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Article

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Abstract: Aquatic environments are generally heterogeneous in space and time, and the marine organisms have their ways response to those environmental heterogeneities. Cutlassfish (*Trichiurus spp.*) once is one of the "Chinese Four Major Marine Fish Species" along the coast of northwest Pacific Ocean. There are some comments on the cutlassfish (*T. spp.*) name identification. In this study, three cutlassfish species, namely, the largehead hairtail (*T. japonicas*) in East China Sea (ECS), Chinese short-tailed hairtail (*T. brevis*), and South China Sea (SCS) cutlassfish (*T. nanhaiensis*), have been identified in the northwest Pacific Ocean. This work integrated 115 studies in cutlassfish population dynamics from 24 sites across 8 countries in the world. The biomass distribution of *T. japonicas* in the ECS and *T. nanhaiensis* in SCS, was found to be highly correlated with water temperature and salinity. Spatiotemporal heterogeneity of cutlassfish is found to correlate with both genetic and environmental characteristics in the northwest Pacific Ocean (e.g., density dependency, primary productivity and climate ocean oscillation). Closely related species coexisting in the same shelf region (e.g., *T. japonicus* and *T. nanhaiensis* in ESC) often differ in diet and microhabitat. The difference of skull phenology between *T. nanhaiens* and *T. brevis* is found to correlate with species separation and environmental heterogeneity. With the implications for the design of ecological research programs on cutlassfish, our study found that the effect of temporal changes outweighs (to some extent) the effect of spatial changes on cutlassfish in those shelf regions.

Keywords: *Trichiurus spp.;* spatiotemporal heterogeneity; population dynamics; meta-analysis; the northwest Pacific Ocean

1. Introduction

Environments are spatially and temporally heterogeneous, and the marine organisms have their ways response to those environmental heterogeneities [1,2]. Temporal heterogeneity shows as variability over time in the extent and quality of habitat, or ecological disturbance [3]. It is important factor to elicit demographic responses, whereas spatial heterogeneity is often related to habitat patchiness [1,4]. For example, the weaker competitors may find a more favorable site or time to spread under environmental stresses. Spatiotemporal heterogeneity in population abundance had been discussed in many studies [3,5–7]. Studies on the distribution and diversity patterns of species traditionally have relied on small-scale and local processes [8–12]. In this study, we drive a pattern to

quantify the effect in the spatial ecosystem and population dynamics model for cutlassfish (*Trichiuridae. spp.* Linnaeus 1758) species.

Cutlassfish (*T. spp.*) (also often referred to as hairtails) is an economically important marine taxa around the world, especially in the China seas [13,14]. The China seas are including the East China Sea (ECS), the South China Sea (SCS), the Yellow Sea (YS) and the Bohai Sea (BH). The scientific name identification and species distribution of the cutlassfish have been summarized in Table 1 [13,15–19]. Based on the complete mitochondrial genome sequence, the improvement name identification has been suggested, namely, the largehead hairtail (*T. japonicas*) in East China Sea (ECS), Chinese short-tailed hairtail (*T. brevis*), and South China Sea (SCS) cutlassfish (*T. nanhaiensis*). The SCS (in Chinese "nanhai") cutlassfish (*T. nanhaiensis*, [20]), was often called *T. lepturus* in some literatures. There are some comments on this species' name identification. Cutlassfish was reported to thrive in 145 countries (or islands) and is classified as endemic, native, or introduced [13,15,17,21]. Since their similarity in morphology and their overlap in distribution, the samples from the normal surveys were often not identified to the species level. In SCS, *T. nanhaiensis* is mostly commonly observed, with a small fraction of *T. japonicas* and *T. brevis*, whereas in the YS, BH, and southern seas of Japan/East Sea (SOJ), the *T. japonicas* is mostly commonly observed [14]. In the ECS, *T. japonicas* is mostly common, with a small fraction of *T. brevis* and is one of the most economically important fish species in the northwest Pacific Ocean [20,22] (Figure 1). According statistics from Japanese fishery, *T. japonicus* is widely distributed offshore in the Sea of Japan (SOJ) around Kyushu [15]. In the seas of Japan/East Sea, cutlassfish (*T. spp.*) is commonly called ribbon fishes or "tachi-uo" (in Japanese) [17]. *T. japonicas* is a widely distributed coastal species that thrives throughout the tropical and temperate waters of the world between the latitudes 60° *N* and 45° *S*, including all China seas [23]. Coastal China seas are rich with high levels of terrigenous nutrients coming from the Asian continent through river runoff, which has led to high primary productivity and increased fish production [12,24].

Table 1. Summary of the three species groups of cutlassfish (*Trichiurus spp.*) in the northwest Pacific Ocean, including seas in China [i.e., South China Sea (SCS), East China Sea (ECS), Yellow Sea (YS) and Bohai Sea (BH)], and southern Seas of Japan/East Sea.

Valid Name	Scientific name (by Authors)	Distribution	Reference
Trichiurus japonicas	*T. lepturus* (Linnaeus,1758) *T. lepturus japonicas* (Temmick&Schlegel,1844) *T. japonicas* (Temmick&Schlegel,1844) *T. japanicus* (Temmick&Schlegel,1844)	Circumtropical and temperate waters (e.g. ECS, BH, YS, and the Seas of Japan/East Sea)	El-Haweet, 1996 Shih, 2004 Zeng 2005 Liu et al 2009 Jin et al. 2010
Trichiurus brevis	*T. minor* (Wang et al. 1993) *T. brevis* (Wang & You, 1992)	Northwest Pacific (e.g. ECS, SCS)	Wang et al. 1993 Zeng 2005
Trichiurus nanhaiensis	*T. lepturus* (Chakraborty et al. 2006) *T. nanhaiensis* (Wang & Xu, 1992)	West Pacific (northwest SCS)	Wang& Xu, 1992 Kwok & Ni, 2000
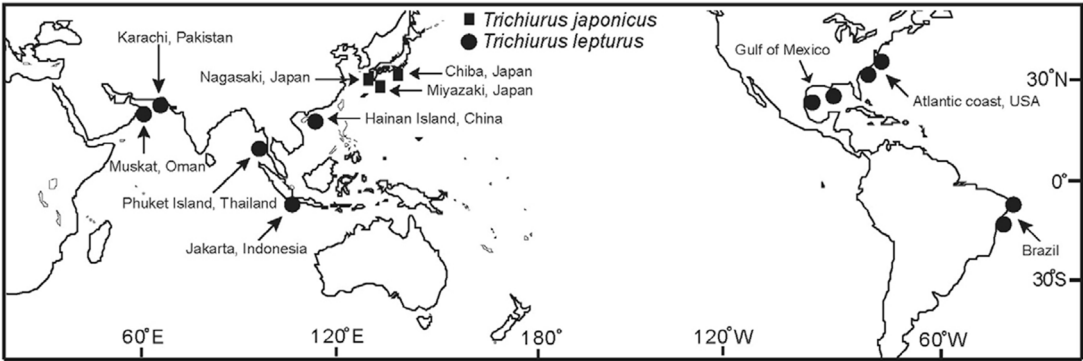
Figure 1. Map indicating fishing locations of *Trichiurus japonicus* (■) and *T. nanhaiensis* (●) in the world. Note that *T. nanhaiensis* (●) (i.e. *T. lepturus*) in South China Sea [SCS].

Previous work on the cutlassfish focused on the growth of individual or reproduction of population [15,16,22]. Cutlassfish are voracious predators and prey on pelagic and benthic species, such as small fish, zooplanktonic and benthic crustaceans, and cephalopods [17,25–27]. The spatial and temporal distribution of fish feeding habits should been changed with the regional and seasonal variations [28]. Comparison of the cutlassfish spatiotemporal heterogeneity in population dynamics and explaining these variations based on the regional oceanographic conditions are largely lacking [29,30]. The seasonal variation was studied in the feeding habits of *T. japonicas* in the ECS [31]. A spatial ecosystem and population dynamics model (SEAPODYM) and metapopulation models were used to address the temporal variation in population growth rates caused by changes in species composition [29,32–34]. SEAPODYM had been used to describe spatial dynamics of many species, such as tuna and tuna-like species [29,30]. Oceans serve as the earth's dominant reservoirs of heat, carbon, and energy, and are in near equilibrium with the atmosphere, lithosphere, and biosphere [27,35]. Meta-analysis is often used as an appropriate method for combining evidence from numerous trials and quantifying homogeneity and heterogeneity among these studies [36–39].

Our study aims to evaluate the dynamic responses of cutlassfish to environmental variation, which will be a challenge because of limited data. More than 100 studies on cutlassfish from 24 sites across 8 countries were compiled in this study, including all China seas and the Sea of Japan. Research history, management foundation and environmental facts will be reviewed in this study, and the meta-analysis method will be used to assess the spatiotemporal features of the population dynamics. The effect of temporal (i.e., maturity age, spawning time, and lifespan) and spatial (i.e., species dispersal distance, longitude, latitude, size, and sea level) factors of the life history of cutlassfish was tested through a meta-analysis of variance. The information will take important implications for the management/conservation of this species in the northwest Pacific Ocean.

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2. Materials and Methods

2.1. Data Collection and Materials

Life history and ecology traits of the *T. japonicas*, *T. nanhaiensis* and *T. brevis* were reported in the published literatures [14,31,40–42]. Biotic factors contain the chlorophyll A concentration (the primary productivity of the ecosystem, available from Ocean Color Web). The fishery data and abundance were extracted from the most recent stock assessment reports. Global climate indices, such as Pacific Decadal Oscillation (PDO), were obtained from National Oceanic and Atmospheric Administration. The natural mortality (*M*), fishing mortality (*F*) and exploitation ratio (*E*) of cutlassfish (*T. spp.*) were obtained from the Chinese-Norwegian "BeiDou" project survey from the bottom trawl fisheries in the China Seas. The growth information of the cutlassfish (*T. spp.*) has been summarized in Table 2. The age–at–maturity of cutlassfish is 1–2 years, and the anal length of species is approximately 50-60 cm [14,22]. The total length of cutlassfish can exceed 200 cm, and it can live for more than 15 years [42]. The catch and effort data of cutlassfish (*T. spp.*) in the China Seas are from the Compilation of the statistics of Chinese fishery (1984-2012) (in Chinese). The variability of the cutlassfish (*T. spp.*) catches and the percentage of the total fish production (from all the seas in China) are from the Compilation of the statistics of Chinese fishery (1950 to 2011).

Table 2. Summary statistics for results of length–weight relationship parameters and growth parameters of the cutlassfish (*Trichiurus spp.*, Linnaeus, 1758).

	Trichiurus japonicas	*Trichiurus nanhaiensis*	*Trichiurus brevis*	**Reference**
East China Sea	κ=(0.27, 0.46) yr^{-1}	κ=(0.17, 0.22) yr^{-1}	κ=(0.11, 0.17) yr^{-1}	Shih et al. 2011
	W_∞=(1911.3, 1950.2)g	W_∞=(2998.8, 3144.4)g	W_∞=(2685.4, 2871.4)g	Lin et al. 2006b
	L_{am}=(43.2, 46.3) cm	L_{am}=(45.7, 54.9) cm	L_{am}=(38.7, 41.6) cm	Tzeng et al. 2007
	PL_∞=(54.1, 85.1)cm	PL_∞=(60.1, 89.1)cm	PL_∞=(42.3, 49.8)cm	-
	t_0=(-1.762, -0.634)	t_0=(-1.762, -0.634)	t_0=(-1.762, -0.634)	Shih et al. 2011
	a=(0.00032, 0.00054)	a=(0.00032, 0.00054)	a=(0.00079, 0.00481)	-
	b=(3.06, 3.22)	b=(3.06, 3.22)	b=(2.92, 3.32)	-
South China Sea		κ=(0.17, 0.22) yr^{-1}	κ=(0.11, 0.17) yr^{-1}	Shih et al. 2011
		W_∞=(2998.8, 3144.4)g	W_∞=(2685.4, 2871.4)g	Kwok & Ni, 2000
		L_{am}=(45.7, 54.9) cm	L_{am}=(38.7, 41.6) cm	-
		PL_∞=(60.1, 89.1)cm	PL_∞=(42.3, 49.8)cm	Shih et al. 2011
		t_0=(-1.762, -0.634)	t_0=(-1.762, -0.634)	-
		a=(0.00032, 0.00054)	a=(0.00079, 0.00481)	Wang et al. 2011a
		b=(3.06, 3.22)	b=(2.92, 3.32)	-
Yellow Sea & Bohai Sea	κ=(0.27, 0.46) yr^{-1}			Shih et al. 2011
	W_∞=(1961.3, 1989.2)g			Lin et al. 2006b
	L_{am}=(43.5, 46.8) cm			Tzeng et al. 2007
	PL_∞=(55.2, 86.9)cm			-
	t_0=(-1.762, -0.634)			Shih et al. 2011
	a=(0.00032, 0.00054)			-
	b=(3.06, 3.22)			-
Sea of Japan	κ=(0.17, 0.22) yr^{-1}			Shih et al. 2011
	W_∞=(1891.6, 1918.5)g			Lin et al. 2006b
	L_{am}=(41.3, 42.6) cm			El-Haweet & Ozawa, 1996
	PL_∞=(50.2, 86.3)cm			-
	t_0=(-1.975, -1.791)			Shih et al. 2011
	a=(0.00032, 0.00054)			-
	b=(3.06, 3.22)			-

Note: *PL* is the preanal length, L_{am} is the length at first maturity, *W* is the whole-body wet weight (*W*), t_0 is the theoretical age at L_t = 0, κ is the growth coefficient, and *a* and *b* are the parameters of the length–weight relationship.

2.2. Modelling Growth Parameters and Population Variability

The dynamic states are based on the production model, which is one of the simplest model-based methods for estimating maximum sustainable yield, such as the Schaefer model (1954) [43]. New simple method (catch-based model) uses catch data plus readily available additional information to approximate maximum sustainable yield with error margins, and this set of viable *r*–*k* combinations can be used to approximate maximum sustainable yield for a given stock [44].

$$r = 0.947 + 1.189k - 0.095\ln(W_\infty) \tag{1}$$

where W_∞ is the von Bertalanffy growth parameter, *k* is the carrying capacity, and *r* is the maximum rate of population increase, and the ranges for the random samples of *r* could be acquired from the resilience assignment in FishBase [44]. Original single-species meta-population model is one of the fundamental ways in which nutrient support is linked to the growth rates of phytoplankton

[29,32,45]. The nutrients across the base of the euphotic layer are thus balanced by the phytoplankton uptake integrated over the euphotic depth, which is given by [12,30],

$$\frac{dp(t)}{dt} = cp(t)(1 - p(t)) - ep(t) \tag{2}$$

$$\langle \omega c' \rangle_{z_{e\mu}} = \int_{z_{eu}}^{0} \langle \mu c \rangle dz \tag{3}$$

where $p(t)$ denotes the proportion of the occupied spatial ecosystem at time t, c is the colonization rate of the empty ecosystem; e is the extinction rate of the occupied ecosystem; μ is an uptake rate for the nutrient (depends on the growth rate of the phytoplankton); $<\omega c'>_{zeu}$ is the vertical supply rate of nutrients; w is the vertical component of the velocity; and z_{eu} denotes the euphotic depth.

2.3. Modelling Feeding and Spawning Migration

Migrations of feeding and spawning are often observed because of their life history and/or prey availability. SEAPODYM that includes feeding habitat index (FHI), spawning habitat index (SHI), and spawning and feeding migration index (SFMI) can be written as,

$$\textbf{(SFMI):} \quad I_a = H_S \frac{1}{1 + e^{\mathrm{K}(G_d - \hat{G}_d)}} + H_{F_A} \frac{1}{1 + e^{\mathrm{K}(\hat{G}_d - G_d)}} \tag{4}$$

$$\textbf{(SHI):} \quad H_S = \Phi_0(t_0) \frac{\Lambda}{\alpha + \Lambda} \tag{5}$$

$$\textbf{(FHI):} \quad H_{F_A} = \sum_n \Phi_{a,n} \Psi_n \frac{F_n}{F_{\max}}, \quad \Psi_n(O_Z) = \frac{1}{1 + e^{\gamma(O_Z - \hat{O})}} \tag{6}$$

where $\Phi_{a,n}$ denotes an accessibility coefficient calculated for each forage (F) component; $\Phi_0(t_o)$ is the spawning temperature index; Ψ_n is the dissolved oxygen content; O_z is the dissolved oxygen concentration in layer z; $\hat{o}$ is the oxygen value for Ψ=0.5; γ is a curvature coefficient. Multiple factors influence the distribution of cutlassfish species distribution. Λ is the ratio between food abundance and predator density; K is a curvature parameter; G_d is the day-length gradient; $\hat{G}$ is the threshold in the day-length gradient at which the switch occurs; and I_a is the fish size at age a.

2.4. Estimating Temporal Heterogeneity and Identifying driving Factors

The temporal heterogeneity of cutlassfish growth is derived from the changes of the marginal growth index (MGI) variability over time; and the average predictive differences (APD) was used to describe how the response variable (e.g., MGI) varies as other potential driving variables change [14,30]:

$$\textbf{(MGI):} \quad H_{MGI} = (\hat{R}_t - \hat{r}_{\max}) / (\hat{r}_{\max} - \hat{r}_{\max - 1}) \tag{7}$$

$$\textbf{(APD}_K\textbf{)} = \frac{1}{n} \sum_{i=1}^{n} [\hat{y}_i | (x_{k,i} = h, x_{(-k),i}, \beta) - \hat{y}_i | (x_{k,i} = l, x_{(-k),i}, \beta)] \tag{8}$$

where $\hat{R}_t$ is the estimated otolith radius (R) at PL_t (preanal length at age t) calculated using equation $\hat{R}_t = 0.652 + 0.009 PL_t$, $(r = 0.905)$, and r_{max} is the estimated size of the outermost annulus [17,37].

2.4. Meta-Analysis

The effect of temporal (i.e. maturity age, spawning time, and lifespan) and spatial (i.e., species dispersal distance, longitude, latitude, size, and sea level) factors of the life history of cutlassfish was tested through a meta-analysis of variance [38,39].

3. Results and Discussion

3.1. Main Marine Ecosystems (i.e. Region 1, Region 2, Region 3 and Region 4)

In the northwest Pacific Ocean, to reveal the regional population dynamics responses of those cutlassfish species to different oceanographic conditions, the data set was divided into different groups corresponding to the four main marine ecosystems (i.e. Region 1, Region 2, Region 3 and Region 4).

3.2. Seas of Japan/East Sea (T. japonicus)

Based on Japanese fishery statistics, *T. japonicus* is widely distributed offshore in the Sea of Japan (SOJ) around Kyushu. The spatial-temporal heterogeneity of cutlassfish was determined from the changes of the MGI variability from April to December in the SOJ. The average predictive difference of MGI for cutlassfish in the SOJ on the variability spatial scale (i.e. distance to land: coastal < 20m, inner shelf 20–80m, outer shelf 80–120m, and Shelf break 120–350m) was compared with temporal changes from April to December (Figure 2). The average annual landing was 225 tons (from 1983 to 1993) with a maximum of 685 tons (1984). The preanal length (PL) of *T. japonicas* ranges from 17.2 cm to 44.7 cm in Kagoshima Bay, southern Japan (Shih, 2004). Previous studies divided the stocks of *T. japonicas* into two or three cohorts in relation to the spawning season in the SOJ, and considered that early sexual maturation would cause the growth rate decrease.
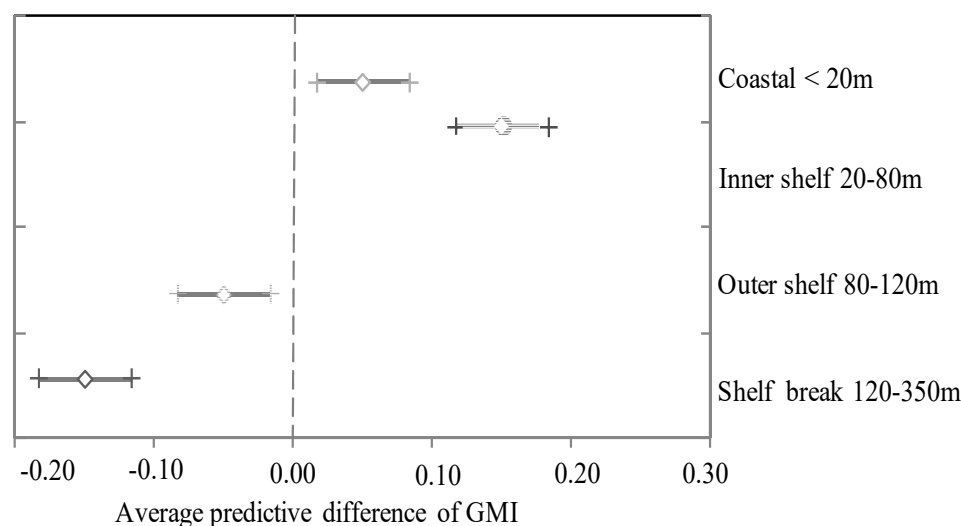
Figure 2. Estimated average predictive difference of marginal growth index (MGI) for cutlassfish (*T. spp.*) in variability spatial scale (i.e. distance to land (km): coastal < 20 nm, inner shelf 20–80 nm, outer shelf 80–120 nm, and shelf break 120–350 nm) in the seas of Japan/East Sea from April to December.

*3.3. Yellow Sea and Bohai Sea (T. japonicas)*

Based on statistics from Chinese fishery (1984–2012), the data set was divided into different groups corresponding to the three main marine ecosystems (i.e. Region 2, Region 3 and Region 4). The YS and BH share a wide and shallow continental shelf with the ECS. In the YS, the first record of fishery of *T. japonicas* was in Zhucheng, Shandong Province, which was established during the Qing Dynasty (A.D. 1644–1912), while other fisheries spun off in other parts of the Shandong Province, such as Laiyang and Muping, during 1950s (the People's Republic of China Period). The *T. japonicus*

catch sharply declined in the BH and YS during the 1960s, which was earlier than the decline in ECS, and was attributed to overfishing. After 1995, *T. japonicus* in this region has been harvested only as bycatch of other target fisheries.

3.4. East China Sea (T. japonicas and T. nanhaiens)

T. japonicas is found throughout Chinese coastal waters whereas *T. nanhaiens* is distributed from the SCS to the southern part of the ECS. Cuttlefish (*Sepia officinalis*), small yellow croaker (*Larimichthys polyactis)*, large yellow croaker (*Pseudosciaena crocea*) and cutlassfish (specially the *T. japonicas*) were once "Chinese Four Major Marine Fish Species" [46]. Currently, the large yellow croaker is already endangered, and although the cutlassfish population has declined significantly, it is still considered as the most caught fish species among the four species [46]. For the *T. japonicas*, the difference of the estimated population sizes between *T. japonicus* (ECS) and *T. japonicus* (YS and BH) reaches an order of magnitude, suggesting that the ECS is approximately 10 times more than conducive for the population growth of *T. japonicus* compared with the other three China Seas. The changes of the catch variability and demographic history of *T. japonicas* in the ESC, BH, and YS have been assessed using the mitochondrial cytochrome *b* sequences. Growth parameters, such as intrinsic growth rate (r), maximum sustainable yield (MSY) and carrying capacity (k), with their relations to catch variability were estimated by the Catch–MSY for *T. japonicas* in the ECS (Figure 3). The response to environmental changes of cutlassfish in the ECS is related to both fishing pressure and climate variability, and the fluctuations in food supply drive recruitment variation in this species [43,47,48]. The versions of SEAPODYM and metapopulation model include the expanded definitions of habitat indices, movements, and natural mortality based on empirical evidences [30]. SEAPODYM showing different biological characteristics of *T. japonicas*, *T. brevis* and *T. nanhaiensis* in ECS is presented to illustrate the capacity of the model to capture many important features of spatial dynamics of cutlassfish. SFMI of *T. japonicas* separated in summer and winter is found to correlate with different sizes (i.e., preanal lengths (mm): 80–200, 201–280, 281–400, and > 400) (Figure 4). Given that population size is closely correlated to primary productivity, the carrying capacities and levels of primary productivity between the ECS and "BH and YS" were comparable. Population size increased with increasing temporal scale and decreased with increasing spatial scale. The population growth rates of *T. japonicas* have declined as human population density increased from 1995 to 2000, which is consistent with density-dependent feedback to survival. Geographical distribution patterns and relationships with temperature, salinity, chlorophyll a, and zooplankton abundance indicated that the *T. japonicas* population in the ECS spawns in the warm Kuroshio Current and in the zone where the warm Kuroshio Current mixed with the ECS shelf water [49,50].
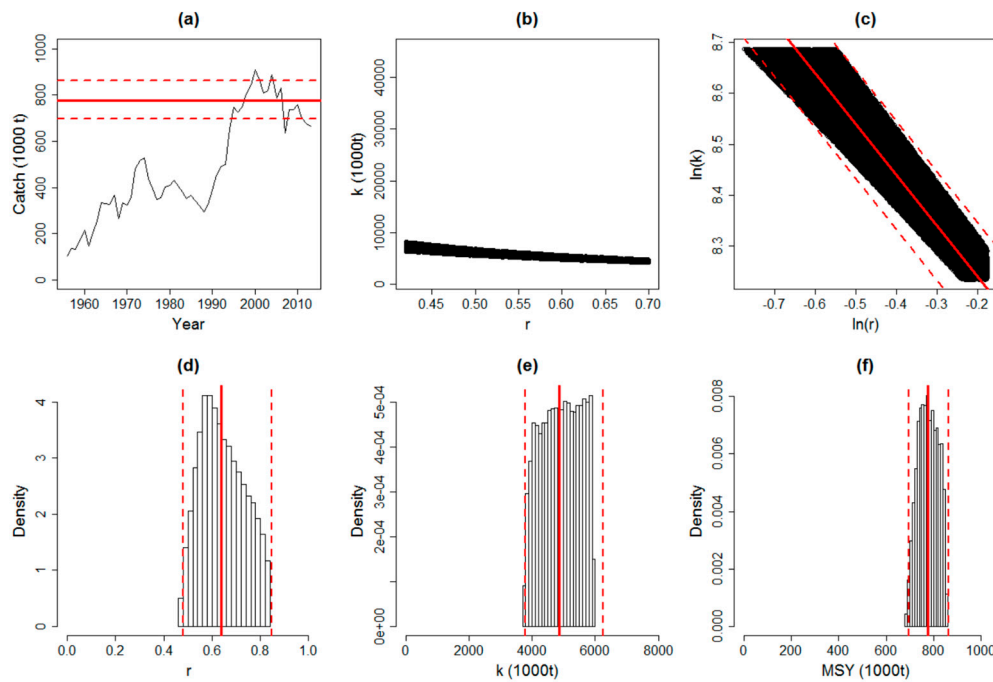
Figure 3. The Catch-MSY model parameters, such as intrinsic growth rate (r), maximum sustainable yield (MSY) and carrying capacity (k), with their relations to catch variability were analyzed for *T. japonicas* in the ECS. (a) The time series of catches with overlaid estimates of MSY (the limits contain about 95% of the estimates). (b) Prior uniform distribution of r–k (the black dots denote the posterior combinations). (c) The relationship between ln(r) and ln(k) with the geometric mean MSY (95% of the estimates). (d–f) Posterior densities of r, k, and MSY (the limits contain about 95% of the estimates).
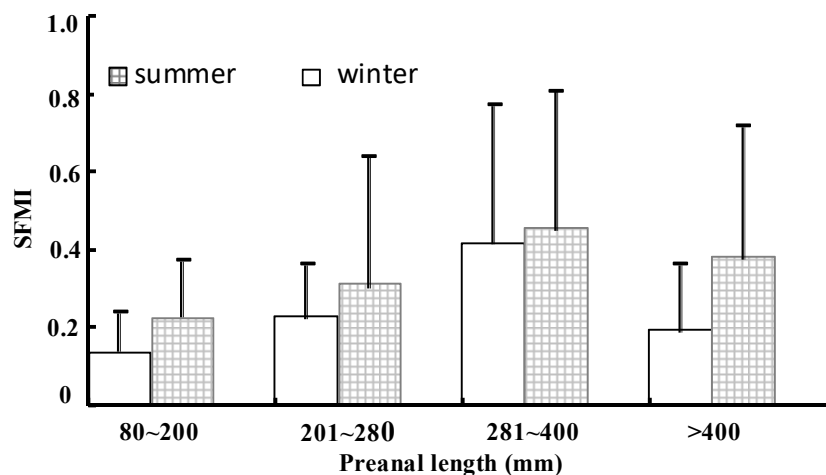
Figure 4. Spawning and feeding migration index (SFMI) for different size classes (i.e. preanal lengths (mm): 80–200, 201–280, 281–400, and > 400) of *T. japonicas* divided according to season (i.e., in summer and winter). Note that the vertical bars denote the standard deviation.

3.5. South China Sea (*T. nanhaiens* and *T. brevis*)

Two species of cutlassfish, *T. nanhaiens* and *T. brevis*, constitute the largest proportion (approximately 80%) of the commercial catches of cutlassfish in the SCS [51]. However, the fishery and population status of cutlassfish stocks in the SCS remain unclear [52]. The two species are partially sympatric in the Beibu Gulf (in the northwest SCS) and has been suggested to be distinguished based on their skull and vertebrae phenotypes (i.e., *T. nanhaiens* has tight frontal bone, whereas *T. brevis* has loose frontal bone) [14]. Main categories of prey groups and regional feeding distributions of the cutlassfish have been summarized in Table 3. Closely related species coexisting

in same shelf region (e.g., *T. japonicus* and *T. nanhaiensis* in ESC) often differ in diet and microhabitat. While the difference of skull phenotypes between *T. nanhaiens* and *T. brevis*, might be influenced by species separation and environmental heterogeneity in the northwest SCS. In coastal waters of Chinese Taiwan, cutlassfish commonly preys on *Benthosema pterotum* and *Acetes intermedius* in the daytime and on *Bregmaceros lanceolatus*, *Benthosema pterotum*, and *Encrasicholina heteroloba* in the nighttime [53].

Table 3. Summary of main categories of prey groups and regional feeding distributions of the cutlassfish (*Trichiurus spp.*, Linnaeus, 1758).

Summary	Regional scales	Feeding area	Prey composition
BH & YS (*T. japonicas*)	35°N-45°N and 117°E-123°E	Few high abundance area (Nowadays only as bycatch)	Fishes(e.g. *engraulis japonicus*, *apogon lineatus*, *T. japonicus*), cephalopod (e.g. *loligo japonica*, *sepiellamaindroni de*), macrura
ECS (*T. japonicas*)	23°N-34°N and 117°E-131°E	30°N-31°N and 123°E-124°E	Pisces (e.g. *T. japonicas*, *decapterus maruadsi*), crustacea (e.g. *mysidacea*, *stomatopoda*, *euphausiacea*) cephalopods (e.g. *abralia multihamata*), urochorda.
SCS (*T. brevis* and *T. nanhaiensis*)	11°N-22°N and 109°E-117°E	22°N-24°N and 109°E-110°E	Fishes (e.g. *Benthosema pterotum*, *Bregmaceros lanceolatus*, *Encrasicholina heteroloba*, *sardinella longiceps*, *decapterus russelli*), crustaceans (e.g. *acetes sp.*, unidentified shrimps), cephalopod (*loligo sp.*)
Through the Korea Strait into the East Japan Sea (*T. japonicas*)	31°N-40°N and 127°E-150°E	35°N-38°N and 128°E-145°E	Fishes(e.g. *T. japonicas*, *engraulis japonicus*, *apogon lineatus*), crustaceans (e.g. Euphausiids, shrimps) cephalopod (e.g. *loligo japonica*, *sepiellamaindroni de*), chaetognaths

3.6. Distributions, Prey Groups, and Spatiotemporal Heterogeneity

In the regions (**1**, **2**, **3**, and **4**), the spatial distribution of the feeding grounds of *T. japonicas*, *T. nanhaiensis* and *T. brevis* are an important factor in determining their prey composition. Regional feeding distributions of *T. japonicas*, *T. nanhaiensis* and *T. brevis* have been summarized in Table 3. Based on the studying the spatial and temporal distribution of fish feeding habits, those species have been shown that their feeding habits are changed with the regional variation, seasonal variations, diurnal variation and ontogenetic. Correlation analysis between cutlassfish catches and environmental factors had implied the spatial heterogeneity in population dynamics (Table 4). The biomass distributions of cutlassfish were found to be correlated with ecological and environmental variations in temperature, salinity, sea level, dissolved oxygen concentration, and primary productions [54]. In the SCS, the tropical cyclones are the major factor affecting fish population, whereas in the ECS, the local runoff and monsoon drive the nutrient distribution directly responsible for the long-term variation of fish population. This study found that the mean sea level trends could be the environmental factor most comprehensively associated with primary productivity distributions (Figure 5).

Table 4. Correlation analysis between environmental factors and catch per unit effort (CPUE) of cutlassfish (*Trichiurus spp.*) in China seas and the distributions of the factors (i.e. depth, temperature, salinity, primary production, and distance to land).

Correlation Analysis	Partial correlation coefficient	Correlation coefficient (R)	P-Significance (2-tailed)
Sea surface temperature (ECS) & CPUE (ECS)	0.52 (3); 0.50 (5)	-0.67	0.01
Summer wind speed (ECS) & CPUE (ECS)	0.46 (0); 0.38 (2)	-0.42	0.02
Winter wind speed (ECS) & CPUE (ECS)	- 0.42 (1); - 0.33 (2)	0.41	0.04
Winter wind speed (YS) & CPUE (ECS)	- 0.44 (3); - 0.50 (4)	0.47	<0.001
Summer wind speed (YS) & CPUE (ECS)	- 0.66 (2); - 0.49 (3)	-0.45	<0.001
Annual precipitation (ECS) & CPUE (ECS)	0.48 (1); 0.56 (2)	-0.37	<0.001
Factors distributions	**Min**	**Pref Min (10th)**	**Pref Max (90th)**	**Max**
Depth (m)	0	100	350	400
Temperature (C°)	8.31	18.45	28.39	29.39
Salinity (psu)	22.7	32.27	35.93	39.36
Primary Production	0	488	1957	4336
Distance to Land (km)	0	10	209	1463
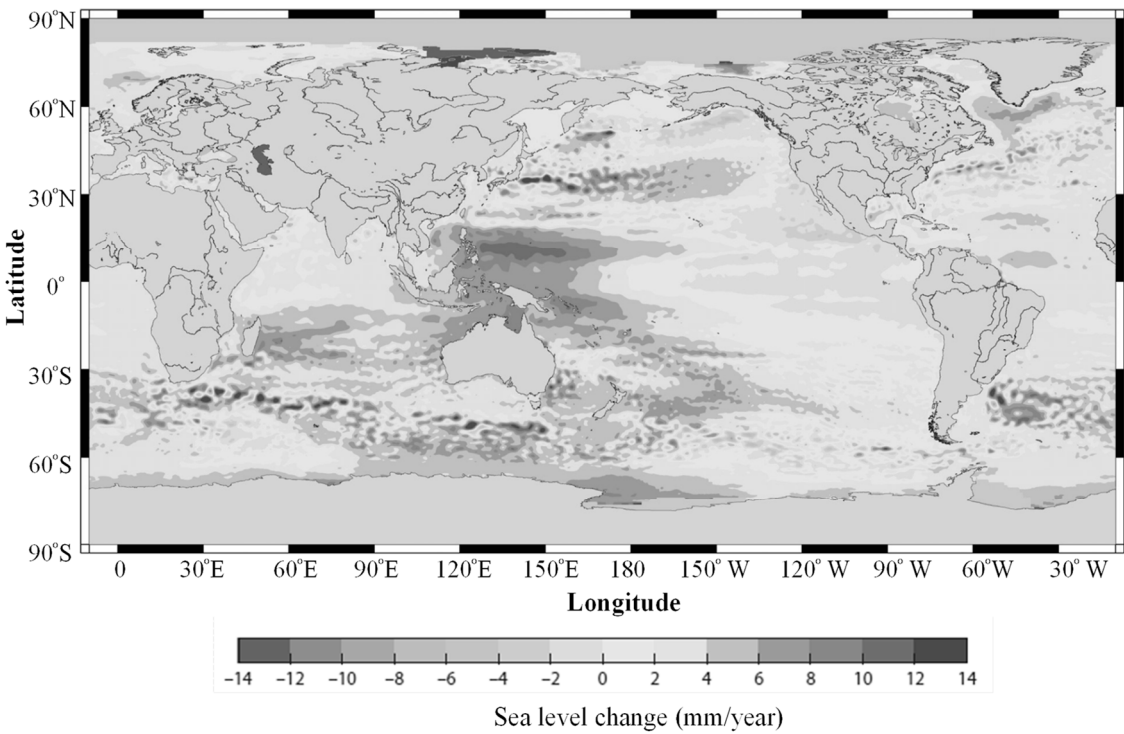
Figure 5. Mean sea level trends determined from altimetry alone from 1993 to 2010. Note that the highest latitudes are not included.

Regions (**1**, **2**, **3**, and **4**) have different fish communities associated with different environmental variables (e.g. temperature, salinity, transparency, and depth) and different abiotic characteristics in the northwest Pacific Ocean [55]. Catches variability and demographic history of cutlassfish (*T. spp.*) have responded the change over time. Effective population size of *T. japonicus*, including geographic groups from ESC, BH and YS the catches variability and demographic history of *T. japonicus* have responded the change over time using the mitochondrial cytochrome *b* sequences (Figure 6). During the Qing Dynasty (A.D. 1644–1912), the coastal regions were closed to fishing because of military

concerns, which possibly explains why the effective population size of *T. japonicas* remained stable during this time [56].
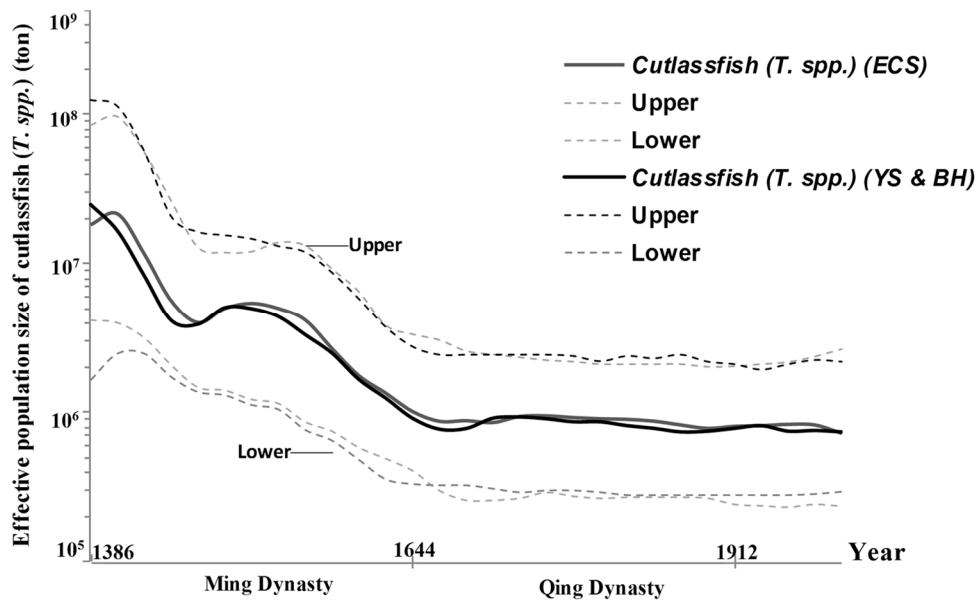

Figure 6. Effective population sizes of cutlassfish (*T. spp.*) of the different geographic groups (e.g. ECS, YS, and BH) using the mitochondrial cytochrome *b* sequences.

Using the SEAPODYM model, the dependency population dynamics of the three cutlassfish species was accounted for from summer to winter and between five spatial scales (i.e., SOJ, ECS, SCS, YS, and BH). Means, 80% confidence intervals of the distributions of water temperature, salinity, depth and distance to land were perfected to the cutlassfish habitation in the northwest Pacific Ocean, including ECS, SCS, YS, BH, and Seas of Japan/East Sea (Figure 7). Data are from FishBase, and separated by season scale (i.e., summer and winter). Water temperatures and salinity strongly influence cutlassfish biology, abundance and habitat, and temporal-spatial distribution.
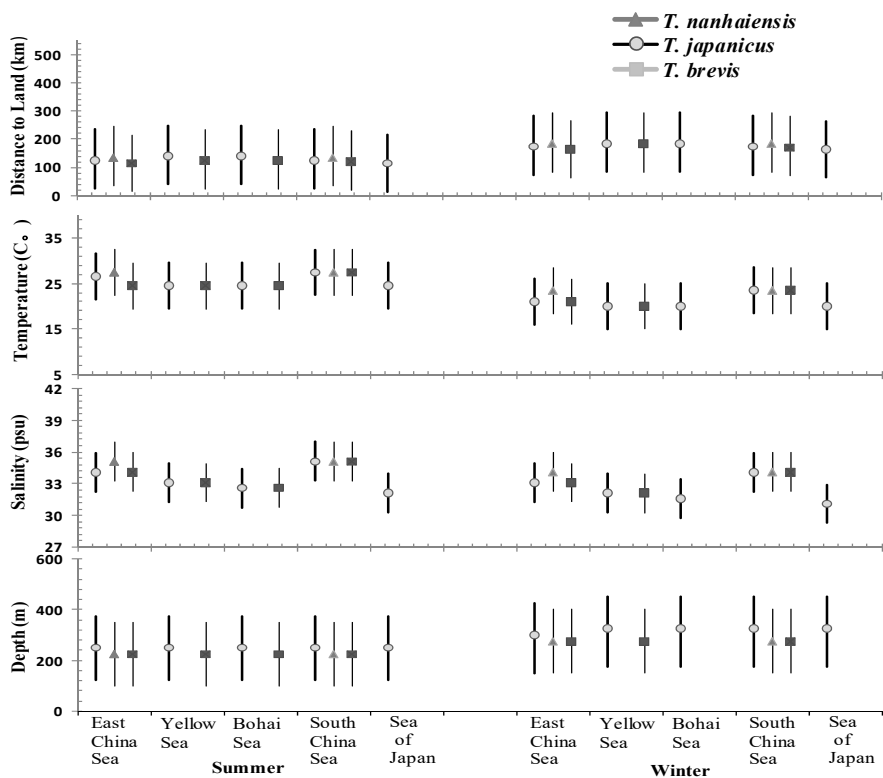
Figure 7. Mean and 80% confidence intervals for the distributions of water temperature, salinity, depth, and distance to land (km) perfected to the cutlassfish (*T. spp.*) in the northwest Pacific Ocean, including ECS, SCS, YS, BH, and seas of Japan/East Sea separated according to summer and winter seasons.

The adult cutlassfish feed on epipelagic (0–100 m) or mesopelagic (100–400 m) organisms in daytime and migrate into the bathypelagic layer (400–1000m) at night [50]. Phytoplanktons affect nutrient uptake in a somewhat non intuitive manner [12]. The observed population dynamics differences among cutlassfish species in the seas along the Chinese coast may reflect the responses of cutlassfish to the differences in the changes of regional primary productivity. Three vertical layers, namely, epipelagic (0–100 m), mesopelagic (100–400m), and bathypelagic (400–1000m), are described in published literature [30,34]. Biomass(gm^{-2}) of epipelagic and mesopelagic mid-trophic functional groups (i.e., prey) in the Pacific Ocean (including Seas in China and Seas of Japan/East Sea) daytime have been illustrated (Figure 8). Approximately two-third of cutlassfish diet are epipelagic group (0–100 m), and migrant mesopelagic groups (e.g. *Decapterus maruadsi*), which are abundant organisms between sunset and sunrise.
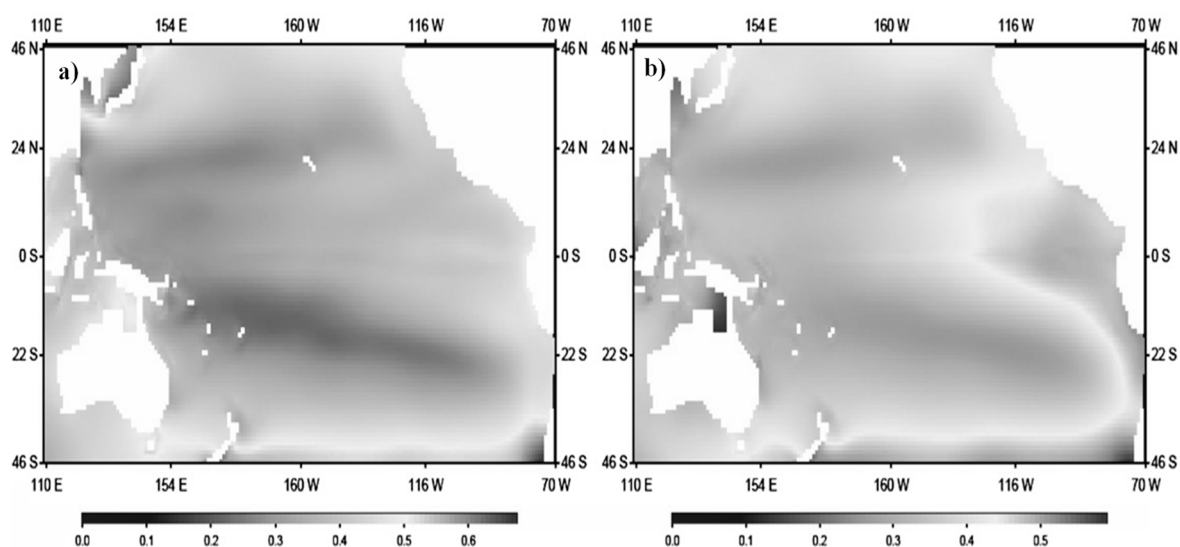
Figure 8. (a) Biomass (g m^{-2}) of epipelagic (0-100 m) mid-trophic functional groups (i.e., prey) in the Pacific Ocean (including Seas in China and Seas of Japan/East Sea) (daytime). (b) Biomass (g m^{-2}) of mesopelagic (100-400 m) mid-trophic functional groups (i.e., prey) in the Pacific Ocean (including Seas in China and Seas of Japan/East Sea) (daytime) (1992–2004).

3.7. Coupling Phytoplankton Production and Physical Transport

Both the anthropogenic and natural causes for the species distribution patterns in the ocean should both be considered [7,57]. The interactions, including mixing, diffusion, and intrusion, in the Yangtze River and Huaihe River produce the complicated hydrographic conditions of the ECS [28,31]. Information on *T. japonicas* in BH and YS, such as spawning and feeding grounds, obtained from the local aquatic archives and history records in the Ming (A.D. 1386–1644) and Qing Dynasties (A.D. 1644–1912) are fully consistent with the modern fishery surveys [56,58]. The variability of the total catches of cutlassfish and the proportion accounted for total fish production in the China Sea (i.e. SCS, ECS, YS, and BH) is a response to changes in sea conditions from 1950 to 2011. SEAPODYM model includes a forage (prey) submodel describing the transfer of energy of stored biomass through functional groups of midtrophic levels and an age-structured population submodel of the predator species and their multifisheries [30]. Nutrients across the base of the euphotic layer are thus balanced by the phytoplankton uptake integrated over the euphotic depth [29,32]. Phytoplankton uptake is one of the fundamental ways in which the physical delivery of nutrients affects linked to the growth

rates of phytoplankton [12]. The existence and stability of equilibriums depend on the extinction threshold condition and metapopulation dynamics [29]. For the *T. japonicas* in the ECS and *T. nanhaiensis* in SCS, the spatiotemporal heterogeneity in population dynamics were found to be correlated with ecological and environmental variations in water temperature, salinity, depth and distance to land, whereas the analysis suggested that water temperature and salinity could be the environmental factor most comprehensively associated with the biomass distributions. Prey and predator dynamics is driven by environmental forces, such as temperature, salinity, dissolved oxygen, and primary production, which can be predicted through coupled physical–biogeochemical models [34].

3.8. Framework of Assessment and Impacts on Ecosystems

Spatial and temporal environmental heterogeneities are known to be important in eliciting on demographic response of species regional environmental conditions [3,59]. An attractive, promising, and frustrating feature of ecology is its conceptual and observational complexity [3,58]. For spatiotemporal heterogeneity, the long-term spatiotemporal variability establishes a regional environmental condition with the complexity and stability [4,59]. Understanding the relationship between an organism and its environment is difficult because all possible environments, which have different scales of heterogeneity, must be studied [3,58]. With the implications for the design of ecological research programs on cutlassfish, our study found that the effect of temporal changes outweighs, to some extent, the effect of spatial changes on cutlassfish in those shelf regions. The situation is much more complex if the goal is to conserve assemblages of species or entire ecosystems [7]. Failure to respond rapidly enough to spatial environmental changes of will result mass extinction of many species. The spawning periods of *T. japonicus* and *T. nanhaiensis* were March to June and April to August [22]. The mature females of cutlassfish are capable of spawning more than once each spawning season. Climate change has substantial ecological impacts on the population dynamics of marine species [60,61]. Correlation analysis between cutlassfish catches and environmental factors had implied the spatial heterogeneity in population dynamics (Table 4). Different anthropogenic and natural causes for the distribution patterns are considered to help understand the impacts of the regional oceanographic conditions on the cutlassfish population dynamics in the northwest Pacific Ocean [62–65]. Using different spatial and temporal scales of observation will enable understanding of many ecological phenomena [66]. The general population size of cutlassfish affected the density to population size growth rate of *T. japonicas* but did not affect the density of *T. nanhaiensis* population [11]. Asides from studying the growth of cutlassfish, our study suggests the population size, survival, and density dependency as considerable factors.

3.9. Heterogeneity and Localization Considered

Regional habitat and associated ecological attributes differ geographically because of biogeoclimatic processes [4,66]. The distribution pattern of three cutlassfish species was closely linked to the different attributes, including hydrographic conditions, primary productivity, climate changes, and physical processes, in local marine ecosystems. Population ecology deals with the dynamics of species populations and their interactions with the environment [67,68]. Geographical distribution patterns and relationships with temperature, salinity, and zooplankton abundance affect cutlassfish population in the Pacific Ocean [34,49,68]. Cutlassfish has the ecological characteristics of wintering, spawning, feeding, and migrating in batches; and the group spaces of *T. brevis*, and *T. nanhaiensis* are overlapping in the SCS. The spatial distribution of *T. japonicus* feeding grounds is an important factor in determining their prey composition [18]. Restoring populations of fish species via reinforcement of existing populations has rarely been included in the ecological study [69]. In marine systems, physical processes not only create structures, but also influence the rates of biological processes in many direct ways, such as shallow mixed layers or fronts within which biological processes may proceed [70]. Climate change is another factor that potentially and drastically impacts the cutlassfish species distribution nowadays [13,70]. Cutlassfish community in the Chinese Taiwan Strait seems to consist of species that have different environmental requirements [18,70]. Some oceanic larvae, such

as *Sigmops gracilis* and *Vinciguerria nimbaria*, may also be carried by the penetrating Kuroshio Branch Current driven by the seasonal monsoon from waters east of Chinese Taiwan into the northern SCS [55,71]. The interactions, including mixing, diffusion, intrusion, of Yangtze River and Huaihe River produce the complicated hydrographic conditions of the ECS, such as water temperatures, salinity, and dissolved oxygen [72,73]. Runoffs provide nutrients to the inshore waters, and monsoons or tropical cyclones control the distribution or availability of nutrients (i.e., the winter monsoon increases primary production, and the summer monsoon reduces availability of nutrients for biological production) in the northern SCS [43]. Environments, or ecosystems, are heterogeneous on many spatial and temporal scales, whereas organisms (e.g., marine species) have scales on which they can respond to environmental heterogeneity [74,75].

4. Conclusions and Recommendations

Spatial and temporal environmental heterogeneity is an important factor that elicits demographic responses of species to regional environmental conditions. The relative effect of temporal scale (i.e., maturity age, spawning time, and lifespan) and spatial scale (i.e., species dispersal distance, longitude, latitude, size, and sea level) on regional population size was tested using meta-analysis in this study, and integrated nested Laplace approximation. Heterogeneity is a part of organization of ecological systems. In this study, spatiotemporal heterogeneity in population dynamics of cutlassfish in the northwest Pacific Ocean has been analyzed in relation to density dependency, primary productivity, and climate ocean oscillation. Fishery sustainability is a process, and further study should compare the effects of Marine Protected Areas (MPA) and the Summer Close Season Management on cutlassfish species. Since 1995, the Chinese government implemented the Summer Close Season Policy, which has effectively protected marine fishery resources to an extent. Before 1995, when Summer Close Season policy is not yet to be implemented, the catch and catch per unit effort (CPUE) changed largely cross years. After 1995, the catch and CPUE were relatively stable. The distribution of marine plankton is influenced by the oceanic physical processes, which not only influence the rates of biological processes in many direct ways, but also create population or stock structures.

Segregation in of the fish species habitat may explain the population dynamics of the species responses to different regional environmental conditions in the northwest Pacific Ocean. Dramatic changes in harvest (or population size) of cutlassfish had been observed in the previous work. Spatiotemporal heterogeneity in their feeding habit (or diet composition) were found to be correlated with regional variation, seasonal variation, diurnal variation and ontogenetic, whereas the analysis suggested that seasonal variation could be the most comprehensively associated with the diet composition. A primary goal of this study is to determine if environments with their intrinsic scales of heterogeneity can be identified. Marine Protected Areas and the Summer Close Season Management provide a geographic framework for predicting recovery from anthropogenic disturbance for fish populations. With the implications for the design of ecological research programs of cutlassfish, this study found that the effect of temporal changes outweighs the effect of spatial changes on cutlassfish in these shelf regions.

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