

Feeding ecology of Japanese Spanish mackerel (*Scomberomorus niphonius*) along the eastern coastal waters of China

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Abstract

Feeding activities provide necessary nutrition and energy to support the reproduction and development of fish populations. The feeding ecology and dietary plasticity of fish are important factors determining their recruitment and population dynamics. As a top predator, Japanese Spanish mackerel (*Scomberomorus niphonius*) supports one of the most valuable fisheries in China. In this study, the feeding ecology and diet composition of Japanese Spanish mackerel spawning groups were analysed based on samples collected from six spawning grounds along the eastern coastal waters of China during spring (March to May) in 2016 and 2017. Both stomach contents and stable isotope analysis were conducted. Stomach content analysis showed that spawning groups of Japanese Spanish mackerel mainly fed on fish, consuming more than 40 different prey species. Diets were significantly different among sampling locations. The most important prey species were *Stolephorus* in Fuzhou, Japanese anchovy *Engraulis japonicus* in Xiangshan, *Euphausia pacifica* in Lüsi, sand lance *Ammodytes personatus* in Qingdao and Weihai, and *Leptochela gracilis* in Laizhou Bay. Stable isotope analysis showed that the trophic level of Japanese Spanish mackerel was relatively high and generally increased with latitude from south to north. In the 1980s, the diet of Japanese Spanish mackerel was dominated solely by Japanese anchovies in the eastern coastal waters of China. The results in the present study showed that the importance of Japanese anchovies declined considerably, and this fish was not the most dominant diet in most of the investigated waters. Both the spatial variations in diet composition and changes in the dominant diet over the long term indicated the high adaptability of Japanese Spanish mackerel to the environment. Combining the results of stomach analysis and stable isotope analysis from different tissues provided more comprehensive and accurate dietary information on Japanese Spanish mackerel. The study provides essential information about the feeding ecology of Japanese Spanish mackerel and will benefit the management of its populations in the future.

Key words: Japanese Spanish mackerel, spawning groups, dietary plasticity, isotopic niche breadth, feeding strategy

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1 Introduction

Coastal ecosystems are continually impacted by climate change and other social stressors, such as rising and warming seas, intensifying storms and droughts, acidifying oceans, and overfishing (Bunce et al., 2010; Chuenpagdee and Jentoft, 2009; Cinner et al., 2012; Perry et al., 2011; Zou and Wei, 2010). Habitat degradation and fishing exploitation have generated a strong impact on marine fauna in recent decades. Fish communities are also threatened by multiple stressors. Most species change their life history strategies to adapt to different stressors by migrating or changing their feeding strategies.

Profound declines in some populations of traditional Chinese

fishery species (e.g., *Larimichthys crocea*, *Pampus argenteus*, *Sepiella maindroni*) have become apparent owing to long-term disturbances such as intense fishing exploitation, pollution and habitat degradation. In contrast, Japanese Spanish mackerel (*Scomberomorus niphonius*) supported major marine commercial fisheries in China with an annual landing of more than 400 000 tonnes (Zhang et al., 2016). It appears that this fish has a unique capacity for adaptation to the changing environment.

Japanese Spanish mackerel is a migratory, coastal pelagic species widely distributed in the northwestern Pacific (Xing et al., 2009). Matured adults of this species spawn in eastern coastal waters from the East China Sea to the Bohai Sea in spring (Qiu

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and Ye, 1996). It was reported that this species might be composed of three stocks, i.e., the southern stock (in the southern East China Sea), the middle stock (in the middle Yellow Sea) and the northern stock (in the northern Yellow Sea and Bohai Sea) (Wei and Zhou, 1988; Zhang et al., 2016). According to previous studies, Japanese Spanish mackerel demonstrated a strong dietary preference for forage fish, especially for Japanese anchovy (*Engraulis japonicus*) (Deng et al., 1986; Wu, 1987). Heavy exploitation of Japanese anchovies in the East China Sea and Yellow Sea has raised concerns about possible resource depletion and recruitment failure of Japanese Spanish mackerel. In addition, the biological characteristics of the Japanese Spanish mackerel population have been continuously adjusted to adapt to intensive fishing, which was obviously manifested in accelerated growth rate, early sexual maturity and extended spawning period. The minimum fork length at first sexual maturity decreased from (52.9 ± 0.3) cm (before 1962) to (42.4 ± 0.2) cm (1977–1989) and further to (38.0 ± 2.3) cm (after 1997) (Sun, 2009). Previous studies have focused more on the individual growth characteristics of Japanese Spanish mackerel, such as fork length and body weight, and feeding ecology has not yet been reported. However, changes in the characteristics of the population are multifaceted and interactive. It is necessary to determine whether feeding activities have changed and what kinds of changes have occurred in feeding patterns to maintain the population of Japanese Spanish mackerel. Therefore, it is worth exploring the mechanism underlying the ecological aspects of basic feeding that facilitate their capacity to adapt, particularly in terms of trophic ecology for reproduction.

Feeding strategies are the key to understanding the mechanisms driving the survival, growth, and reproduction of fish species (Stearns, 1992). Feeding activities provide nutrition and energy to support the maintenance, growth, reproduction, and development of fish populations (Liu et al., 2009). Among these, reproduction has been identified as the most metabolically demanding process, during which high amounts of nutrients and energy are required for the production of hormones and gametes, development of secondary sexual characteristics and reproductive physiology of fishes (Zudaire et al., 2015). Reproductive output is important for determining recruitment and population dynamics (Stearns, 1992; McGraw and Caswell, 1996; Li et al., 2007). Therefore, information about the feeding ecology of spawning groups is critical for the assessment and management of commercially important fish species (Liu et al., 2009).

The trophic ecology of fishes has traditionally been examined by stomach content analysis (Hyslop, 1980; Cortés, 1999). This methodology is one of the most widely used methods to provide detailed information on diet composition, prey size, consumption rates and foraging habitats of species (Chippis and Garvey, 2007), although it might be biased by opportunistic feeding and different digestion rates of prey (Tsai et al., 2015). In addition, stable isotope analysis is able to track diets over longer time periods (Reum and Essington, 2013). The $\delta^{13}\text{C}$ values remain relatively constant between prey and predators but vary between different primary producers and environments (Tieszen et al., 1983; Peterson and Fry, 1987; Boutton, 1991). Therefore, carbon sources can be used to determine the dietary source of a consumer (Munroe et al., 2014). $\delta^{15}\text{N}$ values can be used to estimate the trophic position of individuals. Tissue isotope values more rapidly reflect a recent diet in the liver (weeks) than in muscle (months) (Logan et al., 2006). Analysis of both tissues can provide more comprehensive dietary information over different timescales, showing the changes in dietary resources, and can be

used to estimate residency in sampling regions (Goñi et al., 2011).

The aim of this study was to examine the trophic ecology of Japanese Spanish mackerel spawning groups along the eastern coastal waters of China based on both stomach content analysis and stable isotope analysis. Specifically, the objectives were (1) to investigate the dietary plasticity of Japanese Spanish mackerel over a long-term period by comparison with historical data, (2) to determine the spatial trophic adaptability of Japanese Spanish mackerel spawning groups from six spawning grounds along the eastern coastal waters of China, and (3) to examine the effects of different methods on the feeding ecology of this species. The study could provide essential information about the trophic ecology and dietary plasticity of Japanese Spanish mackerel and help to manage the population of this species.

2 Materials and methods

2.1 Sample collection

Samples were collected from six spawning grounds of Japanese Spanish mackerel along the eastern coastal waters of China ($25.00^\circ\text{--}38.00^\circ\text{N}$, $118.00^\circ\text{--}124.00^\circ\text{E}$) by commercial fisheries (using gillnets) during spring (March to May) in 2016 and 2017 (Fig. 1). Samples were kept on ice for several hours onboard and then frozen (-20°C) in the laboratory. Each individual was weighed to the nearest gram, and the fork length was measured to the nearest millimetre. Total length, weight, gonad weight and liver weight were also measured (China National Standardization Management Committee, 2007). Samples of liver tissue (approximately 5 g) and dorsal muscle (below the first dorsal fin of fish; approximately 5 g) were collected and stored at -20°C for stable isotope analysis.

2.2 Stomach content analysis

A total of 590 stomachs of Japanese Spanish mackerel were

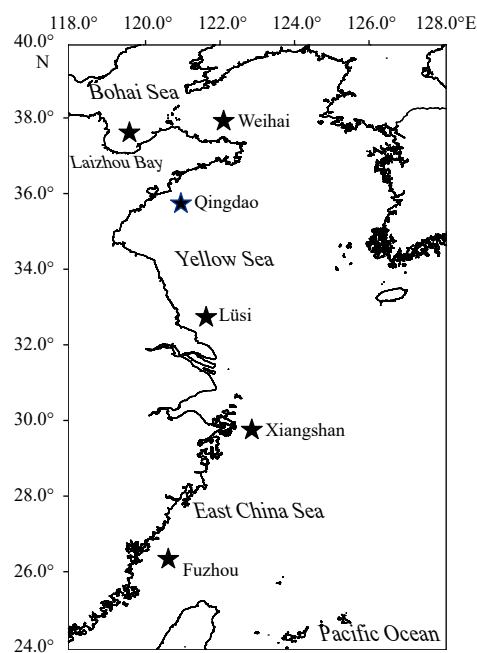


Fig. 1. Sampling locations of Japanese Spanish mackerel from six spawning grounds during spring along the eastern coastal waters of China.

analysed (Table 1). Samples were cleaned thoroughly in distilled water before dissection. Stomach and foreguts of Japanese Spanish mackerel were separated and placed on slides, and all food contents were scraped or squeezed out under a dissecting microscope. Gut contents were then dispersed gently using a dissecting needle with care to avoid damaging food items (China National Standardization Management Committee, 2007). Each prey item was identified as the lowest taxonomic unit. Three indices were calculated, i.e., weight percentage ($W\%$), number percentage ($N\%$), and frequency of occurrence ($F\%$). The index of relative importance (IRI) and percentage IRI (IRI%) were also calculated (Cortés, 1997; Jacob et al., 2005):

$$\text{IRI} = (W\% + N\%) \times F\%, \quad (1)$$

$$\text{IRI}\% = \left[\text{IRI} / \sum (\text{IRI}) \right] \times 100. \quad (2)$$

To examine the ontogenetic variations in the feeding ecology of Japanese Spanish mackerel, individuals were divided into seven fork length classes by 10 cm, i.e., 40–49 cm, 50–59 cm, 60–69 cm, 70–79 cm, 80–89 cm, 90–99 cm and 100–109 cm.

2.3 Stable isotope analysis

A total of 62 samples of white muscle (approximately 5 g) and 30 samples of liver tissue of Japanese Spanish mackerel were collected for stable isotope analysis (Table 1). All 92 samples met three selection criteria: (1) samples were intact; (2) samples covered the range of fork length for each location; and (3) the number of samples was sufficient for statistical analysis ($n \geq 3$). Tissue samples must be acidified to make stable isotope data comparable across taxa with varying CaCO_3 contents (Jacob et al., 2005). Dissected tissues were acidified (3% HCl) to remove residual carbonates, rinsed with distilled water, dried at 60°C for approximately 24 h, and ground into powder. Muscle tissues of potential prey items in sampling locations were treated in the same way.

Stable isotope ratios were expressed in δ notation as deviations from standards in parts per thousand (‰) using the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1\,000, \quad (3)$$

where X is ^{13}C or ^{15}N , R_{sample} is the ratio ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) in samples, and R_{standard} is the ratio in the standard. The standard reference for carbon was Pee Dee Belemnite carbonate, and nitrogen was atmospheric N_2 (Reum and Essington, 2013).

Trophic levels (TL) of Japanese Spanish mackerel and their potential prey items were calculated by the following equation:

$$\text{TL} = \left[\frac{\delta^{15}\text{N}_{\text{sample}} - \delta^{15}\text{N}_{\text{baseline}}}{\text{TEF}} \right] + \text{TL}_{\text{baseline}}, \quad (4)$$

where $\delta^{15}\text{N}_{\text{baseline}}$ and $\text{TL}_{\text{baseline}}$ are the known median $\delta^{15}\text{N}$ value (4.90‰) and trophic level of trophic baseline species (small copepods in this study), respectively (Post, 2002). The trophic enrichment factor (TEF) represents the best estimate of isotopic enrichment between prey and predators. An TEF of 3.4‰ was adopted in this study based on the literature that reported consumer-diet $\delta^{15}\text{N}$ enrichment (Caut et al., 2009).

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of Japanese Spanish mackerel were used to calculate the isotopic niche based on muscle and liver tissue. The isotopic niche was calculated using the SIBER of the SIAR package (Parnell et al., 2010) in RStudio version 1.0.136 as described by Jackson (Jackson et al., 2011). This method uses Bayesian inference techniques to produce (1) the smallest convex hulls that contain all individual $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values within a sample area to represent the total niche breadth area and (2) Bayesian standard ellipses (SEA_b) that incorporate the 90% densest data points within a dataset and thus better represent the “average” isotopic niche breadth of the population (Jackson et al., 2011; Layman et al., 2007; Suca and Llopiz, 2017). This method was chosen because a Bayesian framework for isotopic niche calculations better accounts for sources of uncertainty and variability inherent in stable isotope analysis and allows for more robust comparisons between groups, particularly for small and/or variable sample sizes (Parnell et al., 2010). The relative contributions of all potential prey items to the diet composition of Japanese Spanish mackerel were calculated by a two-source Bayesian mixing model with the SIAR package in RStudio version 1.0.136.

3 Results

3.1 Stomach content analysis

The gonad development stage of all samples of Japanese Spanish mackerel was checked, including all stages I to VI (Table 2). The fork length of samples of Japanese Spanish mackerel ranged from 35.3 cm to 102.5 cm. The minimum 35.3 cm came from a female at gonad development stage IV. The fork lengths of the other samples were all greater than the minimum (35.7 cm) indicated by previous research above, belonging to the mature population. Eighty percent of Japanese Spanish mackerel samples were mature (stage IV–VI).

Among the 590 stomachs of Japanese Spanish mackerel, 63.22% ($n=373$) contained food in their stomachs, and 36.78% ($n=217$) were empty. The empty stomach rates in Xiangshan and Laizhou Bay were much higher than those in the other four locations (67.86% and 68.09%, respectively). A total of 41 prey items were identified, comprising 24 teleost fish species and 17 invertebrate species. Prey items could mainly be classified into three groups, i.e., fish, crustaceans and cephalopods (Table 3). The

Table 1. Sample numbers of Japanese Spanish mackerel collected from six locations for stomach content and stable isotope analysis

Locations	n	Empty-stomach rate	Fork length/cm			Sex		Number for isotopic analysis	
			mean	SD	range	♀	♂	muscle	liver
Fuzhou	83	20.48%	48.26	±4.74	41.5–63.4	59	23	4	3
Xiangshan	112	67.86%	59.65	±7.99	44.2–102.5	10	85	15	6
Lüsi	153	36.60%	48.94	±6.94	40.5–89.5	54	99	11	5
Qingdao	151	19.21%	54.15	±10.92	40.8–90.8	51	100	19	7
Weihai	44	15.91%	54.17	±14.61	35.3–89.6	10	33	8	5
Laizhou Bay	47	68.09%	81.50	±6.68	70.2–101.0	41	6	5	4
Total	590	36.78%	55.20	±12.38	35.3–102.5	225	346	62	30

Table 2. Fork length and body weight of Japanese Spanish mackerel at different gonad development stages collected along the eastern coastal waters of China

Gonad development stage	n	Fork length/cm			Body weight/g		
		mean	SD	range	mean	SD	range
I	21	61.6	11.3	38.8–86.8	806	274	453–1 067
II	59	45.5	2.3	41.5–52.5	783	134	575–1 257
III	38	55.3	7.8	42.3–74.0	1 309	466	629–2 820
IV	71	51.1	9.4	35.3–89.5	1 172	875	371–6 537
V	302	58.8	14.5	40.5–102.5	1 886	1 543	539–10 936
VI	99	51.7	5.5	40.6–70.4	1 078	318	533–2 408

Table 3. Diet composition (IRI%) of Japanese Spanish mackerel in six locations during spring along the coastal waters of China in 2016 and 2017

Prey items	Fuzhou	Xiangshan	Lüsi	Qingdao	Weihai	Laizhou Bay	Total
Pisces							
<i>Engraulis japonicus</i>	1.01	33.55	21.69	0.36	0.97	23.54	6.44
<i>Ammodytes personatus</i>				80.97	91.18	13.22	54.18
<i>Enedrias fangi</i>				0.67	0.09	0.05	0.30
<i>Benthoosema pterotum</i>	0.03		0.09				0.01
<i>Larimichthys polyactis</i>		0.47	0.03				0.01
<i>Liza haematocheila</i>				0.10			0.03
<i>Harpadon nehereus</i>		0.10					-
<i>Champsodon capensis</i>	0.78		0.11				0.10
<i>Gonorynchus abbreviatus</i>	0.02						-
<i>Thryssa mystax</i>	1.29						0.09
<i>Thryssa kammalensis</i>	4.40		4.08				0.89
<i>Callionymus richardsoni</i>				-			-
<i>Coilia mystus</i>	2.20		0.01				0.14
<i>Bregmaceros pescadorus</i>	0.17		0.03				0.02
<i>Synodus macrops</i>	0.04						-
<i>Decapterus maruadsi</i>			0.01				-
<i>Hyporhamphus sajori</i>			2.23				0.08
<i>Liparis</i>			0.56				0.02
<i>Thryssa</i>	0.23	0.47					0.02
<i>Stolephorus</i>	81.52						5.08
<i>Sardinella</i>	0.19			0.05			0.07
<i>Trichiurus</i>	0.01						-
Engraulidae		11.45					0.03
Gobiinae			0.19	0.01			0.02
unidentified pisces	2.83	47.21	1.27	0.04	0.10		1.30
Crustacea							
Euphausiacea							
<i>Euphausia pacifica</i>			48.87				3.00
Decapoda							
<i>Latreutes planircstris</i>				-	0.14		0.01
<i>Leptochela gracilis</i>	5.22		0.06	15.65	5.78	61.11	25.17
<i>Crangon affinis</i>				0.01			-
<i>Acetes chinensis</i>			20.36				1.24
unidentified decapoda	0.01		0.16	-	0.02		0.03
Stomatopoda							
<i>Oratosquilla oratoria</i>				-			-
Mysidacea							
<i>Neomysis japonica</i>				0.01	0.03		0.01
Amphipoda							
<i>Parathemisto gracilipes</i>		1.14		0.62	0.34	2.07	0.73
Gammarus sp.		0.09	0.03	-	0.15		0.02
Copepoda							
Calanidae		5.51		1.46	1.15		0.92

to be continued

Continued from Table 3

Prey items	Fuzhou	Xiangshan	Lüsi	Qingdao	Weihai	Laizhou Bay	Total
Brachyura							
<i>Charybdis bimaculata</i>	0.01						-
Cephalopoda							
<i>Loligo</i> sp.			0.04	0.01			0.01
<i>Euprymna morsei</i>				-			-
<i>Sepiolo birostrata</i>			0.04				-
Sepiolidae	0.03			-			-
Sepiida			0.03	-			-
Unidentified cephalopoda			0.07		0.01		0.01
Gastropoda							
<i>Philine kinglipini</i>			0.01				-
Algae			0.04		0.05		0.01
Unidentified items				0.02			0.01

Note: the dash “-” indicates that a value <0.01, but not a missing value.

most important prey groups were fish. According to IRI%, the dominant prey species were the fish Japanese anchovy and sand lance (*Ammodytes personatus*) and the shrimp *Leptochela gracilis*.

The dominant food of Japanese Spanish mackerel was significantly different among sampling locations (Table 3). The most important prey species were *Stolephorus* (IRI%=81.52%) in Fuzhou, Japanese anchovy (33.55%) in Xiangshan, *E. pacifica* (48.87%) in Lüsi, sand lance (80.97%, 91.18%) in Qingdao and Weihai, and *L. gracilis* (61.11%) in Laizhou Bay. The contribution of other prey items also showed great spatial variations.

3.2 Stable isotope analysis

There were no significant differences in the stable isotopic values of muscle tissue ($p>0.05$) and liver tissue ($p>0.05$) between males and females, so samples of males and females were pooled for further analyses. The $\delta^{15}\text{N}$ values of Japanese Spanish mackerel ranged from 10.50‰ to 15.50‰ ($12.97\text{‰}\pm 1.00\text{‰}$) for muscles and 8.61‰ to 14.20‰ ($11.47\text{‰}\pm 1.10\text{‰}$) for livers. The $\delta^{13}\text{C}$ values of Japanese Spanish mackerel ranged from -19.96‰ to -16.38‰ ($-18.45\text{‰}\pm 0.84\text{‰}$) for muscles and -22.37‰ to -19.38‰ ($-20.76\text{‰}\pm 0.75\text{‰}$) for livers.

The samples were divided into seven size classes of fork length (Fig. 2). The mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in livers were typically lower than the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in muscles for each fork length class (Fig. 2). The mean $\delta^{15}\text{N}$ values of muscles increased from 30–39 cm to 70–79 cm but decreased from 70–79 cm to 90–99 cm. The mean $\delta^{15}\text{N}$ values of the livers increased from

30–39 cm to 60–69 cm but showed a slight decrease from 60–69 cm to 90–99 cm. There was no significant relationship between the mean $\delta^{13}\text{C}$ values and fork length for either muscle or liver ($p>0.05$).

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for Japanese Spanish mackerel and their potential prey items are shown in Fig. 3. Both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values showed large differences across a wide range of prey items (Fig. 3). Potential prey items of Japanese Spanish mackerel were aggregated into nine groups, i.e., Japanese anchovy, sand lance, *Thryssa kammalensis*, other pelagic fishes (*Konosirus punctatus*, *Setipinna tenuifilis*, *Sardinella zunasi*), other demersal fishes (*Ene-drias fangi*, *Callionymus richardsoni*, *Amblychaeturichthys hexanema*, *Chaeturichthys stigmatias*, *Ctenogobius pflaumi*, *Pseudosciaena polyactis*), *L. gracilis*, *E. pacifica*, other crustaceans (*Metapenaeopsis dalei*, *Crangon affinis*, *Trachysalambria curvirostris*, *Latreutes planirostris*), and cephalopods (*Euprymna morsei*, *Loligo* spp.). Mean $\delta^{15}\text{N}$ values of potential prey items ranged from 6.30‰ (*E. pacifica*) to 12.37‰ (cephalopod) ($\Delta 6.07\text{‰}$), and $\delta^{13}\text{C}$ values ranged from -21.99‰ (sand lance) to -18.00‰ (other demersal fishes) ($\Delta 3.99\text{‰}$). The dots with different shapes represent different size classes of Japanese Spanish mackerel individuals. Dots mixed together and could not be separated clearly (Fig. 3). This shows that there was no obvious ontogenetic feeding change between different size classes of Japanese Spanish mackerel.

Trophic levels of Japanese Spanish mackerel showed a positive trend with fork length (Fig. 4). Japanese Spanish mackerel displayed a wide range of trophic levels, shifting from 4.08 ± 0.42 (30–39 cm) to 4.48 ± 0.01 (70–79 cm).

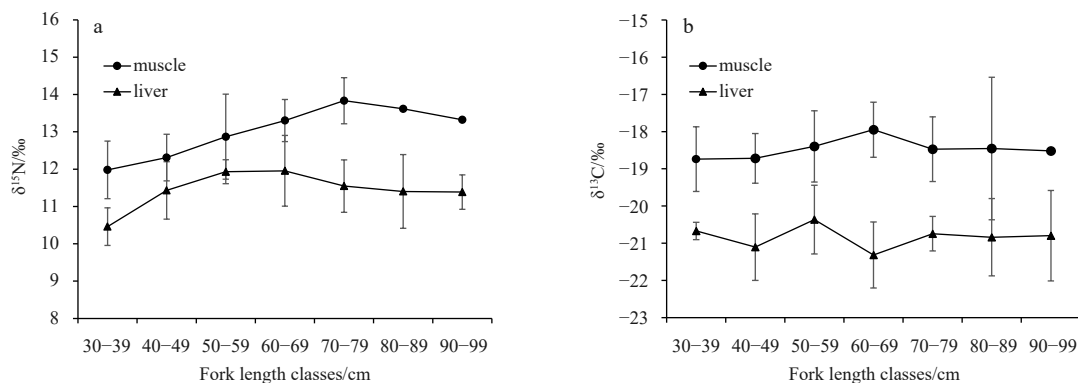


Fig. 2. The mean $\delta^{15}\text{N}$ (a) and $\delta^{13}\text{C}$ (b) values (mean \pm SD) for different fork length classes of Japanese Spanish mackerel.

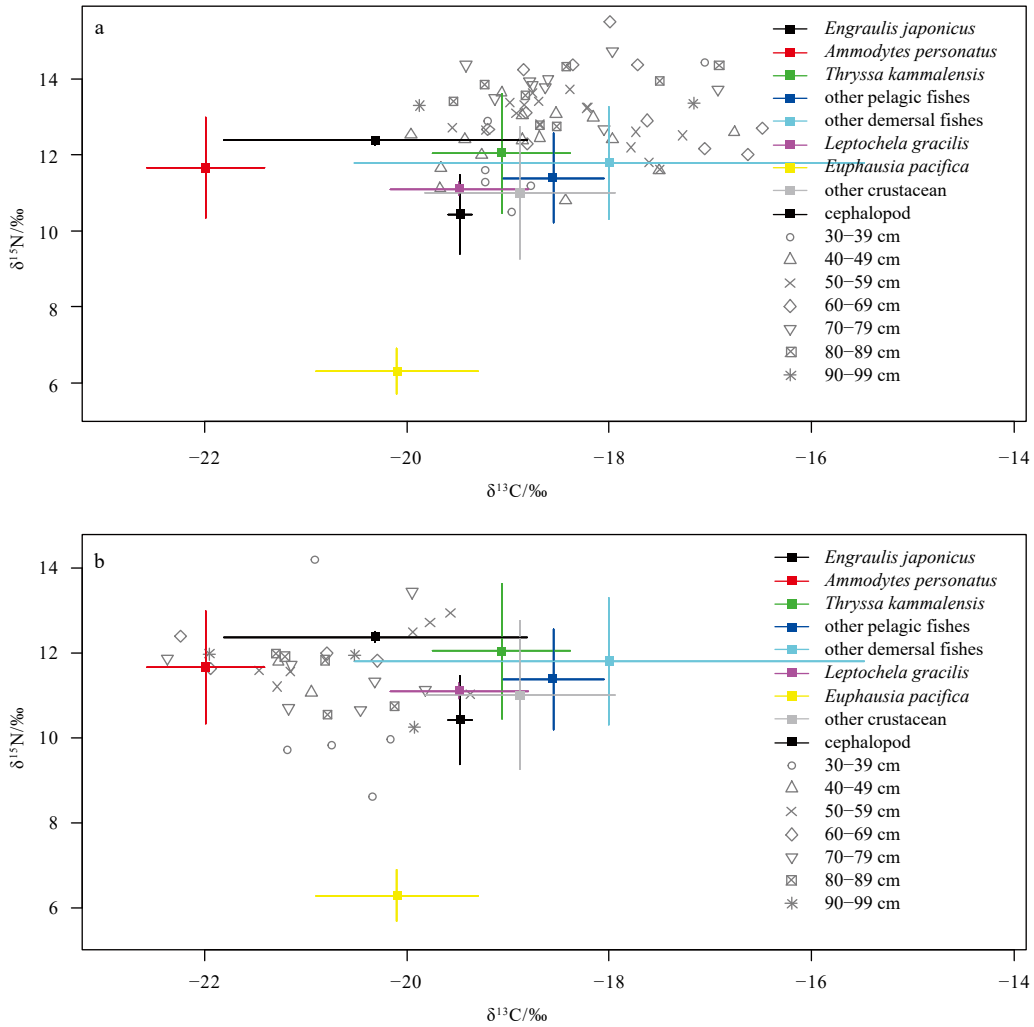


Fig. 3. Stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for muscles (a) and livers (b) of Japanese Spanish mackerel in each size class and potential prey items (mean \pm SD).

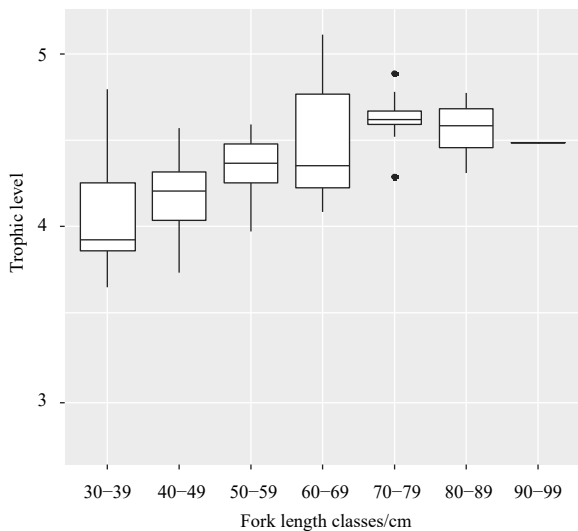


Fig. 4. Trophic levels (mean \pm SD) of different fork length classes of Japanese Spanish mackerel.

3.3 Spatial variations in trophic ecology

The cluster analysis showed the interrelation of diet compositions of Japanese Spanish mackerel in six sampling locations (Fig. 5). The dendrograms displayed similar structures of diet compositions with a convincingly higher value among Qingdao, Weihai and Laizhou Bay. In turn, there was the lowest value of similarity of Xiangshan with the other locations (Fig. 5).

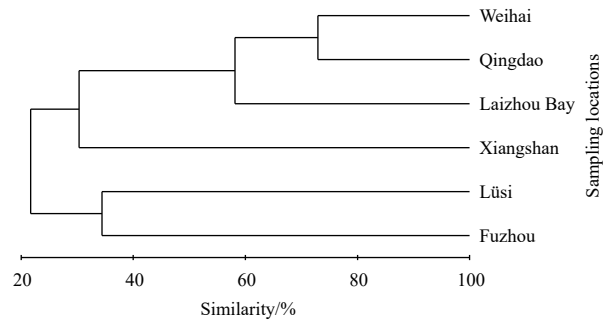


Fig. 5. Dendrogram representing variation in diet composition of Japanese Spanish mackerel in six locations during spring along the eastern coastal waters of China.

The stable isotope values of Japanese Spanish mackerel showed spatial variations (Table 4). The mean $\delta^{15}\text{N}$ values in muscles in Fuzhou and Xiangshan were lower than those in oth-

er locations. The $\delta^{13}\text{C}$ values in muscle and liver showed little difference among locations, suggesting a consistent variation in all sampling locations.

Table 4. Stable isotope values of $\delta^{15}\text{N}$ (‰), $\delta^{13}\text{C}$ (‰) and trophic levels (TL) for samples (muscle and liver) of Japanese Spanish mackerel from six spawning grounds

Locations	Muscle			Liver		
	$\delta^{15}\text{N}/\text{‰}$	$\delta^{13}\text{C}/\text{‰}$	TL	$\delta^{15}\text{N}/\text{‰}$	$\delta^{13}\text{C}/\text{‰}$	TL
Fuzhou	12.39±1.09	-18.23±1.00	4.20±0.32	12.10±0.73	-20.34±0.79	4.12±0.22
Xiangshan	12.47±0.69	-17.52±0.80	4.24±0.21	11.98±1.30	-19.79±0.24	4.08±0.38
Lüsi	13.34±1.08	-18.79±0.63	4.42±0.25	11.47±0.39	-20.92±0.40	3.93±0.11
Qingdao	13.15±0.81	-18.80±0.56	4.43±0.24	11.33±0.66	-21.41±0.69	3.89±0.19
Weihai	13.52±0.78	-18.66±0.71	4.54±0.23	11.65±0.59	-21.15±0.79	3.99±0.17
Laizhou Bay	13.63±0.59	-18.43±0.87	4.57±0.17	11.69±0.48	-20.54±0.74	4.00±0.14

In addition, the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in muscles were higher than those in livers in all sampling locations. Japanese Spanish mackerel exhibited a larger range of $\delta^{15}\text{N}$ values in muscles ranging from 12.39‰ to 13.63‰ (mean ± SD, 13.07‰±0.90‰), with a smaller range in livers from 11.33‰ to 12.10‰ (11.63‰±0.71‰). The $\delta^{15}\text{N}$ values in muscles increased with latitude, while livers changed little with latitude.

The trophic levels of Japanese Spanish mackerel from six sampling locations were significantly different ($p<0.05$) (Table 4). The trophic levels ranged from 4.20±0.32 to 4.57±0.17 (Δ 0.35) in muscle, increasing with latitude from the south (Fuzhou) to the north (Laizhou Bay).

The isotope biplot for Japanese Spanish mackerel is shown in Fig. 6. The isotopic niche of Japanese Spanish mackerel moderately overlapped among six locations, but the degree of overlap varied spatially, with the overlap being the smallest between Xiangshan and Lüsi (0 for muscle and liver) and the largest between Lüsi and Weihai (74.16% and 55.30% for muscle and liver) (Fig. 6). The isotope niche sizes of Japanese Spanish mackerel in Fuzhou and Xiangshan were larger than those in the other four locations.

4 Discussion

4.1 Adaptive feeding strategy of Japanese Spanish mackerel

Stomach content analysis produced similar results as previous studies, showing that Japanese Spanish mackerel mainly fed on fish (W%=92.21%). During the 1980s, Japanese anchovy was the most important prey item (W%>98%) for Japanese Spanish mackerel (Wu, 1987). In this study, Japanese anchovy was still an important prey item for Japanese Spanish mackerel in Xiangshan, Lüsi and Laizhou Bay (W%=67.18%, 25.44%, 42.93%, respectively) but accounted for less than 10% in other locations. The decreased proportion of Japanese anchovies in the diet was mainly due to the sharp decline in its population in Chinese seas caused by overfishing (Zhao et al., 2010; Jin et al., 2005). In this case, Japanese Spanish mackerel showed high dietary adaptability, with its major prey species switching from Japanese anchovy to other prey species, which is probably one of the main reasons that the Japanese Spanish mackerel has survived intense fishing exploitation and other stressors.

Sand lance, a small pelagic fish species, has become the most important prey item for the northern stock of Japanese Spanish mackerel, with weight percentages of 80.77% and 92.23% in Qingdao and Weihai, respectively. Sand lance is a key species in the China seas. Replacing the declining anchovy population, the biomass of sand lance increased and became the dominant prey fish

in the Bohai Sea and Yellow Sea (Li, 2015; Wo et al., 2018). It displays a seasonal energy cycle with a 31% increase in energy density (kJ/g) between February and June (Robards et al., 1999). The lipid content of other prey species also increases rapidly prior to summer (e.g., sand lance and *Ammodytes marinus*) (Sekiguchi, 1977; Hislop et al., 1991). Sand lance may provide enough energy to its predators, including Japanese Spanish mackerel, and become the preferred prey. Japanese Spanish mackerel showed an adaptive feeding strategy and switched its main prey item from anchovy to sand lance and other available prey according to the abundance of these forage species. This dietary plasticity will be beneficial to the maintenance, growth, reproduction and survival of Japanese Spanish mackerel.

The empty stomach rates in Xiangshan and Laizhou Bay were much higher than those in the other four locations. This observation might lead to the assumption that Japanese Spanish mackerel does not ingest significantly until arriving at its final spawning grounds, and its feeding behaviour mainly occurs during pre-spawning migration. It is known that food deprivation may cause increased $\delta^{15}\text{N}$ values and decreased somatic conditions (Gannes et al., 1997; Hobson et al., 1993). However, there was no significant increase in $\delta^{15}\text{N}$ values in Xiangshan and Laizhou Bay, suggesting that either foraging occurs or stored nutrient reserves can cope with the energy costs associated with reproductive migration.

4.2 Spatial variations in trophic ecology of Japanese Spanish mackerel

This study showed that there were obvious spatial variations in the trophic ecology of Japanese Spanish mackerel among six spawning grounds along the coastal China seas. In the southern East China Sea, mackerels mainly consume *Stolephorus* sp. In the northern East China Sea, mackerels mainly consume Japanese anchovies and *E. pacifica*. In the Yellow Sea and Bohai Sea, mackerels mainly consume sand lance, Japanese anchovy and *L. gracilis*. These differences provided phenotypic evidence for the stock identification and migration trajectories of Japanese Spanish mackerel. The three geographic stocks experienced different environments associated with migration trajectories based on analysis of their otolith features (Zhang et al., 2016). The feeding preference of Japanese Spanish mackerel and the availability of local prey species in each spawning ground were the main reasons for the spatial difference in the trophic ecology of Japanese Spanish mackerel.

The $\delta^{15}\text{N}$ value has proven effective in elucidating size-related changes in the trophic level of many fish species (Lindsay et al., 1998; Overman and Parrish, 2001; Jennings et al., 2002). $\delta^{15}\text{N}$

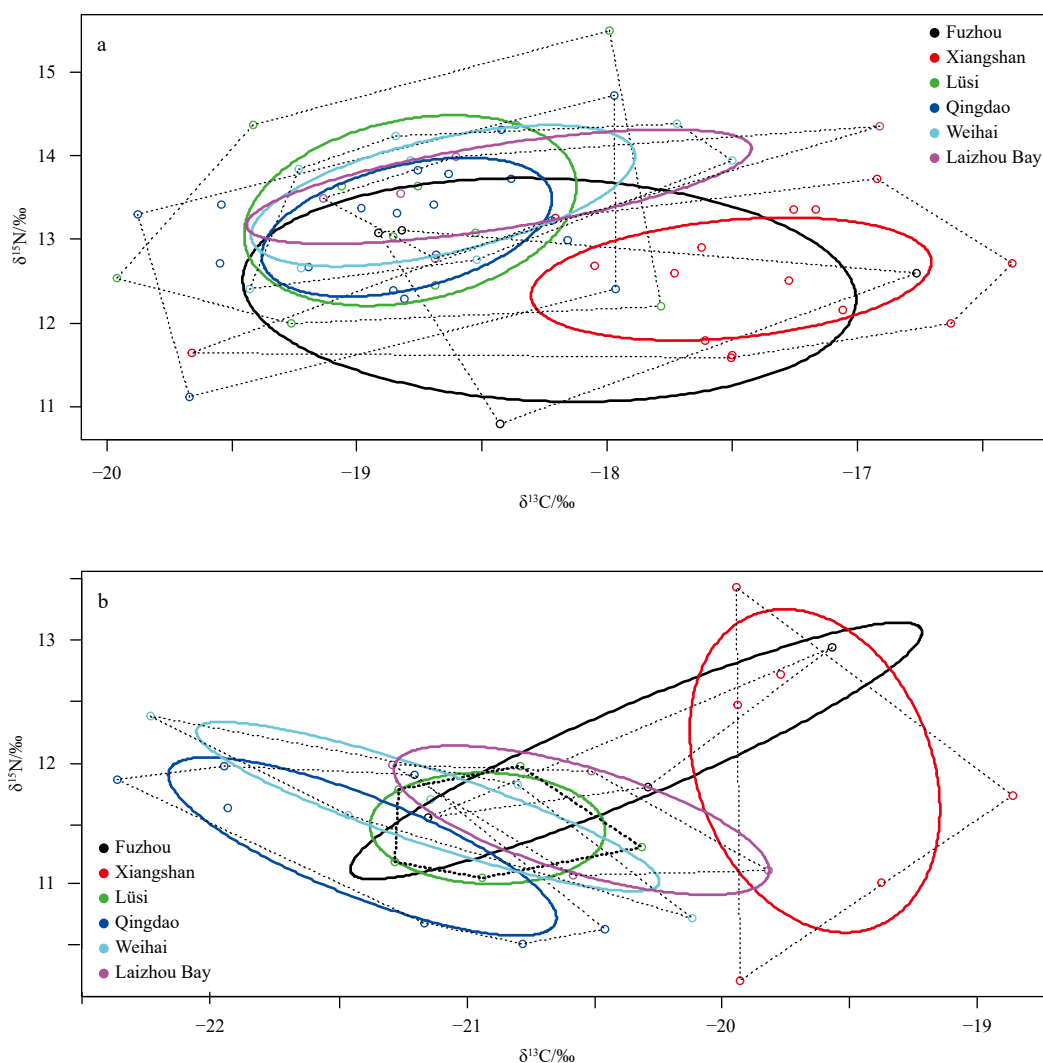


Fig. 6. Isotopic niche breadth in the muscle (a) and liver (b) of Japanese Spanish mackerel from six spawning grounds along the coastal China seas. Convex hulls of the total niche width of the liver and muscle are dotted lines. Bayesian standard ellipses showing isotope niches are shown for different sampling locations.

enrichment across different size classes of fishes demonstrated that trophic positions within a community were largely determined by the size of organisms (Jennings et al., 2002). Thus, the differences in $\delta^{15}\text{N}$ values between sampling locations probably represent differences in the size or trophic positions of prey items consumed. The overall increase in trophic positions with size is generally considered to be the result of intraspecific accumulation of heavy isotopes with somatic growth in body mass (Lindsay et al., 1998; Jennings et al., 2002). For Japanese Spanish mackerel, the $\delta^{15}\text{N}$ values in muscle increased with latitude from south to north along the coastal China seas, and the trophic levels showed a consistent trend with $\delta^{15}\text{N}$ values. These trends are anastomotic with the migration route of Japanese Spanish mackerel from south to north during the spawning period. It has been proven that the gape size of Japanese Spanish mackerel is significantly correlated with its body length (Lin et al., 2017). When migrating from south to north, it probably consumed larger prey to accumulate more energy for growth.

Prey items in the diet and niche breadth could considerably influence the geographic variation in trophic ecology (Munroe et al., 2014). For Japanese Spanish mackerel, the isotopic niche

breadth differed greatly among different locations. The highly overlapping isotopic niches of four spawning grounds (Lüsi, Qingdao, Weihai and Laizhou Bay) suggested a higher level of food competition in their local ecosystems. Moreover, the wider trophic niche of stock in Fuzhou indicated higher variability in individual diets. These differences might be due to geographic variations in local prey items. The lower specialized diets of Japanese Spanish mackerel might result in a larger isotopic niche or larger niche overlap compared with other spawning grounds. The results support the hypothesis that changes in fish growth, size and ultimately accumulation could be due to bottom-up control characterized by changes in food availability and increasing potential trophic competition.

4.3 Comparison between different methods

When prior information on diet composition is limited because of the high empty stomach rate, employing representative prey items in isotope mixing models can provide useful information on diets (Polito et al., 2011). For the parameterization of the multisource SIAR model, pertinent prey items were identified mainly from the analysis of hard remains from the stomach con-

tents and previous studies carried out in the same waters. The results of stomach content analysis and stable isotope analysis could be combined to obtain an accurate diet composition of fishes.

Stable isotope values in the liver and muscle of Japanese Spanish mackerel showed some differences. In general, $\delta^{15}\text{N}$ values increase from prey to predators and accumulate persistently in individuals (Peterson and Fry, 1987; Minagawa and Wada, 1984). In this study, there was a positive correlation between fish fork length and $\delta^{15}\text{N}$ values in muscles. Japanese Spanish mackerel consumed more high-trophic-level prey items with increasing size. However, the stable isotope values in the liver did not show the same result as those in muscle. Japanese Spanish mackerel with 60–69 cm fork length had the highest $\delta^{15}\text{N}$ values in the liver, while mackerel with 70–79 cm fork length had the highest $\delta^{15}\text{N}$ values in muscle. This could be explained by the fact that livers had higher isotopic turnover rates and showed foraging habits over shorter time periods than muscle. It is necessary to consider the difference in stable isotope values in different tissues when using stable isotope analysis.

Although stable isotope analysis provides an alternative method to assess trophic relationships and consumption patterns, it is necessary to exercise caution in their interpretation (Brush et al., 2012). It is suggested to combine stomach content analysis and stable isotope analysis from different tissues to obtain more comprehensive information about the feeding ecology of marine species.

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