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Fishery Biological Characteristics and Changes in the Annual Biomass of Bigeye Kilka (*Clupeonella grimmi*) in the Caspian Sea

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Abstract

Through most of the last century, three endemic kilka species supported the major commercial species in the Caspian Sea. Recent changes in the Caspian Sea ecosystem have occurred as a consequence of climate change and ecological change caused by the invasive ctenophore *Mnemiopsis leidyi*. We examined the impact of these changes on the population biology of bigeye kilka (*Clupeonella grimmi*) in Iranian waters of the Caspian Sea from 1995 to 2001. The overall sex ratio (male:female) was 1.65:1. The length-weight regression was $W = 0.00922L^{2.851}$ (females) and $W = 0.008021L^{2.907}$ (males) indicating a negative growth for both sexes. Growth parameters were estimated as L_∞ = 142 mm, K = 0.28 yr^{-1}, t_0 = -1.39 yr. The instantaneous coefficient of natural mortality was estimated as 0.460 yr^{-1} and the instantaneous coefficient of fishing mortality varied between 0.469 to 0.980 yr^{-1}. Biomass of the bigeye kilka increased from about 36,900 mt in 1995 to more than 53,500 mt in 1998, but declined to less than 5,900 mt in 2001. This decrease in bigeye kilka was simultaneous with a sharp reduction in anchovy kilka due to the combined effects of fishing and changes in zooplankton abundance and composition soon after the appearance of *Mnemiopsis leidyi* in the Caspian Sea.

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Introduction

The most abundant fish of the Caspian Sea are three small clupeids collectively called "kilka", which are anchovy kilka (*Clupeonella engrauliformis* Svetovidov 1941), common kilka (*C. cultriventris caspia* Bordin 1904), and bigeye kilka (*C. grimmi* Kessler 1877) (Svetovidov 1963). All three kilka species are targeted by the local commercial fisheries that use underwater electric lights and fish pumps (Nikonorov 1964). Annual catches of kilka in the Caspian Sea reached about 423,000 mt in 1970 (Ivanov 2000). Kilka fishing in Iran started with six ships in the port of Anzali in 1970. Until 1976, annual kilka catches were less than 4,000 mt (Razavi 1993). Between 1989 and 1998, fishing activities and the number of fishing vessels increased steadily reaching to about 195 vessels. Iran increased its quota of kilka to 95,000 mt in 1999. In the next few years, however, the catch sharply decreased to 19,500 mt in 2004.

Bigeye kilka inhabits the relatively deeper areas of the central and southern Caspian Sea. Bigeye differs from the two other species of kilka in their distinctive adaptation to greater depths (Prikhod'ko 1981). For instance, they have bigger eyes, structural difference in their retinas and greater transparency of the tissues (Prikhod'ko 1981). The larvae of bigeye kilka remain further offshore in depths exceeding 70 m, compared to the anchovy kilka. They are stenohaline and reside at lower water temperature (Prikhod'ko 1981).

Research on bigeye kilka in Iranian waters in the Caspian Sea had been limited to the distribution (Besharat and Khatib 1993) and stock assessment by hydroacoustic methods during 1994-1996 (Poorgholam et al. 1996; Fazli and Besharat 1998). However, quantitative assessments are necessary for the effective utilization and management of the stock. Despite the economic importance of the kilka, little information about sex, age, growth and mortality of kilkas in Iranian waters is available. Further, an invasive jellyfish (Ctenophora, *Mnemiopsis leidyi*), appeared in 1999 (Ivanov et al. 2000). In the 1890s, the invasive species introduced in the Black Sea, radically affected the whole ecosystem (Vinogradov et al. 1989). The objective of the present study is to fill the information gaps on the population biology, estimate the biomass of bigeye kilka (*Clupeonella grimmi*) and provide a basis for improved and effective management of bigeye kilka in Iranian waters.

Materials and Methods

Sampling

Sampling areas were located in the fishing regions in the Iranian Provinces of Mazandaran (with two sampling locations: Amir-abad and Babolsar harbors) and Guilan (with one sampling site: Anazali port) (Fig. 1).

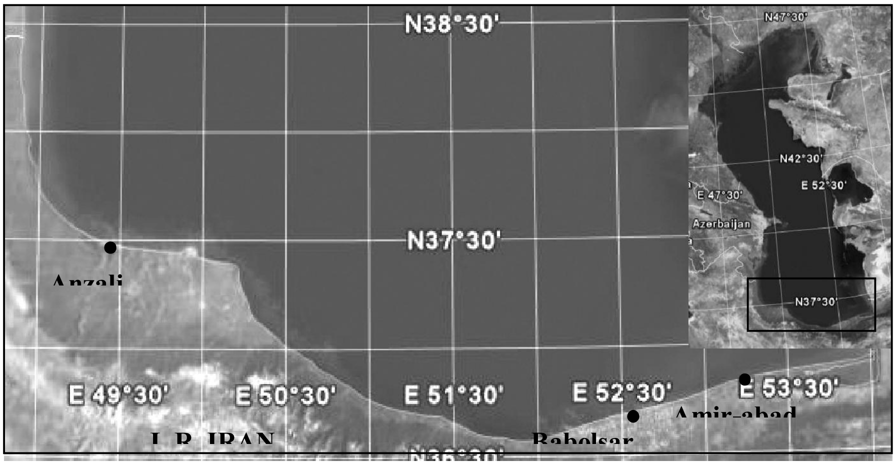


Figure 1. The Caspian Sea (insert) and three Iranian fishing regions of kilkas in the Iranian waters of the Caspian Sea (Amir-abad, Babolsar harbors and Anzali port). Source: http://earth.google.com/

The bigeye kilka examined in this study were caught by commercial vessels at depths ranging from 40 to 100 m using conical lift nets equipped with underwater electric lights. Generally, the diameter of the hoop of a conical lift net is 2.5 to 3 m. There are two underwater electric lamps (about 2 kW) and the length of the net bag is at least 1.25 times greater than the diameter of the hoop (Ben-Yami 1976). The mesh size between two knots of the net was 7-8 mm. To protect the conical net against excessive stress, fishermen use salvage net with a large mesh and a thicker twine mounted to the hoop. The size and configuration of the conical lift nets are nearly identical among all fishing vessels. The fishing vessels are small (15-100 t capacity) and fishing operations are conducted only at night.

Total catches of kilkas by each vessel, recorded by fishermen in both regions, were collected by the Iranian Fisheries Organization (Mazandaran and Guilan branches). Catch data collected during the years of 1995-2001 were used as input data for this study (Fig. 2).

Field sampling of commercial catches was conducted by staff of the Caspian Sea Ecology Research Center and Guilan Fisheries Research Center/IFRO in the Iranian provinces of Mazandaran and Guilan during 1995-2001. During 2002-2004 the catch of bigeye kilka collapsed (Fig. 2), and samples collected were not enough. After identification of the species, 20-150 specimens of bigeye kilka were randomly selected every fortnight in each province. The samples were initially sorted into size bins according to 5 mm (fork) length interval. Then, the total weight (to the nearest 0.1 g), sex and maturity stages of ovary were recorded. Maturity was classified into six macroscopic stages of ovarian development defined by Poorgholam et al. (1996).

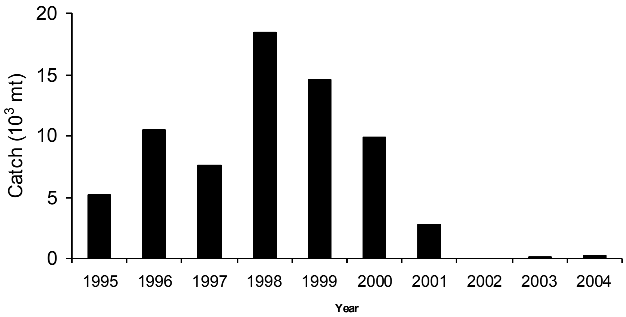


Fig. 2. Annual changes in the catch of bigeye kilka (*Clupeonella grimmi*) in the Iranian waters of the Caspian Sea (1995-2004)

Age determination

Sampling strategy was designed to confirm the age-length relationship, so we emphasized relatively more samples from low and high frequency length intervals. For each sex and in each year we attempted to collect 10 otoliths from each 5 mm size class. Up to 729 of sagitta otoliths of bigeye kilka were removed during 1997-1999. To enhance contrast and facilitate reading and interpretation of growth marks, the whole otolith was dipped in glycerol and inspected under a stereo-microscope with reflected light against a dark background, revealing alternating dark and white rings (hyaline and opaque, respectively) (Fig. 3).

Fig. 3. Whole embedded otolith of bigeye kilka (*C. grimmi*) (130 mm fork length). Arrows indicate opaque zones.

Length-weight relationship and condition factor

The length-weight relationship was derived by applying an exponential regression as following:

$$W = aL^b \tag{1}$$

Where, W is the total weight (g), L is the the fork length (cm), and a and b are parameters to be estimated (Ricker 1975).

The condition factor (CF) of an individual was calculated from subsamples following the equation (Bagenal 1978):

$$CF = \frac{W}{L^3} \times 100 \tag{2}$$

von Bertalanffy growth parameters

The von Bertalanffy growth curve (von Bertalanffy 1938) was fitted to the observed lengths at age for the resulting age-length key using a non-linear estimation method (in the FISAT suite of programs; Gayanilo et al. 1995) the following:

$$L_t = L_\infty (1 - e^{-K(t-t_0)}) \tag{3}$$

where L_t is the fork length (cm) at age t (years), L_∞ is the theoretical maximum length (cm), K is a growth at which L_∞ is approached (1/years) and t_0 is the hypothetical age (years) for *zero length*.

Length at first maturity

To estimate the mean length at 50% maturity, a logistic function was fitted to the proportion of the mature individuals by size class using a non-linear regression. The function used was:

$$P = \frac{1}{1 + e^{(-r(L-Lm))}} \tag{4}$$

where L is the length (mm), P is the mature proportion in each size class, r is a parameter controlling the shape of the curve and Lm is the size at 50% maturity (Saila et al. 1988).

Survival rate and instantaneous coefficient of natural mortality

Survival rate (S) was calculated using the catch curve method (Ricker 1975) to estimate terminal fishing mortalities. To estimate S, age compositions were derived from length composition data collected from the conical lift net during 1998-2001, and age-length key in Iranian waters used as input data. These terminal mortalities were then used as input data for the biomass-based cohort analysis estimating biomass and fishing mortality.

The instantaneous coefficient of total mortality (Z) was transformed from the survival rate as $Z=-\ln S$.

The instantaneous coefficient of natural mortality (M) was estimated using the ZM model (Zhang and Megrey 2006), which is a revised Alverson and Carney model, with von Bertalanffy growth parameters and a maximum age (t_{max}) of 8 (years) for bigeye kilka (Poorgholam et al. 1996). The equation of ZM model is:

$$\hat{M} = \frac{bK}{e^{K(t_{mb}-t_0)}-1} \tag{5}$$

where K is the growth coefficient, b the power parameter of the length-weight relationship, t_0 is the hypothetical age for L_t=0, and t_{mb} is the critical age, which can be estimated as t_{mb} = 0.302 t_{max} (Zhang and Megrey 2006).

When the values of Z and M have been estimated, the value of fishing mortality, F, can be derived from the following equation:

$$F = Z - M \tag{6}$$

Age at first capture

In general, age at first capture of a stock is estimated directly from fishing experiments, either by attaching a small-meshed net cover over the cod-end or from the size composition of the catches of nets of smaller meshes caught at the same time and place (Gulland 1983). Due to lack of fishing experience information, we used Pauly's (1984) length-frequency method, by converting length to age frequencies using the growth parameters. Length composition data collected from the conical lift net during 1998-2001 were used to estimate the age at first capture.

Biomass and instantaneous coefficient of fishing mortality

A biomass-based cohort analysis (Zhang and Sullivan 1988) was used to estimate biomass and instantaneous fishing mortality at age and by year according to the following model equations, assuming that catch is taken instantaneously at mid-year,

$$B_{ij} = B_{i+1,j+1}e^{(M-G_j)} + C_{ij}e^{(M-G_j)/2} \quad (7)$$

$$F_{ij} = \ln(\frac{B_{ij}}{B_{i+1,j+1}}) - M + G_{ij} \quad (8)$$

where B_{ij} and $B_{i+1,j+1}$ are the biomass (mt) at age j and j+1 in year i and i+1, C_{ij} is the catch in weight (mt) at age j in year i, F_{ij} is the instantaneous coefficient of fishing mortality (yr^{-1})at age j in year i, M is the instantaneous coefficient of natural mortality (yr^{-1}), and G_j is the instantaneous coefficient of growth at age j.

The catch in weight at age for the years 1995-2001, an instantaneous coefficient of growth at age, an instantaneous coefficient of natural mortality, and a terminal fishing mortality were used as input data. The instantaneous coefficient of growth at age (G_j) is calculated as the following equation:

$$G_j = \ln(\frac{W_{j+1}}{W_j}) \quad (9)$$

where, W_j and W_{j+1} are the body weight (gr) at age j and j+1, respectively.

The exploitation ratio (E) was estimated as the following equation:

$$E = \frac{F}{Z} \quad (10)$$

where F is the instantaneous coefficient of fishing mortality and Z is the instantaneous coefficient of total mortality (King 1996).

Results

During the years 1995-2001 the fork length and weight of bigeye kilka ranged from 57.5 to 137.5 mm and from 0.6 to 23.0 g and averaged (±SD) 103.6±12.72 mm and 7.6±2.36 g, respectively (Table 1). Age composition of catch was derived from the length composition data and age-length keys, ranged from one to seven years. In the age compositions, age 4 was the most abundant age group during 1995 and accounted for 32.8% of catches (Fig. 4). Age 2 was the most abundant age group during 1996-1998 and represented 41.2, 40.7 and 34.5% of catches, respectively. In 1999, age 3 was the most abundant age group and represented 34.5% of catches. During the years 2000 and 2001, age 4 predominated, representing 30.3 and 31.7% of catches, respectively.

Table 1. Mean fork length (mm) and weight (g) of bigeye kilka (*Clupeonella grimmi*) sampled in the Iranian region of the Caspian Sea during the years 1995-2001

year	N	Fork length (mm)		Weight (g)	
		Mean (S.D.)	Min-Max	Mean (S.D.)	Min-Max
1995	782	103.2 (8.62)	55-135	7.3 (1.79)	0.7-15.6
1996	5801	106.6 (8.74)	60-140	7.9 (1.74)	1.6-18.3
1997	709	95.9 (9.06)	75-125	5.9 (1.98)	2.7-12.7
1998	243	97.7 (7.54)	80-120	5.8 (1.28)	3.1-11.4
1999	527	97.8 (7.78)	70-120	6.1 (1.37)	2.3-11.5
2000	1041	105.0 (10.00)	70-135	8.7 (3.14)	2.6-23.0
2001	144	107.6 (8.82)	85-140	9.0 (2.70)	3.7-20.4
Total	9247	103.6 (12.72)	55-140	7.6 (2.36)	0.6-23.0

The von Bertalanffy growth equation was estimated as shown in figure 5 and table 2:

$$L_t = 142(1 - e^{-0.28(t+1.39)})$$

The fork length and weight relationship from all of the samples was: $W = 0.0083L^{2.894}$ (R^2= 0.92, n=9,247, P<0.001); for female $W = 0.00922L^{2.851}$ (R^2= 0.89, n=2,970, P<0.001) and for male $W = 0.008021L^{2.907}$ (R^2= 0.93, n=4,902, P<0.001).

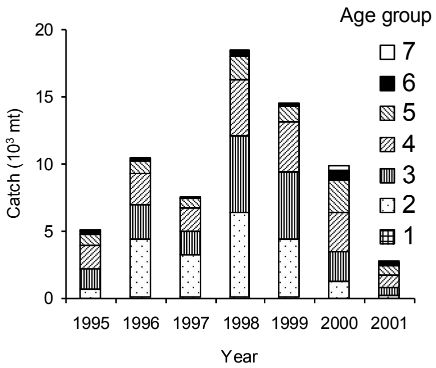


Figure 4. Catch at age of bigeye kilka (*Clupeonella grimmi*) in Iranian commercial catches during 1995-2001

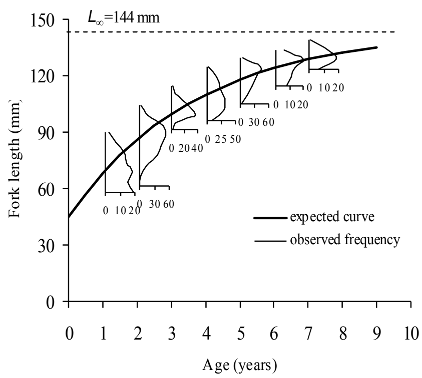


Figure 5. Theoretical growth curve for fork length of bigeye kilka (*Clupeonella grimmi*) in the Caspian Sea

Table 2. Mean fork length and standard deviation and mean weight of bigeye kilka (*Clupeonella grimmi*) in the Iranian waters of the Caspian Sea

Size (mm)	Age group (year)							Total
	1	2	3	4	5	6	7	
n	88	216	96	110	122	59	38	729
$\overline{FL}$ (mm)	68.5	85.4	101.3	108.3	117.2	122.9	128.7	
S.D.	8.08	7.47	5.76	6.26	5.70	6.11	3.76	
$\overline{W}$ (g)	2.1	4.1	6.8	8.3	10.6	12.3	14.0	

The slopes (*b* values) of the length-weight relationships were significantly different between sexes (*t*-test, t=202.9, *P*<0.001). The estimate of *"b"*, 2.851 for females and 2.907 for males were significantly lower than 3.0 (*t*-test, t=429.1, *P*<0.001), indicating a negative allometric growth for both sexes.

Sex ratios varied among seasons. The overall sex ratio (male:female) was 1.65:1, for adult bigeye kilka (n=7,872) which differed significantly from the expected 1:1 (χ^2=474.2, *P*<0.001, Table 3). Males were generally more abundant throughout the year, except in August when females predominated (χ^2=160.1, *P*<0.001) and in April when there was no significant difference (χ^2=0.03, *P*>0.861). Males were most abundant in all the size classes lower than 120 mm (Fig. 6; *P*<0.001). Females predominated in the size classes greater than 120 mm (*P*<0.001).

The condition factor of bigeye kilka declined to the lowest levels between 1995 and 1998, but increased to the highest levels in 2000 and

2001 (Fig. 7). The condition factor differed significantly among the years (P<0.001).

Table 3. Chi-square test for bigeye kilka (*Clupeonella grimmi*) monthly sex ratio comparisons in the Iranian waters of the Caspian Sea samples pooled for all years

Length group	Males	Females	Total	χ^2	P
Jan	225	98	323	49.9	0.001
Feb	1023	409	1432	263.3	0.001
Mar	70	34	104	12.5	0.001
Apr	155	152	307	0.03	0.861
Jul	678	251	929	196.3	0.001
Aug	523	1020	1543	160.1	0.001
Sep	11	2	13	6.2	0.013
Nov	138	36	174	59.8	0.001
Dec	2079	968	3047	405.1	0.001
Total	4902	2970	7872	474.2	0.001

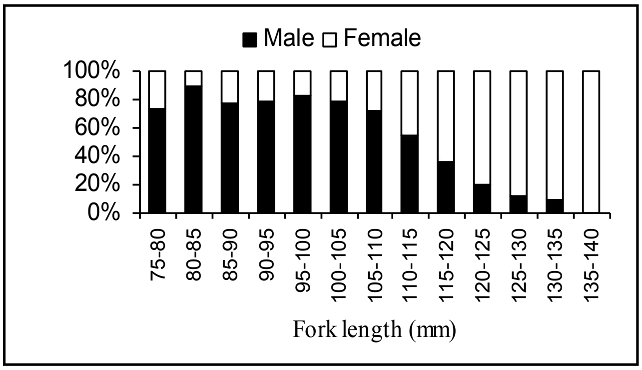


Figure 6. Sex composition of bigeye kilka (*Clupeonella grimmi*) in the Iranian waters of the Caspian Sea

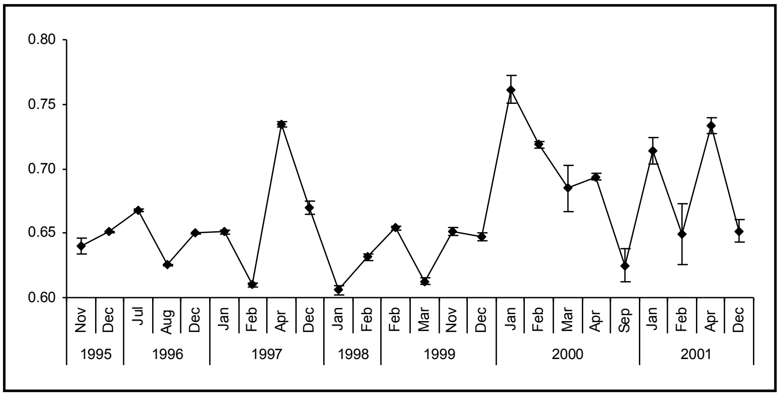
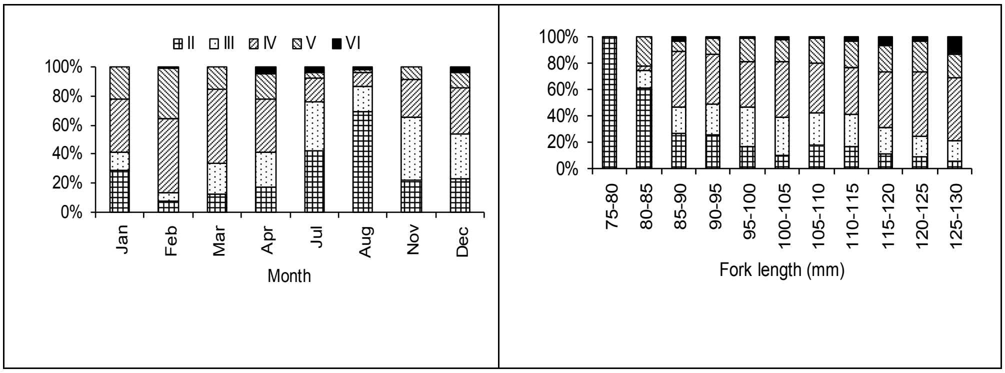


Figure 7. Monthly condition factor (mean±S.E.) of bigeye kilka (*Clupeonella grimmi*) in the Iranian waters of the Caspian Sea, during 1995-2001

The proportion of the specimens with maturing but unripe ovaries declined by 10% from January to February and March (Fig. 8a), but increased to more than 70% in August. These analyses show that reproduction of bigeye kilka occurred throughout the year, but peaked in February and March (Fig. 8a). The optimal period for determining the size-specific maturation schedule of bigeye kilka were in the months of February and March, when most of the fish were in later stages reproduction maturity (Fig. 8a). Figure 8b shows the size class variation of ovarian maturity stages in February and March. The maturity ogive for females of bigeye kilka showed that 50% of samples were sexually mature at a fork length of 88.2 mm (Fig. 9).



(a) (b)

Figure 8. Monthly (a) and size class (b) variation of ovary stages of bigeye kilka (*Clupeonella grimmi*) in the Iranian waters of the Caspian Sea (stage II is not ripe; stage III is almost ripe; stage IV is ripe; stage V is ripe and running and stage VI is spent).

Based on the catch curve method, the annual survival rate (S) of bigeye kilka was estimated as 0.298 (yr^{-1}) (P<0.006). Given these survival rates, the instantaneous coefficient of total mortality (Z) of bigeye kilka was 1.21 yr^{-1}. The estimated instantaneous coefficient of natural mortality (M) for bigeye kilka was obtained from the ZM method (Zhang and Megrey 2006) was 0.460 yr^{-1}.

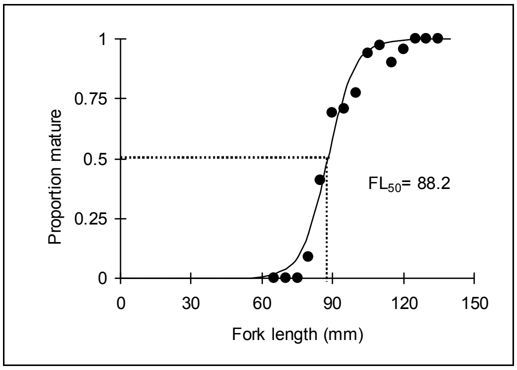


Figure 9. Maturity ogive showing length maturity of bigeye kilka (*Clupeonella grimmi*) from the Caspian Sea

The age at first capture (t_c) of bigeye was 2.75 yr based on the length converted catch curve by the Pauly (1984) method (Fig. 10).

Biomass estimates of bigeye kilka, from the biomass-based cohort analysis (Fig. 11) increased from about 36,900 mt in 1995 to more than 53,500 mt in 1998 and decreased to less than 5,900 mt in 2001. During this period, the average biomass of age 2 represented the highest proportion of total biomass at 30.7% (10,870 mt), followed by the age 3 biomass (25.0%) and age 1 biomass (21.0%). Annual changes in the instantaneous coefficient of fishing mortality had a low C.V. of 0.25 during 1995-2001. With the estimates of instantaneous coefficients of total and fishing mortality, the exploitation ratios for each year were calculated. During the years 1995-2001 the exploitation ratios of bigeye kilka varied from 0.499 to 0.680 (Table 4).

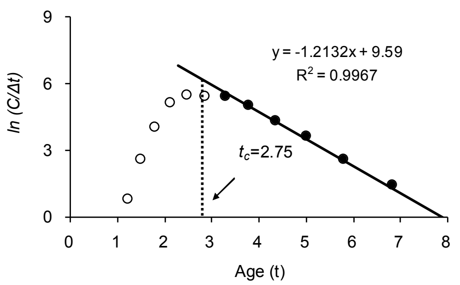


Figure 10. Estimation of the selection ogive of bigeye kilka (*Clupeonella grimmi*) from length-converted catch curve analysis using the Pauly (1984) method

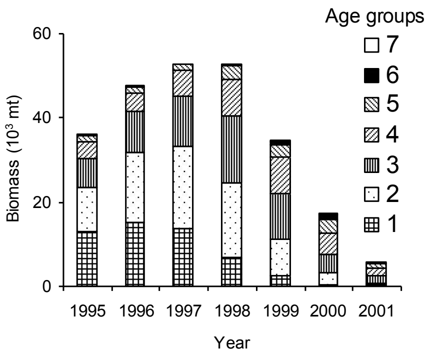


Figure 11. Biomass at age of bigeye kilka (*Clupeonella grimmi*) in Iranian commercial catches during 1995-2001

Discussion

Like two other species of kilka (Fazli et al. 2007a; 2007b), a problem with bigeye kilka is the loss of scales during handling (personal observations). There may also be problems with age determination using scales of older bigeye kilka because the intra-annulus size increment is small at the scale edge and can be missed, resulting in an under-estimate of age in older fish. For instance, Besharat and Khatib (1993) examined the age data from scales and reported that the age of bigeye kilka captured with commercial fishing gear varied from 1+ to 5+ yr. Our otolith analysis of bigeye kilka suggested that ages ranged from 1+ to 7+ yr. Poorgholam et al. (1996) and Fazli and Besharat (1998) reported that bigeye kilka (captured by mid-water trawl) consisted of eight age groups (from 0+ to 7+ yr). Our results are consistent with their observations. Before forming the hyaline zone, there may be some false annuli, which are weak or incompletely formed. With increasing age, bigeye kilka had relatively less calcium on the posterior edge, although there is adequate deposition for detecting annulus formation on the rostrum (our observations). Therefore, otoliths from older fish may exhibit fewer annuli on the posterior edge relative to the rostrum. Alternatively, the annuli may be so closely spaced that it is difficult to distinguish them. Compared with the other two kilka species, however, the hyaline and opaque zones are much clearer in bigeye kilka.

Table 4. Estimated instantaneous fishing mortality (F) and exploitation ratios (E) of bigeye kilka (*Clupeonella grimmi*) in the Caspian Sea during 1995-2001

Parameters		Year						
	Age	1995	1996	1997	1998	1999	2000	2001
F_{ij}	1	0.001	0.006	0.007	0.010	0.041	0.055	0.030
	2	0.062	0.299	0.173	0.449	0.665	0.521	0.444
	3	0.277	0.328	0.180	0.479	0.673	0.783	0.511
	4	0.706	0.840	0.371	0.798	0.704	1.215	0.852
	5	1.396	1.538	0.824	0.966	0.574	1.888	1.318
	6	1.910	1.599	1.147	2.138	0.339	1.342	1.705
	7	0.834	0.942	0.509	0.965	0.556	1.053	0.810
Mean F		0.739	0.793	0.469	0.829	0.507	0.980	0.810
E		0.616	0.633	0.499	0.643	0.524	0.680	0.638

There are no previous estimates of growth rates of bigeye kilka. The present study shows that the growth rate of bigeye kilka was high for the first year of life and then gradually decreased (Table 2).

The exponent (b) of length-weight relationship was 2.894 (pooled data) so growth was negative allometric (i.e. $b \neq 3$). Similar allometric growth was reported by Besharat and Khatib (1993) but with a lower b (2.789).

The overall ratio of males to females (male:female) is 1.65:1, significantly different from 1:1, and there was a seasonal difference in sex ratios. This estimate is close to the ratio of 2.12:1 reported by Besharat and Khatib (1993) who collected samples from 1990-91 using a conical lift net with underwater electric lights. During hydro-acoustic biomass assessment investigations conducted in 1996 and 1997, some samples were collected by mid- water trawl in the Iranian waters of the Caspian Sea (Fazli and Besharat 1998). Their samples were collected in shallow waters (depths between 20 m and 200 m) and offshore (depths >200 m) waters. The sex compositions of the samples varied according to the location of origin (Table 5). In the shallow waters (fishing grounds) males were most common but in the deep waters females predominated in all seasons. These results confirm that the behaviour of females changed with respect to underwater electric lights during the year. Between-sex differences in seasonal attraction to light may explain some of the intra-annual variations in our analysis. Ben-Yami (1976) reported that fish display different behaviours as they respond to light. A key hypothesis is that fish are attracted to light to feed. It is well-known that artificial light attracts many aquatic organisms (Maëda 1951) and perhaps the motivation for attraction is related to increased prey density within the lighted area. With the development of the gonads, females appeared to be less attracted to light. As they approached spawning time, they ceased feeding and disappeared from the catches. In the case of males, they continued to feed during spawning and it seemed that their response to light remained unchanged (Ben-Yami 1976). Our results showed that when the proportion of the specimens with maturing but unripe ovaries had the highest percent in August (70%, Fig. 8a), the females predominated. So some temporal segregation occurs between the sexes.

Table 5. Sex composition of bigeye kilka (*Clupeonella grimmi*) by mid water trawl in the Iranian coastal zone of the Caspian Sea

Month	Region	n	Sex		male:female ratio
			Male	Female	
July-August 1996	Coastal zone	1415	65.8	34.2	1.92:1
	Deep waters	935	15.7	84.3	0.19:1
	Total	2350	27.3	72.7	0.38:1
December 1996	Coastal zone	1530	79.8	20.2	3.95:1
	Deep waters	779	38.9	61.1	0.64:1
	Total	2309	48.9	51.1	0.96:1
February-March 1997	Coastal zone	1822	80.3	19.7	4.07:1
	Deep waters	932	24.7	75.3	0.33:1
	Total	2754	39.9	60.1	0.66:1
April- May 1997	Coastal zone	1976	75.3	24.7	3.05:1
	Deep waters	1111	30.4	69.6	0.44:1
	Total	3087	46.4	53.6	0.87:1

The mean condition factor was lowest in 1998. These changes occurred when an invasive species, the ctenophore *Mnemiopsis* was transported with ballast water from the Black Sea and appeared in 1999 in the Caspian Sea (Ivanov et al. 2001). The ctenophore feeds aggressively on zooplankton, fish eggs and fish larvae (Mutlu 1999) and particularly on zooplankton, which is the food for zooplanktivorous kilka (*Clupeonella* spp) (Kideys et al. 2001; 2005). Total kilka catches declined significantly in 2001 but we found that the condition of bigeye kilka increased after this time (Fig. 6). Similar results were found for two other species of kilka (Fazli et al. 2007a; 2007b). Three species of kilka comprised 70 percent of the total catches in the Caspian Sea (Sedov et al. 1997). Similarly, in the Iranian waters of the Caspian Sea during 1994-1997, Poorgholam et al. (1996) and Fazli and Besharat (1998) reported anchovy kilka comprised more than 70% of the total biomass of kilka. The biomass of the most abundant species of kilka (anchovy kilka) collapsed during 2000-2004 (Fazli et al. 2007a) and our analyses show that the biomass of bigeye kilka also collapsed. It is remarkable that the trends for biomass and condition factor were opposite (the correlation coefficient, R = -0.91, P<0.004), and this may reflect density-dependent growth competition for space or food. Prior to the stock collapse, the species may have been food-limited. Subsequent to the collapse, perhaps reduced inter- and intra-specific competitions may have led to increased availability of zooplankton for the diminished kilka stocks. Therefore their condition increased.

Our analyses show that reproduction of bigeye kilka occurs throughout the year, but peaked from February to March (Fig. 8a). Prikhod'ko (1981) reported that the spawning of bigeye kilka is extended, from January to September but is most intense in spring and autumn which is not consistent with our results.

As Kideys et al. (2001; 2005) reported that *Mnemiopsis* is a voracious predator on zooplankton, which is the food for zooplanktivorous kilka (*Clupeonella* spp) we assume that the ctenophora does not affect annual changes in natural mortality M. Also, some parameters should be constant such as M and growth parameters. Technically, annual differences in these parameters would mean that they are not really "parameters" (or constant) and it is not possible to estimate M different annually in the current fish population dynamics.

Our results showed that, during the period the exploitation ratio of bigeye kilka was >0.5 (except, in 1997 when it was 0.499; Table 4). This is higher than the rate of 0.5, suggested by Gulland (1983), as the theoretical exploitation ratio that could maximize harvest. Therefore, the stock of bigeye kilka is being heavily exploited.

To summarize the changes in the abundance of bigeye kilka might be explained as follows. All three species of kilkas feed on zooplankton but there are substantial differences in their food preferences and composition. The food of common kilka is the most diverse, and is consistent with the greater variety of zooplankton species present in shallow coastal waters (Prikhod'ko 1981). The main food of anchovy kilka is more restricted and consists mainly of two zooplankton species *Eurytemora* spp and *Limnocalanus* sp (Prikhod'ko 1981; Karpyuk et al. 2004). The food of bigeye kilka is least diverse, consisting mainly of large zooplankton (Prikhod'ko 1981). When *Mnemiopsis* appeared in the Caspian Sea, the species composition of meso- and macrozooplankton in the middle and southern Caspian declined drastically (Karpyuk et al. 2004). The species that provided the main food of anchovy kilka, *Eurytemora* and other copepods, were replaced by different copepod species, mainly, *Acartia* sp. (Karpyuk et al. 2004). Therefore, as the biomass of anchovy (Fazli et al. 2007a) and bigeye kilka collapsed due to the combined effects of fishing and the decline in available prey species, the biomass of common kilka increased during the same period (Fazli et al. 2007b). Although our explanation is hypothetical, we suggest that it is the most parsimonious available and is consistent with the available data.

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