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Size variability and natural mortality dynamics of anchovy *Engraulis japonicus* eggs under high fishing pressure

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ABSTRACT: Since the late 1990s, the anchovy *Engraulis japonicus* stock in the Yellow Sea has undergone considerable decline as a result of the enormous fishing pressure there. Reproductive characteristics have changed during the same period. Fisheries surveys were conducted in anchovy spawning grounds off south Shandong Peninsula in the Yellow Sea from 2000 to 2004, and in Laizhou Bay of the Bohai Sea, the wider Yellow Sea, and in coastal waters of the East China Sea from 2003 to 2008. Anchovy eggs from the spawning grounds south of the Shandong Peninsula (16 to 29 June 2003) had long axes ranging from 1.20 to 1.40 mm (1.28 ± 0.04 mm), and short axes ranging from 0.60 to 0.68 mm (0.64 ± 0.02 mm). In the coastal area of the East China Sea (7 to 14 May 2007), the eggs had long axes ranging from 1.12 to 1.40 mm (1.28 ± 0.06 mm) and short axes ranging from 0.55 to 0.68 mm (0.63 ± 0.03 mm). Compared with previous research results on anchovy egg size in Chinese waters and in other coastal regions of the North Pacific from the 1950s to 1970s, egg size was notably decreased both at the spawning grounds off the south Shandong Peninsula and in the coastal waters of the East China Sea. The natural mortality rate of anchovy eggs was 80.15% at the spawning grounds off south Shandong Peninsula, 77.63% in the Yellow Sea, and 82.95% in Laizhou Bay of the Bohai Sea. Based on our survey data, the natural mortality rate of anchovy eggs has been as high as 80% in the Bohai Sea, the Yellow Sea, and the East China Sea since the late 1990s. Compared with survey results for the Yellow Sea from the 1980s, the natural mortality rates of anchovy eggs have shown a significant rising trend. The decreased size and significantly increased natural mortality rate of anchovy eggs are long-term adaptive responses, via the reproductive biology of the anchovy population, to the enormous fishing pressure in the study area.

KEY WORDS: Egg size · Adaptive responses · Yellow Sea

INTRODUCTION

The anchovy *Engraulis japonicus* is one of the most important fish resources in the Yellow and East China Seas (Zhu & Iversen 1990). The annual biomass of anchovy stocks in the Yellow Sea was 205 × 10^4 to 410 × 10^4 t from 1986 to 1996, and its annual yield was almost 100 × 10^4 t from 1997 to 2000 (Fig. 1) (Zhao et al. 2003). Anchovies are an abundant small pelagic fish species in the Yellow Sea. They play an important role in food production and the sustainable use of fisheries. Anchovies mainly feed on zooplankton such as the copepod *Calanus sinicus* or the euphausiid *Euphausia pacifica*. At the same time, they are a major prey species for >40 higher level fishes such as *Scomberomorus niphonius*, *Pseudosciaena polyactis*, and *Trichiurus lepturus* (Wei & Jiang 1992). Hence, anchovies are an important

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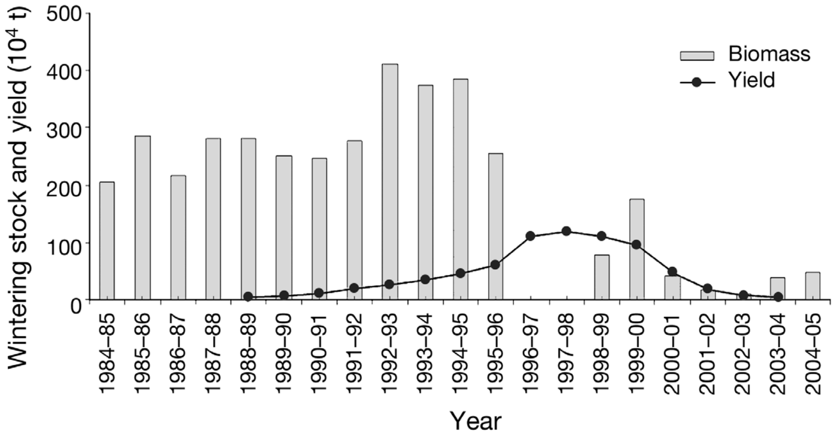

Fig. 1. *Engraulis japonicus*. Acoustic estimates of the wintering stock and annual yield of anchovy in the Yellow Sea, 1985–2005 (Zhao et al. 2003, Zhao 2006)

intermediate link between zooplankton and higher level fish species in food webs. As such, anchovies are one of the key species in the marine ecosystem, playing an important role in energy flow and conversion (Tang et al. 2005).

Since the late 1990s, the anchovy stock in the Yellow Sea has been under enormous fishing pressure and its annual biomass dropped from 410 × 10^4 t in 1993 to 18 × 10^4 t in 2002 (Zhao et al. 2003), and to a historic low in 2003 of only 11 × 10^4 t (Fig. 1) (Zhao 2006). The anchovy stock underwent a serious decline in just 10 yr. The annual biomass remained at a low of 25 × 10^4 to 30 × 10^4 t during 2004 and 2005 (Fig. 1) (Zhao 2006).

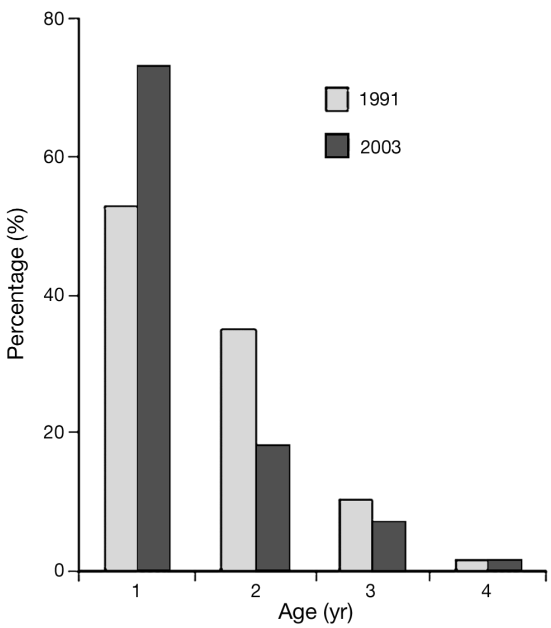

Fig. 2. *Engraulis japonicus*. Annual variation in age composition of anchovy spawning stock (Li et al. 2006)

Moreover, significant changes took place in the biological characteristics of this stock. (1) A trend towards a smaller size and a lower age of the anchovy spawning stock in the Yellow Sea occured (Fig. 2) (Li et al. 2006). (2) Individual fecundity increased significantly within a certain range of fork lengths and body weights (Tables 1 & 2) (Zeng et al. 2005). (3) The growth rates of 1 to 3 yr old recruits increased in terms of both body length and weight (Zhu et al. 2007). These changes in biological characteristics reflect the adaptive responses of anchovy stock to maintain stock survival and sustainable reproduction under enormous fishing pressure (Zeng et al. 2005, Li et al. 2006).

The variation in fishery resources depends on year-class strength, which is determined by the status of stock–recruitment relationships (Hjort 1914). The survival rate in the early life-history stages of fishes is closely related to the status of recruitment to adult

Table 1. *Engraulis japonicus*. Fecundity (number of eggs) within a range of fork lengths (95 to 127 mm) from May to July during the periods 1985–1986 and 2002–2004 (Zeng et al. 2005). Means ± SD for n individual fish. F_L: relative fecundity by length; F_W: relative fecundity by weight

Year	Absolute fecundity (no. of eggs)	F_L (eggs mm^{-1})	F_W (eggs g^{-1})
1985–1986	6187 ± 837 (n = 252)	53 ± 7 (n = 252)	554 ± 62 (n = 252)
2002–2004	12450 ± 537 (n = 147)	106 ± 4 (n = 147)	987 ± 39 (n = 147)
t-test	*t* = 6.2946, p < 0.01	*t* = 6.7071, p < 0.01	*t* = 5.9366, p < 0.01

Table 2. *Engraulis japonicus*. Fecundity (number of eggs) within a range of net body weights (5 to 14 g) from May to July during the periods 1985 to 1986 and 2002 to 2004 (Zeng et al. 2005). Means ± SD for n individual fish. F_L: relative fecundity by length; F_W: relative fecundity by weight

Year	Absolute fecundity (no. of eggs)	F_L (eggs mm^{-1})	F_W (eggs g^{-1})
1985–1986	5908 ± 842 (n = 252)	51 ± 7 (n = 252)	532 ± 62 (n = 252)
2002–2004	11171 ± 542 (n = 147)	98 ± 5 (n = 147)	999 ± 48 (n = 147)
t-test	*t* = 5.2573, p < 0.01	*t* = 5.8137, p < 0.01	*t* = 5.9376, p < 0.01

stocks (Houde 1987, 1989). It has an important role in determining abundance and has been recognized as an important factor in the fluctuation of fishery resources (Campana et al. 1989, Van der Veer et al. 1990, Hovenkamp 1992, Ellis & Nash 1997).

As one of the key species in the marine ecosystem (Tang et al. 2005), the considerable decline of the anchovy stock has had a significant effect on the relationship between food web species in the Yellow Sea, on the structure and function of the ecosystem, on the sustainable development of marine fishery resources, and on food production (Zhao et al. 2003). Determining the survival status of the fish during early life stages will help to better understand the stock–recruitment relationships. This provides important information for management of this fisheries stock and the study of its ecosystem.

The main spawning season of the anchovy extends from March to October in the East China Sea and from April to October in the Yellow Sea. We analyzed the size and survival rate of anchovy eggs during the past 2 decades with reference to previous research results in Chinese waters and in other coastal regions of the North Pacific (Uchida 1958, Jiang & Zheng 1984, Ruan 1984, Chen 1985, Wan & Jiang 1998, Wan et al. 2004, Wan 2005, Wan & Sun 2006). The long-term adaptive response of the reproductive biology of the anchovy stock under high fishing pressure is discussed. This study aims to collect basic information to better understand the early recruitment mechanism and the recruitment process of the anchovy stock, as well as to provide biological information the spawning ground surveys of anchovy in the future.

MATERIALS AND METHODS

A 5 yr multidisciplinary investigation of the *Engraulis japonicus* spawning grounds in waters south of the Shandong Peninsula was conducted aboard the RV 'Beidou' of the Yellow Sea Fisheries Research Institute from May to July in 2000 to 2004. The coordinates of the research area were 33° 30′ N to 37° 00′ N and 120° 00′ to 124° 00′ E. Detailed information on the research surveys is listed in Table 3. Research stations are shown in Fig. 3. Additionally, multidisciplinary investigations, e.g. on the abundance and distribution patterns of fish eggs in the spawning grounds of Laizhou Bay (Bohai Sea) were conducted. The area for this research extended from 37° 15′ to 38° 30′ N and 119° 00′ to 121° 00′ E; 16 stations were investigated from May to June in 2003 and 2006, and 37 stations from May to June in 2008 (Fig. 4). Also, investigations with the same objectives were performed during fishery resource surveys in the Yellow Sea, in which the research area was from 32° 00′ to 39° 00′ N, 121° 30′ to 125° 00′ E. A total of 40 sample stations were set up in September 2006, and 70 sample stations in August 2007. Moreover, investigations on the abundance and distribution patterns of fish eggs in the coastal waters of the East China Sea were conducted from 7 to 14 May 2007. The research area was from 26° 50′ to 32° 00′ N, 120° 50′ to 124° 00′ E, and 32 stations were investigated.

Table 3. Surveys in spawning grounds of *Engraulis japonicus* in waters south of Shangdong Peninsula. A = anchored station, B = background fixed station, T = thick egg area searching, W = water mass drift observation

Date of survey	No. of stations	Method		Geographic coordinates of Stns A or W
13–26 Jun 2000	25	B	A	35° 31.5′ N, 122° 31.4′ E; 34° 59.9′ N, 121° 00.7′ E
16–22 May 2001	25	B		
13–23 Jun 2001	38	T	A	35° 00.9′ N, 121° 00.8′ E; 34° 52.6′ N, 120° 22.3′ E
4–8 Jul 2001	29	T	A	35° 00.1′ N, 120° 59.5′ E
5–11 Jun 2002	48	B		
17–23 Jun 2002	30	T	W	35° 00.0′ N, 120° 41.0′ E
1–4 Jul 2002	30	T	W	35° 10.6′ N, 121° 01.1′ E
11–18 Jun 2003	50	B	W	35° 01.9′ N, 120° 32.9′ E
24–30 Jun 2003	22	T	W	35° 05.1′ N, 120° 35.4′ E; 35° 03.3′ N, 120° 26.4′ E
10–16 Jun 2004	42	B		
26 Jun–3 Jul 2004	20	T	W	35° 00.0′ N, 121° 01.0′ E; 34° 59.0′ N, 120° 38.0′ E; 35° 01.0′ N, 120° 35.0′ E

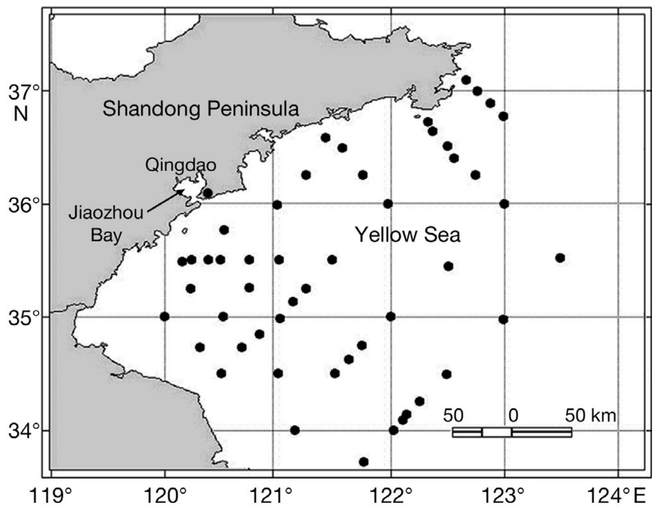

Fig. 3. Sampling stations (●) in spawning grounds of *Engraulis japonicus* south of the Shandong Peninsula, 2000–2004

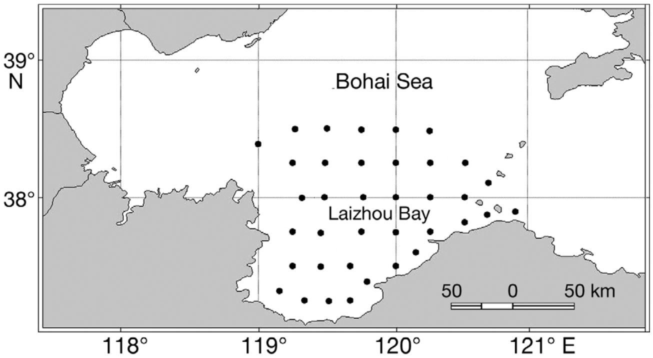

Fig. 4. Sampling stations (●) for *Engraulis japonicus* in spawning grounds in Laizhou Bay, Bohai Sea, May 2008

The eggs were collected mainly by towing a 80 cm diameter plankton net with a mesh size of 0.50 mm along the sea surface. The trawling speed was 3.0 nautical mile h^{-1} for 10 min at each station. The samples were fixed in 5% formalin seawater.

Individual counts, developmental stages, and the egg mortality of the anchovy eggs were determined using a Nikon SMZ1500 photomicroscope equipped with a micrometer ocular lens. Furthermore, the size of anchovy eggs collected both in the spawning grounds off the south Shandong Peninsula from 16 to 29 June 2003 and in the coastal waters of the East China Sea from 7 to 14 May 2007 was measured. However, malformed eggs at the gastrula and embryonic developmental stages were not calculated in measurement of non-viable egg sizes.

The structural basis for discrimination of non-viable eggs includes the lack of a transparent egg membrane; turbidity of the entire egg, with no discernable structures (Fig. 5a); loose, cracked, or broken yolk sacs (Fig. 5b); incomplete epiboly on the underside of the yolk sac, parts of the yolk sac, or tissue free in the egg chamber in the blastula (Fig. 5c–f); and malformations in the blastodisc, blastomeres (Fig. 5g,h), blastula (Fig. 5c), or the embryo (Fig. 5e,f). (Fig. 6a–e) illustrates different developing stages of viable eggs to enable comparison with dead ones. Photographs of eggs were taken by a Nikon SMZ1500.

The methods of sampling anchovy eggs used in our previous studies are described in Table 3.

Egg size variation at the gastrula, tail-bud, and embryonic stages in the spawning grounds off south Shandong Peninsula and in the coastal waters of the East China Sea was examined (Table 4) and initially tested separately by Kruskal-Wallis 1-way ANOVA. A Mann-Whitney *U*-test was used to examine the size variations between viable and non-viable eggs within the spawning grounds off south Shandong Peninsula and in the coastal waters of the East China Sea separately. Variations in the size of viable eggs between spawning grounds off south Shandong Peninsula and in the coastal waters of the East China

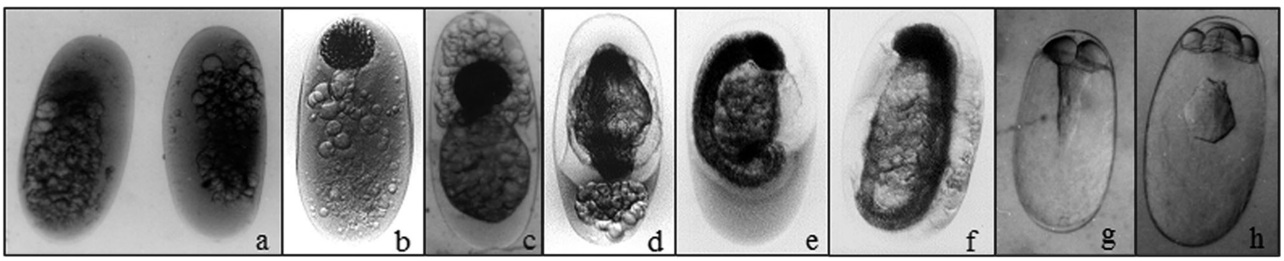

Fig. 5. *Engraulis japonicus*. Malformations during embryonic development: (a) turbidity of the entire egg with no discernable structures; (b) loose and broken yolk sac; (c,d) incomplete epiboly on the underside of the yolk sac, parts of the yolk sac, or tissue free in the egg chamber in the blastula, malformations in embryonic development; (e,f) parts of the yolk sac, or tissue free in the egg chamber, malformations in the blastodisc; (g,h) malformations in the blastomeres

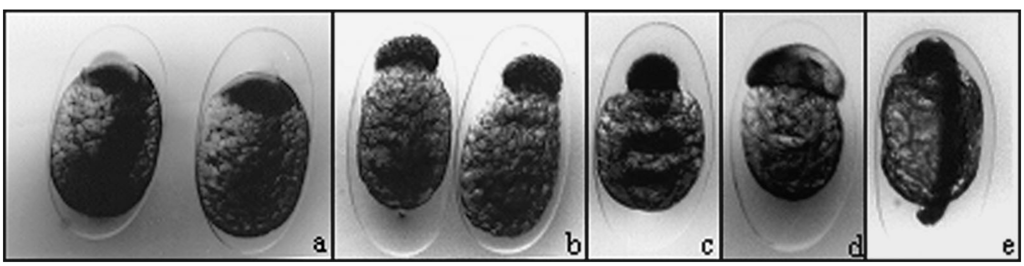

Fig. 6. *Engraulis japonicus*. Normal eggs during embryonic development: (a) unsegmented fertilized, (b) late cleavage stage, (c) early blastula stage, (d) late blastula stage, and (e) embryo three-quarters around yolk sac

Table 4. *Engraulis japonicus*. Anchovy egg size given as a range and mean ± SD (in parentheses). n = number of samples

Area	Developmental stage	Long axis (mm)	Short axis (mm)	Volume (mm^3)	n	Source
Spawning grounds off south Shandong Peninsula (16–29 Jun 2003)	Non-viable eggs	1.20–1.26 (1.24 ± 0.01)	0.60–0.66 (0.63 ± 0.01)	0.234–0.278 (0.256 ± 0.011)	100	Present study
	Gastrula stage	1.20–1.34 (1.28 ± 0.04)	0.60–0.68 (0.64 ± 0.02)	0.226–0.310 (0.276 ± 0.021)	88	
	Tail-bud stage	1.22–1.40 (1.29 ± 0.04)	0.60–0.68 (0.64 ± 0.02)	0.230–0.339 (0.281 ± 0.023)	68	
	Embryonic stage	1.22–1.36 (1.27 ± 0.03)	0.60–0.68 (0.64 ± 0.02)	0.230–0.330 (0.276 ± 0.024)	76	
	Viable eggs	1.20–1.40 (1.28 ± 0.04)	0.60–0.68 (0.64 ± 0.02)	0.226–0.339 (0.278 ± 0.023)	232	
Coastal waters of the East China Sea (7–14 May 2007)	Non-viable eggs	1.10–1.39 (1.25 ± 0.06)	0.55–0.67 (0.62 ± 0.02)	0.192–0.309 (0.254 ± 0.025)	133	
	Gastrula stage	1.12–1.40 (1.28 ± 0.07)	0.55–0.68 (0.63 ± 0.03)	0.204–0.338 (0.264 ± 0.031)	145	
	Tail-bud stage	1.12–1.39 (1.30 ± 0.04)	0.55–0.68 (0.64 ± 0.02)	0.184–0.313 (0.268 ± 0.025)	72	
	Embryonic stage	1.19–1.38 (1.26 ± 0.04)	0.56–0.68 (0.63 ± 0.02)	0.203–0.314 (0.260 ± 0.022)	86	
	Viable eggs	1.12–1.40 (1.28 ± 0.06)	0.55–0.68 (0.63 ± 0.03)	0.184–0.338 (0.264 ± 0.028)	303	
Jiaozhou Bay in Yellow Sea (14 May–3 Jun 1963)		1.21–1.71 1.34[a]	0.57–0.85 0.67[a]	0.315[a]		Ruan (1984)
East China Sea (1958–1964)		1.08–1.57	0.55–0.70			Chen (1985)
Fishing ground of the south Fujian and Taiwan Bank (Apr 1974–Mar 1977)		1.16–1.40 1.29[b]	0.60–0.71 0.63[b]	0.268[b]		Jiang & Zheng (1984)
Coastal ocean of Japan (1958)		1.4–1.6	0.6–0.7			Uchida (1958)

[a]Mean in June; [b]mean

Sea were determined by Mann-Whitney *U*-test. A one-sample *t*-test was run to determine the variations in anchovy egg size between the current study and previous research results in Chinese waters from the 1950s to 1970s. The volume of anchovy eggs used in comparisons was calculated as:

$$\text{Egg volume} = \frac{4}{3}\pi \times \frac{(\text{long axes})}{2} \times \left[\frac{(\text{short axes})}{2}\right]^2 \quad (1)$$

Natural mortality rates of anchovy eggs, i.e. the percentage of naturally occurring dead eggs, was calculated based on the abundance of dead anchovy eggs and the abundance of all eggs examined during 1 cruise:

$$\text{Non-viable eggs (\%)} = \frac{\text{No. of non-viable eggs}}{\text{No. of total eggs}} \times 100\% \quad (2)$$

Natural mortality rates of anchovy eggs in the Bohai Sea, Yellow Sea, and East China Sea surveys (Table 5) after 1990 were compared with the survey results from the 1980s (Table 5) in the Yellow Sea by using the chi-squared test.

RESULTS

Changes in size of the anchovy egg

Engraulis japonicus eggs are ellipsoid, isolated, and pelagic (Uchida 1958, Jiang & Zheng 1984, Ruan 1984, Chen 1985). The analysis of the measurements showed that there was no variation in the size of anchovy eggs at the gastrula, tail-bud, or embryonic stages in spawning grounds off the south Shandong Peninsula ($H_{(2,n = 232)}$ = 0.923, p = 0.6302 > 0.05; Kruskal-Wallis 1-way ANOVA) or in the coastal waters of the East China Sea ($H_{(2, n = 303)}$ = 2.64, p = 0.267 > 0.05; Kruskal-Wallis 1-way ANOVA) (Table 4). The viable eggs off the southern Shandong Peninsula had long axes ranging from 1.20 to 1.40 mm (1.28 ± 0.04 mm) and short axes from 0.60 to 0.68 mm (0.64 ± 0.02 mm). The non-viable eggs, with long axes ranging from 1.20 to 1.26 mm (1.24 ± 0.01 mm) and short axes ranging from 0.60 to 0.66 mm (0.63 ± 0.01), were significantly smaller than viable eggs (*U* = 1298.5, p < 0.01; Mann-Whit-

Table 5. *Engraulis japonicus.* Natural mortality rates of anchovy eggs. n = number of eggs

Survey area	Survey time	n	Non viable eggs (%)	Source
Spawning grounds off south Shandong Peninsula	13–18 Jun 2000	28 907	83.41	Present study
	16 May–6 Jul 2001	86 872	84.87	
	5–20 Jun 2002	51 231	81.34	
	11–17 Jun 2003	175 115	80.42	
	10–19 Jun 2004	124 510	75.22	
	Total	466 635	80.15	
Yellow Sea	Sep 2006	344	77.33	
	Aug 2007	3473	77.66	
	Total	3817	77.63	
Laizhou Bay of Bohai Sea	May 2003	116 194	82.52	
	May 2004	8391	87.70	
	Jun 2005	4311	70.38	
	May 2006	11 575	87.02	
	May–Jun 2008	10 035	84.68	
	Total	150 506	82.95	
East China and Yellow Seas	26 Mar–24 Apr 2001	14 379	88.09	Wan & Sun (2006)
Yellow Sea	15 May–18 Dec 1998	59 838	83.57	Wan (2005)
Bohai Sea	25 May–16 Oct 1998	118 933	91.33	Wan et al. (2004)
Yellow Sea	11 Mar–14 Jun 1985	800 999	64.10	Wan & Jiang (1998)

ney *U*-test). The viable eggs in the coastal waters of the East China Sea had long axes ranging from 1.12 to 1.40 mm (1.28 ± 0.06 mm) and short axes ranging from 0.55 to 0.68 mm (0.63 ± 0.03 mm). The non-viable eggs, with long axes ranging from 1.10 to 1.39 mm (1.25 ± 0.06 mm) and short axes ranging from 0.55 to 0.67 mm (0.62 ± 0.02 mm), were also significantly smaller than viable eggs ($U = 13423$, $p = 0.002 < 0.01$; Mann-Whitney *U*-test).

The anchovies distributed in the Northwest Pacific Ocean belong to the same population (Liu et al. 2006). The geographical distribution area includes the western and northern East China Sea, the Yellow Sea, the Sea of Japan, the western coast of Kyushu in Japan, the Seto Inland Sea, and the Pacific coast of the Japanese archipelago (Whitehead et al. 1988). Thus, the anchovy eggs from different sea areas were comparable in size. The anchovy eggs collected at the spawning grounds off the south Shandong Peninsula from 16 to 29 June 2003, were significantly smaller than those collected in Jiaozhou Bay of the Yellow Sea from 14 May to 3 June 1963 ($t = -26.479$, df = 231, tested value = 0.629, $p < 0.01$; 1-sample *t* test) (Table 4). The anchovy eggs collected in the coastal waters of the East China Sea in May 2007 were slightly smaller than those collected in the same areas from 1958 to 1964 (Table 4), but they were significantly smaller than those collected at the fishing ground off the southern Fujian and Taiwan Bank from April 1973 to March 1977 ($t = -2.409$, df = 302, tested value = 0.536, $p = 0.017 < 0.05$; 1-sample *t*-test). Also, the anchovy eggs currently collected were significantly smaller than those distributed off the coasts of Japan in 1958 (Table 4). The comparison above indicates that the egg size both in the spawning grounds off the south Shandong Peninsula and in the coastal waters of the East China Sea decreased significantly under the enormous fishing pressure.

The spawning grounds off the south Shandong Peninsula are located at a higher latitude than the coastal waters of the East China Sea. As a rule, egg sizes of a certain teleost species increase with increasing latitude (Xia & Liu 1981). Though the anchovy stock has undergone serious decline in just 10 yr, the anchovy eggs currently collected at spawning grounds off south Shandong Peninsula were still significantly larger than those collected in the coastal waters of the East China Sea ($U = 11875$, $p < 0.01$; Mann-Whitney *U*-test). This coincides with the rule of geographical variation.

Natural mortality rates of anchovy eggs

Based on a 5 yr consecutive survey performed at the spawning grounds off south Shandong Peninsula during May to June from 2000 to 2004, the natural mortality rates of anchovy eggs were always >80 %, except for that from 10 to 19 June 2004 when it was only 75.22%. The 5 yr total mean natural mortality rate of anchovy eggs was 80.15% (Table 5). The natural mortality rate of anchovy eggs is 77.63% according to Yellow Sea fishery resource surveys conducted in September 2006 and August 2007 (Table 5). The natural mortality rate of anchovy eggs in Laizhou Bay of Bohai Sea also reached >80% from May 2003 to June 2008, except in June 2005, when the natural mortality rate was only 70%. The 5 yr total mean natural mortality rate of anchovy eggs distributed in Laizhou Bay of the Bohai Sea was 82.95% (Table 5). In this study, non-viable eggs included those with malformations at embryonic developmental stages (Bunn et al. 2000).

Based on the data outlined in Table 5, the natural mortality rates of anchovy eggs in the Bohai Sea, the Yellow Sea, and the East China Sea have all reached up to 80% since the late 1990s. Compared with the 1980s survey results in the Yellow Sea, the natural mortality rates of anchovy eggs showed a significantly rising trend under the enormous fishing pressure there (χ^2 = 38.88, df = 5, $p < 0.01$; chi-squared test).

Based on microscopial inspection of total egg numbers, 5 to 10% of the >80% of non-viable anchovy eggs were fertilized and developed to either the gastrula stage or the late embryonic stage. However, among the rest it could not be discriminated whether they were fertilized or not.

DISCUSSION

The high natural mortality rate of fish eggs reduces the effective fecundity of the brood stock (Anderson 1988). In particular, given the severe decline of the anchovy *Engraulis japonicus* stock in recent years, the significant increase in mortality rates of anchovy eggs is extremely unfavorable for the recovery of anchovy resources, which may even affect the balance of the marine ecosystem (Zhao et al. 2003). The numerous factors that cause natural mortality of fish eggs can be broadly divided into 2 categories, exogenous and endogenous (Heath 1992). Exogenous causes include predation (Hunter & Kimbrell 1980, Toesen 1985), diseases and parasites (Ojaveer 1981, Menses & Ré 1989), effects of harmful and toxic algae (Aneer 1987), pollutants (Longwell & Hughes 1981), and physical damage (Wood 1981). Endogenous sources of mortality stem from inherited genetic, physiologic, or other non-external factors that induce dysplasia (Heath 1992), such as poor quality of eggs and sperm (Kjørsvik et al. 1990) and fertilization restrictions (the relative density of sperm and eggs or unfavorable aquatic environment) among other factors (Bobe & Labbé 2010). The quality of eggs, immature or overmature, may result in failed fertilization or abnormal development after fertilization (McEvoy & McEvoy 1992). However, until now, much of the mechanism through which endogenous factors cause mortality of fish eggs remains unclear (Bunn et al. 2000, Bobe & Labbé 2010).

Anchovies are multiple spawners typically displaying group-synchronous ovary development and batch spawning (Funamoto & Aoki 2002). Egg quality among the different age groups of the spawning stock varies greatly (Solemdal et al. 1995). Variations may also exist among different batches (McEvoy & McEvoy 1992). A significant proportion of anchovy eggs spawned in the field may have been unsuitably mature, which led to the high mortality rate of the eggs. Moreover, egg mortality of first-time spawners is significantly higher than that of repeat spawners in the same spawning stock (Solemdal 1997). Additionally, gonadal development and the quality of eggs and sperm are significantly affected by the lower age and decreased mean length of anchovy spawning stock (Li et al. 2006), as well as by significantly increased individual fecundity (Zeng et al. 2005). All of these factors could affect fertilization rates, causing a marked increase in the mortality rates of anchovy eggs (Bobe & Labbé 2010).

In anchovy, ovulation, ejaculation, and fertilization of the brood stock all occur within a short period. The abundance and density of the spawning stock sharply dropped due to the decline in anchovy resources (Li et al. 2006). These changes might affect the relative density of eggs and sperm in the aquatic environment, thereby causing the low fertilization rates and significantly increased mortality of eggs. Thus, it is necessary to conduct further studies on spawning behavior, including the duration of egg viability after ovulation and the initiation of the fertilization process.

Pseudo-gamy and pseudo-cleavage also occur in teleost eggs (Lou & Zheng 1981). Accurately determining egg status, i.e. whether they are already fertilized or not, through a morphologic method is difficult. Thus, non-viable eggs that had developed until the cell division stage were not included in the aforementioned 80% natural mortality rate. Consequently, mortality rates might be slightly underestimated. To better understand the mechanism of early recruitment in the anchovy stock, the causes of egg mortality should be interpreted; the fertilization status of non-viable eggs, including those that develop to the cell division stage, should be determined; and the endogenous and exogenous factors, as well as the pathogenesis of mortality should be clarified. The standard cytological features of fertilized and pseudo-gamy eggs should be defined to provide a more reliable basis for testing samples collected in the field. Therefore, determination of fertilization status of non-viable eggs is one of the most important scientific issues in studying the process and mechanism behind anchovy recruitment. Furthermore, monitoring of the anchovy fishery, as well as regulating the fishing effort and fishing capacity to ensure sustainable utilization of the anchovy stock, is of great significance.

The size of anchovy eggs declined in the spawning grounds off south Shandong Peninsula and in the coastal waters of the East China Sea. Non-viable eggs were significantly smaller than the viable ones.

A characteristic trend towards lower age and decreased mean length has been reported for the anchovy spawning stock (Li et al. 2006). Moreover, individual fecundity has increased at comparable fork lengths and weight ranges (Zeng et al. 2005). All of the above have contributed to decreases in anchovy egg size. The perivitelline spaces of the eggs swelled insufficiently due to the absorption of water, causing non-viable eggs to be significantly smaller than viable eggs, both in the spawning grounds off south Shandong Peninsula ($U = 1298.5$, $p < 0.01$; Mann-Whitney U-test) and in the coastal waters of the East China Sea ($U = 13423$, $p = 0.002 < 0.01$; Mann-Whitney U-test).

The decreased size and significantly increased natural mortality rates of anchovy eggs are long-term adaptive responses, via the reproductive biology of the anchovy population, to an enormous fishing pressure.

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