



# Long-term variations in body length and age at maturity of the small yellow croaker (*Larimichthys polyactis* Bleeker, 1877) in the Bohai Sea and the Yellow Sea, China

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## ABSTRACT

This study focused on changes in the maturation schedules, as depicted in maturity ogives, of female small yellow croaker (*Larimichthys polyactis*) in the Bohai Sea and the Yellow Sea during the 1960–2010 spawning seasons. The two stocks studied were the northern Yellow Sea-Bohai Sea stock (the NYBS,  $n = 1283$ ) and the southern Yellow Sea stock (the SYS,  $n = 2024$ ). Body length ( $L_{50}$ ) and age at median sexual maturity ( $A_{50}$ ) were estimated by an arcsin-square-root (ASR) transformative logistic model and an inverse von Bertalanffy growth function, respectively. The results show that  $L_{50}$  decreased from 152.8 mm to 105.3 mm between 1960 and 2003–2005 in the NYBS and from 184.4 mm to 110.1 mm between 1960 and 2010 in the SYS. Over the same period,  $A_{50}$  decreased from approximately 1.5 years in the NYBS and 2.4 years in the SYS to about 1 year in both stocks. Significant intrastock changes ( $P < 0.01$ ) in length–maturation curves were found in both stocks over long time periods ( $\geq 4$  years); however, there were no significant changes ( $P > 0.05$ ) over short time intervals ( $< 4$  years). Significant interstock changes ( $P < 0.01$ ) were observed in length–maturation curves in corresponding sampling years. Significant positive correlations were found between the instantaneous rate of maturation ( $\delta$ ) and the growth potential index ( $\omega$ ) in the NYBS and between  $L_{50}$  and asymptotic body length ( $L_{\infty}$ ) in the SYS. Significant negative correlations were found between  $L_{50}$  and the sea surface temperature (SST) daily rise rate in the NYBS and between  $\delta$  and the mean monthly SST in the SYS. These correlations suggest that declines in length and age at maturation primarily reflect changes in growth associated with overfishing and rising SST. Additionally, a fisheries-induced evolutionary response has contributed to changes in maturation schedules in both stocks. The principal pressures are the stress of continuously higher fishing intensity and an increasing proportion of yearling fish in the catches over time.

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## 1. Introduction

The small yellow croaker *Larimichthys polyactis* (Bleeker, 1877), an economically and ecologically important demersal fish, is found in the Bohai Sea, the Yellow Sea and the East China Sea. It is the target of bottom trawling in China, Japan and Korea (Jin et al., 2005). In the 1950s and the early 1960s, small yellow croaker was a dominant species in the Yellow Sea and the Bohai Sea (Jin and Tang, 1996; Jin, 2004), with an annual production greater than 0.19 million tons (Liu et al., 1990). Overfishing and environmental changes,

however, led to a major decline in abundance over the following two decades, and the fisheries were on the verge of collapse by the early 1990s (Liu et al., 1990; Jin, 1996; Kim et al., 1997). The stock recovered significantly and again came to dominate the Yellow Sea fish community (Xu and Jin, 2005; Zhang et al., 2009). Consequently, the catch began a continual increase and exceeded 0.38 million tons in 2008 (FAO, 2010). Unfortunately, most of the landings ( $> 80\%$ ) were  $< 1$  year old, especially after 2000 (Jin et al., 2005; Yan et al., 2006). Thus, it is apparent that new management strategies are urgently needed for the sustainable use of this species.

Body length and age at median sexual maturity ( $L_{50}$  and  $A_{50}$ ) are important reference points in fishery management (Hilborn and Walters, 1992). Declines in  $L_{50}$  and  $A_{50}$  have been observed in many heavily exploited fisheries, such as cod *Gadus morhua* (Cardinale and Modin, 1999; Chen and Mello, 1999; Olsen et al., 2005; Nash

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et al., 2010) and herring *Clupea harengus* (Engelhard and Heino, 2004a).

Shifts in age of maturity are mainly ascribed to overfishing (Trippel, 1995) and changes in environmental factors (Gerritsen et al., 2003; Domínguez-Petit et al., 2008). Overfishing led directly to decreased stock density, and compensatory growth contributed to changes in maturation (Trippel, 1995; Chen and Mello, 1999). Johannessen et al. (2001) suggested that the decrease in mean total length at maturity in the small yellow croaker was a density-dependent response to low stock density in the Yellow Sea. Years of heavy fishing pressure has led to evolutionary responses in fish maturation for some species (Law, 2000; Heino and Godø, 2002; Ernande et al., 2004), particularly via encounters with schools of only mature or only immature individuals (Engelhard and Heino, 2004b). Moreover, maturation is also related to environment factors, such as water temperature. Changes in water temperature significantly affect gonad development (Brown et al., 2010). Since the early 1990s, sea surface temperature (SST) has been rising due to global warming, which significantly impacted fish growth and reproduction (Brander, 2010; Strüßmann et al., 2010).

In particular, the asymptotic body length and weight of the small yellow croaker declined significantly (Guo et al., 2006; Yan et al., 2006; Zhang et al., 2010), as did the average body length and average total length at maturity (Jin, 1996; Johannessen et al., 2001; Lin and Cheng, 2004). In addition, absolute and relative fecundity of this fish significantly increased with fisheries exploitation and environmental changes over the past forty years (Zeng et al., 2005; Lin et al., 2009). However, relationships between the changes in growth and maturation in the small yellow croaker, particularly the long-term variations in  $L_{50}$  and  $A_{50}$ , have not been fully investigated. In this study, we estimate the  $L_{50}$  and  $A_{50}$  of the small yellow croaker in its different stock statuses and to explore the correlations between growth, maturation and the environment. This study will provide useful information for stock assessment, protection and management.

## 2. Materials and methods

### 2.1. Study areas and stocks

The Bohai Sea (37.0–41.0°N, 117.5–122.0°E) and the northern Yellow Sea (37.5–39.5°N, 121.0–125.5°E) together cover an area of about 160,000 km<sup>2</sup>. Both are semi-enclosed seas with average depths of 18 and 40 m (Cheng et al., 2004). These seas are important spawning and feeding grounds for northern Yellow Sea-Bohai Sea stock (NYBS), a major geographical stock of the small yellow croaker (Liu et al., 1990).

The southern Yellow Sea (32.0–34.0°N, 120.5–126.0°E) covers an area of about 130,000 km<sup>2</sup>, with an average depth of 45 m. It includes the Yellow Sea Cold Water Mass (YSCWM) and the Yellow Sea warm current, a branch of the Kuroshio Current (Su et al., 1994). The environment in this area is complex and forms a well-known spawning and feeding ground for the southern Yellow Sea stock (the SYS), the biggest geographical stock of small yellow croaker, as well as the overwintering ground for this species (Liu et al., 1990; Jin and Tang, 1996).

### 2.2. Data collection

The study focused on female small yellow croaker sampled by the Yellow Sea Fisheries Research Institute (YSFRI) in the Bohai Sea and the Yellow Sea during spawning seasons (April–May) between 1960 and 2010 (Fig. 1). These specimens for the NYBS were collected from stations in the Bohai Sea and along the northern Shandong Peninsula in 1960, 1985, 1986, 1993, 2003, 2004 and

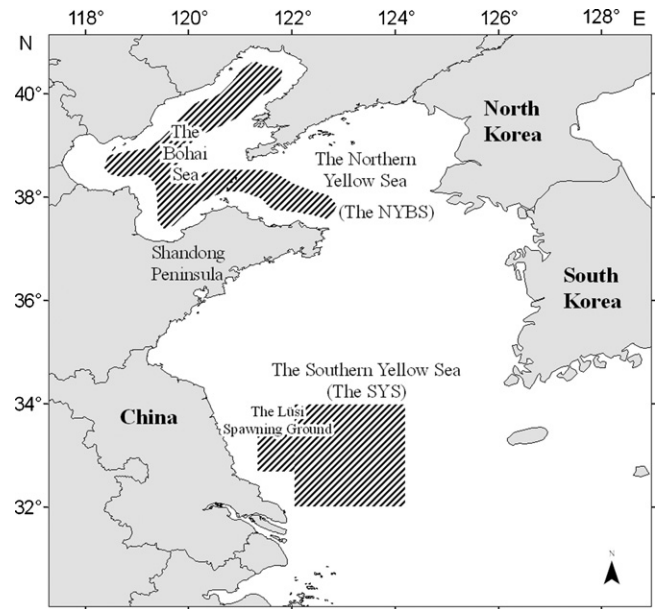


Fig. 1. Sampling areas in the Bohai Sea, the northern Yellow Sea and the southern Yellow Sea. Hatched areas denote the principal sampling areas.

2005. To compensate for the small sample size in the mid-1980s and the 2000s, specimens from 1985–1986 and 2003–2005 were pooled, respectively. To exclude individuals from nearby stocks, the SYS was represented only by specimens collected from the area 32.0–34.0°N, 121.0–124.5°E in 1960, 1986, 1994, 1998, 2001, 2005, 2007 and 2010.

In the Bohai Sea and the northern Yellow Sea, all samplings were carried out by bottom pair trawlers (200 horsepower) during the day; in the southern Yellow Sea in the 1960s, samples were collected over 24 h by bottom pair trawlers (200 horsepower); since 1984, the R/V “Bei Dou” (2250 horsepower) was used. In every 0.5°N × 0.5°E area, four to five sampling stations were predetermined. Trawling lasted approximately 1 h per station at an average speed of 3 knots. The gear used in sampling is shown in Table 1.

If there were fewer than 25 individuals in a catch of small yellow croaker, all were cryopreserved for laboratory bioassays; otherwise, 25–50 individuals were randomly sampled for measurement. In total, 1283 fish from the NYBS and 2024 from the SYS were measured for body length to the nearest mm. The maturity stages of all specimens were macroscopically distinguished by the development of the ovaries, and each specimen was assigned to one of six stages (Qiu and Jiang, 1965). The females with gonad development at stages I–III were considered sexually immature; those at stage IV–VI were considered sexually mature.

### 2.3. Body length and age at median sexual maturity

Body length at median maturity,  $L_{50}$ , was estimated based on the relationships between the arcsin-square-root (ASR) transformative percentage  $P_i$  of sexually mature females in each 5.0-mm body length interval and midpoint value of the body length interval ( $X_i$ ), which is described by the ASR transformative logistic model (Chen and Paloheimo, 1994):

$$\text{ASR}(P_i) = \frac{\text{ASR}(G)}{1 + \exp(-\delta * (X_i - L_{50}))} + \varepsilon_i, \quad (1)$$

where  $\delta$  is the instantaneous rate of maturation. A large  $\delta$  indicates that fish mature over a short time interval, and  $G$  is the maximum attainable proportion of the mature fish. Because all individuals

**Table 1**  
Vessels and trawls used in the surveys.

Sampling area	Year	Vessel	Mesh number × mesh size (cm)	Codend/liner size (cm)	Vertical opening (m)
The Bohai Sea and the northern Yellow Sea	1960	“Huang Hai” 3/4	600 mesh × 8.0	4.3/–	7–8
	1985–2004	Pair-trawlers	1740 mesh × 6.3	10.0/2.0	5–6
The southern Yellow Sea	1960	“Huang Hai” 3/4	600 mesh × 8.0	4.3/–	7–8
	1986	R/V “Bei Dou”	450 mesh × 17.0	10.0/2.0	5–7
	1994–2010	R/V “Bei Dou”	836 mesh × 12.0	10.0/2.4	5–7

will attain maturity after reaching a specific body length,  $G$  equals 1.  $ASR(P_i)$  is the ASR transformative  $P_i$  and is given by:

$$ASR(P_i) = \arcsin \sqrt{P_i}. \quad (2)$$

$ASR(G)$  in Eq. (1) equals  $\pi/2$  when  $G = 1$ , and  $\varepsilon_i$  in Eq. (1) is the error term. The  $L_{50}$ ,  $\delta$  and their 95% confidence intervals were estimated using the nonlinear regression in IBM® SPSS® Statistics 19.

Age at median maturity,  $A_{50}$ , was calculated by the inverse von Bertalanffy growth function (von Bertalanffy, 1938):

$$A_{50} = t_0 - \frac{1}{K} \ln \left( 1 - \frac{L_{50}}{L_{\infty}} \right), \quad (3)$$

using the asymptotic body length ( $L_{\infty}$ ), growth coefficient ( $K$ ) and theoretical age at zero length ( $t_0$ ) of the fish in the two stocks (Table 2) and the  $L_{50}$  values with their 95% confidence intervals estimated in this study.

#### 2.4. Potential factors affecting maturity

Changes in SST, rate of daily increase in SST, growth rate of young fish and asymptotic body length were considered as factors that could potentially affect the maturation of the small yellow croaker.

The monthly SST ( $2^\circ \times 2^\circ$ ) for the Bohai Sea, the northern Yellow Sea and the southern Yellow Sea (from March to May) was downloaded from the IRI/LDEO climate data library of Columbia University (Smith et al., 2008) [July 8th 2010 from IRI Data Library: <http://iridl.ldeo.columbia.edu/>]. The mean SST values from March to May in the sampling years (Fig. 2) were used. The rate of daily increase in SST ( $T_{DIR}$ ) between March and May was calculated as:

$$T_{DIR} = \frac{SST_{MAY} - SST_{MAR}}{D}, \quad (4)$$

where  $SST_{MAR}$  and  $SST_{MAY}$  are the average SSTs in March and May, respectively, and  $D$  is the number of days between March and May. In addition, the mean SSTs from March to May in 1985–1986 and 2003–2005 for the NYBS were calculated from the monthly SST weighted by the percent of total specimens collected in a given year, as were the rates of daily increase in SST.

A growth parameter  $\omega$  ( $\omega = KL_{\infty}$ ) proposed by Gallucci and Quinn (1979) was calculated for the small yellow croaker as a measure of overall growth potential of the young fish (Chen and Harvey, 1994; Chen and Mello, 1999).

**Table 2**  
Growth parameters for the two stocks of small yellow croaker.

Stock	Survey year	$L_{\infty}$ (mm)	$k$ (year <sup>-1</sup> )	$t_0$ (year)	Estimation method	Referenced from
The NYBS	1960	339.4	0.28	−0.61	Ford–Walford	Guo et al. (2006)
	1982	302.9	0.33	−0.41	ELEFAN	
	1993	275.4	0.46	−0.50		
	2003	245.3	0.49	−0.28		
The SYS	1960	342.1	0.26	−0.58	ELEFAN	Zhang et al. (2010)
	1985	301.7	0.40	−0.37		
	1998	255.4	0.48	−0.30		Lin and Cheng (2004)
	2001	251.6	0.55	−0.27	ELEFAN	
	2002–2003	212.6	0.43	−0.69	Ford–Walford	Yan et al. (2006)
	2008	240.6	0.56	−0.25	ELEFAN	

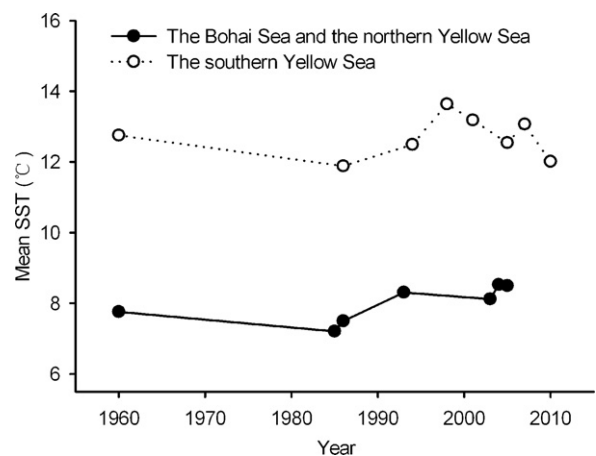
#### 2.5. Statistical analyses

Interannual and interstock changes to the logistic model were explored using an analysis of the residual sum of squares (ARSS) to assess significant differences between body length–maturation curves (Chen et al., 1992). The  $F$ -statistic was calculated as follows:

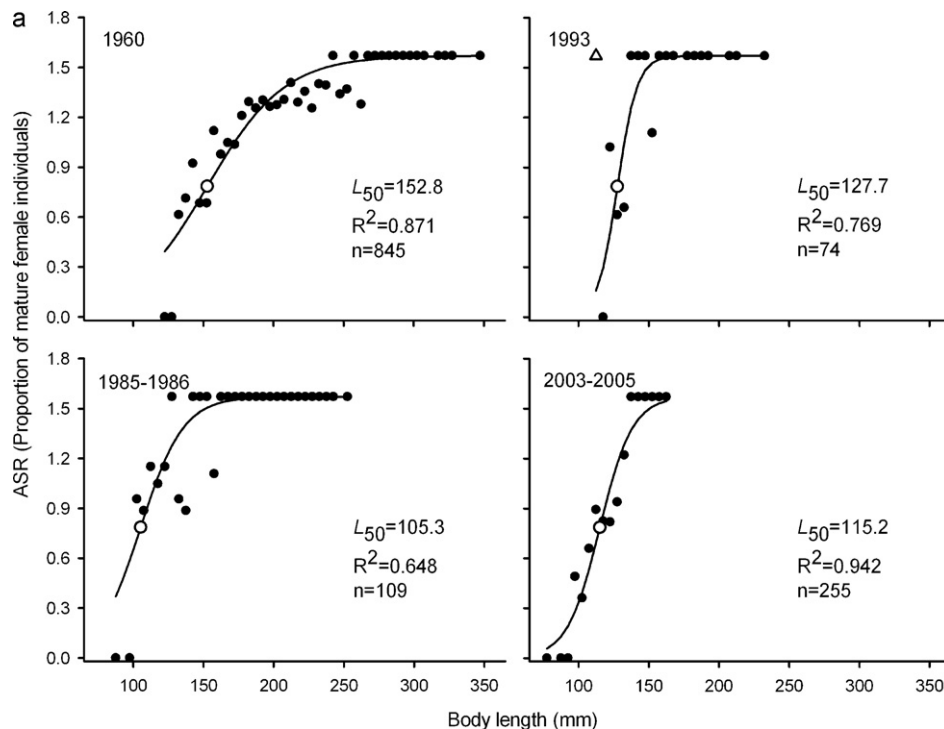
$$F = \frac{(RSS_p - RSS_s)/(DF_p - DF_s)}{RSS_s/DF_s} = \frac{(RSS_p - RSS_s)/(3(M - 1))}{RSS_s/(N - 3M)}, \quad (5)$$

where  $RSS_p$  is the residual sum of squares (RSS) of the ASR model that is fitted by the ASR transformative pooled proportion of mature fish;  $RSS_s$  is the sum of the RSS of each ASR model fitted by the ASR transformative mature fish proportions of comparative years;  $DF_p$  is the pooled degrees of freedom (DF);  $DF_s$  is the sum of DF from comparative years,  $M$  is the number of years in the comparison (2 in this study); and  $N$  is the sum of body length groups in each year. The calculated  $F$  value was then compared with the critical  $F$ , the DF of the numerator and the denominator equal to 3 and  $N - 6$ , respectively.

The significance of Pearson's correlation coefficient for relationships between maturation characteristics ( $L_{50}$  and  $\delta$ ) and environmental factors (the SST and the SST daily rise rate) and between maturation characteristics ( $L_{50}$  and  $\delta$ ) and growth param-



**Fig. 2.** Variations in mean monthly sea surface temperature (SST) in the spring in the Bohai Sea, the northern Yellow Sea and the southern Yellow Sea.



**Fig. 3.** The observed and ASR model-fitted maturity ogives for female small yellow croakers in (a) the NYBS and (b) the SYS. ●: observed data; ○:  $L_{50}$ ; lines denote predicted maturity ogives based on the ASR model.  $L_{50}$ : body length at 50% sexual maturity;  $R^2$ : correlation coefficient;  $n$ : sample size; △ in 1993; (a) shows the observed abnormal proportion of sexual maturity in the body length class 110.0–115.0 mm in which only one specimen was sampled.

eters ( $\omega$  and  $L_{\infty}$ ) was examined. All analyses were processed with the aid of IBM® SPSS® Statistics 19.

### 3. Results

#### 3.1. Variations in maturation characteristics

Sigmoid relationships between body lengths and the corresponding ASR transformative proportions of sexually mature individuals were plotted by stock and year (Fig. 3). Changes in  $L_{50}$  and  $A_{50}$  are shown in Fig. 4. In the NYBS,  $L_{50}$  decreased significantly from 1960 to 1985–1986, increased in 1993 and then decreased in 2003–2005.  $A_{50}$  decreased from about 1.5 years to around 0.9 years from 1960 to 1985–1986 and has changed very little since the mid-1980s. In the SYS,  $L_{50}$  also decreased significantly from 1960 to 1986 but increased significantly in 1994 and then fluctuated, tending to decline until 2005. SYS  $L_{50}$  finally increased in 2010 until it reached the level recorded in 2001.  $A_{50}$  decreased significantly from about 2.4 years to around 1 year from 1960 to 1986 and then slightly changed.

Values of  $\delta$  varied from year to year in the two stocks (Fig. 5A). In the NYBS,  $\delta$  increased greatly from 1985–1986 to 1993 but decreased from 1993 to 2003–2005. In the SYS,  $\delta$  increased greatly in 1986 but gradually decreased from 1986 to 2001.

Length–maturation curves showed significant differences between surveys in the NYBS ( $P < 0.01$ ), as did the surveys over long time intervals ( $\geq 4$  years) in the SYS ( $P < 0.01$ ). No significant difference ( $P > 0.05$ ) was found between the surveys over short time intervals ( $< 4$  years) (Table 3).

$L_{50}$  in the SYS were both higher than those found in the NYBS in 1960, the mid-1980s, and the mid-1990s.  $A_{50}$  values were higher in the SYS than in the NYBS in 1960 and the mid-1980s. The 95% confidence intervals of  $L_{50}$  and  $A_{50}$  in the two stocks did not overlap in these periods, but did overlap in the mid-2000s. Significant differences were found between the length–maturation

curves ( $P < 0.01$ ) of corresponding sampling years in both stocks (Table 4).

#### 3.2. Changes in potential affecting factors

The mean monthly SST from March to May in the Bohai Sea and the northern Yellow Sea was approximately  $4.7^{\circ}$  lower than in the southern Yellow Sea. The most striking features are a rise in temperature since the beginning of the 1990s in the Bohai Sea and the northern Yellow Sea and the decadal warming from the mid-1990s to the mid-2000s in the southern Yellow Sea (Fig. 2).

In the Bohai Sea and the northern Yellow Sea, the daily rate of increase in SST from March to May was greater in 1985–1986 and 2004–2005 than in the other measured years. In the southern Yellow Sea, the daily rate of increase in SST gradually rose from 1960 to 1998 and then continuously decreased until 2010 (Fig. 5B).

In the NYBS, the  $\omega$  values found in 1993 and 2003 were higher than those found in 1960 and 1982. In the SYS,  $\omega$  increased significantly from 1960 to 1985 and remained high in the following years, except in 2002–2003 (Fig. 5C).

#### 3.3. Correlations among maturation, growth and environmental factors

According to the correlation analysis, sexual maturation of the small yellow croaker is structured by growth parameters and environmental factors (Table 5). In the NYBS, a significant negative correlation was found between  $L_{50}$  and the rate of daily increase in SST ( $P < 0.1$ ), indicating that small yellow croaker in areas with a rapid temperature rise in the spring tended to mature earlier. Values of  $\delta$  increased significantly with increasing  $\omega$  ( $P < 0.1$ ), indicating that the small yellow croaker with higher growth rates during early development tend to mature faster. In the SYS, a significant positive relationship was identified between  $L_{50}$  and asymptotic body length  $L_{\infty}$  ( $P < 0.05$ ), but a significant negative correlation was found

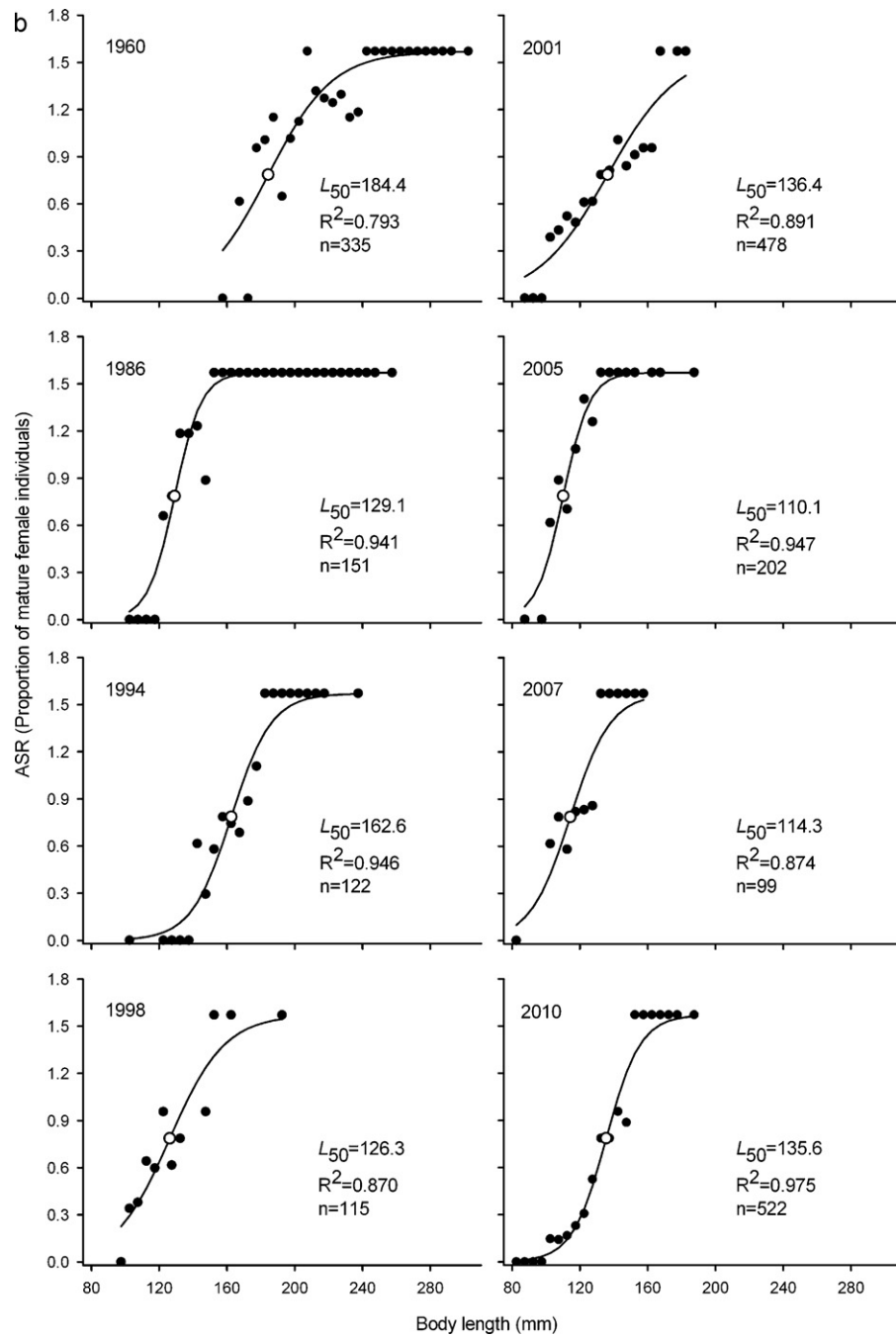


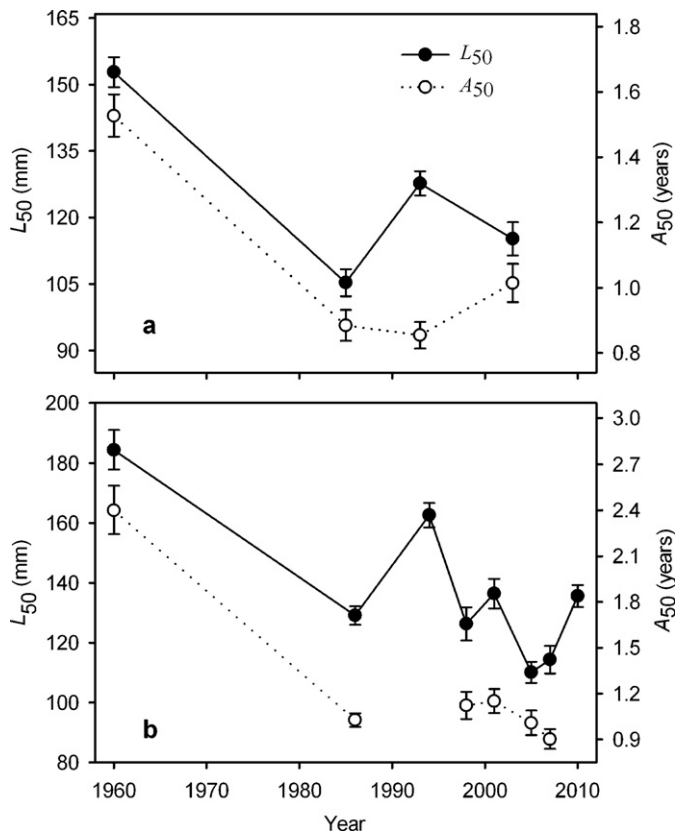
Fig. 3. (Continued).

**Table 3**

Comparison of length–maturation curves of female small yellow croaker between years in the two stocks.

Stock	Comparison between	RSS <sub>p</sub>	DF <sub>p</sub>	RSS <sub>s</sub>	DF <sub>s</sub>	F	Significance
The NYBS	1960 and 1985–1986	5.97	70	2.66	67	27.85	<0.001
	1985–1986 and 1993	3.73	46	2.67	43	5.69	<0.01
	1993 and 2003–2005	1.72	32	1.17	29	4.59	<0.01
The SYS	1960 and 1986	7.08	56	1.67	53	57.29	<0.001
	1986 and 1994	4.71	50	1.01	47	57.40	<0.001
	1994 and 1998	3.50	31	0.86	28	28.76	<0.01
	1998 and 2001	1.05	28	0.85	25	1.96	>0.05
	2001 and 2005	3.15	32	0.72	29	32.62	<0.001
	2005 and 2007	0.85	26	0.67	23	2.00	>0.05
	2007 and 2010	2.22	33	0.67	30	23.33	<0.001



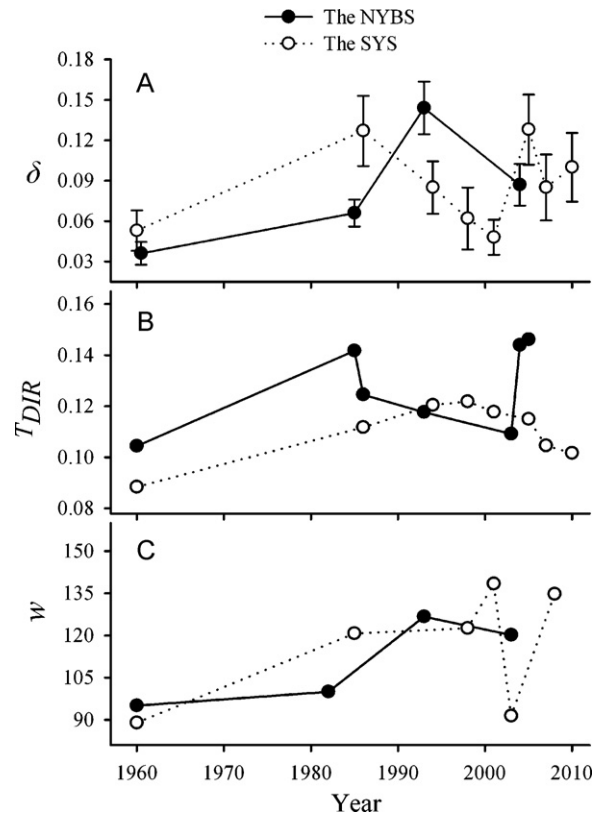


**Fig. 4.** Variations in  $L_{50}$  and  $A_{50}$  of female small yellow croakers in (a) the NYBS and (b) the SYS. Error bars show the 95% confidence intervals.

between  $\delta$  and the mean monthly SST ( $P < 0.05$ ). Hence, small yellow croaker with smaller  $L_{\infty}$ , living in relatively low-temperature waters tends to mature earlier and faster.

#### 4. Discussion

There are several stocks of small yellow croaker living in or migrating between the Bohai Sea, the Yellow Sea and the East China Sea. The stocks have been distinguished by their spawning and foraging grounds (Liu et al., 1990; Meng et al., 2003). The NYBS and the SYS are the two major stocks. The latter is the largest stock, accounting for 50% of the landings of this species (Jin et al., 2005). Growth patterns varied between stocks owing to the different habi-



**Fig. 5.** Variations in (A) the instantaneous rate of maturation ( $\delta$ ), (B) the daily rate of increase in SST from March to May ( $T_{DIR}$ ), and (C) growth potential at early age ( $\omega$ ) for the two stocks of small yellow croaker. Error bars show the 95% confidence intervals.

tats and fishing intensity. The entire Bohai Sea and most parts of the Yellow Sea were included in routine surveys (e.g., Jin and Tang, 1996; Tang et al., 2003). The sampling stations used for the analyses of this article were restricted to avoid the accidental inclusion of specimens from nearby stocks, which could introduce some bias in the result. Furthermore, small yellow croaker was infrequently caught in the areas far from spawning grounds in the spawning seasons, especially in the mid-1980s and the 1990s, which might be due to heavy fishing stress on the species. Hence, the impact of fish coming from stocks other than the NYBS or the SYS should not be significant, and the data represent the stocks alone.

**Table 4**  
Comparison of length–maturation curves of female small yellow croaker between the two stocks in the nearest years.

Stock	Comparison between	RSS <sub>p</sub>	DF <sub>p</sub>	RSS <sub>s</sub>	DF <sub>s</sub>	F	Significance
The NYBS and the SYS	1960 and 1960	3.08	67	1.96	64	12.27	<0.001
	1985–1986 and 1986	4.54	59	2.37	56	17.13	<0.001
	1993 and 1994	5.64	37	1.31	34	37.48	<0.001
	2003–2005 and 2005	5.71	30	0.58	27	79.12	<0.001

**Table 5**  
Results of the correlation analysis. Only the correlation coefficient tests with  $P < 0.1$  are shown.

Stock	Parameters	$\omega$	$L_{\infty}$	Mean monthly SST	Rate of daily increase in SST
The NYBS	$L_{50}$	–	–	–	–0.95*
	$\delta$	0.92*	–	–	–
The SYS	$L_{50}$	–	0.88**	–	–
	$\delta$	–	–	–0.72**	–

–: Denotes the test for the correlation coefficient was non-significant ( $P > 0.1$ ).

\* Significance at  $P < 0.1$  level.

\*\* Significance at  $P < 0.05$  level.

A significant decline in body length and age at median sexual maturity of the small yellow croaker was observed in this study. Jin (1996) also showed that the average body length in a spawner school was 227 mm for the SYS in the 1960s but was reduced to 147 mm in the 1980s. Lin and Cheng (2004) found that the mean body length at maturity of the small yellow croaker was 173.6 mm in 1983 and 123.4 mm in 2001 in the northern East China Sea. Although these values were calculated using different methods with data from a different sampling area, they also showed significant declines in body length at maturity. Johannessen et al. (2001) reported that the average total length at maturity of the small yellow croaker decreased by 10.0 mm from 1986 to 1994 in the Yellow Sea. A comparison of the trends in  $L_{50}$  between the results of Johannessen et al. (2001) and the present study in the Yellow Sea from 1986 to 1994 showed differences in results, with the present analysis tending to show that  $L_{50}$  increased over the period. These differences might be caused by different data sources; Johannessen et al. (2001) used the data obtained from pre-spawning seasons (March–April) in the Yellow Sea, whereas the results in the present study were based on the SYS specimens collected in the spawning season (April–May).

Previous studies identified a significant decrease in the small yellow croaker density due to overfishing and environment changes from 1960 to the beginning of 1990s (Liu et al., 1990; Jin and Tang, 1996; Kim et al., 1997). Over the same period, the most significant decreases in  $L_{50}$  and  $A_{50}$  occurred (Fig. 4). These declines might be attributed to the reductions in stock density, as supported by Johannessen et al. (2001). However, why  $L_{50}$  and  $A_{50}$  declined is still unclear. One hypothesis considered the declines in length (a proxy for age) at reproductive maturity as density-dependent phenotypic plasticity (Trippel, 1995; Heino and Godø, 2002; Ernande et al., 2004). The low stock density, caused by the overfishing or environmental changes, could release stocks from the intraspecific competition, therefore providing for more food per individual and enabling faster growth and earlier maturation if sexual maturity were size-based (Trippel, 1995). This density-dependent compensatory growth has been previously observed (Cardinale and Modin, 1999; Lorenzen and Enberg, 2002; Plaistow et al., 2004; Engelhard and Heino, 2004b) and was also proven in the NYBS and the SYS when higher growth rates were found in younger fish since the mid-1980s (Fig. 5C). The higher  $\omega$  value indicated faster maturity in the NYBS, and the smaller the size at maturity, the smaller the asymptotic body length in the SYS (Table 5). These results are in accordance with the current life history theory (Stamps et al., 1998; Roff, 2000). Hence, the variations in  $L_{50}$  and  $A_{50}$  of the small yellow croaker might be strongly density-dependent.

Since the early 1990s, stock assessments of the small yellow croaker have indicated an increase both in the relative stock density (catch per unit effort) and the percentile of total catches by weight (Jin, 2004; Xu and Jin, 2005; Zhang et al., 2009); however,  $L_{50}$  increased only in the early 1990s and then decreased continually;  $A_{50}$  changed slightly during stock recovery in two stocks, contrary to compensatory theory. These changes may be related to an evolutionary response and changes in environmental factors. The landings of the small yellow croaker have consisted principally of immature individuals since the mid-1990s (Jin et al., 2005; Yan et al., 2006). Consequently, fishery-induced genetic change in  $A_{50}$  could not be ruled out over the last twenty years (Engelhard and Heino, 2004b; Ernande et al., 2004; Law, 2007), resulting in difficulties to reverse in maturation schedule (Law, 2000). The fast warming and relatively high SST in the spring from the mid-1990s to the mid-2000s negatively impacted sexual maturation (Table 5). In the Bohai Sea and the northern Yellow Sea, fast warming may cause a rapid increase in sea water temperature. This change could accelerate sexual maturation by increasing the growth rate of fish and changing physiological characteristics (Domínguez-Petit et al.,

2008; Brander, 2010; Brown et al., 2010; Strüssmann et al., 2010). However, SST was usually higher in the SYS than the optimal hatching temperature (from 9.65 to 12.17 °C); the higher SST might compel spawners to migrate to deep water in the areas between strong YSCWM and other water masses (Lin et al., 2008). This pressure might be one reason that the instantaneous rate of maturation ( $\delta$ ) is negatively correlated with SST. In addition, the spawning season and grounds extended farther in the southern Yellow Sea (Lin et al., 2008). These changes might be adaptive strategies by this stock to survive the warmer spring.

The spawning stock of the small yellow croaker was dominated by one-year-old spawners recently. For example, 84.25% of female spawners were one-year-old fish in 2008 (Zhang et al., 2010). Continual heavy exploitation had led to a significant increase in absolute and relative fecundity (Zeng et al., 2005; Lin et al., 2009); however, the reproductive potential of young spawners was still lower than that of older spawners, as measured by low fecundity and small egg size (Trippel, 1995; Lin et al., 2009). The decrease in  $L_{50}$  and  $A_{50}$  would have prevented the decline in spawning stock biomass, further contributing to stock recovery. Nevertheless, these factors might have adverse effects on fish quality and the sustainable use of fishery resources. A new management program for stock conservation is urgently needed to reduce the proportion of immature fish in the catch. Such a strategy may be not effective to reverse the changes in the length and age at maturity but will alleviate the decrease in  $L_{50}$  and  $A_{50}$ . A new minimum legal size for fishing and marine reserves for spawning areas may be two such useful strategies for management (Heino and Godø, 2002; Mithé et al., 2010).

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## References

- Brander, K.M., 2010. Cod *Gadus morhua* and climate change: process, productivity and prediction. *J. Fish Biol.* 77, 1899–1911.
- Brown, M., Kawaguchi, S., Candy, S., Virtue, P., 2010. Temperature effects on the growth and maturation of Antarctic krill (*Euphausia superba*). *Deep-Sea Res. II* 57, 672–682.
- Cardinale, M., Modin, J., 1999. Changes in size-at-maturity of Baltic cod (*Gadus morhua*) during a period of large variations in stock size and environmental conditions. *Fish. Res.* 41, 285–295.
- Chen, Y., Harvey, H.H., 1994. Maturation of white sucker, *Catostomus commersoni*, population in Ontario. *Can. J. Fish. Aquat. Sci.* 51, 2066–2076.
- Chen, Y., Jackson, D.A., Harvey, H.H., 1992. A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. *Can. J. Fish. Aquat. Sci.* 49, 1228–1235.
- Chen, Y., Mello, L.G.S., 1999. Growth and maturation of cod (*Gadus morhua*) of different year classes in the Northwest Atlantic, NAFO subdivision 3Ps. *Fish. Res.* 42, 87–101.
- Chen, Y., Paloheimo, J.E., 1994. Estimating fish length and age at 50% maturity using a logistic type model. *Aquat. Sci.* 56, 206–219.
- Cheng, J., Qiu, S., Li, P., Cui, Y., 2004. The Eco-Environment and Bio-Communities in the Coastal Waters of the Bohai Sea and the Yellow Sea. China Ocean University Press, Qingdao (in Chinese).
- Domínguez-Petit, R., Korta, M., Saborido-Rey, F., Murua, H., Sainza, M., Piñeiro, C., 2008. Changes in size at maturity of European hake Atlantic populations in relation with stock structure and environmental regimes. *J. Mar. Syst.* 71, 260–278.
- Engelhard, G.H., Heino, M., 2004a. Maturity changes in Norwegian spring-spawning herring before, during, and after a major population collapse. *Fish. Res.* 66, 299–310.

- Engelhard, G.H., Heino, M., 2004b. Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary responses? *Mar. Ecol. Prog. Ser.* 272, 245–256.
- Ernande, B., Dieckmann, U., Heino, M., 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. *Proc. R. Soc. Lond. B* 271, 415–423.
- FAO, 2010. FIGIS – Web Site. Fisheries Global Information System (FIGIS). FAO Fisheries and Aquaculture Department [online], Rome, Updated 13.07.10 (cited 11.08.10) <http://www.fao.org/fishery/figis/en>.
- Gallucci, V.F., Quinn, T.J., 1979. Reparameterizing, fitting, and testing a simple growth model. *Trans. Am. Fish. Soc.* 108, 14–25.
- Gerritsen, H.D., Armstrong, M.J., Allen, M., McCurdy, W.J., Peel, J.A.D., 2003. Variability in maturity and growth in a heavily exploited stock: whiting (*Merlangius merlangus* L.) in the Irish Sea. *J. Sea Res.* 49, 69–82.
- Guo, X., Jin, X., Dai, F., 2006. Growth variations of small yellow croaker (*Pseudosciaena polyactis* Bleeker) in the Bohai Sea. *J. Fish. Sci. China* 13, 243–249 (in Chinese, with English abstract).
- Heino, M., Godø, O.R., 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. *Bull. Mar. Sci.* 70, 639–656.
- Hilborn, R., Walters, C.J., 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman & Hall, London.
- Jin, X., 1996. Ecology and Population Dynamics of Small Yellow Croaker (*Pseudosciaena polyactis* Bleeker) in the Yellow Sea. *J. Fish. Sci. China* 3, 32–46 (in Chinese, with English abstract).
- Jin, X., 2004. Long-term changes in fish community structure in the Bohai Sea. *China. Estuar. Coast. Shelf S.* 59, 163–171.
- Jin, X., Tang, Q., 1996. Changes in fish species diversity and dominant species composition in the Yellow Sea. *Fish. Res.* 26, 337–352.
- Jin, X., Zhao, X., Meng, T., Cui, Y., 2005. Biology Resources and Habitat Environment in Yellow and Bohai Seas. Science Press, Beijing (in Chinese).
- Johannessen, A., Iversen, S.A., Jin, X., Li, F., 2001. Biological investigations of anchovy and some selected fish species caught during the R/V “Bei Dou” surveys 1984–1999. *Mar. Fish. Res.* 22, 45–56.
- Kim, S., Jung, S., Zhang, C.L., 1997. The effect of seasonal anomalies of seawater temperature and salinity on the fluctuation in yields of small yellow croaker, *Pseudosciaena polyactis*, in the Yellow Sea. *Fish. Oceanogr.* 6, 1–9.
- Law, R., 2000. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* 57, 659–668.
- Law, R., 2007. Fisheries-induced evolution: present status and future directions. *Mar. Ecol. Prog. Ser.* 335, 271–277.
- Lin, L., Cheng, J., 2004. An analysis of the current situation of fishery biology of small yellow croaker in the East China Sea. *Period. Ocean Univ. China* 34, 565–570 (in Chinese, with English abstract).
- Lin, L., Cheng, J., Jiang, Y., Yuan, X., Li, J., Gao, T., 2008. Spatial distribution and environmental characteristics of the spawning grounds of small yellow croaker in the southern Yellow Sea and the East China Sea. *Acta Ecol. Sin.* 28, 3485–3494 (in Chinese, with English abstract).
- Lin, L., Jiang, Y., Yan, L., Gao, T., Wang, J., 2009. Study on the distribution characteristics and fecundity of spawning stock of *Larimichthys polyactis* in the southern Yellow Sea and the East China Sea. *J. Shanghai Ocean Univ.* 18, 453–459 (in Chinese, with English abstract).
- Liu, X., Wu, J., Han, G., 1990. Investigation and Division of the Yellow Sea and Bohai Sea Fishery Resources. Ocean Press, Beijing, p. 295 (in Chinese).
- Lorenzen, K., Enberg, K., 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proc. R. Soc. Lond. B* 269, 49–54.
- Meng, Z., Zhuang, Z., Jin, X., Tang, Q., Su, Y., 2003. Genetic diversity in small yellow croaker (*Pseudosciaena polyactis*) by RAPD analysis. *Biodivers. Sci.* 11, 197–203 (in Chinese, with English abstract).
- Miethe, T., Dytham, C., Dieckmann, U., Pitchford, J.W., 2010. Marine reserves and the evolutionary effects of fishing on size at maturation. *ICES J. Mar. Sci.* 67, 412–425.
- Nash, R.D.M., Pilling, G.M., Kell, L.T., Schön, P.-J., Kjesbu, O.S., 2010. Investment in maturity-at-age and length in northeast Atlantic cod stocks. *Fish. Res.* 104, 89–99.
- Olsen, E.M., Lilly, G.R., Heino, M., Morgan, M.J., Bratley, J., Dieckmann, U., 2005. Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 62, 811–823.
- Plaistow, S.J., Lapsley, C.T., Beckerman, A.P., Benton, T.G., 2004. Age and size at maturity: sex, environmental variability and developmental thresholds. *Proc. R. Soc. Lond. B* 271, 919–924.
- Qiu, W., Jiang, D., 1965. In: 1962 Committee of Marine Fisheries Resources Symposiums (Ed.), Primary Study on Reproductive Habit of Small Yellow Croaker, *Pseudosciaena polyactis*, in Southern Yellow Sea and East China Sea. Memoir of Marine Fisheries Resources, Shanghai, pp. 58–71 (in Chinese).
- Roff, D.A., 2000. Trade-offs between growth and reproduction: an analysis of the quantitative genetic evidence. *J. Evol. Biol.* 13, 434–445.
- Smith, T.M., Reynolds, R.W., Peterson, T.C., Lawrimore, J., 2008. Improvements to NOAA's Historical Merged Land-Ocean Surface Temperature Analysis (1880–2006). *J. Climate* 21, 2283–2296.
- Stamps, J.A., Mangel, M., Phillips, J.A., 1998. A new look at relationships between size at maturity and asymptotic size. *Am. Nat.* 152, 470–479.
- Strüssmann, C.A., Conover, D.O., Somoza, G.M., Miranda, L.A., 2010. Implications of climate change for the reproductive capacity and survival of New World silver-sides (family Atherinopsidae). *J. Fish Biol.* 77, 1818–1834.
- Su, J., Yuan, Y., Jiang, J., 1994. Advances in physical oceanography in China since the establishment of the PRC. *Acta Geophys. Sin.* 37 (Suppl. 1), 85–95 (in Chinese, with English abstract).
- Tang, Q., Jin, X., Wang, J., Zhuang, Z., Cui, Y., Meng, T., 2003. Decadal-scale variations of ecosystem productivity and control mechanisms in the Bohai Sea. *Fish. Oceanogr.* 12, 223–233.
- Trippel, E.A., 1995. Age at maturity as a stress indicator in fisheries. *BioScience* 45, 759–771.
- von Bertalanffy, L., 1938. A quantitative theory of organic growth (inquiries on growth laws II). *Hum. Biol.* 10, 181–213.
- Xu, B., Jin, X., 2005. Variations in fish community structure during winter in the southern Yellow Sea over the period 1985–2002. *Fish. Res.* 71, 79–91.
- Yan, L., Hu, F., Ling, J., Li, S., 2006. Study on age and growth of *Larimichthys polyactis* in the East China Sea. *Period. Ocean Univ. China* 36, 95–100 (in Chinese, with English abstract).
- Zeng, L., Jin, X., Li, F., Li, X., Dai, F., 2005. Fecundity and its variations of small yellow croaker (*Pseudosciaena polyactis*) in the Bohai Sea. *Mar. Sci.* 29, 80–83 (in Chinese, with English abstract).
- Zhang, B., Jin, X., Tang, Q., 2009. Functional groups of high trophic level communities in adjacent waters of Changjiang estuary. *Chin. J. Appl. Ecol.* 20, 344–351 (in Chinese, with English abstract).
- Zhang, G., Li, X., Jin, X., Zhu, J., Dai, F., 2010. Changes of biological characteristics of small yellow croaker (*Larimichthys polyactis*) in the central and southern Yellow Sea. *Acta Ecol. Sin.* 30, 6854–6861 (in Chinese, with English abstract).