.197 | 0.200 | 0.988 |
| 11 | *Metapenaeopsis barbata* | 0.196 | 6.096 | 26.052 | 0.234 | 0.200 | 0.946 |
| 12 | Other shrimp | 0.721 | 4.634 | 21.018 | 0.220 | 0.200 | 0.962 |
| 13 | Cephalopod | 0.027 | 3.937 | 15.725 | 0.250 | 0.200 | 0.920 |
| 14 | Sea urchin | 15.062 | 5.806 | 22.126 | 0.262 | 0.200 | 0.013 |
| 15 | Starfish | 0.018 | 2.359 | 8.710 | 0.271 | 0.200 | 0.829 |
| 16 | Other gastropod | 0.486 | 5.379 | 23.632 | 0.228 | 0.200 | 0.607 |
| 17 | *Turritella terebra bacillum* | 0.369 | 5.904 | 24.040 | 0.246 | 0.200 | 0.156 |
| 18 | Barnacle | 30.000 | 6.145 | 27.160 | 0.226 | 0.200 | 0.003 |
| 19 | Oyster | 22.493 | 4.610 | 20.830 | 0.221 | 0.400 | 0.078 |
| 20 | Mytilus | 22.964 | 5.059 | 19.440 | 0.260 | 0.400 | 0.097 |
| 21 | Other bivalve | 1.512 | 4.299 | 21.924 | 0.196 | 0.400 | 0.763 |
| 22 | Other macrobentho | 0.339 | 3.705 | 13.887 | 0.267 | 0.350 | 0.881 |
| 23 | Zooplankton | 4.348 | 32.045 | 192.151 | 0.167 | 0.400 | 0.564 |
| 24 | Phytoplankton | 32.780 | 113.820 | | | | 0.479 |
| 25 | Detritus | 49.420 | | | | | 0.207 |

**Table 3 Biomass, *P*/*B*, *Q*/*B*, *P*/*Q*, and EE values of each functional group in control area**

| No. | Functional group | Biomass (t/km$^2$) | Production/ biomass (/a) | Consumption/ biomass (/a) | Production/ consumption (/a) | Unassimilated consumption | EE |
|---|---|---|---|---|---|---|---|
| 1 | Pelagic fish | 0.016 | 0.815 | 15.374 | 0.053 | 0.200 | 0.000 |
| 2 | Large and medium benthic fish | 0.160 | 1.205 | 11.317 | 0.106 | 0.200 | 0.823 |
| 3 | Seabream | 0.012 | 1.540 | 15.886 | 0.097 | 0.200 | 0.416 |
| 4 | Leiognathidae | 0.043 | 2.344 | 13.932 | 0.168 | 0.200 | 0.982 |
| 5 | Small benthic fish | 0.054 | 1.942 | 12.125 | 0.160 | 0.200 | 0.957 |
| 6 | Scorpaenidae | 0.026 | 0.736 | 10.941 | 0.067 | 0.200 | 0.211 |
| 7 | Gobiidae | 0.068 | 2.236 | 12.662 | 0.177 | 0.200 | 0.674 |
| 8 | *Oratosquilla oratoria* | 0.622 | 5.865 | 30.386 | 0.193 | 0.200 | 0.020 |
| 9 | Large crab | 0.454 | 5.252 | 28.834 | 0.182 | 0.200 | 0.958 |
| 10 | Other crab | 0.266 | 5.856 | 31.438 | 0.186 | 0.200 | 0.974 |
| 11 | *Metapenaeopsis barbata* | 0.168 | 6.953 | 29.141 | 0.239 | 0.200 | 0.983 |
| 12 | Other shrimp | 0.714 | 5.042 | 22.537 | 0.224 | 0.200 | 0.984 |
| 13 | Cephalopod | 0.046 | 4.367 | 15.989 | 0.273 | 0.200 | 0.904 |
| 14 | Other gastropod | 0.134 | 5.198 | 23.972 | 0.217 | 0.200 | 0.947 |
| 15 | *Turritella terebra bacillum* | 0.093 | 5.438 | 24.034 | 0.226 | 0.200 | 0.934 |
| 16 | Other bivalve | 3.987 | 3.695 | 21.765 | 0.170 | 0.400 | 0.812 |
| 17 | Other macrobentho | 0.060 | 4.803 | 20.205 | 0.238 | 0.350 | 0.893 |
| 18 | Zooplankton | 3.601 | 32.265 | 192.550 | 0.168 | 0.400 | 0.262 |
| 19 | Phytoplankton | 31.330 | 113.820 | | | | 0.141 |
| 20 | Detritus | 52.455 | | | | | 0.085 |

energy flow was also from zooplankton at 693.4 t/(km$^2$·a), but followed by other bivalves sharply decreasing to 78.1 t/(km$^2$·a) (Table 5). The unutilized productivity of various functional groups in the ecosystem eventually flowed into the detritus group, with the largest flow to detritus in both the marine ranching and control area ecosystems being from phytoplankton at 1 942.609 and 3 062.162 t/(km$^2$·a), respectively, followed by zooplankton at 394.901 and 363.070 t/(km$^2$·a).

The proportion of total system throughput from low trophic levels to high trophic levels gradually decreased in both the marine ranching and control area ecosystems (Fig.4). Most energy flow occurred at trophic levels I and II, accounting for 98.10% and 99.33%, respectively. The average transfer efficiency in the marine ranching and control areas was 4.57% and 7.64%, respectively (Table 7).

### 3.4 Mixed trophic impact and key functional group

In both marine ranching and control ecosystems, prey groups had positive impacts on their predators, such as detritus and phytoplankton positively affecting most functional groups (Fig.5). Predator groups had negative impacts on other groups, such as large and medium benthic fishes and seabreams negatively affecting their prey functional groups. The diagonal line in the mixed trophic impact matrices showed that most functional groups had negative impact within their own group. In the marine ranching area (Fig.5a), fishery catch had a significant negative impact on seabreams, *Oratosquilla oratoria*, and large crabs. Similarly, in the control area (Fig.5b), fishing exerted a significant negative impact on seabreams, Gobiidae, and *Oratosquilla oratoria*.

In the marine ranching area, the functional group with the highest keystone species indices was *Oratosquilla oratoria* ($KS_{1i}$=0.053, $KS_{2i}$=2.642, $KS_{3i}$=1.133), while seabreams showed the highest indices in the control area ($KS_{1i}$=0.035, $KS_{2i}$=3.560, $KS_{3i}$=1.314) (Table 6).

### 3.5 Ecological network analysis

The ecological network analysis of the marine ranching and control area ecosystems revealed that

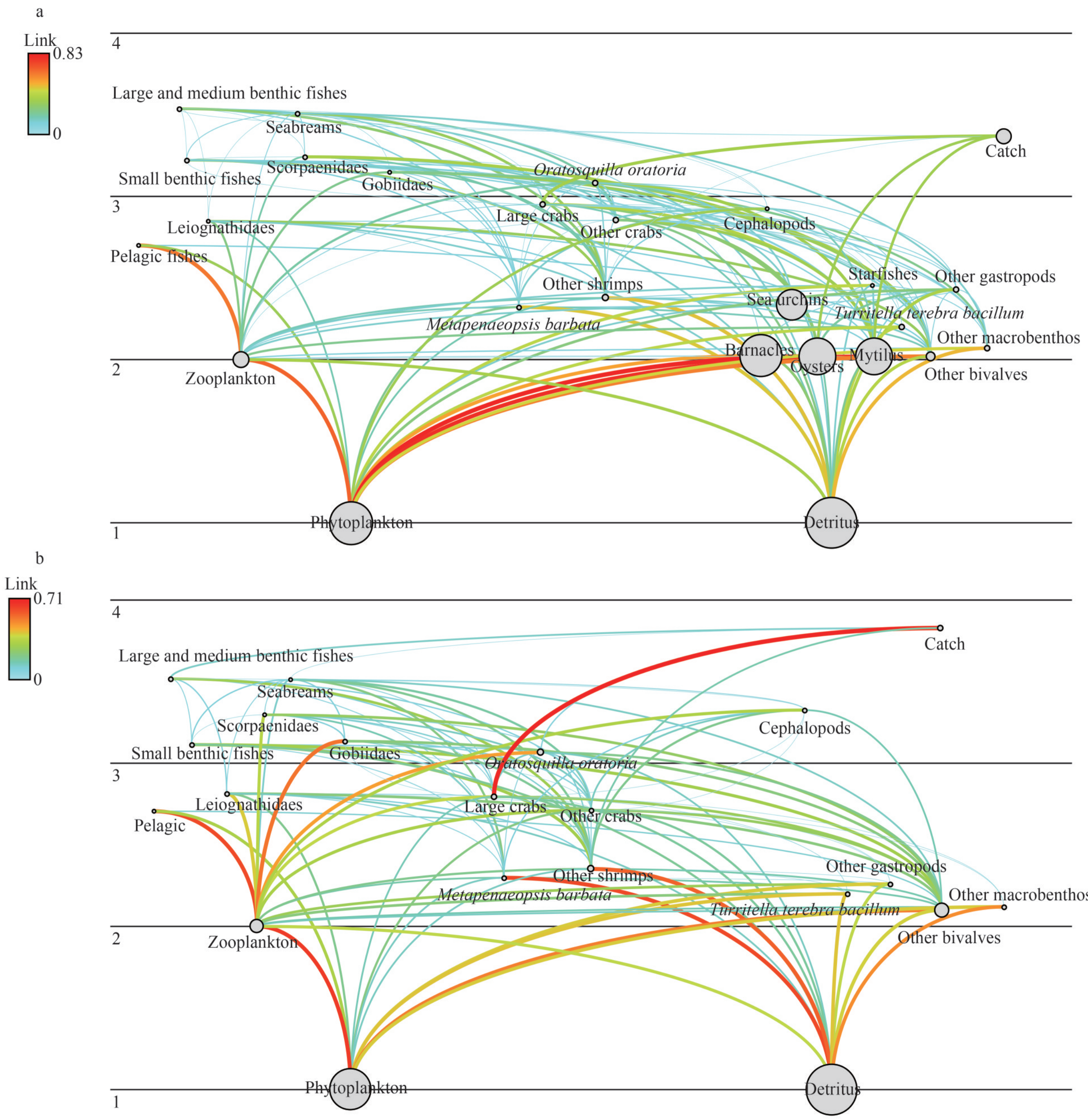


**Fig.3 Flow diagrams representing food web structure in marine ranching (a) and control area (b)**

Circle sizes are proportional to the logarithm of biomass. The color of the line indicates the proportion of prey in the predator's food composition.

the TPP/TR ratios were greater than 1 in both areas, specifically 2.67 and 9.36, and the TPP/TB ratios were 28.10 and 85.20, respectively. The TST and TB in the marine ranching area increased by 33.92% and 217.28%, respectively, and FCI and FMPL were higher compared to the control area (Table 7). Conversely, the CI and SOI were slightly higher in the control area than marine ranching ecosystem.

### 3.6 Ecological carrying capacity

There were 14 functional groups in the marine ranching area with higher ecological carrying capacities compared to the control area (Table 8). In the marine ranching area, the highest ecological carrying capacity was observed by mytilus (149.937 t/km$^2$), followed by barnacles (145.552 t/km$^2$), with the lowest being cephalopods (0.040 t/km$^2$). In the control area, the highest ecological carrying capacity was observed for other bivalves (43.361 t/km$^2$), followed by other macrobenthos (35.406 t/km$^2$), with the lowest being seabreams (0.015 t/km$^2$). Sea urchins, starfish, barnacles, oysters, and mytilus were only observed in the marine ranching area.

**Table 4 Trophic flow matrix of marine ranching ecosystem according to model groups and trophic levels (TLs)**

| No. | Functional group | Effective TL | Absolute flow (t/(km²·a)) | | | | | Flow to detritus (t/(km²·a)) |
|---|---|---|---|---|---|---|---|---|
| | | | I | II | III | IV | V | |
| 1 | Pelagic fish | 2.70 | | 0.098 | 0.225 | 0.001 | | 0.082 |
| 2 | Large and medium benthic fish | 3.54 | | | 1.130 | 1.153 | 0.114 | 0.516 |
| 3 | Seabream | 3.51 | | | 0.299 | 0.224 | 0.022 | 0.113 |
| 4 | Leiognathidae | 2.85 | | 0.043 | 0.121 | 0.014 | 0.001 | 0.038 |
| 5 | Small benthic fish | 3.22 | | 0.083 | 0.423 | 0.187 | 0.015 | 0.163 |
| 6 | Scorpaenidae | 3.24 | | | 1.081 | 0.273 | 0.019 | 0.288 |
| 7 | Gobiidae | 3.15 | | | 0.297 | 0.041 | 0.002 | 0.078 |
| 8 | *Oratosquilla oratoria* | 3.08 | | 1.116 | 7.598 | 1.498 | 0.082 | 3.925 |
| 9 | Large crab | 2.95 | | 1.416 | 8.278 | 0.792 | 0.036 | 2.171 |
| 10 | Other crab | 2.86 | | 1.900 | 6.290 | 0.427 | 0.012 | 1.747 |
| 11 | *Metapenaeopsis barbata* | 2.32 | | 3.549 | 1.477 | 0.079 | 0.001 | 1.086 |
| 12 | Other shrimp | 2.38 | | 9.837 | 5.064 | 0.249 | 0.004 | 3.159 |
| 13 | Cephalopod | 2.92 | | 0.176 | 0.173 | 0.070 | 0.005 | 0.093 |
| 14 | Sea urchin | 2.33 | | 222.200 | 111.100 | | | 152.931 |
| 15 | Starfish | 2.45 | | 0.087 | 0.068 | 0.001 | | 0.039 |
| 16 | Other gastropod | 2.43 | | 6.729 | 4.653 | 0.103 | | 3.324 |
| 17 | *Turritella terebra bacillum* | 2.20 | | 7.097 | 1.774 | | | 3.613 |
| 18 | Barnacle | 2.03 | | 794.400 | 20.370 | | | 346.718 |
| 19 | Oyster | 2.02 | | 459.200 | 9.371 | | | 283.056 |
| 20 | Mytilus | 2.02 | | 437.500 | 8.928 | | | 283.431 |
| 21 | Other bivalve | 2.02 | | 32.490 | 0.663 | | | 14.803 |
| 22 | Other macrobentho | 2.07 | | 4.378 | 0.330 | | | 1.798 |
| 23 | Zooplankton | 2.00 | | 835.500 | | | | 394.901 |
| 24 | Phytoplankton | 1.00 | 3 731.000 | | | | | 1 942.609 |
| 25 | Detritus | 1.00 | 3 441.000 | | | | | |

# 4 DISCUSSION

The methodology used in this study for artificial reef areas can be extended to other marine ranching zones, such as bottom-sown aquaculture areas and seagrass bed conservation areas, to assess the health status and ecological carrying capacity of marine ranching ecosystems. For example, Ecopath models have been applied by Han et al. (2018) and Lee et al. (2021) in the clam farming area of Jiaozhou Bay and the seagrass bed area of Dongsha Island, respectively, to evaluate the local ecosystem status. Compared to their models, our model further calculates the ecological carrying capacity, providing additional valuable information for the assessment of marine ranching ecosystem models.

## 4.1 Ecosystem energy flow

The overall energy flow distribution in the Beibu Gulf marine ranching ecosystem decreases progressively from lower to higher trophic levels, in accordance with the energy pyramid principle. The characteristic of this ecosystem is that the biomass of low trophic level organisms, such as filter-feeding bivalves, is relatively high on the artificial reefs. These sessile bivalves are constrained by artificial reefs and are unable to fully exploit the primary productivity of the entire marine area. Consequently, many producers flows into detritus, resulting in low transfer efficiency within the ecosystem. Meanwhile, the biomass of benthic bivalve predators, such as crustaceans, is relatively low, which hinders the efficient transfer of energy from

**Table 5 Trophic flow matrix of control area ecosystem according to model groups and trophic levels (TLs)**

| No. | Functional group | Effective TL | Absolute flow (t/(km$^2$·a)) | | | | | Flow to detritus (t/(km$^2$·a)) |
|---|---|---|---|---|---|---|---|---|
| | | | I | II | III | IV | V | |
| 1 | Pelagic fish | 2.71 | | 0.074 | 0.168 | 0.002 | | 0.062 |
| 2 | Large and medium benthic fish | 3.52 | | | 0.922 | 0.793 | 0.088 | 0.396 |
| 3 | Seabream | 3.51 | | | 0.111 | 0.077 | 0.010 | 0.051 |
| 4 | Leiognathidae | 2.81 | | 0.160 | 0.386 | 0.044 | 0.002 | 0.120 |
| 5 | Small benthic fish | 3.11 | | 0.119 | 0.367 | 0.153 | 0.013 | 0.135 |
| 6 | Scorpaenidae | 3.30 | | | 0.205 | 0.067 | 0.007 | 0.071 |
| 7 | Gobiidae | 3.14 | | | 0.763 | 0.095 | 0.005 | 0.222 |
| 8 | *Oratosquilla oratoria* | 3.07 | | 1.897 | 14.140 | 2.669 | 0.183 | 7.355 |
| 9 | Large crab | 2.79 | | 3.556 | 8.714 | 0.784 | 0.029 | 2.718 |
| 10 | Other crab | 2.71 | | 2.987 | 5.009 | 0.362 | 0.005 | 1.713 |
| 11 | *Metapenaeopsis barbata* | 2.30 | | 3.526 | 1.281 | 0.090 | | 0.999 |
| 12 | Other shrimp | 2.35 | | 10.890 | 4.898 | 0.301 | | 3.274 |
| 13 | Cephalopod | 3.33 | | | 0.611 | 0.122 | 0.007 | 0.167 |
| 14 | Other gastropod | 2.26 | | 2.370 | 0.833 | | | 0.677 |
| 15 | *Turritella terebra bacillum* | 2.20 | | 1.798 | 0.449 | | | 0.483 |
| 16 | Other bivalve | 2.10 | | 78.090 | 8.677 | | | 37.474 |
| 17 | Other macrobentho | 2.12 | | 1.067 | 0.145 | | | 0.455 |
| 18 | Zooplankton | 2.00 | | 693.400 | | | | 363.070 |
| 19 | Phytoplankton | 1.00 | 3 566.000 | | | | | 3 062.162 |
| 20 | Detritus | 1.00 | 3 482.000 | | | | | |

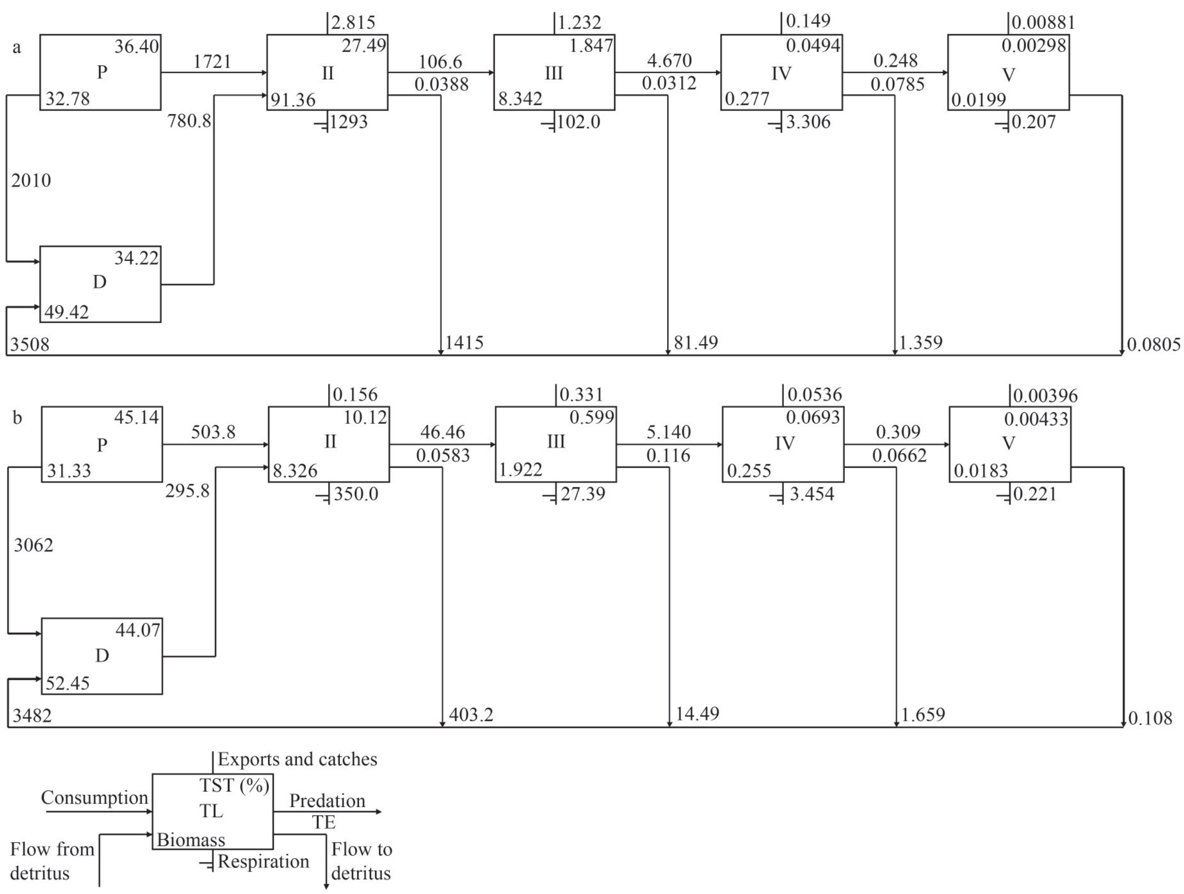


**Fig.4 Lindeman energy flow diagram between trophic levels for two scenarios for marine ranching (a) and control area (b)**

D: detritus; P: primary producer; TE: transfer efficiency; TL: trophic level; TST: total system throughput.

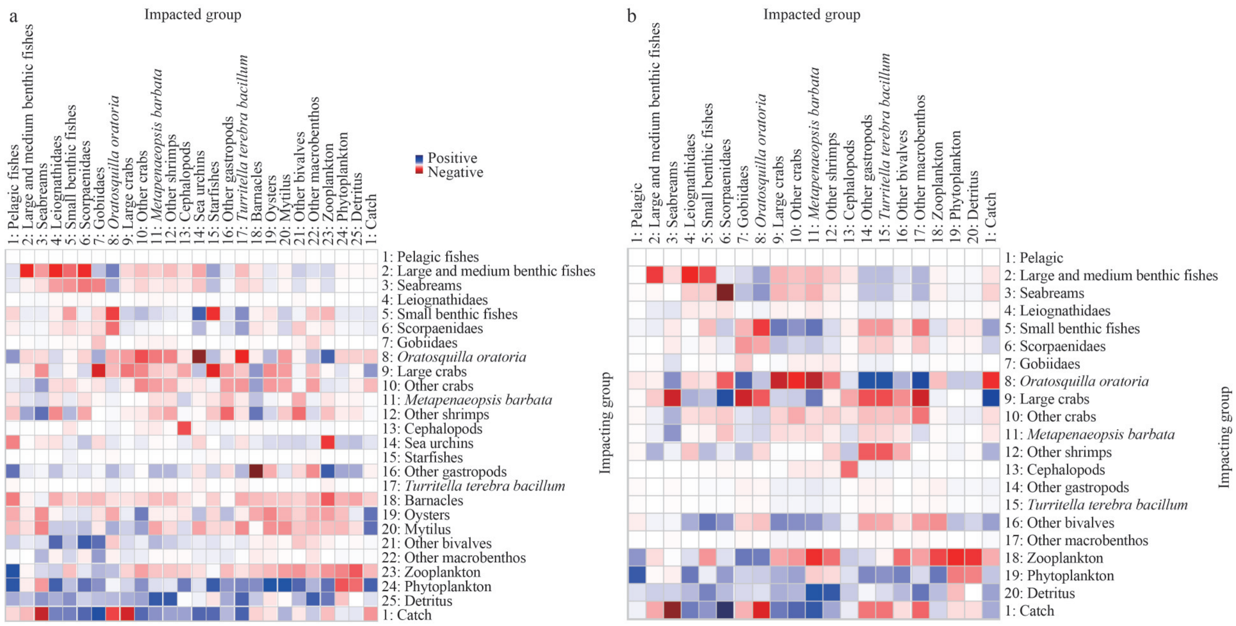


**Fig.5 Mix trophic impacts analysis for the marine ranching (a) and control area (b) ecosystems**

Positive impacts are denoted in blue rectangles and negative impacts in red rectangles, and the color concentration represents the impact strength.

**Table 6 The $KS_{1i}$, $KS_{2i}$ and $KS_{3i}$ of the marine ranch and the control area**

| Functional group | Marine ranching | | | Control area | | |
|---|---|---|---|---|---|---|
| | $KS_{1i}$ | $KS_{2i}$ | $KS_{3i}$ | $KS_{1i}$ | $KS_{2i}$ | $KS_{3i}$ |
| Pelagic fish | -2.239 | 1.542 | -0.896 | -2.316 | 1.106 | -1.061 |
| Large and medium benthic fish | -0.130 | 2.663 | 1.047 | -0.133 | 2.287 | 0.823 |
| Seabream | -0.380 | 2.988 | 0.899 | 0.035 | 3.560 | 1.314 |
| Leiognathidae | -1.704 | 2.273 | -0.324 | -1.064 | 1.929 | 0.140 |
| Small benthic fish | -0.181 | 3.171 | 1.074 | -0.136 | 2.756 | 1.010 |
| Scorpaenidae | -0.489 | 2.789 | 0.742 | -0.488 | 2.728 | 0.743 |
| Gobiidae | -1.208 | 2.501 | 0.115 | -1.172 | 1.617 | -0.092 |
| *Oratosquilla oratoria* | 0.053 | 2.642 | 1.133 | 0.216 | 2.051 | 0.922 |
| Large crab | -0.080 | 2.477 | 0.922 | 0.182 | 2.152 | 0.965 |
| Other crab | -0.344 | 2.322 | 0.803 | -0.401 | 1.799 | 0.447 |
| *Metapenaeopsis barbata* | -0.685 | 2.146 | 0.519 | -0.568 | 1.830 | 0.337 |
| Other shrimp | -0.245 | 2.023 | 0.661 | -0.259 | 1.517 | 0.351 |
| Cephalopod | -1.303 | 2.389 | -0.002 | -1.269 | 1.688 | -0.093 |
| Sea urchin | -0.398 | 0.599 | 0.353 | – | – | – |
| Starfish | -1.668 | 2.199 | -0.307 | – | – | – |
| Other gastropod | -0.011 | 2.427 | 0.944 | -1.248 | 1.250 | -0.246 |
| *Turritella terebra bacillum* | -1.557 | 1.000 | -0.515 | -1.432 | 1.220 | -0.390 |
| Barnacle | -0.435 | 0.322 | -0.023 | – | – | – |
| Oyster | -0.444 | 0.408 | 0.239 | – | – | – |
| Mytilus | -0.424 | 0.421 | 0.136 | – | – | – |
| Other bivalve | -0.307 | 1.642 | 0.544 | -0.230 | 0.835 | 0.115 |
| Other macrobentho | -0.719 | 1.875 | 0.396 | -1.611 | 1.233 | -0.497 |
| Zooplankton | -0.138 | 1.362 | 0.655 | -0.046 | 1.058 | 0.470 |
| Phytoplankton | -0.109 | 0.622 | 0.014 | -0.727 | -0.002 | -0.127 |

– means no data.

**Table 7 Ecological indicators estimated by the Ecopath models of marine ranching and control area ecosystems**

| Indicator | Acronym | Marine ranching | Control area |
|---|---|---|---|
| Statistics and flows | | | |
| Total system throughput (t/(km$^2$·a)) | TST | 10 583.08 | 7 902.59 |
| Total production (t/(km$^2$·a)) | TP | 4 385.38 | 3 711.55 |
| Total biomass (t/km$^2$) | TB | 132.78 | 41.85 |
| Total consumption/TST (%) | TQ/TST | 28.47 | 10.80 |
| Total exports/TST (%) | EX/TST | 25.81 | 40.32 |
| Flows to detritus/TST (%) | FD/TST | 32.51 | 44.06 |
| Total respiration/TST (%) | TR/TST | 13.21 | 4.82 |
| Ecosystem maturity status | | | |
| Total primary production/total respiration | TPP/TR | 2.67 | 9.36 |
| Total primary production/total biomass | TPP/TB | 28.10 | 85.20 |
| Finn's cycling index (%) | FCI | 4.15 | 2.27 |
| Finn's mean path length | FMPL | 2.56 | 2.22 |
| Connectance Index | CI | 0.27 | 0.32 |
| System Omnivory Index | SOI | 0.16 | 0.19 |
| Trophic indices | | | |
| Mean transfer efficiency (%) | mTE | 4.57 | 7.64 |
| mTE from primary production (%) | mTEpp | 4.57 | 7.63 |
| mTE from detritus (%) | mTEd | 4.56 | 7.65 |
| Proportion of total flow from detritus (%) | PFFD | 42.71 | 48.09 |
| Proportion of total flow from primary producers (%) | PFFPP | 57.29 | 51.91 |

bivalves to higher trophic levels. Instead, the majority of this energy is redirected into the detritus. As a result, the overall trophic transfer efficiency is only 4.57%, significantly lower than the average of 10% observed in natural ecosystems (Lindeman, 1942).

Compared to other marine ranching ecosystems, the energy transfer efficiency in the Beibu Gulf marine ranching ecosystem remains at a relatively low level. Currently, the energy transfer efficiency from trophic level 2 to trophic level 3 in the Beibu Gulf marine ranching ecosystem is 3.9%, which is similar to that of the Zhongjieshan Islands (4.1%) and Lvsi fishing ground (3.6%). The ecological transfer efficiencies from trophic level III to IV and from trophic level IV to V are also low, at only 3.1% and 7.9%, respectively, while marine ranching ecosystems being compared to this study show values exceeding 10% (Gao et al., 2022; Qu et al., 2024). The artificial reef ecosystem is still in the developmental stage, and its ecosystem structure and function depend on the stage of community succession. Currently, high-trophic-level predators are scarce in the artificial reef areas, leading to low energy transfer efficiency between higher trophic levels (Wang et al., 2022a). Increasing the biomass and diversity of organisms at trophic levels III and IV through measures such as fishing restrictions and stocking may help optimize the food web and improve the energy transfer efficiency of the system (Feng et al., 2025).

### 4.2 Ecosystem scale

Total system throughput (TST), which includes total consumption, total export, total respiration, and the flow to detritus, along with TB, reflects the ecosystem scale (Ju et al., 2020). The deployment of artificial reefs plays a significant role in influencing ecosystem processes and cycles, ultimately affecting the overall scale of the ecosystem. Chen et al. (2008) reported a 24.21% increase in the TST in reef areas following artificial reef deployment at a similar latitude to our study, indicating an expansion in ecosystem scale. Hydrodynamic processes and the physical characteristics of the substrate in the artificial reef area are some of the main direct

**Table 8 The carrying capacity and reproductive potential of economic species in the marine ranching and the control areas**

| Group name | Marine ranching | | Control area | |
|---|---|---|---|---|
| | Carrying capacity (t/km$^2$) | Potential stock enhancement (t/km$^2$) | Carrying capacity (t/km$^2$) | Potential stock enhancement (t/km$^2$) |
| Pelagic fish | 1.335 | 1.313 | 2.265 | 2.249 |
| Large and medium benthic fish | 0.233 | 0.019 | 0.162 | 0.002 |
| Seabream | 0.070 | 0.013 | 0.015 | 0.003 |
| Leiognathidae | 0.055 | 0.041 | 0.077 | 0.034 |
| Small benthic fish | 0.084 | 0.025 | 0.070 | 0.016 |
| Scorpaenidae | 0.081 | 0.011 | 0.040 | 0.014 |
| Gobiidae | 0.059 | 0.033 | 0.096 | 0.028 |
| *Oratosquilla oratoria* | 0.355 | 0.012 | 0.635 | 0.013 |
| Large crab | 0.394 | 0.024 | 0.503 | 0.049 |
| Other crab | 0.389 | 0.102 | 0.326 | 0.060 |
| *Metapenaeopsis barbata* | 0.606 | 0.410 | 0.251 | 0.083 |
| Other shrimp | 1.382 | 0.661 | 0.822 | 0.108 |
| Cephalopod | 0.040 | 0.013 | 0.063 | 0.017 |
| Sea urchin | 43.429 | 28.367 | – | – |
| Starfish | 0.362 | 0.344 | – | – |
| Other gastropod | 0.697 | 0.211 | 13.883 | 13.749 |
| *Turritella terebra bacillum* | 13.423 | 13.054 | 17.921 | 17.828 |
| Barnacle | 145.552 | 115.552 | – | – |
| Oyster | 134.854 | 112.361 | – | – |
| Mytilus | 149.937 | 126.973 | – | – |
| Other bivalve | 144.661 | 143.149 | 43.361 | 39.375 |
| Other macrobenthos | 64.907 | 64.568 | 35.406 | 35.346 |

– means no data.

factors influencing the local ecological scale (Layman and Allgeier, 2020). Artificial reefs significantly reduce water flow velocity, creating a turbulence flow field to provide a favorable environment for the benthic organisms’ recruitment and assemblage (Danovaro et al., 2002). At the same time, the formation of upwellings transports particulate carbon and nutrients to the surface layers, enhancing nutrient cycling and promoting plankton growth, which in turn supports fish aggregation (Machado et al., 2013). Artificial reefs also provide attachment substrates for filter-feeding benthic organisms, and their shells, through aggregation and deposition, can form oyster reefs (Reeves et al., 2020). The newly formed oyster reefs, in turn, create additional habitats for other benthic species, thereby establishing a positive feedback loop. Newly settled benthic organisms enhance the ecosystem’s TB. Through behaviors such as predation and respiration, they further strengthen the ecosystem’s TST, while increasing the proportion of TQ and TR within the ecosystem’s TST (Krohling et al., 2006). It is through this mechanism that the ecosystem scale effect of artificial reef deployment is enhanced.

Compared to artificial reef ecosystems at similar latitudes, the scale of our marine ranching ecosystem is larger than that of the Zhujiang River estuary artificial reef area (Xu et al., 2022) but smaller than the artificial reef area in the Sea of Oman (Al Ismaili and Dutta, 2023). One potential explanation for this phenomenon may lie in the variation in primary production across different reef areas. Artificial reef deployment has been shown to be strongly positively correlated with primary production (Esquivel et al., 2022). Higher primary productivity leads to greater TB, which results in increased respiration and consumption rates. This ultimately elevates the TST, thereby enhancing the overall scale of the ecosystem. The Sea of Oman is well-known for its local upwelling system, which delivers abundant nutrients (Ismail and Al Shehhi, 2022). The accumulated effects of upwelling and the back-eddy flow generated by artificial reefs significantly enhance primary productivity, with phytoplankton biomass being 3.36 times higher than that of the Beibu Gulf marine ranching area. This results in a larger ecosystem scale in the region. When the biological community structure and nutrient levels are favorable, the deployment of artificial reefs has the potential to significantly enhance ecosystem scale (Paxton et al., 2022).

### 4.3 Ecosystem maturity

Following the approach of Wang et al. (2022b), this study uses TPP/TR, TPP/TB, CI, SOI, FCI, and FMPL to assess the maturity of the ecosystem. When the ratios of TPP/TR and TPP/TB approach 1, it indicates that primary productivity is being utilized more efficiently, leading to greater ecosystem stability and an enhanced ability to withstand external disturbances (Christensen, 1995). Artificial reefs in marine ranching areas attract benthic mollusks, leading to an increase in TB. These benthic organisms consume large amounts of phytoplankton through their feeding behavior, thereby making more efficient use of primary productivity, while their respiration further increases TR. Under the condition of similar TPP values, the TPP/TR and TPP/TB ratios in the marine ranching area are lower than those in the control area (e.g., TPP/TR is 2.69 vs. 9.36). Consequently, the marine ranching ecosystem is considered more mature (Odum, 1969). The CI and SOI, representing the ratio of actual to potential connections in the food web and the logarithmic weighted average of all consumers' food consumption, respectively, reflect the complexity of the food web. More mature ecosystems have more complex food web structures (Heymans et al., 2014). In the marine ranching area, the CI and SOI were slightly lower than in the control area, which could be attributed to the dietary habits of the significantly increased benthic sessile animals, such as oysters and mussels. These sessile organisms, characterized by shorter food chains, accounted for over 60% of the total biomass in the marine ranching area. The simplified food chain—from phytoplankton/detritus to oysters/mussels, and then to carnivorous benthic animals—reduces the complexity of the food web, streamlining the overall structure (Heymans et al., 2014). FCI and FMPL, representing the proportion of nutrients recirculated into the system and the average length of energy flowing through the food chain during recycling, often show more recycling in more mature systems (Finn, 1976). In the marine ranching area, a large amount of benthic organisms such as mollusks flows into the detritus pool. This detritus is subsequently recycled, thereby increasing both FCI and FMPL. The benthic organisms attracted by the artificial reefs, through their strong filter-feeding activity, more efficiently utilized primary productivity. This process helped prevent potential eutrophication of the water due to nutrient accumulation (Karlson et al., 2007). Additionally, the detritus produced by benthic organisms was utilized by other functional groups, enhancing the internal circulation of ecosystem resources and thereby increasing the stability of the ecosystem (Xu et al., 2019).

Compared to other coastal artificial reef ecosystems in China, the ecosystem maturity of marine ranching from our study is lower than that of the Laizhou Bay artificial reef area (Yuan et al., 2022). The TPP/TR and TPP/TB in the Beibu Gulf marine ranching area are higher than those in the Laizhou Bay artificial reef area, while the FCI and FMPL are lower. This suggests that the biomass and respiration are relatively low, that primary productivity is not fully utilized. Additionally, the functional groups of this study exhibit more homogeneous feeding habits, the food web structure is simpler, and fewer nutrients are involved in recycling. This may be related to the relatively short deployment period of the artificial reefs, which has been only two years, leading to insufficient ecological development and an inability to reach full maturity (Toledo et al., 2020). Based on ecosystem changes observed over ten years following artificial reef deployment (Perkol-Finkel and Benayahu, 2005), the Beibu Gulf marine ranching ecosystem is expected to become more stable over time.

### 4.4 Ecological carrying capacity

This study estimated the ecological carrying capacity of various functional groups in both the marine ranching area and the control area of Beibu Gulf. Ecopath is based on a steady-state model, which describes the constant energy flow between functional groups. In calculating ecological carrying capacity, the biomass of other functional groups remains constant (Srithong et al., 2021). Compared to the control area, the EE values of the phytoplankton and detritus functional groups in the marine ranching area were higher, indicating a more efficient utilization of primary productivity. However, the EE values of phytoplankton and detritus remain well below 1, indicating that their potential as a food source for filter-feeding bivalves still offers significant room for utilization. This explains the high ecological carrying capacity and population growth potential of functional groups such as oysters and mussels in the northern Gulf of Beibu Sea marine ranching area. At the same time, the high biomass of filter-feeding bivalves in the northern Gulf of Beibu Sea marine ranching area provides a food source for predators (such as gastropods, crabs, etc.), thereby enhancing the ecological carrying capacity and potential population growth of these predators.

Compared to northern China (latitude higher than 33°N), the ecological carrying capacity of large, high-trophic-level fish in the Beibu Gulf is lower than that in Laizhou Bay (Yuan et al., 2022). This is related to the lower EE values of lower trophic level functional groups, indicating that they are not fully utilized. In contrast, the carrying capacity for shellfish is higher than in the Changshan Islands area of the Bohai Sea (Zhang et al., 2023). The ecological carrying capacity of shellfish largely depends on the biomass of phytoplankton and detritus as their food sources (Zhao et al., 2022), with the biomass of phytoplankton and detritus in the Beibu Gulf being 2.16 and 1.59 times that of the Changshan Islands, respectively. The primary productivity in the Beibu Gulf marine ranching area remains at a relatively high level. To better utilize primary productivity and enrich fishery resources, it is recommended to refer to the ecological carrying capacity of each functional group for restocking and stock enhancement activities (Mace, 2001). However, excessive restocking and stock enhancement activities can lead to the EE values of other functional groups approaching 1, which may result in energy imbalance even under weak disturbances, thereby causing additional ecological risks (May, 1977). Therefore, it is crucial to adopt appropriate stocking strategies based on ecological carrying capacity, such as stocking functional groups with lower biomass up to half of their ecological carrying capacity and simultaneously stocking species across different trophic levels (Yang et al., 2023).

## 5 CONCLUSION

This study established two Ecopath models for the marine ranching and control area ecosystems in Beibu Gulf, comparing their trophic interactions, energy flows, ecosystem characteristics, key species analysis, and ecological carrying capacity differences. The deployment of artificial reefs increased ecosystem scale, contributed to ecosystem maturity, and has significant potential to enhance the ecological carrying capacity for top predator groups and large benthic animal populations. This study provides a basis for stock enhancement practices in marine ranching in the Beibu Gulf, grounded in the ecological carrying capacity.

## 6 DATA AVAILABILITY STATEMENT

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

**References**

Al Ismaili S, Dutta S. 2023. Ecosystem characteristics and trophic model of the artificial reef ecosystem in the Sea of Oman, Sultanate of Oman. *Sustainability*, **15**(24): 16574, https://doi.org/10.3390/su152416574.

Baynes T W, Szmant A M. 1989. Effect of current on the sessile benthic community structure of an artificial reef. *Bulletin of Marine Science*, **44**(2): 545-566.

Becker A, Taylor M D, Lowry M B. 2017. Monitoring of reef associated and pelagic fish communities on Australia's first purpose built offshore artificial reef. *ICES Journal of Marine Science*, **74**(1): 277-285, https://doi.org/10.1093/icesjms/fsw133.

Brey T. 1999. Growth performance and mortality in aquatic macrobenthic invertebrates. *Advances in Marine Biology*, **35**: 153-223, https://doi.org/10.1016/S0065-2881(08)60005-X.

Champion C, Suthers I M, Smith J A. 2015. Zooplanktivory is a key process for fish production on a coastal artificial reef. *Marine Ecology Progress Series*, **541**: 1-14, https://doi.org/10.3354/meps11529.

Chen Z Z, Qiu Y S, Jia X P et al. 2008. Using an ecosystem modeling approach to explore possible ecosystem impacts of fishing in the Beibu Gulf, northern South China Sea. *Ecosystems*, **11**(8): 1318-1334, https://doi.org/10.1007/s10021-008-9200-x.

Christensen V. 1995. Ecosystem maturity—towards quantification. *Ecological Modelling*, **77**(1): 3-32, https://doi.org/10.1016/0304-3800(93)E0073-C.

Christensen V, Pauly D. 1992. ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling*, **61**(3-4): 169-185, https://doi.org/10.1016/0304-3800(92)90016-8.

Christensen V, Walters C J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling*, **172**(2-4): 109-139, https://doi.org/10.1016/j.ecolmodel.

2003.09.003.

Christensen V, Walters C J, Pauly D. 2005. Ecopath with Ecosim: A User's Guide. University of British Columbia, Vancouver, Canada.

Colléter M, Valls A, Guitton J et al. 2015. Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. *Ecological Modelling*, **302**: 42-53, https://doi.org/10.1016/j.ecolmodel.2015.01.025.

Coll M, Bundy A, Shannon L J. 2009. Ecosystem modelling using the Ecopath with Ecosim approach. *In*: Megrey B A, Moksness E eds. Computers in Fisheries Research. Springer Netherlands, Dordrecht. p.225-291, https://doi.org/10.1007/978-1-4020-8636-6_8.

Danovaro R, Gambi C, Mazzola A et al. 2002. Influence of artificial reefs on the surrounding infauna: analysis of meiofauna. *ICES Journal of Marine Science*, **59**(S1): S356-S362, https://doi.org/10.1006/jmsc.2002.1223.

Dupont J M. 2008. Artificial reefs as restoration tools: a case study on the West Florida shelf. *Coastal Management*, **36**(5): 495-507, https://doi.org/10.1080/08920750802395558.

Esquivel K E, Hesselbarth M H K, Allgeier J E. 2022. Mechanistic support for increased primary production around artificial reefs. *Ecological Applications*, **32**(6): e2617, https://doi.org/10.1002/eap.2617.

Feng J, Yu H L, Wu L J et al. 2025. Evaluating ecosystem characteristics and ecological carrying capacity for marine fauna stock enhancement within a marine ranching system. *Animals*, **15**(2): 165, https://doi.org/10.3390/ani15020165.

Finn J T. 1976. Measures of ecosystem structure and function derived from analysis of flows. *Journal of Theoretical Biology*, **56**(2): 363-380, https://doi.org/10.1016/S0022-5193(76)80080-X.

Gao J S, Wu G D, Ya H Z. 2017. Review of the circulation in the Beibu Gulf, South China Sea. *Continental Shelf Research*, **138**: 106-119, https://doi.org/10.1016/j.csr.2017.02.009.

Gao S K, Chen Z, Lu Y N et al. 2022. Comparison of marine ecosystems of Haizhou Bay and Lvsi fishing ground in China based on the Ecopath model. *Water*, **14**(9): 1397, https://doi.org/10.3390/w14091397.

Gorbatenko K M, Dolganova N T. 2007. Comparing the catch efficiency with different types of plankton nets in the high production zones of the Pacific Ocean. *Oceanology*, **47**(2): 205-212, https://doi.org/10.1134/S0001437007020075.

Hale S L, Koprowski J L. 2018. Ecosystem-level effects of keystone species reintroduction: a literature review. *Restoration Ecology*, **26**(3): 439-445, https://doi.org/10.1111/rec.12684.

Han D Y, Chen Y, Zhang C L et al. 2018. Evaluation of effects of shellfish aquaculture and capture fishery on a semi-closed bay ecosystem. *Estuarine, Coastal and Shelf Science*, **207**: 175-182, https://doi.org/10.1016/j.ecss.2018.04.005.

Heymans J J, Coll M, Libralato S et al. 2014. Global patterns in ecological indicators of marine food webs: a modelling approach. *PLoS One*, **9**(4): e95845, https://doi.org/10.1371/journal.pone.0095845.

Heymans J J, Coll M, Link J S et al. 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecological Modelling*, **331**: 173-184, https://doi.org/10.1016/j.ecolmodel.2015.12.007.

Heymans J J, Tomczak M T. 2016. Regime shifts in the Northern Benguela ecosystem: challenges for management. *Ecological Modelling*, **331**: 151-159, https://doi.org/10.1016/j.ecolmodel.2015.10.027.

Hong X F, Zhang K, Li J J et al. 2023. Effects of climate events on abundance and distribution of major commercial fishes in the Beibu Gulf, South China Sea. *Diversity*, **15**(5): 649, https://doi.org/10.3390/d15050649.

Ismail K A, Al Shehhi M R. 2022. Upwelling and nutrient dynamics in the Arabian Gulf and Sea of Oman. *PLoS One*, **17**(10): e0276260, https://doi.org/10.1371/journal.pone.0276260.

Jiang W M, Gibbs M T. 2005. Predicting the carrying capacity of bivalve shellfish culture using a steady, linear food web model. *Aquaculture*, **244**(1-4): 171-185, https://doi.org/10.1016/j.aquaculture.2004.11.050.

Ju P L, Cheung W W L, Chen M R et al. 2020. Comparing marine ecosystems of Laizhou and Haizhou Bays, China, using ecological indicators estimated from food web models. *Journal of Marine Systems*, **202**: 103238, https://doi.org/10.1016/j.jmarsys.2019.103238.

Jung S, Van Chau T, Kim M et al. 2022. Artificial seaweed reefs that support the establishment of submerged aquatic vegetation beds and facilitate ocean macroalgal afforestation: a review. *Journal of Marine Science and Engineering*, **10**(9): 1184, https://doi.org/10.3390/jmse10091184.

Karlson K, Bonsdorff E, Rosenberg R. 2007. The impact of benthic macrofauna for nutrient fluxes from Baltic Sea sediments. *AMBIO: A Journal of the Human Environment*, **36**(2): 161-167, https://doi.org/10.1579/0044-7447(2007)36[161:TIOBMF]2.0.CO;2.

Krohling W, Brotto D S, Zalmon I R. 2006. Functional role of fouling community on an artificial reef at the northern coast of Rio de Janeiro State, Brazil. *Brazilian Journal of Oceanography*, **54**(4): 183-191, https://doi.org/10.1590/S1679-87592006000300002.

Latham II L G. 2006. Network flow analysis algorithms. *Ecological Modelling*, **192**(3-4): 586-600, https://doi.org/10.1016/j.ecolmodel.2005.07.029.

Layman C A, Allgeier J E. 2020. An ecosystem ecology perspective on artificial reef production. *Journal of Applied Ecology*, **57**(11): 2139-2148, https://doi.org/10.1111/1365-2664.13748.

Lee C L, Lin W J, Liu P J et al. 2021. Highly productive tropical seagrass beds support diverse consumers and a large organic carbon pool in the sediments. *Diversity*, **13**(11): 544, https://doi.org/10.3390/d13110544.

Lee H T, Chang Y C, Liao C H et al. 2022. Development of integrated multitrophic aquaculture-based cage rearing system in an underutilized fishing port and its application in marine stock enhancement. *Frontiers in Marine Science*, **9**: 998198, https://doi.org/10.3389/fmars.2022.998198.

Leitão F, Santos M N, Monteiro C C. 2007. Contribution of artificial reefs to the diet of the white sea bream (*Diplodus sargus*). *ICES Journal of Marine Science*, **64**(3): 473-478, https://doi.org/10.1093/icesjms/fsm027.

Li Z P, Chen Y, Wang G et al. 2023. Ecological carrying capacity and carbon sequestration potential of bivalve shellfish in marine ranching: a case study in Bohai Bay, China. *Frontiers in Marine Science*, **10**: 1174235, https://doi.org/10.3389/fmars.2023.1174235.

Libralato S, Christensen V, Pauly D. 2006. A method for identifying keystone species in food web models. *Ecological Modelling*, **195**(3-4): 153-171, https://doi.org/10.1016/j.ecolmodel.2005.11.029.

Lin H Y, Lin P Y, Chang N N et al. 2014. Trophic structure of megabenthic food webs along depth gradients in the South China Sea and off northeastern Taiwan. *Marine Ecology Progress Series*, **501**: 53-66, https://doi.org/10.3354/meps10681.

Lindeman R L. 1942. The trophic-dynamic aspect of ecology. *Ecology*, **23**(4): 399-417, https://doi.org/10.2307/1930126.

Lorenzen K, Leber K M, Lee Blankenship H. 2010. Responsible approach to marine stock enhancement: an update. *Reviews in Fisheries Science*, **18**(2): 189-210, https://doi.org/10.1080/10641262.2010.491564.

Mace N. 2001. A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. *Fish and Fisheries*, **2**(1): 2-32, https://doi.org/10.1046/j.1467-2979.2001.00033.x.

Machado P M, de Sá F S, de Rezende C E et al. 2013. Artificial reef impact on macrobenthic community on south-eastern Brazil coast. *Marine Biodiversity Records*, **6**: e40, https://doi.org/10.1017/S1755267213000183.

May R M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, **269**(5628): 471-477, https://doi.org/10.1038/269471a0.

Odum E P. 1969. The strategy of ecosystem development: an understanding of ecological succession provides a basis for resolving man's conflict with nature. *Science*, **164**(3877): 262-270, https://doi.org/10.1126/science.164.3877.262.

Outeiro L, Byron C, Angelini R. 2018. Ecosystem maturity as a proxy of mussel aquaculture carrying capacity in Ria de Arousa (NW Spain): a food web modeling perspective. *Aquaculture*, **496**: 270-284, https://doi.org/10.1016/j.aquaculture.2018.06.043.

Palomares M L D, Pauly D. 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Marine and Freshwater Research*, **49**(5): 447-453, https://doi.org/10.1071/MF98015.

Pan Y, Tong H H, Wei D Z et al. 2022. Review of structure types and new development prospects of artificial reefs in China. *Frontiers in Marine Science*, **9**: 853452, https://doi.org/10.3389/fmars.2022.853452.

Pasquaud S, Pillet M, David V et al. 2010. Determination of fish trophic levels in an estuarine system. *Estuarine, Coastal and Shelf Science*, **86**(2): 237-246, https://doi.org/10.1016/j.ecss.2009.11.019.

Pauly D. 1990. Length-converted catch curves and the seasonal growth of fishes. *Fishbyte*, **8**(3): 24-29.

Paxton A B, Steward D N, Harrison Z H et al. 2022. Fitting ecological principles of artificial reefs into the ocean planning puzzle. *Ecosphere*, **13**(2): e3924, https://doi.org/10.1002/ecs2.3924.

Perkol-Finkel S, Benayahu Y. 2005. Recruitment of benthic organisms onto a planned artificial reef: shifts in community structure one decade post-deployment. *Marine Environmental Research*, **59**(2): 79-99, https://doi.org/10.1016/j.marenvres.2004.03.122.

Post D M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, **83**(3): 703-718, https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2.

Power M E, Tilman D, Estes J A et al. 1996. Challenges in the Quest for Keystones: identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. *BioScience*, **46**(8): 609-620, https://doi.org/10.2307/1312990.

Qu Y, Wang Z M, Zhou Y D et al. 2024. Ecosystem structure and function in the Sea Area of Zhongjieshan islands based on Ecopath model. *Journal of Marine Science and Engineering*, **12**(11): 2086, https://doi.org/10.3390/jmse12112086.

Raj K D, Mathews G, Edward J K P. 2020. Long-term benefits of artificial reef modules for reef recovery in gulf of Mannar, Southeast India. *Journal of Coastal Conservation*, **24**(5): 53, https://doi.org/10.1007/s11852-020-00773-5.

Ramm L A W, Florisson J H, Watts S L et al. 2021. Artificial reefs in the Anthropocene: a review of geographical and historical trends in their design, purpose, and monitoring. *Bulletin of Marine Science*, **97**(4): 699-728, https://doi.org/10.5343/bms.2020.0046.

Raoux A, Salaun J, Pezy J P et al. 2022. Ecosystem approach of artificial reef through trophic web modelling. *IOP Conference Series*: *Materials Science and Engineering*, **1245**(1): 012004, https://doi.org/10.1088/1757-899X/1245/1/012004.

Reeves S E, Renzi J J, Fobert E K et al. 2020. Facilitating better outcomes: how positive species interactions can improve oyster reef restoration. *Frontiers in Marine Science*, **7**: 656, https://doi.org/10.3389/fmars.2020.00656.

Sambrook K, Hoey A S, Andréfouët S et al. 2019. Beyond the reef: the widespread use of non-reef habitats by coral reef fishes. *Fish and Fisheries*, **20**(5): 903-920, https://doi.org/10.1111/faf.12383.

Srithong N, Jensen K R, Jarernpornnipat A. 2021. Application of the Ecopath model for evaluation of ecological structure and function for fisheries management: a case study from fisheries in coastal Andaman Sea, Thailand. *Regional Studies in Marine Science*, **47**: 101972, https://doi.org/10.1016/j.rsma.2021.101972.

Su L, Chen Z Z, Zhang K et al. 2021. Decadal-scale variation in mean trophic level in Beibu Gulf based on bottom-trawl survey data. *Marine and Coastal Fisheries*, **13**(3):

174-182, https://doi.org/10.1002/mcf2.10144.

Suo A N, Li H Y, Zhou W G et al. 2023. Estimation of ecological carrying capacity of small-scale fish in marine ranch of the Pearl River Estuary, China. *Regional Studies in Marine Science*, **61**: 102901, https://doi.org/10.1016/j.rsma.2023.102901.

Toledo M I, Torres P, Díaz C et al. 2020. Ecological succession of benthic organisms on niche-type artificial reefs. *Ecological Processes*, **9**(1): 38, https://doi.org/10.1186/s13717-020-00242-9.

Ulanowicz R E, Puccia C J. 1990. Mixed trophic impacts in ecosystems. *Coenoses*, **5**(1): 7-16.

Valls A, Coll M, Christensen V. 2015. Keystone species: toward an operational concept for marine biodiversity conservation. *Ecological Monographs*, **85**(1): 29-47, https://doi.org/10.1890/14-0306.1.

Wang X, Feng J, Lin C G et al. 2022a. Structural and functional improvements of coastal ecosystem based on artificial oyster reef construction in the Bohai Sea, China. *Frontiers in Marine Science*, **9**: 829557, https://doi.org/10.3389/fmars.2022.829557.

Wang Z G, Feng J, Lozano-Montes H M et al. 2022b. Estimating ecological carrying capacity for stock enhancement in marine ranching ecosystems of Northern China. *Frontiers in Marine Science*, **9**: 936028, https://doi.org/10.3389/fmars.2022.936028.

Wu Z X, Tweedley J R, Loneragan N R et al. 2019. Artificial reefs can mimic natural habitats for fish and macroinvertebrates in temperate coastal waters of the Yellow Sea. *Ecological Engineering*, **139**: 105579, https://doi.org/10.1016/j.ecoleng.2019.08.009.

Xu M, Qi L, Zhang L B et al. 2019. Ecosystem attributes of trophic models before and after construction of artificial oyster reefs using Ecopath. *Aquaculture Environment Interactions*, **11**: 111-127, https://doi.org/10.3354/aei00284.

Xu M, Yang X Y, Song X J et al. 2021. Seasonal analysis of artificial oyster reef ecosystems: implications for sustainable fisheries management. *Aquaculture International*, **29**(1): 167-192, https://doi.org/10.1007/s10499-020-00617-x.

Xu P, Zhou W G, Xie M J et al. 2022. Temporal and spatial comparison of food web structure in marine pastures in the Pearl River Estuary: implications for sustainable fisheries management. *Ecology and Evolution*, **12**(5): e8903, https://doi.org/10.1002/ece3.8903.

Xu S C, Wang X, Yue S D et al. 2024. Coastal ecological connectivity between seagrass bed and marine ranching 30 km apart: a case study of *Apostichopus japonicus* feeding on seagrass debris in the Bohai Sea, China. *Sustainability*, **16**(7): 2944, https://doi.org/10.3390/su16072944.

Yan Y R, Li Y Y, Yang S Y et al. 2013. Biological characteristics and spatial—temporal distribution of mitre squid, *Uroteuthis chinensis*, in the Beibu Gulf, South China Sea. *Journal of Shellfish Research*, **32**(3): 835-844, 810, https://doi.org/10.2983/035.032.0327.

Yan Y R, Zhang Y Y, Wu G R et al. 2015. Seasonal feeding habits, reproduction, and distribution of *Harpiosquilla harpax* (Stomatopoda: Harpiosquillidae) in the Beibu Gulf, South China Sea. *Journal of Crustacean Biology*, **35**(6): 776-784, https://doi.org/10.1163/1937240X-00002386.

Yang W, Zhang Z Y, Wu Y et al. 2023. Ecosystem-based fishery management that accounts for trade-offs between fishing and enhancement stocking: a case study of Juehua Island in the Bohai Sea. *Ecological Indicators*, **156**: 111081, https://doi.org/10.1016/j.ecolind.2023.111081.

Yuan Y, Feng J, Xian W W et al. 2022. Analysis of the ecosystem characteristics and ecological carrying capacity of the main commercial fish in the artificial reef ecosystem in Laizhou bay using the Ecopath model. *Sustainability*, **14**(21): 13933, https://doi.org/10.3390/su142113933.

Zhang R L, Zhang Q Q, Zhao J M et al. 2022. Using ecopath models to explore differences in ecosystem characteristics between an artificial reef and a nearby natural reef on the coast of the North Yellow Sea, China. *Frontiers in Marine Science*, **9**: 911714, https://doi.org/10.3389/fmars.2022.911714.

Zhang X P, Song H J, Zhuang H F et al. 2023. Calculating the carrying capacity of bivalve mariculture in the Changshan Archipelago (Bohai Strait, China): ecopath modeling perspective. *Journal of Sea Research*, **192**: 102367, https://doi.org/10.1016/j.seares.2023.102367.

Zhao Q S, Huang H M, Zhu Y G et al. 2022. Analysing ecological carrying capacity of bivalve aquaculture within the Yellow River Estuary ecoregion through mass-balance modelling. *Aquaculture Environment Interactions*, **14**: 147-161, https://doi.org/10.3354/aei00430.

Zhou X J, Zhao X, Zhang S Y et al. 2019. Marine ranching construction and management in East China Sea: programs for sustainable fishery and aquaculture. *Water*, **11**(6): 1237, https://doi.org/10.3390/w11061237.

## Electronic supplementary material

Supplementary material (Supplementary Tables S1–S4) is available in the online version of this article at https://doi.org/10.1007/s00343-025-4285-z.