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ARTICLE

Population Dynamics of Fish Species in a Marine Ecosystem: A Case Study in the Bohai Sea, China

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Abstract

There were rapid shifts of the dominant species in the Bohai Sea from the 1950s to the 1990s, with large-sized, high-valued species (e.g., Small Yellow Croaker *Larimichthys polyactis* and Largehead Hairtail *Trichiurus lepturus*) being replaced by small-sized, low-valued species (e.g., Japanese Anchovy *Engraulis japonicus* and Hairfin Anchovy *Setipinna taty*). From the 1990s to the present, the Small Yellow Croaker and some of the small-sized species (Hairfin Anchovy and Dotted Gizzard Shad *Konosirus punctatus*) have become the dominant species. The food web is now simple, with species from relatively low trophic levels controlling the energy flow within the fishery ecosystem. Along with the shift in community structure, the abundance of dominant species changed, the diversity of fish species and species number density decreased, and interannual and seasonal variations in species number density were found. Fish abundance had a decreasing trend and fish interannual and seasonal

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distribution greatly changed. Variation in the sizes of the ecological niches of the dominant species regulated the succession of the fish community, and the alteration of ecological niches caused changes in the fishery community.

Coastal ecosystems are important spawning grounds, feeding grounds, and nursery grounds for many fish species, and they are important fishing grounds for humans. These ecosystems provide approximately 25% of the global primary productivity, and they support approximately 90% of the global catch (Field et al. 2002). Since the 1950s, more than 90% of the marine fisheries catch in China is captured in its coastal waters (Ministry of Agriculture Bureau of Fisheries 2000–2014). The Bohai Sea is an inland sea of China that was previously known as the "fisheries cradle" of both the Bohai Sea and Yellow Sea. Over the past 30 years, fisheries in the Bohai Sea have greatly declined because of overfishing (Deng and Jin 2001; Jin, 2004; Shan et al. 2012). Additionally, the rapid development of the coastal economy of the Bohai Sea has exposed the coastal environment to multiple stressors, such as large-scale reclamation along its entire coast. By 2020, this reclamation, which is caused by the development of the Caofeidian Industrial District, will reach 310 km^2, directly impacting wetlands, intertidal zones, and the gulf, and causing further loss and fragmentation of essential fish habitat (CCICED 2013). Land-sourced pollution continues to increase; and most of the coastal waters in the Bohai Sea have experienced eutrophication, increased exposure to elevated concentrations of heavy metals, persistent organic pollutants, and other emerging contaminants (Ning et al. 2010; Zhou et al. 2013). There is evidence that these pollutants have caused a substantial decrease in the hatching and survival rates of the fish targeted by fisheries (subsequently referred to as "fishery species"), leading to reductions in their population growth rates and abundance (Cui et al. 2003; Cao et al. 2012). In addition, the decreasing runoff from the Yellow River, Liao River, Hai River, and others rivers, has negatively affected the fish habitat along the Bohai Sea coast, causing changes in water temperature and salinity, and reducing sedimentation (Ding et al. 2013). Furthermore, large-scale mariculture has directly impacted essential fish habitat and the food foundation for some fish species, and it has even led to eutrophication and associated algal blooms (Cui et al. 2003; Zhou et al. 2013). In the Bohai Sea, the changes have increased stress on the coastal ecosystem and have reduced fish yields (Su and Tang 2002; Shan et al. 2013).

Many studies have focused on the fish and fisheries of the Bohai Sea (Zhu and Tang, 2002; Tang et al. 2003; Jin, 2004; Shan et al. 2012; Zhang et al. 2012). In the Bohai Sea, retrospective studies show that the fishery resources have exhibited (1) abrupt shifts in species dominance (Zhu and Tang 2002; Xu and Jin 2005; Shan et al. 2012); (2) decreased species abundance; (3) juvenation of spawning populations; (4) reductions in the size at age in some species (Meng 1998; Guo et al. 2006); and (5) a decrease in both the species diversity and trophic structure (Tang et al. 2003; Zhang and Tang 2004; Jin 2004). In this study, we conducted a retrospective analysis of fish data from surveys in the Bohai Sea to (1) evaluate the temporal population dynamics of fish species; (2) document changes in the fish community; (3) identify shifts in species dominance; and (4) describe changes in the sizes of ecological niches. The results provide scientific information related to the conservation and management of fishery resources in coastal waters.

METHODS

Study area and data source.—The Bohai Sea is a shallow, semi-enclosed sea with an average depth of 18 m. The hydrographic conditions in this area are substantially influenced by river discharges, wind–tide–thermohaline circulation, stratification in the summer, and mixing in the winter (Ning et al. 2010). There are more than ten rivers (the Yellow River, Hai River, etc.) that flow into the Bohai Sea and which bring abundant land-sourced nutrients to support higher primary productivity. The Bohai Sea is presently the main spawning ground for many of the fish species captured by fisheries in the coastal waters of North China, and both the Bohai Sea and Yellow Sea are important nursery grounds for several species targeted by fisheries. At the same time, the coastal regions of the Bohai Sea, which are "hot spots" of economic development in China, have recently caused significant changes in the coastal environment (CCICED 2013).

The Yellow Sea Fisheries Research Institute conducted surveys of the Bohai Sea using a pair of trawlers that ran at approximately 200 horsepower (1 horsepower = 746 W). Spring surveys were conducted in May of 1959, 1982, 1993, 1998, 2004, and 2010. Summer surveys were conducted in June of 1959, 1982, 1992, 1998, and 2010. In 1959, the circumference of the trawl was about 7 m and the headline height was 3 m, but the other parameters of the fishing gear were not recorded; therefore, the fishery data in 1959 was not directly comparable to the recent data but was still included as a reference. In recent years (1982–2010), paired bottom trawl surveys were conducted in the spring and summer. The distance between their wings was 22.6 m, their headline height was between 5 m and 6 m, their cod end mesh size was 2 cm, and their circumference was 30.6 m. The 1982–2010 surveys were conducted on a fixed station grid that measured 0.5°N × 0.5°E and which was comprised

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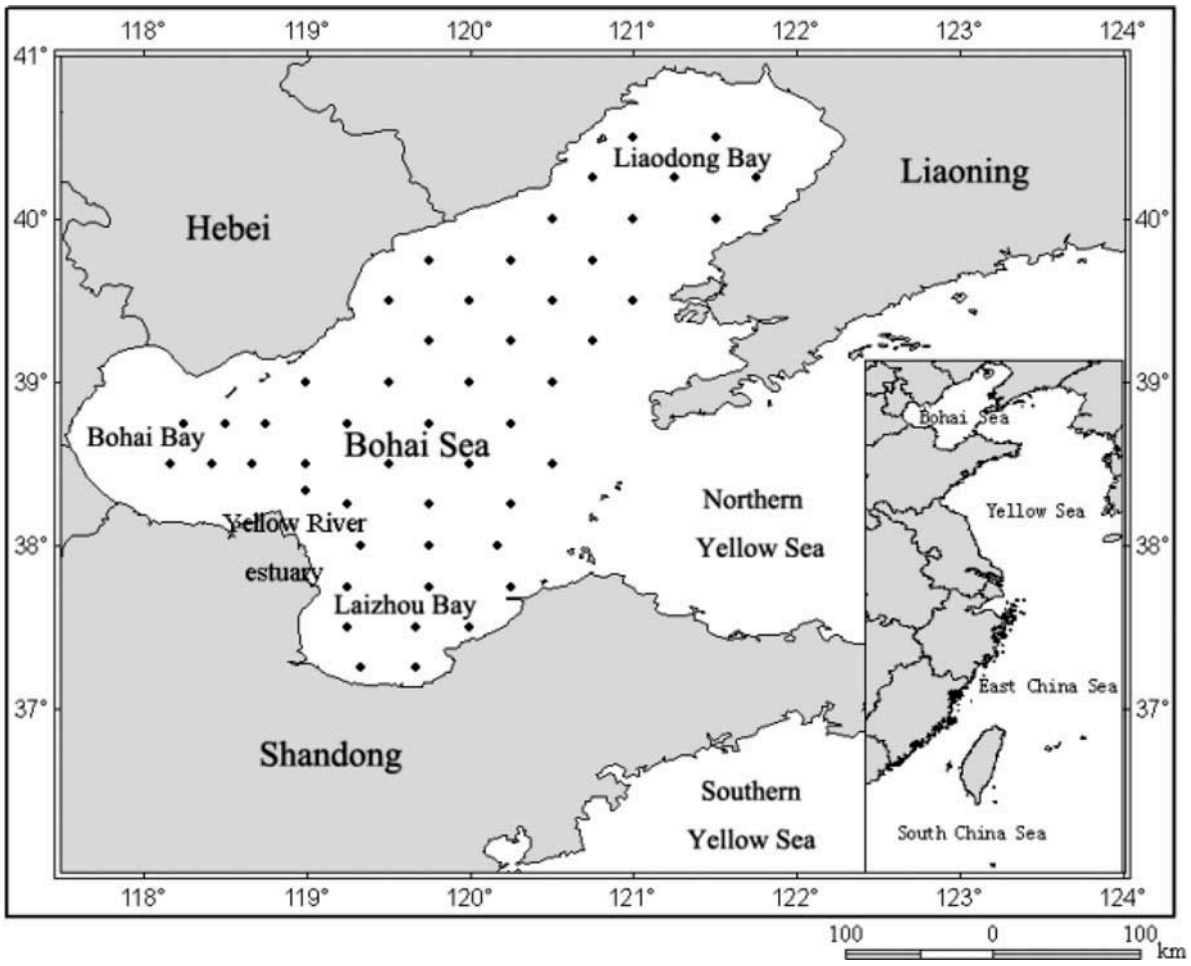


FIGURE 1. Sampling stations in the Bohai Sea, 1959–2010.

of 4–5 stations, with around 50 sampling stations, that covered the entire Bohai Sea (Figure 1). The surveys were performed during the daytime, and the tows were one hour in duration. All specimens were sorted to species level and they only included fish specimens.

For each fish species, its CPUE (kg/hr) was expanded to provide an estimate of mean abundance in a standard survey area (kg/km^2). Although the headline height of the trawls was slightly different during the 1982–2010 surveys, all other parameters were the same. During 1982–2010, the modest changes in the headline height likely did not affect either fish composition or body size because all of the trawls had the same mesh size during the times that the surveys were conducted.

Fish in the Bohai Sea were partitioned into three groups according to their optimal spawning temperature: above 20°C for warmwater species, 12–20°C for warm-temperate species, and 4–12°C for cold-temperate species (Tian et al. 1993).

Diversity indices.—Average abundances (kg/km^2) were used to calculate three diversity indices: Margalef's (D) (Margalef 1958) for species richness, Shannon–Wiener (H') (Shannon and Wiener 1949) for species diversity, and Pielou (J) (Pielou 1975) for species evenness:

$$d = (S - 1)/\ln N$$

$$H' = -\sum_{i=1}^{S} P_i \ln P_i$$

$$J = H'/\ln S$$

where S is the species number, N is the total number of individuals, and P_i is the ratio of species i abundance to the total abundance. Any difference in mean abundance between groups was identified with a t-test.

A dominance curve, which was a plot of the cumulative abundance (divided by abundance) against the species rank, was used to investigate temporal changes in species dominance. This analysis was run in PRIMER for Windows version 5 (Clarke and Warwick 2001).

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Correspondence analysis was used to analyze decadal and seasonal changes in the fish community of the Bohai Sea. This analysis was run with *R* software.

Index of relative importance.—Dominant species were identified with an index of relative importance (IRI; Pianka 1971):

$$\mathrm{IRI} = (N\% + W\%) \cdot F,$$

where $N\%$ and $W\%$ are the ratios of abundance of each fish species relative to the total abundance of captured species, by number (N) and by weight (W); and F is the frequency occurrence of that fish species. A dominant species had an IRI value greater than 1,000, while a common species ranged from 100 to 1000. The important species in a fish community include both the dominant and common ones (Zhu and Tang, 2002).

Ecological niches.—Ecological niches explain the *n*-dimensional space associated with the survival and reproduction of living organisms, and they are widely used to analyze the evolution of species diversity, community structure, and interspecific relationships (Zhu and Tang 2002; Li et al. 2013). For example, temporal ecological niches explain the dominance of species over time; spatial ecological niches explain the dominance of species across space; trophic ecological niches explain the diet composition of species; and individual ecological niches explain the dominance of fish size to the body length spectrum of the fishery ecosystem. Here, the formula applied for an ecological niche analysis followed that of Levins (1968) and Washington (1984):

$$B_i = -\sum_{j=1}^{r} P_{ij} \ln P_{ij}$$

where B_i is an ecological niche and $P_{ij} = n_{ij}/N_{ij}$. For temporal ecological niches, P_{ij} is the ratio of species i in survey j (n_{ij} hereinafter) relative to the total number of fish in survey j (N_{ij} hereinafter), and r is the total number of surveys. For spatial ecological niches, P_{ij} is the ratio of species i at sampling station j relative to the total number of fish at sampling station j, and r is the total number of sampling stations. For trophic ecological niches, P_{ij} is the ratio of the diet of species i consisting of food item type j, and r is the total number of types of food items. For individual ecological niches, P_{ij} is the ratio of all the individuals of species i belonging to body length group j, and r is the total number of body length groups. The differences in the ecological niches of the principal species between years were determined with a *t*-test.

RESULTS

Fish Species Composition

A total of 97 fish species were collected in the Bohai Sea from 1959 to 2010. The samples included both Osteichthyes and Chondrichthyes from 13 orders, 42 families, and 78 genera. The richest species order was the Perciformes, with 35 species, followed by the Pleuronectiformes, Clupeiformes, and Tetraodontiformes. No more than 10 species from other orders was observed. The fish community was composed of warm-water species, warm-temperate species, and cold-temperate species. In the spring, the number of species in each ecotype exhibited a slight increase from 1959 to 1982 and had a decreasing trend since 1982. In the summer, the number of cold-temperate species, warm-temperate species, and warm-water species displayed the same changes, increasing from 1959 to 1982. After 1982, the number of cold-temperate and warm-temperate species decreased until 1998 and then it slightly increased; while the number of warmwater species showed a decreasing trend since 1982 (Figure 2). The Silver Pomfret *Pampus argenteus*, Small Yellow Croaker, and Bartail Flathead *Platycephalus indicus* occurred in all surveys. Four species (Hairfin Anchovy, Dotted Gizzard Shad, Belanger's Croaker *Johnius belangerii*, and Joyner´s Tongue Sole *Areliscus joyneri*) occurred in 90% of all the surveys; three species (White Croaker *Argyrosomus argentatus*, Sappa *Sardinella zunasi*, and Malayan Hairtail *Eupleurogrammus muticus*) occurred in 80% of all the surveys; and species that were observed only one time accounted for 28.9% of the total species number (Tables 1, 2).

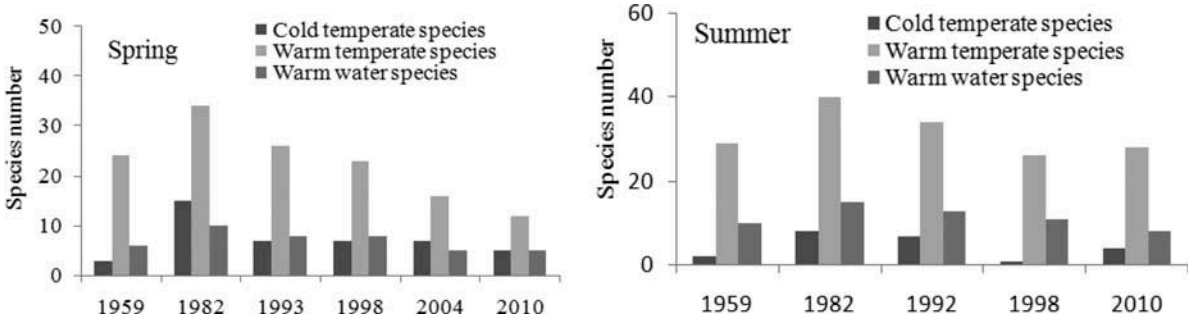


FIGURE 2. Variations in fish species numbers in the Bohai Sea, 1959–2010.

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TABLE 1. Important species and their resource density (kg/km^2)/frequency (%) in the Bohai Sea during the spring, 1959–2010. Abbreviations are as follows: D = dominant species (IRI > 1,000) and C = common species (1,000 > IRI > 100).

	Year					
Species	1959	1982	1993	1998	2004	2010
Trichiurus lepturus[a]	1,209.903/45.3 (D)		0.557/4.5			0.159/2.5
Larimichthys polyactis[b]	1,074.200/84.0 (D)	2.389/59.6	7.168/90.9	0.557/53.3	2.389/51.1 (D)	0.080/1.2
Eupleurogrammus muticus[a]		1.593/68.1	3.186/79.5	1.593/96.7 (C)	0.398/66.7 (C)	0.637/12.5
Raja porosa[b]	135.703/62.7	19.114/57.4 (C)	15.928/61.4 (C)	0.478/6.7		
Konosirus punctatus[a]		3.186/21.3	4.778/54.5			0.637/2.5
Thrissa kammalensis[a]			9.55768.2 (C)	6.371/90.0 (D)	0.398/24.4 (C)	
Nibea albiflora[b]	0.714/5.3	54.951/38.3 (C)		0.080/3.3		
Engraulis japonicus[a]		162.465/66.0 (D)	272.368/81.8 (D)	3.982/60.0 (D)		
Lateolabrax japonicus[b]	25.712/25.3	42.209/42.6 (C)	12.742/18.2			217.416/5.0 (C)
Setipinna taty[a]		219.009/80.6 (D)	15.928/93.2 (C)	4.778/100.0 (D)	3.186/73.3(D)	14.335/30.0(C)
Pampus argenteus[a]	8.571/22.7	3.982/61.7	1.593/68.2	0.796/43.3	0.319/28.9	1.593/40.0
Argyrosomus argentatus[a]	11.428/5.3	0.796/21.3	0.796/45.5	0.040/10.0		
Ctenotrypauchen chinensis[b]						3.186/30.0(C)
Myersina filifer[b]						3.186/35.0(C)
Ammodytes personatus[c]					0.398/31.1	
Pholis fangi[c]		1.593/55.3	0.239/40.9		0.319/60.0(C)	1.593/40.0
Liparis tanakae[c]		0.080/31.9			0.319/51.1(C)	0.159/5.0
Scomberomorus niphonius[a]	0.143/6.7		0.717/6.8	0.159/3.3		
Sphyraena pinguis[b]	0.129/1.3		0.557/11.4			
Collichthys lucidus[b]		0.008/4.3	0.159/9.1			

[a]Warmwater species.

[b]Warm-temperate species.

[c]Cold-temperate species.

TABLE 2. Important species and their resource density (kg/km^2)/frequency (%) in the Bohai Sea during the summer, 1959–2010. See Table 1 for additional details.

	Summer				
Species	1959	1982	1992	1998	2010
Trichiurus lepturus[a]	222.839/83.6 (D)	0.159/10.3	1.593/33.3		0.159/18.8
Larimichthys polyactis[b]	418.538/72.7 (D)	71.676/81.0 (D)	102.735/97.8(D)	0.796/47.7 (C)	2.389/39.6
Eupleurogrammus muticus[a]		3.186/46.6	4.778/84.4	1.593/2.3 (C)	
Raja porosa[b]	29.998/50.9 (C)	17.521/51.7	19.910/42.2		
Okamejei kenojei[b]		3.982/8.6 (C)			
Konosirus punctatus[a]	12.856/40.0	3.186/17.2	81.232/95.6 (D)	0.796/40.9 (D)	445.186/29.2 (D)
Thrissa kammalensis[a]		8.760/25.9	39.023/71.1	2.389/47.7	1.593/33.3
Nibea albiflora[b]	0.857/14.5	1.593/8.6	0.398/24.4	0.072/9.1	
Engraulis japonicus[a]		18.317/51.7 (C)	191.135/75.6 (D)	0.159/15.9	3.186/27.1
Lateolabrax japonicus[b]	12.856/5.5	7.168/15.5	39.820/20.0		2.389/2.1
Setipinna taty[a]	134.275/89.1 (C)	118.663/44.8 (D)	112.292/80.0 (D)	3.982/52.3 (D)	3.982/43.8 (C)
Pampus argenteus[a]	22.855/58.2	16.724/63.4 (C)	2.389/53.3	3.982/56.8 (D)	34.245/50.0 (C)
Argyrosomus argentatus[a]	45.711/41.8 (C)	19.910/81.0 (C)	12.742/88.9	0.398/27.2	
Pholis fangi[c]		0.398/20.7	0.159/28.9		
Liparis tanakae[c]		7.964/20.7	0.159/8.9		0.239/27.1
Scomberomorus niphonius[a]	0.714/9.1	47.784/82.8 (C)	3.186/51.1	12.742/90.9 (C)	8.760/31.3 (C)
Sphyraena pinguis[b]	0.571/9.1	2.389/31.0	18.317/51.1 (C)	0.040/4.6	
Collichthys lucidus[b]			17.521/51.1 (C)		

[a]Warmwater species.

[b]Warm-temperate species.

[c]Cold-temperate species.

Shifts in Dominant Species

In the spring of 1959, the dominant species were the Small Yellow Croaker and Largehead Hairtail, whose cumulative abundance accounted for 85.1% of the total abundance (including fish, crustaceans, and cephalopods). In 1982, the dominant species were the Hairfin Anchovy and Japanese Anchovy *Engraulis japonicas*; and the common species were the Yellow Drum *Nibea albiflora*, Rayfish *Raja porosa*, and Japanese Seaperch *Lateolabrax japonicus*. In 1993, the dominant species was the Japanese Anchovy, accounting for 66.0% of the total fish abundance; and the common species were the Hairfin Anchovy, Rayfish, and Rednose Anchovy *Thrissa kammalensis*. In 1998, the dominant species were the Hairfin Anchovy, Japanese Anchovy, and Rednose Anchovy; the common species was the Malayan Hairtail; and the cumulative abundance of important species accounted for 53.3% of the total fish abundance. In 2004, the dominant species were the Hairfin Anchovy and Small Yellow Croaker; the common species were the Malayan Hairtail, Rednose Anchovy, Fang's Blenny *Pholis fangi*, and Snailfish *Liparis tanakae*; and the cumulative abundance of important species accounted for 57.2% of the total fish abundance. According to the IRI value for dominant species, only common species were found in 2010, which included the Hairfin Anchovy, Japanese Seaperch, the goby *Ctenotrypauchen chinensis*, and Filamentous Shrimpgoby *Myersina filifer* (Table 1). Based on the above results, the dominant species in the Bohai Sea during the spring (excluding Largehead Hairtail and Small Yellow Croaker) were mainly small-sized, pelagic species, such as the Japanese Anchovy, Rednose Anchovy, and Hairfin Anchovy; and the dominance of single species was relatively high (27–78%): Small Yellow Croaker and Largehead Hairtail were dominant in 1959, Japanese Anchovy in 1993, and Japanese Seaperch in 2010 (Figure 3).

In the summer of 1959, the dominant species were the Small Yellow Croaker and Largehead Hairtail; the common species were the White Croaker, Hairfin Anchovy, and Rayfish; and the cumulative abundance of important species accounted for 63.7% of the total fish abundance. In 1982, the dominant species were the Small Yellow Croaker and Hairfin Anchovy; and the common species were the Ocellate Spot Skate *Okamejei kenojei*, Silver Pomfret, White Croaker, Japanese Anchovy, and Japanese Spanish Mackerel *Scomberomorus niphonius*. In 1992, the dominant species were the Japanese Anchovy, Small Yellow Croaker, Dotted Gizzard Shad, and Hairfin Anchovy; the common species were the Red Barracuda *Sphyraena pinguis* and Spinyhead Croaker *Collichthys lucidus*; and the cumulative abundance of important species accounted for 68.4% of the total fish abundance. In 1998, the dominant species were the Hairfin Anchovy, Silver Pomfret, and Dotted Gizzard Shad; the common species were the Small Yellow Croaker, Malayan Hairtail, and Japanese Spanish Mackerel; and the cumulative

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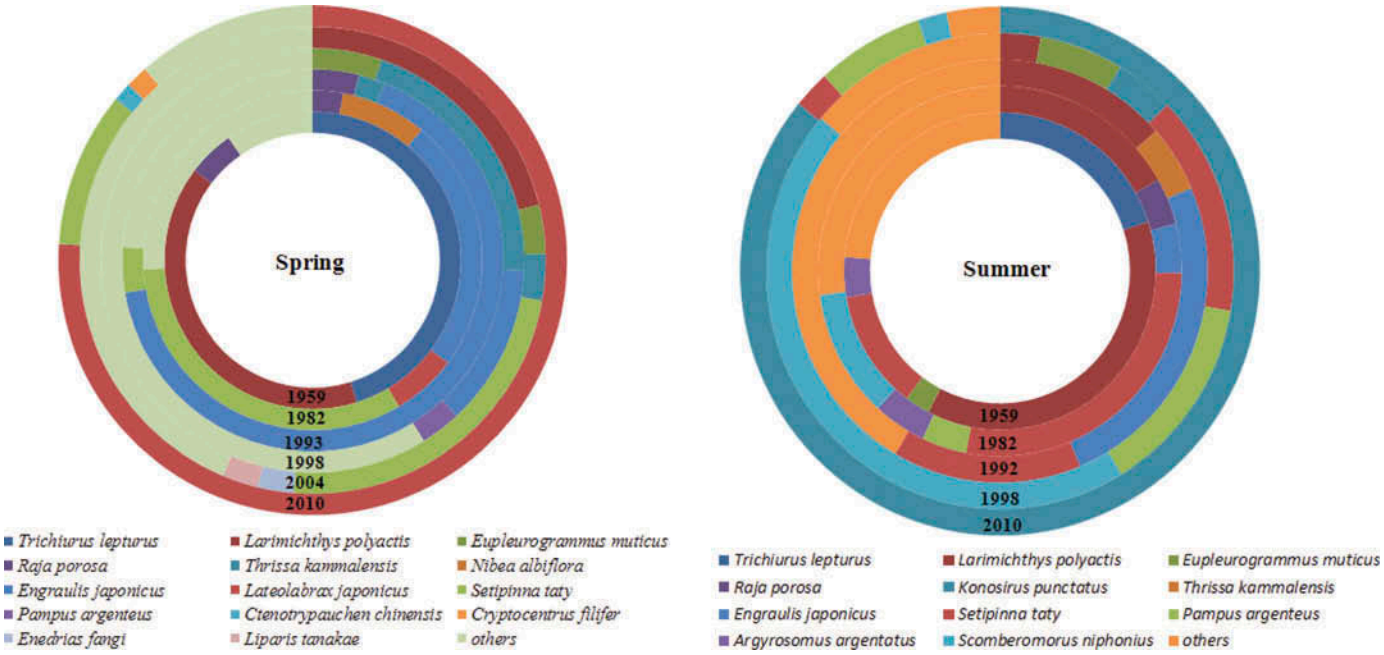


FIGURE 3. Shift in dominant species in the Bohai Sea, 1959–2010.

abundance of the important species accounted for 87.3% of the total fish abundance. In 2010, Dotted Gizzard Shad was the absolutely dominant species; the common species were Silver Pomfret, Hairfin Anchovy, and Japanese Spanish Mackerel; and the cumulative abundance of the dominant species and common species accounted for 87.8% of the total fish abundance (Table 2; Figure 3). The dominant species (excluding Silver Pomfret and Small Yellow Croaker) were mainly composed of small-sized, pelagic species, such as Dotted Gizzard Shad, Hairfin Anchovy, and Japanese Anchovy. The dominance of Dotted Gizzard Shad was highest, and all of the other dominant species showed dominance levels above 25% (Figure 4).

Diversity of the Fish Community

The fish community in the Bohai Sea was divided into three groups according to correspondence analysis: high similarities between the fish communities in May and August of 1959, high similarities in other study years (excluding August, 2010), and high similarities among fish communities in the 1980s and 1990s. The highest seasonal similarities were observed in the spring (May) and summer (August) of the same year for 1959, 1982, and 2010; and high similarities were also observed between adjacent years (e.g. 1992 and 1993). The key species that determined similarities in fish communities were Small Yellow Croaker, Largehead Hairtail, and Silver Pomfret (1959); Branded Goby *Chaeturichthys stigmatias* and Dotted Gizzard Shad (August 2010); Bartail Flathead, Hairfin Anchovy, Dotted Gizzard Shad, Joyner's Tongue Sole, Malayan Hairtail, and Japanese Anchovy, etc. (other years) (Figure 5).

In the springtime months, *D*, *H*′, and *J* showed the same changing trends (increasing from 1959 to 1982, decreasing until 1993, slightly increasing from 1993 to 1998, and decreasing

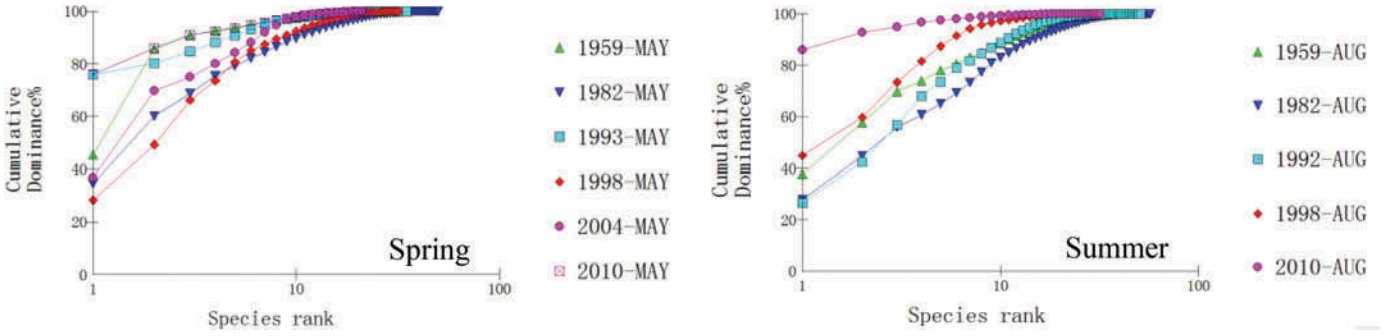


FIGURE 4. Dominance curve of the fish community in the Bohai Sea, 1959–2010.

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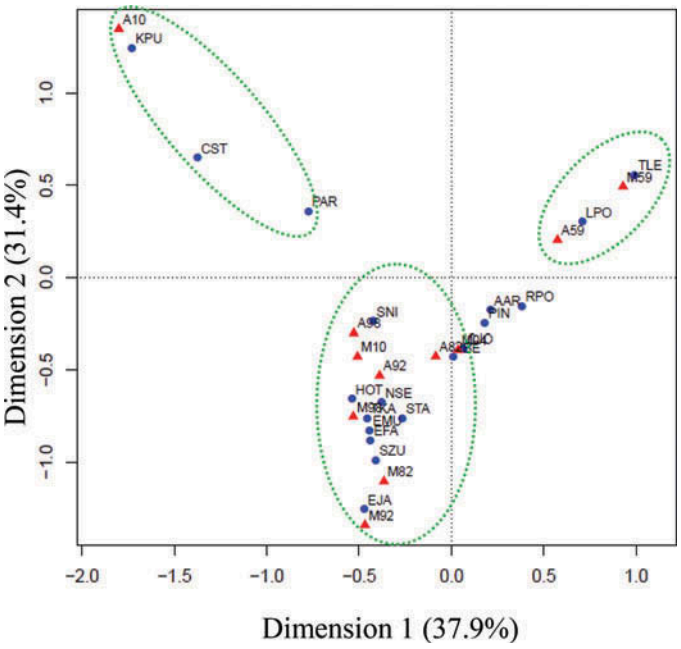


FIGURE 5. Correspondence analysis of the fish community in the Bohai Sea. Blue dots denote species as follows: LPO, *Larimichthys polyactis*; PAR, *Pampus argenteus*; PIN, *Platycephalus indicus*; STA, *Setipinna taty*; KPU, *Konosirus punctatus*; CJO, *Cynoglossus joyneri*; JBE, *Johnius belangerii*; AAR, *Argyrosomus argentatus*; SZU, *Sardinella zunasi*; EMU, *Eupleurogrammus muticus*; EJA, *Engraulis japonicus*; RPO, *Raja porosa*; SNI, *Scomberomorus niphonius*; NSE, *Navodon septentrionalis*; CST, *Chaeturichthys stigmatias*; EFA, *Pholis fangi*; HOT, *Hexagrammos otakii*; TLE, *Trichiurus lepturus*; TKA, *Thrissa kammalensis*. Red triangles denote months and years (e.g., M59 = May 1959, A59 = August 1959, etc.).

since 1998) and H' and D were higher relative to J (Figure 6). Species number density was relatively high and mainly distributed in the central part of the Bohai Sea in 1982, lower and mainly distributed in Bohai Bay and Liaodong Bay in 1993, much lower and mainly distributed in northeastern Laizhou Bay in 1998, and it continued to decrease in Bohai Bay and Liaodong Bay but was relatively stable in Laizhou Bay in 2010 (Figure 7). During the summer months, H', D, and J increased slightly from 1959 to 1982, followed by a decrease since 1982; H' and D had relatively high values (Figure 6). The relatively high species number density was mainly distributed in the central part of the Bohai Sea, Bohai Bay, and Liaodong Bay in 1982; increased and was mainly distributed in the central part of the Bohai Sea and the Liaodong Bay in 1992; greatly decreased and was mainly distributed in the Bohai Bay and Laizhou Bay in 1998; and was high in the central part of the Bohai Sea, Bohai Bay, and Laizhou Bay in 2010 (Figure 7).

Abundance Dynamics of the Different Fish Ecotypes

The warmwater and warm-temperate fish species dominated the Bohai Sea, and the cold-temperate species were a lower proportion of the total catch (Figures 8, 9). In the spring of 1959, the abundance of the warmwater species (1240.6 kg/km^2) approached that of warm-temperate species (1419.9 kg/km^2); the ratio of warmwater species in the total fish catch was lower than 25% after 1959; and the abundance of warmwater and warm-temperate species decreased until 2004, at which time a slight increase occurred from 2004 to 2010 (Figure 8). In 1982, the highest abundance of fish was observed in Laizhou Bay in the spring, with shifts to the central part of the Bohai Sea in the summer. In 1993, dense concentrations of fish were observed farther north in the central part of the Bohai Sea, Liaodong Bay, and the coastal waters of Laizhou Bay. In 1998, the abundance decreased, with the highest abundance mainly distributed in the central part of the Bohai Sea and the mouths of Bohai Bay and Laizhou Bay. In 2010, fish abundance was more evenly distributed in the spring, with higher concentrations of fish in the same area as they were in the summer of 1998 (Figure 10).

During the summer, the abundance of both warmwater and warm-temperate fish species slightly increased from 1959 to 1992, and then decreased from 1992 to 1998, after which they both increased slightly. The warm-temperate species dominated the fishery ecosystem from 1959 to 1998. In 2010, the warmwater species dominated the fish community, mainly due to a

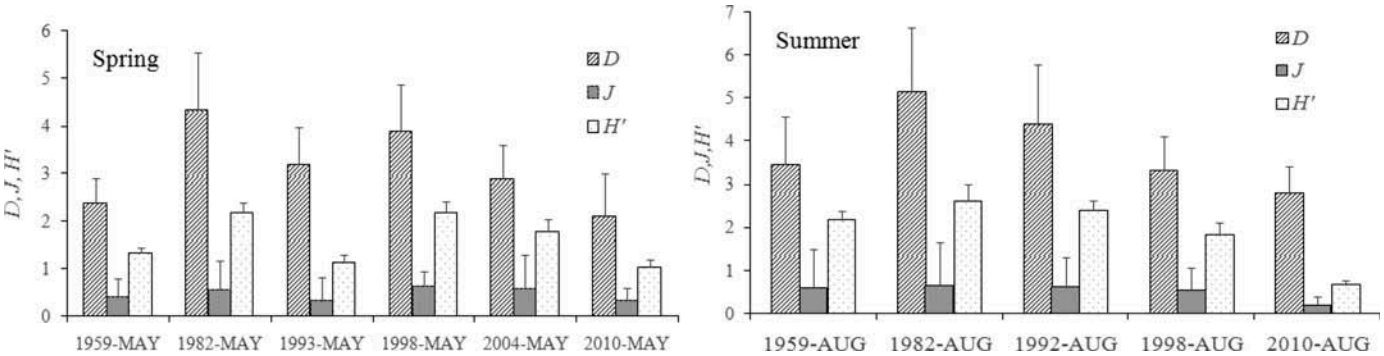


FIGURE 6. Diversity of the fish community in the Bohai Sea, 1959–2010, as indicated by the Margalef (D), Pielou (J), and Shannon–Wiener (H') diversity indices.

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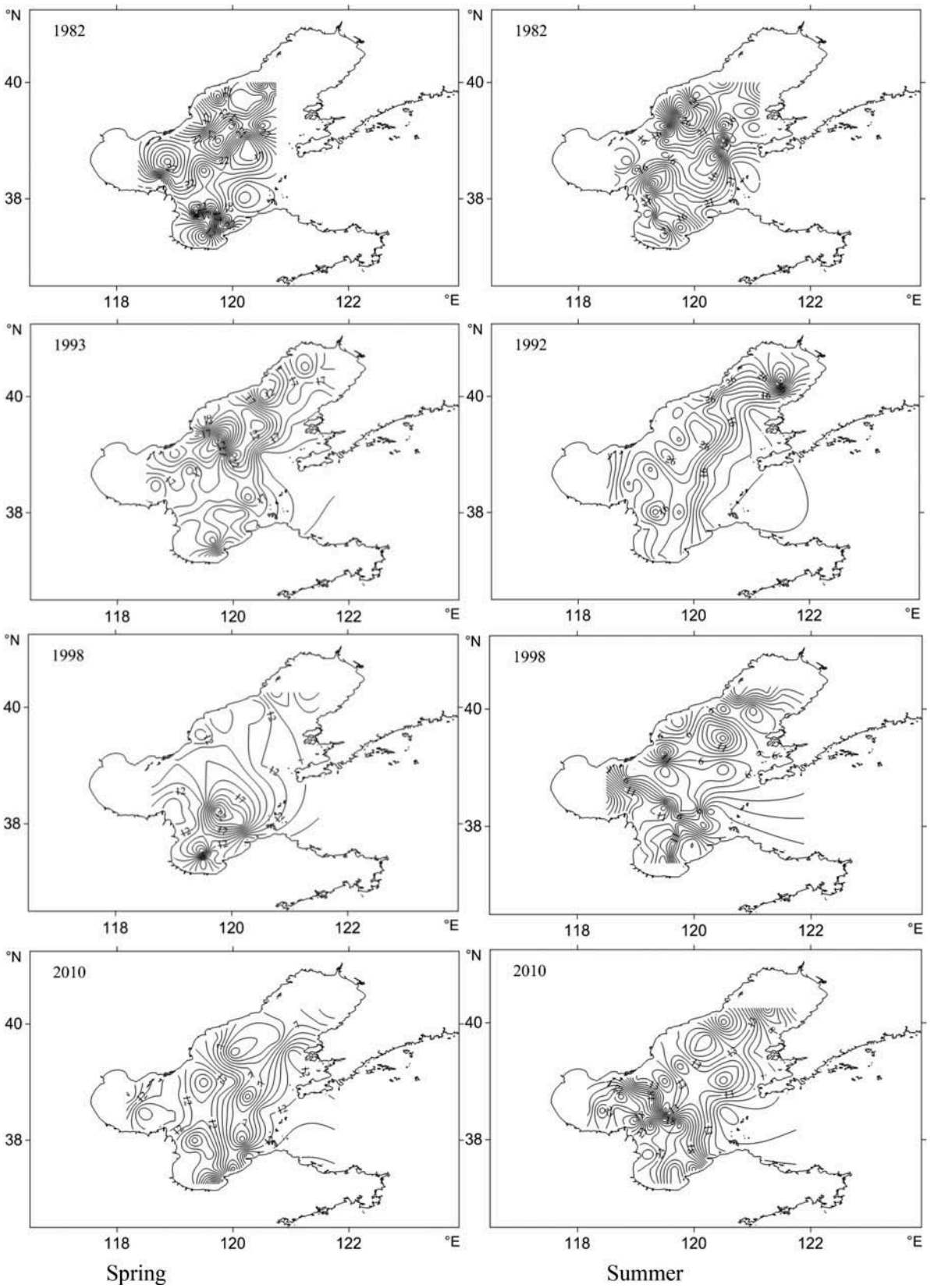


FIGURE 7. Fish species distribution (number of species/km^2) in the Bohai Sea, 1959–2010.

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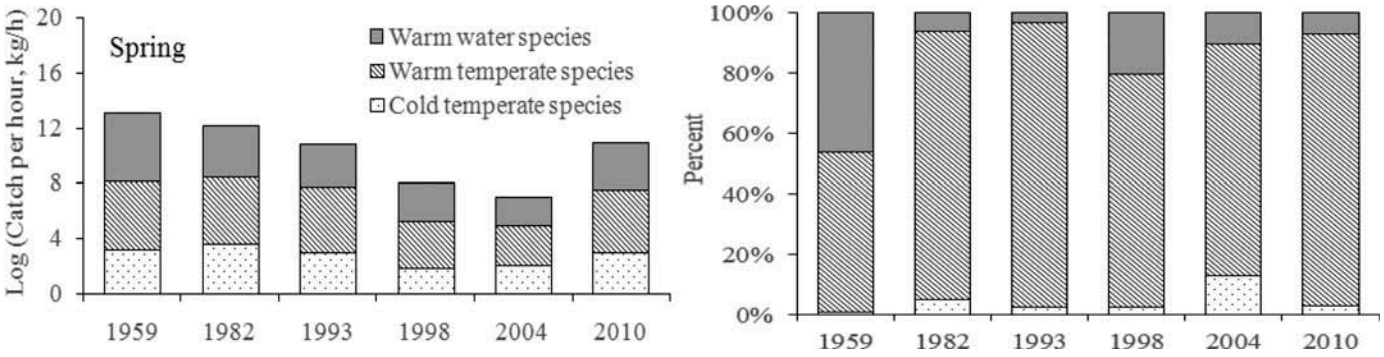


FIGURE 8. Spring CPUEs of the different ecotypes and the proportions of the total catch, in the Bohai Sea, 1959–2010.

significant increase in Dotted Gizzard Shad, which accounted for 85.3% of the total fish catch (Figure 9). In 1982, the higher abundance was mainly distributed in the central part of the Bohai Sea and an estuary of the Yellow River; in 1992, the higher abundance was mainly distributed in the mouths of the Liaodong Bay, but it was lower in other areas; in 1998, the abundance greatly decreased and was higher in the coastal waters of Laizhou Bay; in 2010, the abundance greatly increased and the higher abundance was mainly distributed in the Laizhou Bay and Bohai Bay (Figure 10).

Abundance Dynamics of Important Species

Largehead Hairtail.—During the spring, the abundance of Largehead Hairtail was 1,209.90 kg/km^2 in 1959, accounting for 45% of the total abundance; then it decreased greatly to just 0.56 kg/km^2 in 1993; and no Largehead Hairtail were collected in 1998 and 2004. During summer, Largehead Hairtail abundance was 222.84 kg/km^2 in 1959, accounting for 16.8% of the total fish abundance; and then it decreased greatly to < 1 kg/km^2, accounting for a maximum of 1% of the total fish abundance (Tables 1, 2).

Small Yellow Croaker.—During the spring, the abundance of Small Yellow Croaker decreased from 1,074.20 kg/km^2 in 1959 to 2.39 kg/km^2 in 1982; after which time it stabilized at, or below, 10.0 kg/km^2. The highest proportion of this species in the total abundance was observed in 1959, and the next highest occurred in 2004. During summer, the abundance decreased from 418.54 kg/km^2 in 1959 to 71.68 kg/km^2 in 1982. A slight increase was observed in 1992 (102.73 kg/h), followed by a decreasing trend since 1992. The summer abundance was only 2.39 kg/km^2 in 2010, and the proportion of this species in the total abundance decreased from 31.5% in 1959 to 0.4% in 2010 (Tables 1, 2).

Japanese Anchovy.—During the spring, the abundance of Japanese Anchovy increased greatly from 1959 to 1993, reaching 272.37 kg/km^2; it decreased in 1998 to below 10 kg/h; and no Japanese Anchovy samples were collected in 2010. The proportion of this species in the total fish abundance showed a changing pattern similar to the abundance pattern described above. During the summer, the abundance exhibited the same trend as it did in the spring, increasing greatly from 1959 to 1992 (reaching 191.14 kg/km^2), and then it decreased. The abundance has been less than 5 kg/km^2 since 1998, and it was only 0.80 kg/km^2 in 1998 (Tables 1, 2).

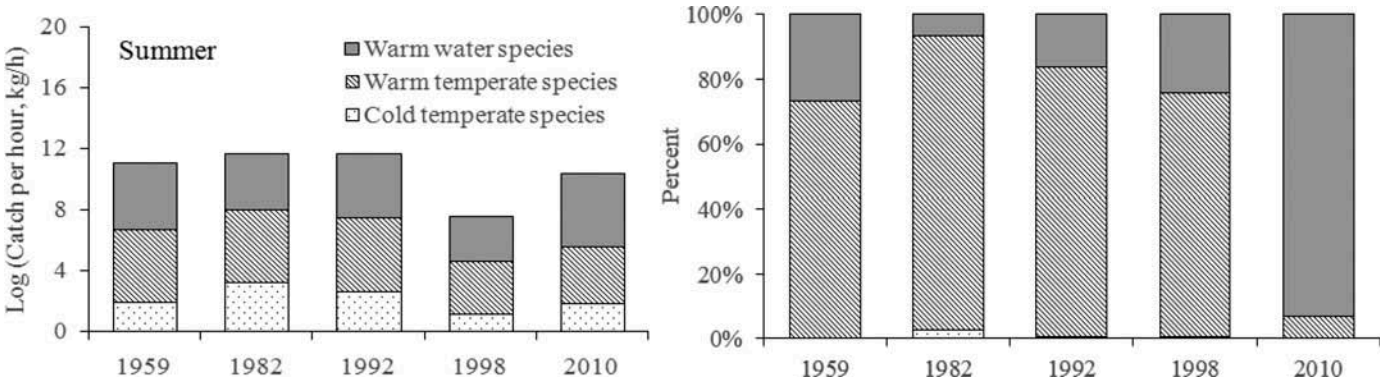


FIGURE 9. Summer CPUEs of the different ecotypes and the proportions of the total catch, in the Bohai Sea, 1959–2010.

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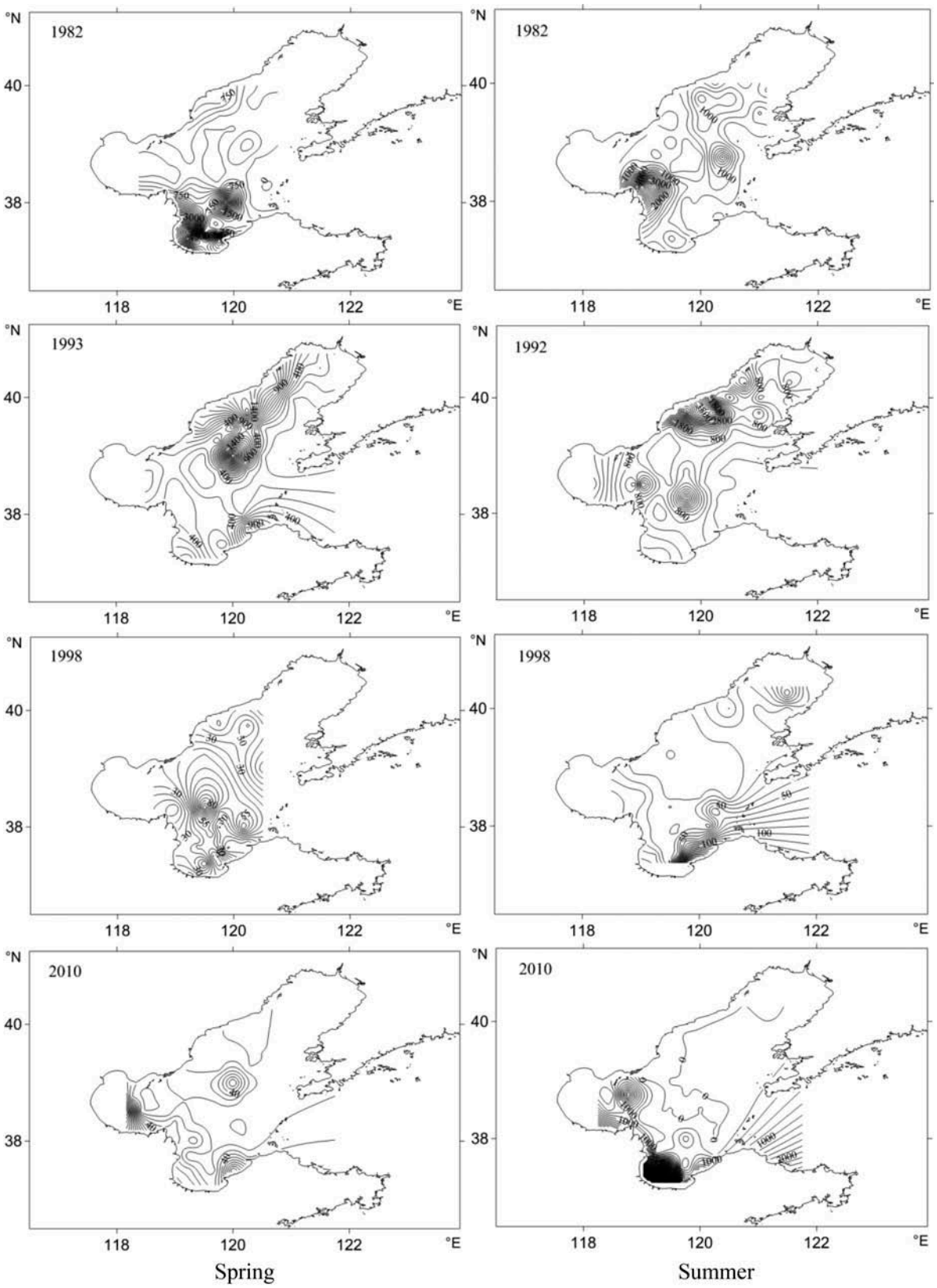


FIGURE 10. Resource density distribution (kg/km^2) in the Bohai Sea, 1959–2010.

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Hairfin Anchovy.—From 1959 to 1982, the abundance of Hairfin Anchovy increased, reaching 219.01 kg/km^2 in the spring of 1982. Since that time, this species has decreased greatly. A similar changing pattern was found for the proportion of this species in the total fish abundance. During the summer, the abundance decreased from 134.28 kg/km^2 in 1959 to 118.66 kg/km^2 in 1982, it remained stable from 1982 until 1992, and then it decreased. Hairfin Anchovy abundance was 3.98 kg/km^2 in 2010, and its proportion in the total fish abundance increased at first and then decreased in that same year (Tables 1, 2).

Silver Pomfret.—The abundance of Silver Pomfret in the spring decreased consistently, from 8.57 kg/km^2 in 1959 to 0.32 kg/km^2 in 2004, and then it increased to 1.593 kg/km^2. Silver Pomfret proportion in the total fish abundance reached its highest value of 5% in 2010. During the summer, its abundance showed a slight increase from 1959 to 1982, and then it decreased greatly until 1992, at which time it showed an increasing trend. Silver Pomfret abundance reached 34.25 kg/km^2 in 2010; however, its proportion in the total abundance was at its highest in 1998, yet only 3.98 kg/km^2 (Tables 1, 2).

Dotted Gizzard Shad.—During the spring, the abundance of Dotted Gizzard Shad increased from 1959 to 1993, and then it decreased, maintaining a relatively low level until the present. The proportion of this species in the total abundance increased greatly from 1959 to 1998, followed by a decreasing trend since 1998. During the summer, Dotted Gizzard Shad abundance increased from 12.86 kg/km^2 in 1959 to 81.23 kg/km^2 in 1992, after which time it decreased until 1998, reaching its highest value of 445.186 kg/km^2 in 2010. Its proportion in the total fish abundance showed an overall increasing trend (Tables 1, 2).

Japanese Spanish Mackerel.—The abundance of Japanese Spanish Mackerel in the spring decreased greatly from 1959 to 1982, and then it increased slightly until 1993, followed by another decrease. During the summer, the abundance increased from 1959 to 1982, and then it decreased (Tables 1, 2).

Rednose Anchovy.—During the spring, Rednose Anchovy was not collected in the surveys between 1959 and 1982. The abundance of this species was 9.56 kg/km^2 in 1993, accounting for 2.26% of the total fish abundance. Since that time, the abundance decreased, and this species was never collected in 2010. During the summer, the abundance showed changing patterns that were similar to the patterns in the spring. No samples were collected in 1959, the abundance increased from 8.76 kg/km^2 in 1982 to 39.02 kg/km^2 in 1992, and then the abundance decreased. The abundance was only 1.54 kg/km^2 in 2010, and this species accounted for 0.23% of the total fish abundance (Tables 1, 2).

Ecological Niches.—The ecological niches of the dominant species in the Bohai Sea, and those species with frequencies of occurrence greater than 80%, were analyzed. For all of the analyzed species, the temporal ecological niches ranged between 0.71 and 1.58, the individual ecological niches ranged between 0.45 and 1.36, the spatial ecological niches ranged between 1.13 and 3.69, and the trophic ecological niches ranged between 1.21 and 2.89. For all species, the values of both the trophic and spatial ecological niches were significantly higher than those of either the individual or temporal ecological niches. Furthermore, the values of the trophic ecological niches were similar to those of the spatial ecological niches, and the values of the temporal ecological niches were similar to those of the individual ecological niches. For most of the analyzed species, the spatial ecological niches were larger than the trophic ecological niches (excluding Large-head Hairtail and Japanese Spanish Mackerel), and the temporal ecological niches were larger than the individual ecological niches (excluding Hairfin Anchovy, Small Yellow Croaker, White Croaker and Rednose Anchovy) (Figure 11).

The top three species with the largest temporal ecological niches were the Silver Pomfret, Bartail Flathead, and Belanger's Croaker. Silver Pomfret, Hairfin Anchovy, and Small Yellow Croaker occupied the top three spatial ecological niches. Belanger's Croaker, Small Yellow Croaker, and Largehead Hairtail had the broadest trophic ecological niches. Small Yellow Croaker, Bartail Flathead, and White Croaker dominated the individual ecological niches. Silver Pomfret was the dominant species within the trophic and individual ecological niches; Bartail Flathead was the dominant species within the temporal and spatial ecological niches; Belanger's Croaker was the dominant species within the temporal and trophic ecological niches; and Small Yellow Croaker was the dominant species within the trophic and individual ecological niches (Figure 11).

DISCUSSION

Species Composition and Dominant Species Shift

The fish community in the Bohai Sea was mainly composed of warmwater and warm-temperate species whose cumulative abundance accounted for more than 95% of the total fish abundance (excluding the spring, of 2004). The warm-temperate species were mainly composed of Small Yellow Croaker, Red Barracuda, the goby *Ctenotrypauchen chinensis*, Yellow Drum, etc.; and their proportions in the total fish abundance increased from 1959 to 1982 and then stabilized around 80%, (excluding the summer of 2010). The warmwater species were mainly composed of Largehead Hairtail, Dotted Gizzard Shad, Rednose Anchovy, Japanese Anchovy, Hairfin Anchovy, Silver Pomfret, etc. In the spring, their proportions in the total fish abundance decreased from 1959 to 1993, increased slightly from 1993 to 1998, and decreased after 1998. In the summer, their proportions in the total fish abundance decreased from 1959 to 1982, increased after 1982, and reached more than 90% in 2010, which greatly attributed to a sharp increase in the proportion of Dotted Gizzard Shad in the total fish abundance (85.3%). In addition, the Bohai Sea is located at a relatively high latitude in China where many cold-temperate species are found. Fifteen cold-temperate species were found,

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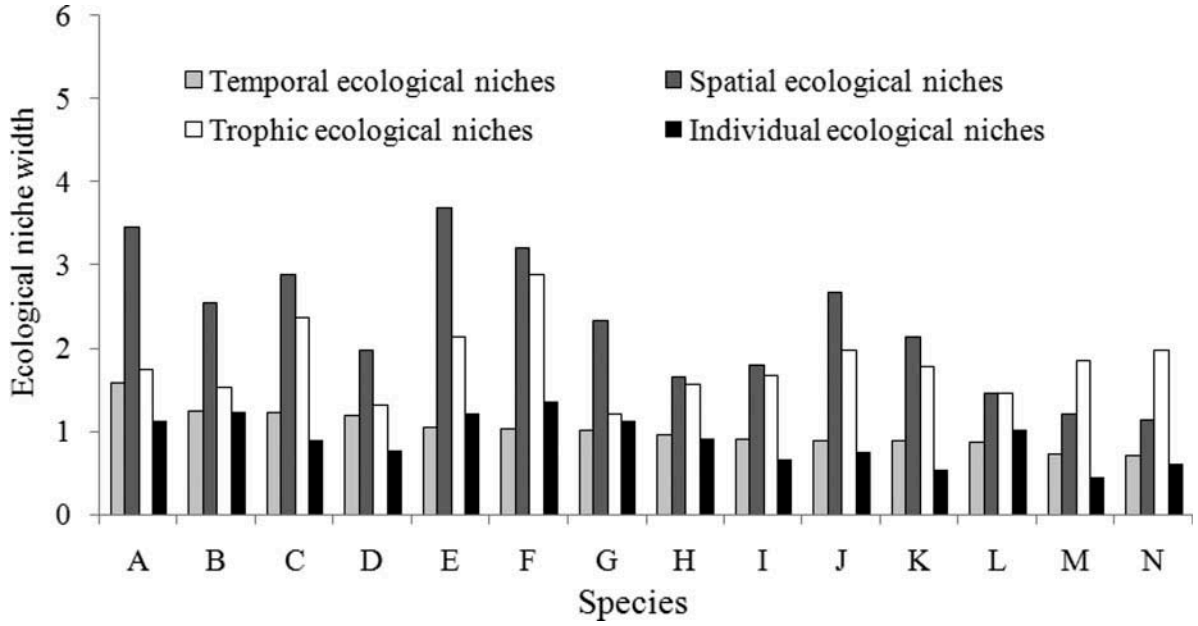


FIGURE 11. Ecological niches of the main fish species in the Bohai Sea (A, *Pampus argenteus*; B, *Platycephalus indicus*; C, *Johnius belangerii*; D, *Sardinella zunasi;* E, *Setipinna taty*; F, *Larimichthys polyactis*; G, *Argyrosomus argentatus*; H, *Konosirus punctatus*; I, *Areliscus joyneri*; J, *Eupleurogrammus muticus*; K, *Engraulis japonicus*; L, *Thrissa kammalensis;* M *Trichiurus lepturus*, N, *Scomberomorus niphonius*).

1959–2010, including Sand Lances (Ammodytidae), Fang's Blenny, and Snailfish, accounting for 15.5% of the total species number but no more than 10% of the total fish abundance (excluding the spring of 2004).

The fish community in the Bohai Sea has significantly changed since the 1950s. Dominant, large-sized, demersal species, such as the Largehead Hairtail, were replaced by small-sized, pelagic fishes, such as the Hairfin Anchovy and Japanese Anchovy, changes which are also supported by an analysis of fish recruitment in the Bohai Sea (Wang et al. 2010). Similar results were found by Tang et al. (2003) and Jin (2004), as well as in the other coastal areas of China (Xu and Jin 2005; Shan et al. 2010; Li et al. 2013).

Some of the apparent changes in species dominance may have been caused by those factors during the early survey that differed from the more current surveys, such as the fishing power of the vessels and the catchability/selectivity of the nets. However, recent surveys indicate that the biomass of the small-sized pelagic species (e.g., Japanese Anchovy) is declining, while the biomass of large-sized, demersal species (e.g., Small Yellow Croaker) is increasing (Tang and Fang 2012; Tang 2014).

There are several explanations for the shifts in fish communities that we observed in this study. The successional characteristics of the fish community, (e.g., spatiotemporal heterogeneity) are consistent with adaptations of fish to their specific environments (Zhu and Tang 2002). Significant changes in the environmental conditions were indeed observed over the study period. Increased temperature, salinity, dissolved inorganic nitrogen, and N/P ratio may influence changes in fish communities (Ning et al. 2010; Jin et al. 2013). Dissolved oxygen, phosphorus, silicon, and the Si/P ratio decreased, which can have direct and/or indirect effects on primary productivity and fish recruitment, further altering community structure (Ning et al. 2010).

The shift in the dominant species of the Bohai Sea has been closely related to the abovementioned variations in the environment as well as to the migration behavior of those fish (Liu, 1990; Zhu and Tang, 2002; Ning et al. 2010). For example, Small Yellow Croaker spawns in coastal waters, then migrates to its feeding and nursery grounds in offshore waters, and finally migrates to its overwintering grounds in deep waters. Since the overwintering grounds of Small Yellow Croaker in both the Bohai Sea and Yellow Sea are located in the central part of the Yellow Sea (Figure 12), climate change, pollution (e.g., red tides, green tides, jellyfish blooms, and oxygen deficiencies that lead to serious eutrophication), and overfishing in the Yellow Sea and East China Sea may directly influence the recruitment and resource dynamics of Small Yellow Croaker in the Bohai Sea (Shui 2003; Xu and Jin 2005; Zhu et al. 2011; Tang 2014). These factors can also cause changes in hydrographic conditions in the Bohai Sea.

The observed shifts in the fish community structure of the Bohai Sea may have also been influenced by its large-scale stock enhancement programs (Jin et al. 2014). However, the abundance of the species used for stock enhancement is far from its highest historical production, and the stocked species

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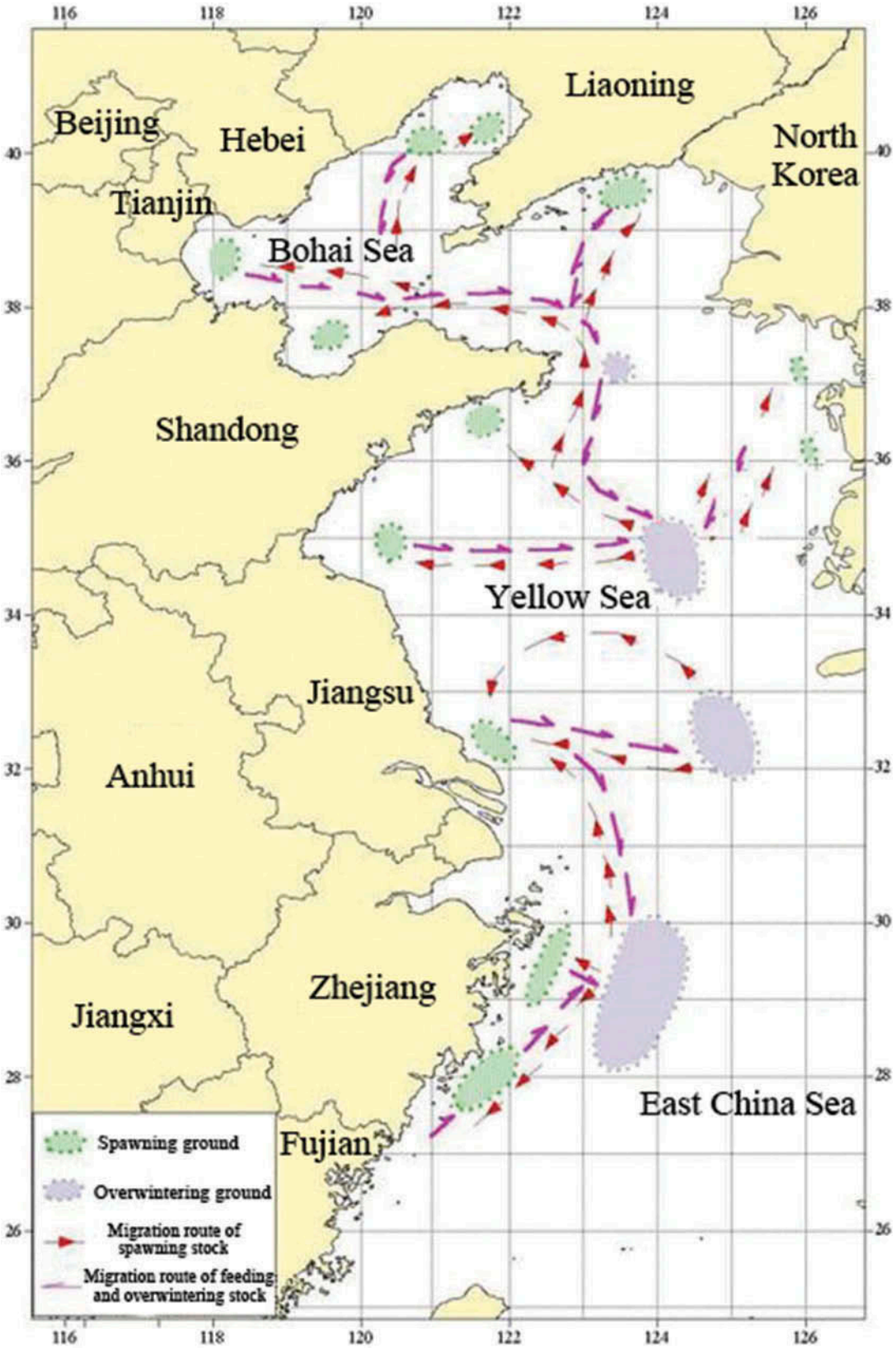


FIGURE 12. Migration routes of the Small Yellow Croaker in the coastal waters of China.

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do not appear to have reached their carrying capacity in the Bohai Sea (Shan et al. 2012). Nonetheless, released species, such as the Olive Flounder *Paralichthys olivaceus* and Japanese Seaperch, are the top predators, and their resources have declined in the fishery ecosystem (Jin et al. 2014). In addition, the sudden introduction of these species to the fishery ecosystem might influence the self-regulation of the fish community (Shan et al. 2012), as supported by observed associations between competition for ecological niches and decreased fish diversity in marine ecosystems that have large-scale stock enhancements (Kitada et al. 2009; Araki and Schmid 2010).

In this study, Hairfin Anchovy, Japanese Anchovy, and Dotted Gizzard Shad were found to be the dominant species since the 1980s. The Hairfin Anchovy showed a relatively consistent abundance during the survey. The Dotted Gizzard Shad alternated with the Hairfin Anchovy and Japanese Anchovy as the dominant species (excluding the summer of 1992): the dominance of the Hairfin Anchovy and Japanese Anchovy was high at the same time that the dominance of Dotted Gizzard Shad was low, and vice versa. According to analyses of stomach contents, the Hairfin Anchovy and Japanese Anchovy mainly fed on zooplankton, but the specific organisms in their diets were different (Liu 1990). For example, the organisms in the diet of the Japanese Anchovy mainly consisted of the North Pacific Krill *Euphausia pacifica*, the copepod *Calanus sinicus*, and the mysid *Acanthomysis longirostris*; while the Hairfin Anchovy mainly fed on *Acanthomysis longirostris, Sagitta crassa*, and the Northern Mauxia Shrimp *Acetes chinensis*; and the Dotted Gizzard Shad mainly fed on the diatoms, *Navicula spp*. and *Nitzschia closterium* (Jin et al. 2014). Tang (2014) hypothesized that the shifts in species dominance may be attributable to either systematic or ecological replacement and that the dynamics of the fish populations in the Bohai Sea have been regulated by these two types of shifts.

Population Characteristics of the Dominant Species

According to our analysis of the ecological niches of the fish species in the Bohai Sea (excluding Bartail Flathead and Malayan Hairtail), a number of the commercial species, such as Small Yellow Croaker, Silver Pomfret, Belanger's Croaker, and White Croaker, occupied wide ecological niches in the fish community of the Bohai Sea during the survey. Other species, such as Japanese Anchovy, Dotted Gizzard Shad, Rednose Anchovy, and Sappa, were found in the narrow ecological niches. These changes are supported by studies on the species that occupy high trophic levels (Zhang and Tang 2004; Jin et al. 2010). For example, the trophic levels of the Japanese Spanish Mackerel and Small Yellow Croaker decreased from 4.9 and 4.1 (1982–1983) to 3.89 and 3.99 (1992–1993), respectively; while the proportion of zooplankton in their diets increased (Zhang and Tang 2004). When the trophic level of the diet species in the dominant species decreased, the trophic level of its landings greatly decreased. In the fishery ecosystem of the Bohai Sea, the trophic level has decreased from 0.16 to 0.19 over a 10 year period (Zhang and Tang, 2004), and the rate of decrease is high relative to observed changes in global landings (0.10 over 10 years) (Pauly et al. 1998). The high rate of decrease in the trophic level of landings might be attributable to the fact that zooplanktivorous species dominated the fish community in the Bohai Sea at that time (Meng 1998).

The above shift in the dominant dietary species is also related to the variations in the sizes of the ecological niches in the Bohai Sea (Jin et al. 2010). For instance, Small Yellow Croaker mainly fed on the Northern Pacific Krill after the large-scale decline of Japanese Anchovy resources at the end of the 1990s (Shan et al. 2011; Shan et al. 2013). Individual ecological niches are important characteristics that influence the function and structure of fish populations, and niche changes are mainly caused by food availability, age structure, and life history strategies (Zhu and Tang 2002). The body lengths of the dominant species (e.g., Small Yellow Croaker, Silver Pomfret, and Japanese Anchovy) showed a decreasing trend, with the distributions of the dominant body lengths becoming more concentrated and shifting from double-peak to single-peak distributions (Shui 2003; Shan et al. 2011). In contrast, the body length of Japanese Spanish Mackerel increased in 2010, which might have been caused by an increase in the biomass of pelagic species, such as Dotted Gizzard Shad. In addition, the sea surface temperature increased from an El Niño event in 2010, which might have caused spawning to occur earlier, and higher growth rates to occur in fish, thus contributing to the relatively large sizes of Japanese Spanish Mackerel observed in 2010. Similar results were also found in Small Yellow Croaker in both the Yellow Sea and Bohai Sea (Li et al. 2011).

Although rapid shifts were observed in the dominant species of the Bohai Sea, the Small Yellow Croaker, Silver Pomfret, and Bartail Flathead were collected in every survey and they maintained a level of consistent abundance. This consistency may have been related to the different life history strategies that were observed relative to the spatial and trophic ecological niches (Zhu and Tang 2002); Small Yellow Croaker is a demersal species, Silver Pomfret is a pelagic species, and Bartail Flathead is a bottom species. These three fish occupy different spatial ecological niches, and they also have different trophic ecological niches as a result of variations in their feeding habits, which greatly decreases the competition that they have for living spaces and food. These results partially explain the observed continuity of fish stocks under multiple stressors; however, methods for maintaining that continuity in the Bohai Sea, under multiple stressors, are not completely clear. In the Yellow Sea, where the same multiple stressors exist, the biomass of some commercial

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species was either relatively stable (e.g., Japanese Spanish Mackerel), recovered (e.g., Small Yellow Croaker), or decreased (e.g., Japanese Anchovy) (Tang 2014).

Dynamics of Fishery Resource Structure

The cumulative abundance of the important species (i.e., the dominant species and the common species) in the Bohai Sea accounted for more than 85% of the total fish abundance and 50% of the total abundance of captured species (including fish, crustaceans and cephalopods; Jin 2004; Shan et al. 2012). The abundance of the main commercial species (e.g., Largehead Hairtail, Silver Pomfret, and Small Yellow Croaker) peaked in 1959, and then it continuously decreased. However, the abundance of the Silver Pomfret showed a slight increase during the summer of 2010. The abundance of the small-sized, low-valued species (e.g., Japanese Anchovy and Hairfin Anchovy) was relatively high in the 1980s and 1990s. In recent years, the abundance and landings of the other small-sized species (excluding the Dotted Gizzard Shad) decreased. The population structure of the Dotted Gizzard Shad in the Bohai Sea and Yellow Sea is currently similar to that observed in the 1980s, and the age structure and growth characteristics of the spawning stock have also been relatively stable (Jin 2004).

For the Bohai Sea fishery, the fish community greatly changed; the abundance of most target species declined; the size of the ecological niches for the species in the landings declined (Figures 11, 13); the landings were mainly composed of either 1-year-old or juvenile

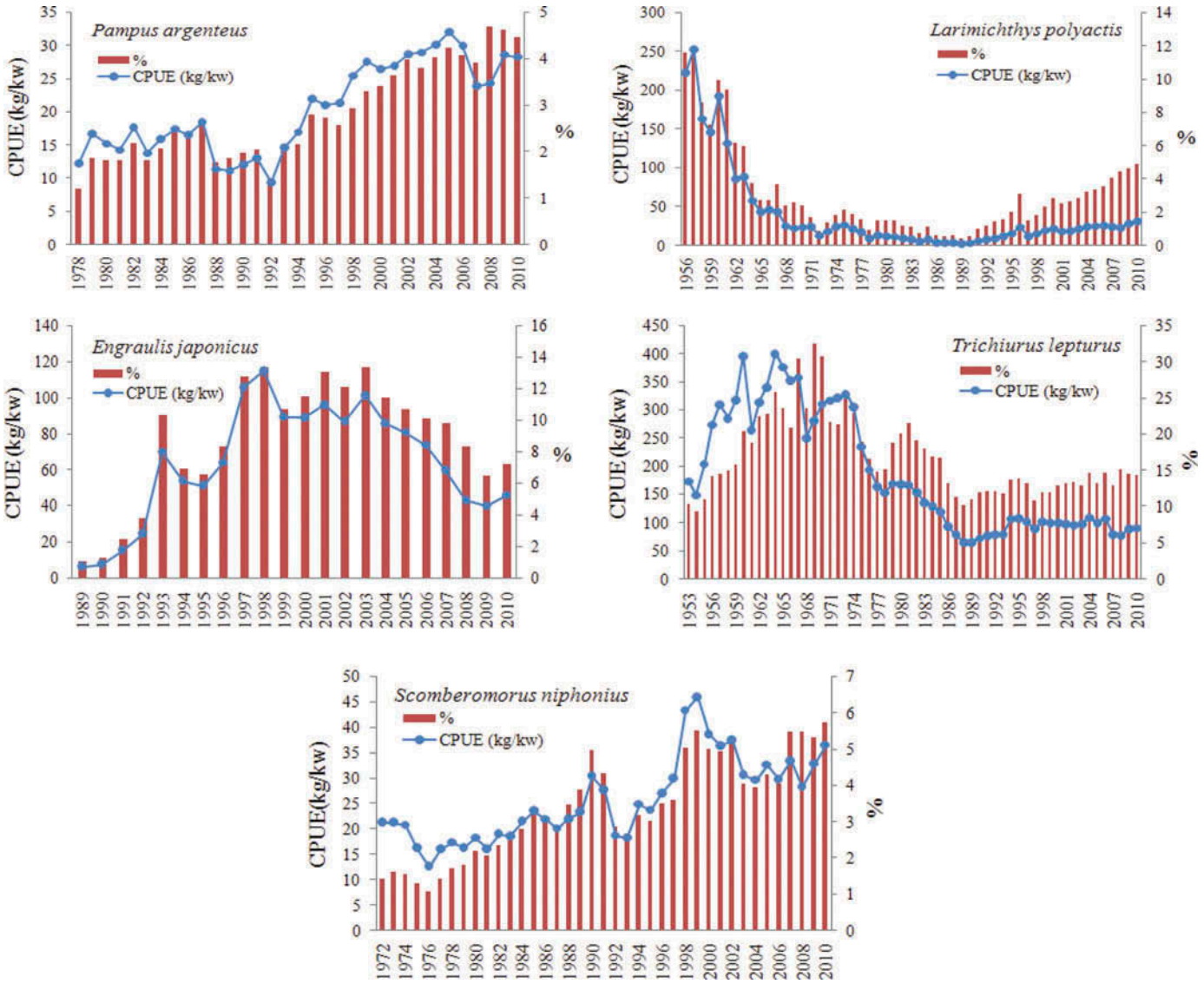


FIGURE 13. The CPUEs of the main commercial fish species and their percent contributions to the total catch.

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commercial species; and small-sized, low-valued species and recruitment populations were the main targets (Jin 2004; Shan et al. 2013; CCICED 2013). These findings are consistent with the hypothesis that, as certain species are fished down, they retreat to their core habitats. The abundance of several small, pelagic fish species in the region has also decreased in recent years, and this decline is often associated with the shrinking distributions of these species (Zhao et al. 2003). Other indicators of overfishing include smaller sizes and earlier maturity in fish species. For example, the body length of Small Yellow Croaker has decreased from 20 cm in the 1970s to approximately 10 cm in recent years (Jin 2004; Zhang and Tang 2004; CCICED 2013). These changes are mainly attributed to the high fishing intensity in the Bohai Sea, where fishing effort has increased 40 times since the 1950s (Shan et al. 2013). In addition, habitat loss due to large-scale reclamation and mariculture in the Bohai Sea has increasingly influenced the dynamics of fishery resources in recent years (CCICED, 2013). Land reclamation, pollution, oil spills, mariculture, and climate change have all had serious negative influences on the natural productivity and ecosystem health of the Bohai Sea, as well as on the self-regulation of fishery resources (CCICED 2013). The kind of control mechanism (e.g., bottom-up, top-down, or wasp-waist) that is regulating the dynamics of the fishery resources in the Bohai Sea, is not known, and it is difficult to directly and clearly explain the observed changes with any established theory (Tang et al. 2003).

Given the current status of the coastal fisheries in China, exploration and implementation management is urgently needed. Two management strategies are currently being used: fishery management techniques (closed season, stock enhancement, etc.) and environmentally friendly aquaculture (e.g., a new production model called integrated multi-trophic aquaculture is very popular in China). In addition, to sustain fishery resources, adaptive management, which is based on the changing biological characteristics, life history, and habitats of fishery species, as well as social and economic factors, needs to be a part of resource conservation programs.

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