

Biological responses of small yellow croaker (*Larimichthys polyactis*) to multiple stressors: a case study in the Yellow Sea, China

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Abstract

Temporal changes in biological characteristics of small yellow croaker *Larimichthys polyactis* in the Yellow Sea were examined for the period of 1960–2008. The body size and age of small yellow croaker decreased substantially, in particular, average length of fish in 2008 was reduced by ~85% than those occurring in 1985, and at that time ~93% of the total catch was dominated by one-year-old individuals. Correspondingly, growth parameters also varied significantly over the years, i.e., k (growth coefficient) and t_0 (zero-length age) gradually increased from 0.26 and –0.58 year in 1960 to 0.56 and –0.25 year in 2008, respectively. Although, L_∞ (body length) sharply decreased from 34.21 cm in 1960 to 24.06 cm in 2008, and t_r (inflection age) decreased from 3.78 year in 1960 to 1.61 year in 2008. There was a great increase both in natural mortality coefficient and fishing mortality coefficient. However, according to the gray correlation analysis, changes in the biological characteristics of small yellow croaker were induced by different stressors ranked as: fishing vessel power>feeding grade>sea surface temperature. This study suggests that the active fishery management measures for biological characters of fish populations should be considered.

Key words: small yellow croaker *Larimichthys polyactis*, biological characteristics, multiple stressors, responses, temporal changes, the Yellow Sea

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1 Introduction

Fish are an essential part of marine ecosystems and play significant roles to meet market demands, ensure food security and provide large amounts of high-quality protein for humans, especially in developing countries. Because of anthropogenic activities (e.g., overfishing, pollution) and climate change, the marine ecosystems are affecting negatively, therefore, the biological characteristics and population dynamics of marine fish (Law, 2000; Heino and Godø, 2002) and their genetic makeup (Kim et al., 2010; Sun et al., 2012) have been changing significantly. For example, the body length of small yellow croaker *Larimichthys polyactis* in the Yellow Sea was changed from 20 cm in the 1980s to 10 cm in the present, as well as the population attribute and its life history characteristic (Shan et al., 2011). Even if the fishing intensity were to decrease, some of these changes are likely irreversible (Law, 2000; Heino and Godø, 2002) that might threaten the function of marine ecosystems.

The small yellow croaker is widely distributed throughout the Bohai Sea, Yellow Sea and East China Sea. The species is commercially important and predominantly caught/harvested by the

bottom trawl fishery in China, Japan and Korea. In China, the fish are mainly distributed in the bays of Liaodong, Laizhou and Haizhou, and in the fishing grounds of Yanwei, Lüsi and Dasha. Because of intense fishing pressure, the population of small yellow croaker has declined from 160 000 tons in 1957 to 16 000 tons in 1989 (The Ministry of Agriculture Fisheries Bureau of People's Republic of China, 1958, 1990). In recent years, their population has recovered to a mentionable level because of the implementation of effective fishing measures, i.e., closed season/closed areas and “zero growth” in production from capture (Cheng et al., 2004; Lin et al., 2009a). Moreover, the population composition of small yellow croaker has changed during this period, with individual miniaturization and growing predominance of young fish (Jin and Tang, 1996; Guo et al., 2006). Many studies were conducted to investigate and assess the resources (Jin and Tang, 1996; Zheng et al., 2003; Ding et al., 2007), growth (Guo et al., 2006) and diet composition (Zhang and Tang, 2004; Xue et al., 2004; Yan et al., 2006) of this species. These studies mainly focused on qualitative analysis of biological characteristics and stock assessment, the biological adaptations to multiple stressors are not well ad-

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dressed. In this study, long-term variations in biological characteristics of small yellow croaker in southern Yellow Sea were analyzed, as well as biological responses of small yellow croaker to multiple stressors were evaluated. These results are expected to provide the important implications for understanding responses of fish to multiple stressors in marine ecosystem.

2 Materials and methods

2.1 Study area and data collection

The Yellow Sea is characterized by the presence of both Yellow Sea Cold Water Mass and Yellow Sea Warm Current, which is a branch of the Kuroshio Current (Su et al., 1994). Thus, environments of this area are complex, but composed of several fishing grounds, such as the Lüsi fishing ground along coastal waters of Jiangsu Province. The Lüsi is a well-known spawning ground of small yellow croaker that spawns between April and May (Jin and Tang, 1996; Jin et al., 2005). The southern Yellow Sea is also an overwintering habitat and feeding ground of small yellow croaker (Liu, 1990; Jin and Tang, 1996).

The data of this study obtained from bottom trawl survey of the southern Yellow Sea (32°30′–37°00′N, 121°30′–125°00′E, Fig. 1). The small yellow croaker samples in survey area were belong to the same geographical stock by morphological characteristics (Lin et al., 1965), RAPD and AFLP analysis (Meng et al., 2003; Lin et al., 2009b), and collected from 1960, 1985, 1998 and 2008. Samples were collected in January, March, May, August, October and December (but in April instead of March in 2008), and analysis of the spawning stock was conducted using the data collected in May. In 1960, the samples were collected by bottom pair trawlers (200 horsepower). After 1985, the R/V *Beidou* (2 250 horsepower) was used. The characteristics of trawler and gears used in the surveys were described by Li et al. (2011). Because of the gear differences between 1960 and the other survey years, the data in 1960 could not be standardized with the data in the other survey years, so, the data in 1960 was just as a reference. To collect data, four to five sampling stations were sampled in each 0.5°N×0.5°E plot. The trawling time at each station lasted approximately 1 h at an average speed of three knots. A total of 7 500 randomly selected small yellow croaker were collected, of which

2 000 sampled in 1960, 1 500 sampled in 1985 from 40 sampling stations, 2 000 sampled in 1998 from 46 sampling stations and 2 000 sampled in 2008 from 52 sampling stations. Age of the fish was determined by otolith section analysis. Monthly water temperature was obtained from the IRI/LDEO Climate Data Library.

2.2 Biological parameters

2.2.1 Growth equation

The body length-weight relationship of fish is described by the equation $W=aL^b$, where W is the body weight, L is the body length, and a and b are the condition factor and allometric factor, respectively.

The growth equation was that of von Bertalanffy growth equation:

$$L_t = L_{\infty}[1 - e^{-k(t-t_0)}], \quad (1)$$

where k is the growth coefficient, L_{∞} is the asymptotic total length, t is the age of the mid-value body length group, and t_0 is the zero-length age. The growth parameters L_{∞} and k were calculated with the Electronic Length Frequency Analysis I (ELEFAN I).

2.2.2 Mortality coefficient

Total mortality coefficient (Z) was calculated with the help of catch curve equation (Lin and Cheng, 2004):

$$\ln(N/\Delta t) = a + bt, \quad (2)$$

where N is the ratio of the length of each body length group to that of all samplings, Δt is the time required for the lower limit to reach the upper limit in the corresponding body length group. Negative slope of the regression of data points that tended to decrease ($Z=-b$) is defined as total mortality coefficient.

Natural mortality coefficient (M) was calculated as per the equation:

$$\ln M = -0.0066 - 0.279 \ln L_{\infty} + 0.6543 \ln k + 0.4634 \ln T, \quad (3)$$

where T (°C) is the average water temperature of the habitat of the small yellow croaker, a value of 13.6°C, the average sea temperature in the southern Yellow Sea was used in the present study according to Tang (2006). Body length (BL) and total length (TL) of 100 randomly selected small yellow croaker were used to establish the relationship between BL and TL :

$$TL = 0.9814BL + 3.281 \quad (R = 0.9537), \quad (4)$$

which was used to calculate the asymptotic total length.

Inflexion age (t_r) was calculated after the equation:

$$t_r = \ln b/k + t_0, \quad (5)$$

where b is the power exponent in the relationship between body length and body weight.

2.2.3 Diet composition

The composition of diet was determined by following equation (Pinkas et al., 1971):

$$IRI = (W\% + N\%) \times F, \quad (6)$$

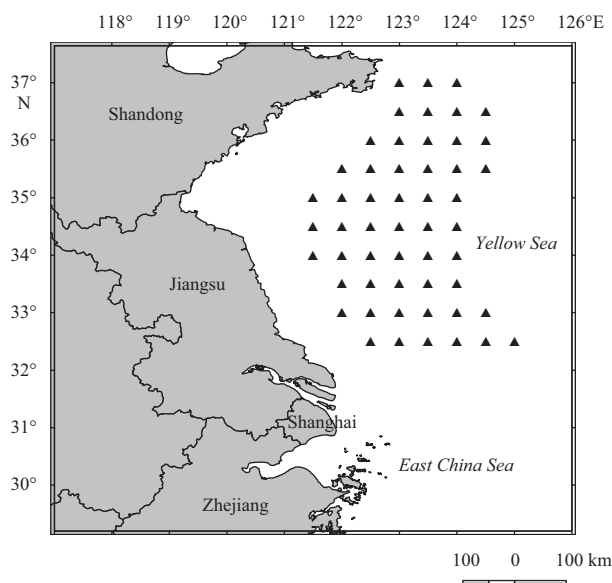


Fig. 1. Sampling stations in the southern Yellow Sea.

where $W\%$ represents the weight of species in diet relative to the weight of total diet, $N\%$ is the proportion of species in diet relative to total number of species in the diet, and F is the frequency at which dietary species are encountered in the diet.

2.3 Gray correlation analysis

Assuming geometric similarity among the influencing factors, thus a gray correlation analysis was used to analyze the degree of influence or contribution of the governing factors on the marine ecosystem (Lv, 2005). The SST, feeding grade and fishing vessel power (fishing intensity) were chosen as influencing factors.

The raw data were converted by mean normalization to obtain a new sequence: X_0 (biological parameters), X_2 (SST) and X_3 (fishing vessel power).

For the reference system, the absolute values were obtained by following equation:

$$\Delta i(m) = |X_0(m) - X_i(m)| \quad (i = 1, 2, 3), \quad (7)$$

where $\Delta i(m)$ is the absolute difference between X_0 and X_i , and i and m represent the row and column of the data, respectively, after mean normalization.

The correlation coefficient $\varepsilon_i(m)$ was calculated after the equation:

$$\varepsilon_i(m) = \frac{\text{Min}\Delta i(m) + p\text{Max}\Delta i(m)}{\Delta i(m) + p\text{Max}\Delta i(m)}, \quad (8)$$

where p is the distinguishing coefficient and ranges from 0 to 1 (a

value of 0.5 was used in the present study).

Gray correlation value y_i was obtained from the correlation coefficient of each data sequence as follows:

$$y_i = \frac{1}{n} \sum_{k=1}^n \varepsilon_i(m) \quad (i = 1, 2, 3, \dots, m), \quad (9)$$

which forms a Gray correlation value sequence: $\{y_i\} = \{y_1, y_2, y_3, \dots, y_n\}$.

The order of gray correlation values, the results of analysis and the degree of influence of each sequence on the reference system were evaluated by ranking the elements in $\{y_i\}$.

2.4 Data analysis

The significant differences between parameters were determined by t -test. All analyses were processed with Microsoft Excel 2010, Surfer 8.0 and FiSAT II softwares (Pauly, 1990).

3 Results

3.1 Body size

Body length of both male and female small yellow croaker was decreased from 1960 to 2008 (Fig. 2). In particular, body length of female in 1960 ranged from 13 cm to 34.9 cm, with majority ranged from 18 cm to 30.9 cm. An average body length of female in 1985, 1998 and 2008 were (14.4 ± 3.3) cm, (11.8 ± 1.5) cm and (12.3 ± 1.9) cm, with body length of maximum female ranged from 10–15.9 cm (71.72%), 10–13.9 cm (84.36%) and 10–13.9 cm (77.78%), respectively.

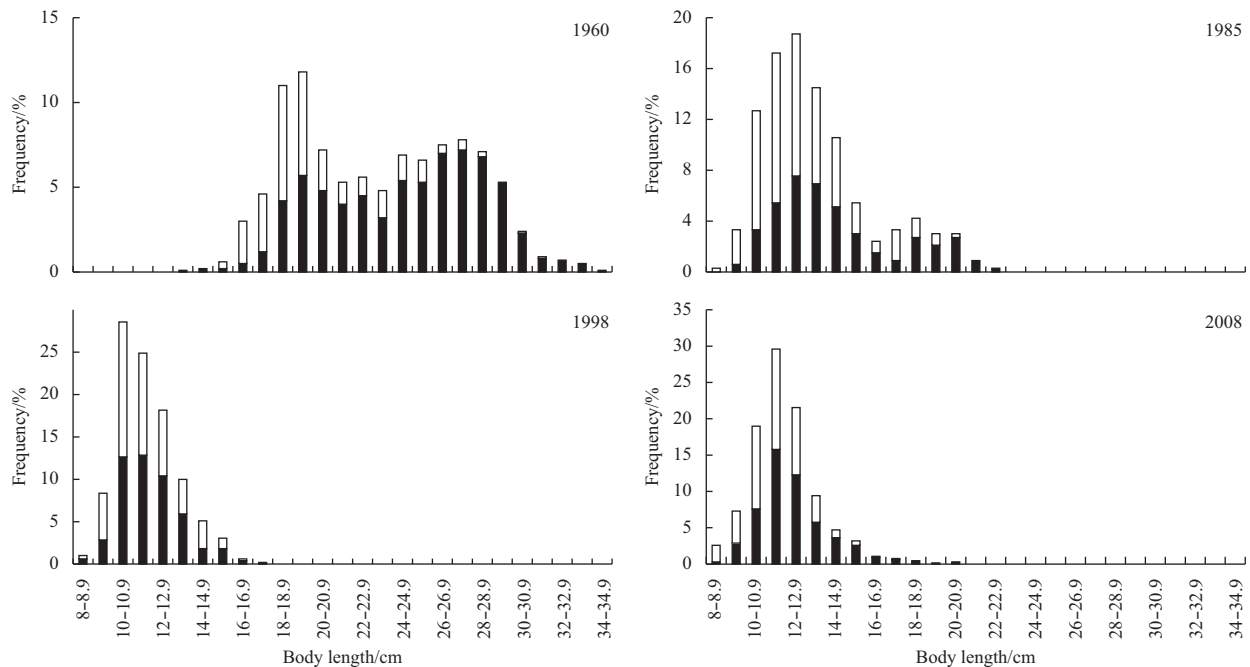


Fig. 2. Body length distribution of small yellow croaker in the Yellow Sea from 1960 to 2008. White bar represents males and black bar females.

A change in the body length of spawning stocks was also observed from 1960 to 2008. Fish in the dominant body-length group in 1960 had a double peak distribution at length ranged 17–20 cm and at 25–28 cm, while an average body length was 23.55 cm. However, later in 1985, length of fish in the dominant

body-length group decreased to 11–14 cm and also an average body length decreased to 14.78 cm. Incidentally, length of fish in the dominant body-length group has been relatively stable since 1985 (i.e., 10–13 cm in 1998, with an average length 11.90 cm). In 2008, the dominant and average body length of spawning stocks

increased slightly from 11 cm to 14 cm with an average 12.69 cm (Fig. 3).

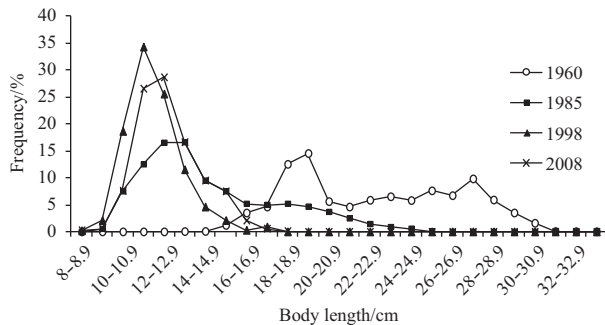


Fig. 3. Body length distribution of the small yellow croaker spawning stock in the Yellow Sea from 1960 to 2008.

3.2 Body length-weight relationship

A power function relationship between body length and body weight of small yellow croaker was observed (Table 1). The allometric factors of female decreased from 1960 to 1998, but increased after 1998. The trends in allometric factors of male were

similar to those of female, i.e., the allometric factors were approximately equal to 3 in 1960 and 2008, and significantly lower than 3 for other years. The lowest value was observed in 1998.

The condition factors for female greatly decreased from 1960 to 1985, but an increase was noted from 1985 to 2008. A similar trend was also observed for male fish. Female, in general, had relatively higher condition factors than male, and the difference was significant ($P < 0.01$) in 2008. In addition, significant negative correlation ($P < 0.01$) was observed between condition factors and allometric factors of male and female, and the allometric factors showed a significant positive correlation ($P < 0.05$) with average body length (Table 2).

3.3 Age structure

Age structure of small yellow croaker in the Yellow Sea was largely altered from 1960 to 2008, with numbers of younger fish becoming increasingly dominant ($P < 0.05$). The dominant age group ranged 2–5 year in 1960 that composed of 89.40% of all individuals in the age group. However, the age of fish in the dominant age group decreased to 1–2 year in 1985 and to a minimum 1 year in 1998 and 2008. Average age of fish was 4.49 year in 1960 and 1.99 year in 1985, but less than 1.5 year in 1998 and 2008 (Table 3).

Table 1. Parameters defining the body length-weight relationship of small yellow croaker in the Yellow Sea

Year	Female				Male			
	$a/10^{-2}$	b	R^2	t	$a/10^{-2}$	b	R^2	t
1960	0.61	3.35	0.97	5.85**	2.47	2.87	0.94	1.27 ^{ns}
1985	4.30	2.61	0.82	1.10 ^{ns}	6.54	2.41	0.87	3.50**
1998	4.29	2.65	0.95	3.19**	8.13	2.39	0.85	3.19**
2008	2.62	2.81	0.90	1.21 ^{ns}	2.51	2.82	0.90	1.07 ^{ns}

Note: a and b represent parameters defining the body length (cm)-weight (g) relationship, R^2 correlation coefficient; t t test for b ($H_0: b=3$), ^{ns} no significant difference between b and 3, * significant difference between b and 3 ($P < 0.05$), and ** strongly significant difference between b and 3 ($P < 0.01$).

Table 2. Correlations between the parameters defining the body length-weight relationship of small yellow croaker in the Yellow Sea and potential influencing factors

Sex		Allometric factor b	Average body length	Feeding grade	Proportion of mature females
Female	Condition factor a	-0.95**	-0.51	-0.44	-0.58
	Allometric factor b	-	0.73*	0.38	0.66
Male	Condition factor a	-0.97**	-0.18	-0.17	-
	Allometric factor b	-	0.37	0.07	-

Note: Values in the table represent correlation coefficients, * a significant correlation between the mean body length and b ($P < 0.05$), and ** very strong significant correlations between b and a ($P < 0.01$).

Table 3. Age structure of small yellow croaker in the Yellow Sea

Year	Age structure/%										Average age/year
	1	2	3	4	5	6	7	8	9	Beyond 10	
1960	0.9	16.4	33.6	23.2	6.2	2.6	3.8	3.8	2.0	7.5	4.49
1985	28.8	55.5	8.7	3.3	2.6	0.9	0.2				1.99
1998	97.6	2.36	0.04								1.02
2008	93.4	5.7	0.9								1.08

Maximum age of small yellow croaker belonging spawning stocks was 23 year in 1960, but individuals aging 1–4 year was dominating in the stocks since 1985. After 1998, the spawning stocks mostly consisted of individuals aging 1–2 year (>90%). Average age of fish in the spawning stocks was in the order of 4.13 year in 1960 >1.36 year in 1985 >1.05 year in 1998, but 1.12 year in 2008. These facts indicate that, by now, stocks of older fish has been exhausted in the Yellow Sea and that the younger stocks occupied the most of capture production (Table 3).

3.4 Feeding habits

Food items in the diet of small yellow croaker had changed from 1960 to 2008 (Table 4). In 1960, the dominant prey species by weight were *Euphausia pacifica* and *Crangon affinis* and *Engraulis japonicus* according to the IRI. Moreover, *Thrisa kamalensis*, *Collichthys lucidus* and *Apogonichthys lineatus* were recorded in their diet, *E. japonicus* being the dominant prey-food in 1985, followed by *C. affinis* and *Metapenaeopsis dalei*. The proportion of species in diets by weight was also similar. *E. pacifica*

Table 4. Changes in the composition of small yellow croaker diet in the Yellow Sea

Prey composition	1960			1985*			1998			2008		
	W/%	F/%	IRI	W/%	F/%	IRI	W/%	F/%	IRI	W/%	F/%	IRI
<i>Engraulis japonicus</i>	13.56	26.30	418.17	45.18	31.91	1 577.31	4.67	0.92	4.36	14.54	5.00	79.78
<i>Thrissa kammalensis</i>	9.68	8.69	88.03				9.59	4.47	44.03	24.40	4.50	116.80
<i>Collichthys lucidus</i>	5.36	7.98	43.73	9.37	2.13	20.47						
<i>Apogonichthys lineatus</i>	8.65	4.57	40.67				3.36	1.39	4.77			
<i>Enedrias fangi</i>							1.59	0.77	1.26			
<i>Crangon affinis</i>	19.63	39.70	990.52	13.10	21.28	344.10	9.38	7.70	77.69	28.22	13.00	473.77
<i>Metapenaeopsis dalei</i>				15.13	12.80	220.93						
<i>Palaemon gravieri</i>				3.21	2.13	8.35						
<i>Trachypenaeus curvirostris</i>				2.54	2.13	5.92						
<i>Euphausia pacifica</i>	16.25	45.78	1 968.08				47.28	60.86	6 807.80	18.71	42.00	4 122.19
<i>Leptochelia gracilis</i>							7.21	10.79	102.40	6.58	10.00	116.82
<i>Eualus sinensis</i>							2.44	3.85	11.13	3.07	5.00	25.26
<i>Alpheus distinguendus</i>							1.51	0.46	0.70			
<i>Parathemisto gracilipes</i>							1.31	9.40	127.46			
<i>Calanus sinicus</i>							4.67	0.92	4.36			

Note: * Tang et al. (1990); W represents the weight of species in the diet relative to the weight of the total diet, F the frequency at which dietary species are encountered in the diet, and IRI the dominance of diet composition.

was the dominant prey species in 1998 and 2008, and both *C. affinis* and *T. kammalensis* occupied higher proportions in diets accounting more than 20% by weight. *E. japonicus* was a predominant food type in 2008 accounting 14.54% of total diet weight. After 1985 (and particularly after 1998), *E. pacifica* was the dominant prey species. *C. affinis* and *E. japonicus* were the main species, followed by *T. kammalensis*, found in the diet of small yellow croaker between 1960 and 2008.

3.5 Reproductive characteristics

The proportion of small yellow croaker reaching maturity decreased from 88.1% in 1960 to 5.9% in 1985, with record of average 47.1% matured individuals. Such a large difference may be occurred due to error in sample collection, i.e., fish during their peak spawning period were probably not sampled (Fig. 4).

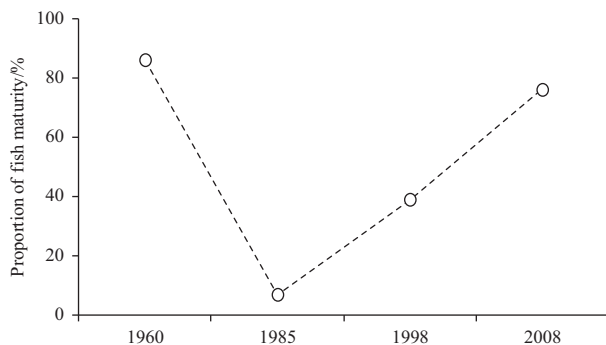


Fig. 4. Proportion of mature individuals in the female spawning stock of small yellow croaker in the Yellow Sea.

3.6 Biological parameters and influencing factors

The biological parameters of small yellow croaker in the Yellow Sea changed noticeably between 1960 and 2008 (Table 5). The growth coefficient and zero-length age gradually increased, whereas the asymptotic body length and age at inflexion of body weight decreased by 29.67% and 57.41%, respectively. Mortality coefficient also changed, i.e., in 2008, both natural mortality coefficient and fishing mortality coefficient greatly increased, with

Table 5. Biological parameters of small yellow croaker in the Yellow Sea from 1960 to 2008

Biological parameter	Year			
	1960	1985	1998	2008
Growth coefficient k	0.26	0.40	0.48	0.56
Zero-length age t_0	-0.58	-0.37	-0.30	-0.25
Asymptotic length L_{∞} /cm	34.21	30.17	25.54	27.00
Age at inflexion of body weight growth t_i	3.78	2.44	1.99	1.61
Total mortality coefficient Z	0.51	1.80	2.84	2.40
Natural mortality coefficient M	0.24	0.33	0.39	0.77
Fishing mortality coefficient F	0.27	1.47	2.45	1.63
Goodness of fit R_n		0.30	0.26	0.27

fishing mortality coefficient 2.12 times as large as natural mortality coefficient.

The results of gray correlation analysis relating to SST, feeding grade, fishing vessel power and changes in the biological parameters of small yellow croaker were shown in Table 6. Influences of these factors on the fishing mortality coefficient were ranked in the order of feeding grade > fishing vessels power > SST. The fishing vessel power primarily had an influence on the growth coefficient, natural mortality coefficient, zero-length age, and age at inflexion of body weight, feeding grade and SST. Moreover, influence of these factors on the total mortality coefficient was ranked as fishing vessel power > SST > feeding grade. However, the asymptotic length was closely related to SST. The overall impact levels were ranked as fishing vessel power > feeding grade > SST.

4 Discussion

4.1 Biological adaptation

Small yellow croaker accounts for a large proportion of total catch in the Yellow Sea, however, their population composition is characterized by fish with small body size and relatively young age; therefore, the catch production was mainly composed of the recruitment populations (Fig. 3) (Jin and Tang, 1996; Shan et al., 2011). Biological characteristics, which are the most variable traits of fish, are affected by a broad array of selective factors

Table 6. Correlations between the decadal changes in the biological parameters of small yellow croaker and influencing factors

Biological parameter	Sea surface temperature (SST)/°C	Feeding grade	Fishing vessel power/MW
Growth coefficient k	0.649 1	0.692 3	0.727 3
Zero-length age t_0	0.624 9	0.735 2	0.759 6
Asymptotic length L_∞ /cm	0.754 9	0.653 6	0.736 1
Age at inflection of body weight growth t_i	0.607 3	0.742 7	0.768 9
Total mortality coefficient Z	0.640 4	0.634 6	0.727 3
Fishing mortality coefficient F	0.640 3	0.709 2	0.675 6
Natural mortality coefficient M	0.560 6	0.664 5	0.671 6
Mean value	0.639 6±0.019 3	0.690 3±0.013 5	0.723 8±0.035 6

mainly related to environmental variables and predation pressure that fish confront continuously in their habitats. The body size and age of small yellow croaker in the Yellow Sea decreased from 1960 to 2008, the individuals with body length 16–17 cm were seldom found in recent years. The average body length of fish in 2008 was reduced to 85.9% compared to the length of fish in 1985. Additionally, one-year-old individuals accounted for 93.4% of total catch in 2008. The body size of samples in 1960 was greatly bigger than that in the other survey years, which might be attributed to the gear in 1960 with bigger mesh size, and higher selectivity for larger body size samples. Correspondingly, the gear selectivity also brought some influences on the growth parameters. The growth parameters of small yellow croaker k and t_0 , which are closely related to the growth rate, gradually increased from 0.26 and –0.58 year in 1960 to 0.56 and –0.25 year in 2008, respectively. However, L_∞ sharply decreased from 34.21 cm in 1960 to 24.06 cm in 2008, and t_i decreased from 3.78 year in 1960 to 1.61 year in 2008. Similar results on the above mentioned facts were reported for small yellow croaker in the East China Sea and Bohai Sea (Lin and Cheng, 2004; Guo et al., 2006). Moreover, minimum size and age of small yellow croaker at sexual maturity was reported to decrease in these regions (Shui, 2003). A decrease in the age and body length of small yellow croaker might be related to overfishing of large aged individuals (Shin et al., 2005). Small yellow croaker individuals beyond 3 year have already experienced several years of fishing pressure, as a result, their numbers have sharply decreased. However, their population has recovered to a certain extent during the 1990s, mostly due to large recruitment events. Resource miniaturization has been observed in other fishery species of the Yellow Sea, including *Scomberomorus niphonius* (Shui et al., 2009), *E. japonicus* (Wan and Bian, 2012) and *Gadus macrocephalus* (Li et al., 2012), and this is in agreement with data obtained from other coastal waters of China such as the East China Sea (Zhou et al., 2002).

The size of the population of targeted species has greatly declined, leading to the dominance of small-sized and short-lived stocks and an imbalance in predator-prey dynamics. These changes have caused a “miniaturization ecological adaption” of fishery resources (Myers and Worm, 2003), thus limiting minimum catchable size of fish, and resulted variations in their biological, genetic and behavioral characteristics (Conover and Munch, 2002; Walsh et al., 2006). When subjected to multiple stressors, fishery species could regulate the population dynamics by natural selection, which could result in a series of ecological responses due to environmental changes. Biological adaptations are determined both by the life history of fishery species and dynamics of fishery populations, therefore, the life history of fishery species is regulated by environmental changes and resource exploration (Smale et al., 2010). The small yellow croaker has a K-type life history and elements of an r-type life history (Luo et al., 1993). The age and body length of small yellow croaker at sexual

maturity has decreased, although the fecundity of this species reported to increase greatly (Jin and Tang, 1996; Shui, 2003; Zeng et al., 2005; Guo et al., 2006), indicating that life history of the fish transformed to r-type. The mechanisms regulating the transformation of life history of small yellow croaker warrant further investigation.

Both male and female small yellow croaker experienced negative allometric growth from 1960 to 2008. Additionally, b decreased during resource recession period (1985) and also during resource recovery period (1998). The age at sexual maturity decreased from 2 year in 1960 to 1 year in 1985 (Li et al., 2011), therefore, more energy was used to support gonad development that caused body weight of the fish to reduce (i.e., lean body mass weight), leading to a decrease in condition factors (Pitcher and Hart, 1982). Since the 1980s, SST, growth rate, feeding rate and condition factors of small yellow croaker have increased. Fish stocks with small-sized individuals were characterized by a higher b value because of the predominance of juvenile or young fish, and a similar trend was observed for *Perca fluviatilis* (Wang et al., 2006). However, no significant difference ($P>0.05$) was observed for the proportion of individuals in younger and older populations that did not reach to sexual maturity. This point to the fact that age was not a dominant factor affecting the b value and that the variations in b were mainly determined by the proportion of individual attained maturity (Le Cren, 1951). Improved synergistic relationships were observed between the variations in b of male and fishing efforts, and also between higher fishery stock densities and larger b values. A decrease in the conditions factors of small yellow croaker from the 1960s to the 1980s was mainly associated with decreasing age of fish at sexual maturity. Since the 1990s, the condition factors of small yellow croaker increased with an increasing SST.

4.2 Factors affecting biological characteristics

4.2.1 Overfishing

The technological development of fishing gear and increases in fishing power of individual vessels have resulted an increased fishing mortality, and a disproportional distribution of recruited populations and surplus populations. In consequence, both yield-per-recruit and spawning-biomass per recruit of fishery species have sharply decreased. However, total catch of small yellow croaker remained relatively high in the Yellow Sea in recent years. But, the body length, body weight and age of the fish have greatly decreased, and the per-unit-effort has sharply decreased, mostly because of overfishing (Jin and Tang, 1996; Zhou et al., 2002). In addition, overfishing had resulted variations in the intraspecies and interspecies dynamics of small yellow croaker, i.e., competition for food. Reductions in the number of competitors (*S. niphonius*) and predators (*Miichthys miiuy*, *Lateolabrax japonicus*) of small yellow croaker associated with high fish-

ing intensity (Wei and Jiang, 1992) that has relieved the interspecific stress on the fish. The changes in intraspecific dynamics consist mainly of increases in the production of growth hormones, a more rapid metabolism rate, a lower age at the inflexion of body weight/length, a lower age at sexual maturity and higher individual fecundity (Shen and Shi, 2002). An unfavorable genetic change was significantly correlated with long-term overfishing, and the evolution of this species that occurred over a long period of time has resulted in irreversible impacts on its biological traits (Walsh et al., 2006). Therefore, the recovery of many fish populations that had experienced a decline was delayed far more than expected (Olsen et al., 2004).

According to the suitable exploitation rate of fish (0.5) proposed by Gulland (1984), small yellow croaker, which was characterized by an exploitation rate of 0.68 (Zhang et al., 2010), has been over-exploited. The exploitation rate of small yellow croaker was typical of a situation of overfishing and overwhelmed the required size of renewable population of small fish proposed in the Beverton-Holt model (Zhang et al., 2010). In 1985, catchable age of small yellow croaker in the Yellow Sea was 0.3 year, the fishing mortality was 1.2 (fishing industry standard at that time) and the yield-per-recruit was 45.3 g (Jin and Tang, 1996). While in 2008, the catchable age of small yellow croaker was 0.3 year, the fishing mortality was 1.63 (the current fishing industry standard) and the yield-per-recruit was 15.15 g (Zhang et al., 2010), representing 33.5% value of the year 1985. Prior to 1990, the catchable size of fish in the Yellow Sea and Bohai Sea was measured by the China government and found to be 6–20 cm in 2008 with average body length 10.2 cm. The prospects of small yellow croaker in the Yellow Sea are bleak and thus Zhang et al. (2010) recommended changing the catchable size of small yellow croaker to 15 cm.

4.2.2 Feeding habit

E. pacifica has been the dominant prey species in the diet of small yellow croaker, particularly since 1998. *C. affinis* and *E. japonicus* were the main species by composition from 1960 to 2008, followed by *T. kammalensis*. Variations in the composition of diet might be associated with interspecific dynamics and also competition in the fishery ecosystem. Recently, populations of *Lophius litulon* and *Liparis tanakae* have greatly increased in size in the Yellow Sea. Also, fecundity and survival rate of these two species are very high, and the abundant feeding of juvenile commercial fish has resulted in significant interspecies competition (Tang and Ye, 1990). In addition, changes in the composition of diets of fish in the fishery ecosystems have greatly contributed to the variations of diet composition of small yellow croaker and other species (Zhang et al., 2012). The spectra of organisms that compose the diets of fish are related to the heterogeneity of fish population, which is a result of the response of fishery species to changes in the composition and biomass of dietary organisms.

The trophic level of small yellow croaker in the Yellow Sea decreased from 3.7 in 1985–1986 to 3.4 in 2000–2001 (Zhang and Tang, 2004), but in the East China Sea (Lin et al., 2009a), decrease in the trophic level of small yellow croaker was more pronounced than that of the global fishery catch (0.1 per decade) (Pauly et al., 1998). Changes in the trophic levels of marine fish were determined by both feeding habits and fishing intensity (Pauly et al., 1998; Linke et al., 2001; Anastasopoulou et al., 2013). In this study, gray correlation index relating the feeding grade to variations in biological characteristics was 0.609 3, and the degree of influence of feeding grade was higher than that of SST but lower than the fishing intensity. Therefore, the variation in biolo-

gical characteristics of small yellow croaker in the Yellow Sea ecosystem was mostly fishery-induced. In addition, the proportions of dominant prey species were similar in 1960 and 2008, which might reflect an ecosystem revision following a long period of disturbance. The regulatory mechanisms underlying this process should be further investigated.

4.2.3 Sea surface temperature

Increasing influence of human activities on global climate change has resulted in a gradual increase of SST by 0.64°C in the Yellow Sea than that observed in the 1960s. Temperature influences all aspects of physiology of ectotherms, plays an important role in the survival and growth, and controls the metabolic rate of fish by regulating the activities of enzymes. It also affects physiological and biochemical procedures such as feeding intensity, metabolic rate and protein synthesis rate (Sun et al., 2000; Hurst et al., 2012; Bergstad, 2013; Trueman et al., 2013). The responses of fish populations and communities to climate forcing represent the cumulative effects of changes in physiological and behavioral characteristics (Rijnsdorp et al., 2009; Ottmar and Hurst, 2012). Variations in physiological and morphological traits among fish serve as an indicator of persistent response to environmental history, for example, thermal reaction varied among the growth of different Pacific cod cohorts (Hurst et al., 2012). The correlation index relating to SST and biological characteristics of the fish was relatively low in the Yellow Sea, which might be attributable to the fact that water temperatures in the Yellow Sea remained within a suitable range for small yellow croaker (Ding et al., 2007). In addition, large-scale climatic phenomena such as the North Atlantic Oscillation (NAO) and El Niño-Southern Oscillation (ENSO) also affect the spawning, recruitment and distribution of fish populations (Alheit et al., 2005; Rojas-Mendez and Mendoza, 2008). During the ENSO years, SST increased and the thermal layer structure changed, which resulted variations in the primary and secondary productivity of fishery species (Hong et al., 1998) and further changed the community structure, distribution and stock density of these species (Fan et al., 2001). The habitat range of *Katsuwonus pelamis* was markedly increased during ENSO events and extended an additional 6 000 km along the equator because of the warm pool caused by ENSO (Lehodey et al., 1997). The effects of ENSO on biomass varied for different fishery species, for example, the biomass of *Sardinops sagax*, *T. murphyi* and *Scomber japonicus* increased during ENSO years or after ENSO events. However, ENSO events led to a significant decline in the biomass of *E. ringens* (Niquen and Bouchon, 2004). The biomass of small yellow croaker also appeared to increase during ENSO years, or one to two years after ENSO events (Li et al., 2011). This increase in biomass might have been caused by high water temperatures contributing to a high metabolic rate and short hatching period, which increased the survival rate and recruitment stock density of this species, or changes in environmental factors of the Yellow Sea led to an increased biomass of zooplankton in the spawning and feeding grounds of small yellow croaker and thus, an abundant food to support the growth and development of larvae and juveniles. Although the recruitment of small yellow croaker benefited from an increased SST, a high natural mortality was also observed during this period. Therefore, a positive correlation between natural mortality index and SST was evident. Climate change and human activities caused spatial and temporal heterogeneity, which resulted in changes in the migratory habits of fish along latitudes (Cury et al., 2000; Perry et al., 2005; Cheung et al., 2009, 2013) and water depths (Dulvy et al., 2008; Theisen and Baldwin, 2012).

The impacts of human activities and environmental changes on fishery resources have become more pronounced (CCICED, 2013), thus, as observed in this study, the attributes and life history characteristics of small yellow croaker in the Yellow Sea have changed significantly. Small yellow croaker is characterized by environment-specific genotypes and morphological variations. The aforementioned changes could dramatically impact the performance and biomass of small yellow croaker that able to influence the structure and dynamics of the Yellow Sea ecosystem by inducing trophic cascade variations. Therefore, an understanding of the variations in biological characteristics of small yellow croaker is very much important for an effective fisheries management and conservation.

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