Fish Biology and Ecology

Chapter · September 2014

DOI: 10.1007/978-94-017-8944-8_16

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Chapter 16
Fish Biology and Ecology

Ilia Ostrovsky, Menachem Goren, James Shapiro, Gregory Snovsky and Alex Rynskiy

Abstract The chapter summarizes current knowledge on fish biology in Lake Kinneret. Nineteen native fish species belonging to six families populate the lake. Three of these species are endemic to the lake and four other species are endemic to the Jordan Valley system. Eight alien species are found in the lake. Four of them are breeding in nature, three cannot breed but are regularly stocked, and one is a hitchhiker that cannot breed. Growth rate equations and weight-length relationships are presented for the dominant cyprinids (*Mirogrex terraesanctae, Hypophthalmichthysmolitrix, Cyprinus carpio, Barbuslongiceps, Capoetadamascina, Carasobarbuscanis*), cichlids (*Oreochromisaureus, Sarotherodon galilaeus, Tilapiazillii, Tristramellasimonis*), grey mullets (*Lizaramada, Mugilcephalus*), and catfish (Clariasgariepinus). The long-term changes in fish community composition in the lakewere associated with introduction and invasion of fishes; changes in fishing intensity; modifications of the littoral, and changes of the lake ecological regime. Temporal dynamics, spatial distribution, total abundance and biomass of fish in the lake were studied based on long-term hydroacoustic monitoring. The size structure and abundance of fish in the pelagic zone of the lakedisplay explicitseasonal changes associated with fish spawning migrations and winter-spring recruitment of the dominant bleak M. terraesanctae. Water level fluctuations beyond natural have modified the littoral habitats, which are of specific importance during different life

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T. Zohary et al. (eds.), *Lake Kinneret, Ecology and Management,* Aquatic Ecology Series 6,
DOI 10.1007/978-94-017-8944-8_16, © Springer Science+Business Media Dordrecht 2014

stages of fish. Water level has an immense impact on fishreproduction, survival, recruitment, population dynamics, and eventually determines the catches of commercially important species.

Keywords Cichlids · Mugilids · Cyprinids · Water-level fluctuations

16.1 Introduction

Interest in the fishes of Lake Kinneret goes back to the dawn of human history, when hunter-gatherer peoples fished in the lake (Zohar 2003). As evident from the New Testament (Luke 5:1–11), fishing was a common practice among the inhabitants of the Galilee. The first modern scientist to study the fishes of the lake was the Swedish naturalist Hasselquist[1] (1757), who collected the St. Peter's fish *Sarotherodon galilaeus,* which was described by Linnaeus (1758) as *Sparus galilaeus*. The last of the lake fish species to be described as new to science is the most common fish in the lake—*Mirogrex terraesanctae* (Steinitz 1952), referred to in some publications as *Acanthobrama terraesanctae*. In the mid-nineteenth century, the Holy Land became a fashionable target for European scientists, who have published since then articles on the fishes of the Jordan Valley and Lake Kinneret (Cuvier and Valenciennes 1840, 1842; Heckel 1843; Günther 1865, 1866; Lortet 1875, 1876, 1883; Tristram 1884; Pellegrin 1911, 1923, 1933; Tortonese 1938, 1952; Trewavas 1942, 1965; Ricardo-Bertram 1944; Kosswig 1950, 1961, 1967; Komarovsky 1952; Banarescu et al. 1982; Krupp 1987; Krupp and Schneider 1989). The first Israeli scientist to study the Jordan Valley fishes was Bodenheimer (1935). He was followed by Steinitz (1952, 1953, 1954, 1959), Ben-Tuvia (1959), Steinitz and Ben-Tuvia (1957, 1960), Fishelson (1962, 1966, 1967), Goren (1972, 1975, 1983), and Goren et al. (1973).

Nineteen native fish species belonging to six families have been reported from Lake Kinneret (Table 16.1). Three of these species are endemic to the lake and four species are endemic to the Jordan Valley system. One species that was identified as *Paracobitis tigris* is probably an undescribed one. Eight alien species are common in the lake. Four of them are breeding in nature (*Cyprinus carpio, Gambusia affinis, Oreochromis aureus* hybrids*, Xiphophorus hellerii*), three of them do not breed in the lake but are regularly stocked (*Hypophthalmichthys molitrix, Mugil cephalus, Liza ramada* = *Mugil capito*; Cuvier 1829), and one is a hitchhiker (*Anguilla anguilla*) that arrived with the stocked *Mugil* but does not reproduce in the lake (Goren and Ortal 1999; Roll et al. 2007).

[1] *Fredrik Hasselqvist (1722–1752) died while touring the Middle East. His notes were edited and published by Linnaeus.*

Table 16.1 The fishes of Lake Kinneret, their habitat, food and biogeographic affiliation (numbers in parentheses represent the references listed in the table footnotes)

Family	Species	Common name	Hebrew name	Habitat	Food (in Lake Kinneret)	Origin
	Native species					
Blenniidae	*Salaria fluviatilis* (Asso, 181)	Blenny	Karnun naharoni	Shallow waters among stones (3, 8)	Benthic invertebrates (3)	Mediterranean
Cichlidae	*Astatotilapia flaviijosephi* (Lortet, 1883)[a]		Amnunit yosef	In shallow water among rocks and stones (8)	Benthic invertebrates (16)	Africa
Cichlidae	*Oreochromis aureus* (Stiendachner 1864)	Blue tilapia	Amnun ha'yarden	Throughout the lake (8)	Adults: filter feeders, herbivorous, detritus, zooplankton (15, 19)	Africa
Cichlidae	*Sarotherodon galilaeus* (Linnaeus, 1758)	Mango tilapia, St. Peter's fish	Amnun ha'galil	Pelagic schools in winter, littoral in couples in spring and summer	Young: visual feeding, mostly zooplankton; adults and young (>50 mm): filter feeding, large algae, mostly *Peridinium* (5, 13, 19)	Africa
Cichlidae	*Tilapia zillii* (Gervais 1848)	Common St. Peter's fish	Amnun matsuy	Throughout the lake (20)	Omnivorous: zooplankton, zoobenthos, and higher plants (14)	Africa
Cichlidae	*Tristamella sacra* (Günther 1864)[b]		Tvarnun listani	Among immersed vegetation around the lake (8)	Fish, crustaceans, insects (2)	Africa
Cichlidae	*Tristramella simonis* (Günther 1864)[b]		Tvarnun hakinneret	Throughout the lake (8)	Plankton, benthic plants, invertebrates, zooplankton, small fish (2)	Africa
Clariidae	*Clarias gariepinus* (Burchell 1822)	Catfish	Sfamnun	Benthic, littoral, during winter concentrates near hot springs in winter (8, 9)	Omnivorous: invertebrates, fish, plants, seeds, mollusks (9, 20)	Africa
Cyprinidae	*Barbus longiceps* (Valenciennes 1842)[a]	Barbel	Binit arukat rosh	Benthic, littoral, adults descend in winter to deeper waters (8)	Zoobenthos and young fish (2, 9)	Asia

Table 16.1 (continued)

Family	Species	Common name	Hebrew name	Habitat	Food (in Lake Kinneret)	Origin
Cyprinidae	*Mirogrex terraesanctae* (Steinitz 1952)[b]	Kinneret bleak	Lavnun ha'kinneret	Pelagic (8)	Zooplankton: prefer cladocera in winter feed from bottom: musquito larvae, nematods (1, 2, 6, 7, 10, 19)	Middle East
Cyprinidae	*Acanthobrama lissneri* Tortonese 1952[a]		Lavnun lisner	Vegetated and stony habitats around the lake (8)	Zoobenthos and algae (9)	Middle East
Cyprinidae	*Carasobarbus canis* (Valenciennes, 1842)[a]		Binit gdolat kaskas	Benthic and pelagic (8)	Juvenile fish (Lavnun) and pelagic and benthic invertebrates (16)	Asia–Africa
Cyprinidae	*Capoeta damascina* (Valenciennes, 1842)		Hafaf	Benthic (8)	Algae, detritus, benthic invertebrates (8)	Middle East
Cyprinidae	*Garra rufa* (Heckel 1843)	Reddish log sucker, Levantine sucker	Agulest	Benthic, on stones in littoral and thermal sprigs (8)	Scratching algae and detritus from surface of rocks, benthic invertebrates (9)	Asia
Cyprinidae	*Hemigrammocapoeta nana* (Heckel 1843)		Yableset	Vegetated and stony habitats around the lake (8)	Zoobenthos and algae (8)	Middle East
Cyprinidae	*Pseudophoxinus kervillei* (Pellegrin 1911)		Lavnunit ha'galil	Stony habitats around the lake (8)	Zoobenthos and algae (8)	Asia–Europe
Cyprinodontidae	*Aphanius mento* (Heckel 1843)	Pupfishes	Na'avit kahula	Vegetated habitats around the lake (8)	Zooplankton, zoobenthos, and filamentous algae (8)	Asia
Balitoridae	*Oxynoemacheilus tigris* (Heckel 1843)[c]		Binun kinnarti	Stony habitats around the lake (8)		Asia–Europe
	Alien species					
Cichlidae	*Oreochromis aureus hybrids*		Amnun ha'yarden	Throughout the lake (8)	Zooplankton benthic organisms and detritus (15)	Oreochromis niloticus X O. aureus
Cyprinidae	*C. carpio Linnaeus* 1758	Common carp	Karpion matsui	Inshore throughout the lake (8)	Bottom invertebrates and detritus (20)	Asia

Table 16.1 (continued)

Family	Species	Common name	Hebrew name	Habitat	Food (in Lake Kinneret)	Origin
Poeciliidae	*Gambusia affinis* (Baird and Girard 1853)	Mosquito fish	Gambusia metsuya	Littoral, protected bays in shallow water among plants (20)	Crustaceans, insects, fish larvae, and algae (8)	North America
Poeciliidae	*Xiphophorus hellerii* Heckel 1848	Green swordtail	Saifan	Rare, vegetated areas (20)	Aquatic insects, zoobenthos, and fish larvae (18)	North America
	Regularly stocked species (alien)					
Cyprinidae	*Hypophthalmichthys molitrix* Valenciennes, 1844	Silver carp	Kasif	Pelagic (20)	Filter feeder, phytoplankton (Peridinium bloom), and zooplankton (11, 16)	China
Mugilidae	*Mugil cephalus* Linnaeus 1758	Flathead grey mullet	Kipon gdol rosh	Inshore pelagic (20)	Planktonic and benthic organisms and detritus (2, 18)	Mediterranean Sea
Mugilidae	*Liza ramada* (Risso, 1827) (=*Mugil capito* Cuvier 1829)	Thinlip grey mullet	Kipon tober	Inshore pelagic, in small schools (18)	Planktonic and benthic organisms and detritus (12)	Mediterranean Sea
	Hitchhiker species (alien)					
Anguillidae	*Anguilla anguilla* Linnaeus 1758	European eel	Tslofach	Benthic (18)	Piscivore (4)	Atlantic Ocean, Mediterranean, and Black Sea

1 Azouly and Gophen 1992, *2* Ben-Tuvia 1978, *3* Gasith and Goren 2009, *4* Golani et al. 1988, *5* Gophen 1980, *6* Gophen and Landau 1977, *7* Gophen and Scharf 1981, *8* Goren 1983, *9* Goren and Gasith 1999, *10* Landau et al. 1988, *11* Shapiro 1985, *12* Shapiro 1998, *13* Spataru 1976, *14* Spataru 1978, *15* Spataru and Zorn 1978, *16* Spataru and Gophen 1985b, *17* Spataru et al. 1987, *18* Zismann 1976, *19* Zohary et al. 1994, *20* Personal unpublished data

[a] Endemic to the Jordan Valley system

[b] Endemic to Lake Kinneret

[c] Taxonomic status needs clarification

Table 16.2 The weight–length and von Bertalanffy growth equations of dominant fish species in Lake Kinneret

Species	Weight–length relationship $W = a L^b$			von Bertalanffy growth equation $L_t = L_\infty (1\text{-}e^{-kt})$		
	a	b	Reference	L_∞	k	Reference
S. galilaeus	0.0177	3.07	1	35.0	0.495	3
O. aureus	0.0958	2.47	1	31.3	0.598	3
T. simonis	0.0148	3.12	1	20.0	0.635	3
T. zillii	0.0179	3.06	1	20.7	0.480	1
*M. terraesanctae**	0.0047	3.24	2	34.2	0.173	4
Male	–	–	–	22.4	0.326	4
Female	–	–	–	29.2	0.247	4
C. carpio	0.0074	3.22	1	105.8	0.390	1
H. molitrix	0.0106	3.04	1	133.0	0.267	5
B. longiceps	0.0171	2.86	1	–	–	–
C. canis	0.0254	2.77	1	–	–	–
C. damascina	0.114	2.31	1	–	–	–
C. gariepinus	0.0204	2.75	1	125.0	0.444	1
M. cephalus	0.0088	3.04	1	89.1	0.194	6
L. ramada	0.0078	3.03	1	57.6	0.237	6

L is total length in cm, W is weight in g, L_t is the total fish length in cm at age t(yr), k is growth coefficient in yr^{-1}, Fish age is counted from the moment of time when $L = 0$

1 author's original data, 2 Ostrovsky and Walline 2001, 3 recalculated from Ben-Tuvia 1959, 4 recalculated from Ostrovsky and Walline 1999, 5 recalculated from Snovsky 2000, 6 recalculated from Snovsky 1993

*Growth rates of *M. terrascantae* males and females are different. For practical reasons a "mixed" von Bertalanffy equation was computed taking into consideration the difference in growth rate of males and females and decrease in proportion of males with length. The "mixed" equation allows calculating reasonably well size-specific growth rate of the bleak; however, the coefficients of such a "mixed" equation are unrealistic

16.2 Fish Biology

The biology of Lake Kinneret fish was reviewed by Ben-Tuvia (1978), Reich (1978), Goren (1975), and Ben-Tuvia et al. (1992). A summary of the available information on habitat and food preferences of the Kinneret fishes and their geographical region of origin are presented in Table 16.1. Information on body growth and weight–length relationships of the dominant fish species is summarized in Table 16.2. Additional information regarding the most abundant species is presented hereafter.

Cichlidae Four out of the six Kinneret cichlids have commercial value (*O. aureus, S. galilaeus, Tristramella simonis,* and *Tilapia zillii*), and another two are either too small (*Astatotilapia flaviijosephi*) or too rare (*Tristramella sacra*). All cichlids in the lake are fish of African origin. Two species of this group (*Tilapia sacra, T. simonis*) are endemic to the lake, one (*A. flaviijosephi*) is endemic to the central Jordan River basin, while the other three cichlids (*O. aureus, S. galilaeus,* and *T. zillii*) are widely distributed in Israel and Africa. The presence of these two groups of cichlids in the Jordan Valley may reflect at least two waves of biogeographical migration from the coastal system (Goren and Ortal 1999). As these fishes are of tropical and subtropical origin, they are sensitive to low temperatures and show poor growth and high mass mortality during winter (Chervinski and Lahav 1976). Due to their affiliation to warm water, some of Kinneret cichlids concentrate near the warm salt springs in the western side of the lake when water temperature drops below 14–16 °C in winter. In extremely cold winters (e.g., 1991–1992), when temperature dropped below 12–13 °C, high mortality of these fish was reported (Shapiro and Snovsky 1997).

S. galilaeus is a biparental mouthbrooder fish spawning up to five times from April to August, with each progressive spawn containing smaller numbers of eggs (Ben-Tuvia 1978; Balshine-Earn 1994). During the nesting season, these fish show territorial behavior. The most intensive reproduction occurs in April–May. During this period adults inhabit shallow (< 1.5 m) areas protected from the wind and waves by either lagoons or inundated vegetation that has developed around the lake at low water levels over the past two decades (Gasith and Gafny 1990). During most of the year, adult *S. galilaeus* move in schools of various sizes in open waters, while breeding adults and juveniles inhabit the littoral. *S. galilaeus* is the most commercially valuable cichlid species in Lake Kinneret (Chap. 36).

The other cichlid species (except *T. zillii*) are female mouthbrooders. During the breeding season (spring and summer), males possess territories in shallow water and court females that enter their territory. After spawning, the females take the fertile eggs into their mouth cavity and leave the area. Females of *T. zillii* spawn in nests or burrows, dug by the males. Both parents guard the brood and later the school of juveniles for a few days (Ben-Tuvia 1959; Goren 1983; Bruton and Gophen 1992).

Juveniles of all cichlids live in rocky or vegetated areas in the littoral, while adults of *T. simonis* and *O. aureus* are found during most of the year forming schools in the open water. *T. sacra* was found among reeds near the shore and in springs around the lake. Multiannual decrease in water level caused disappearance of its habitat and *T. sacra* have been listed as extinct since 1990 (Goren 2003).

Clariidae The African catfish *Clarias gariepinus* is the largest native freshwater fish in Israel (up to 1.5 m in length and 20 kg body weight). The fish is an omnivore and feeds on invertebrates and fish (Spataru et al. 1987; Goren and Gasith 1999). Being a scavenger (in addition to being a predator), the catfish plays a "sanitary" role in the lake as it preys on carrion of fish and birds. Its breeding season starts in March–April when the catfish migrate into the lagoons and remain there until June. The number of eggs ranges between 150,000 and 200,000 per kg of body weight (Goren and Gasith 1999).

Cyprinids Four out of the eight native lake cyprinids are objects of fisheries. The most important cyprinid from both, ecological and economical aspects is the Kinneret bleak *M. terraesanctae* (Hebrew name: lavnun ha'kinneret). This is the dominant fish in Lake Kinneret by abundance (> 80 %) and biomass (> 50 %; Walline et al. 1992). *M. terraesanctae* spawns from November to March when water levels rise. The bleak eggs are adhered to freshly inundated, epiphyton-free stones in very shallow water (< 30 cm; Gafny et al. 1992). The emerged larvae stay for some time in shallow area, but usually they are dispersed by currents to the pelagic zone and inhabit the upper part of the water column during winter and early spring; then the young-of-the-year fish form schools that live in the open water. Due to its high abundance and feeding on zooplankton (Gophen and Landau 1977; Gophen and Scharf 1981; Landau et al. 1988; Azoulay and Gophen 1992), the bleak has a significant impact in the food web of the lake (Walline et al. 2000; Ostrovsky et al. 2013). The dependence of *M. terraesanctae* reproduction success on the availability of freshly inundated stones in the shallow littoral causes the population dynamics of this species to be sensitive to large fluctuations in water level taking place in Lake Kinneret over the past two decades, as discussed below.

The three barbel species (*Carasobarbus canis, Barbus longiceps,* and *Capoeta damascina*) inhabit mainly the shallow water. *C. canis* and *B. longiceps* are frequently observed together with *M. terraesanctae* fry, which is one of the barbel's food components (G Snovsky and J Shapiro, unpublished data). Barbels spawn from November to March. *B. longiceps, and C. damascina* migrate in autumn upstream the surrounding rivers, where they spawn. A hybrid of these two species has been often observed in the lake and surrounding rivers (Stoumboudi et al. 1992; Fishelson et al. 1996).

The carp, *C. carpio,* was stocked only at the end of the 1940s with the scaled carp variety. Stocking was not repeated, but since then the population was bolstered by escapees (mirror carp variety) from the surrounding fishponds. Since the late 1980s, conditions for the natural reproduction of carp in the lake became favorable due to the formation of large littoral areas with flooded vegetation, and the catch of carps has increased considerably (see Chap. 36). At the same time, the mirror carp variety, which was abundant in the 1960s–1980s, was replaced by the wild-type-scaled carp, such that in the late 1990s the all-scaled fish already accounted for >96% of the entire population (Shapiro and Snovsky, unpublished data). This reflects a decrease in abundance of escapees (mirror carps) and possibly more advantageous conditions for scaled carp reproduction in the lake.

The silver carp *H. molitrix,* which was stocked periodically since 1969, grows in the lake as fast as in ponds (Shefler and Reich 1977) and achieves a weight of 20–30 kg in 5–8 years (Snovsky 2000). Leventer and Teltsch (1990) reported that in the Netofa reservoirs *H. molitrix* achieves a weight of 6–15 kg in 6–8 years. Silver carp is stocked in an attempt to reduce the amount of phytoplankton and improve water quality (Shapiro 1985; Spataru and Gophen 1985a; Snovsky and Pizanty 2002; Chap. 36).

Mugilildae The grey mullets *L. ramada* and *M. cephalus* have been stocked in the lake since 1963 in order to make use of benthic resources while supporting the commercial fishery (Bar-Ilan 1975; Reich 1978; Shapiro 1998). About 28% of stocked grey mullets are landed. The mean natural mortality rates were 0.39 yr_{-1} and 0.30 yr_{-1} for L. *ramada*, M. *cephalus*, respectively (Snovsky and Ostrovsky 2014). *L. ramada* is the more abundant (>75%) grey mullet species in the lake. In November–January, *L. ramada* forms large schools, which become an easy target for fishermen, leading to winter catch maxima. In contrast, *M. cephalus* does not form large schools and its catches are distributed more uniformly throughout the year. Since the decline of the harvest of cichlids and bleak in recent years, grey mul-

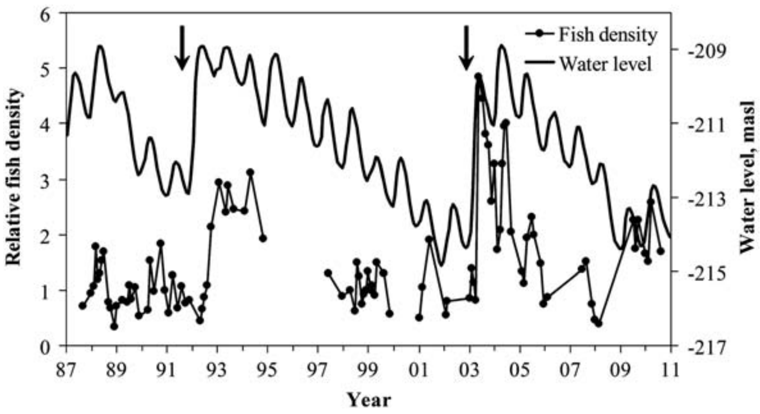

Fig. 16.1 Time series of water level and fish abundance in Lake Kinneret. *Arrows* mark the two events of 4 m (winter 1991–1992) and 4.7 m (winter 2002–2003) rise in water level. Fish density (mainly *M. terraesanctae*) was determinated based on hydroacoustic surveys. The relative density of fish in a given date was computed as a ratio of the estimated density of fish (acoustic targets >−60 dB) to the mean density prior to the rapid rise in water level, computed for two periods of averaging: 1987–1991 and 1997–2002. The fish abundance data were collected with a 70-kHz Simrad single-beam echo sounder (model EY-M) during 1987–1994, 120-kHz Biosonics dual-beam echo sounder (model 102) during 1997–1999, and 120-kHz Biosonics dual-beam echo sounder (model DE5000) after 2001. For more details on the acoustic surveys see Walline et al. (1992). (Adapted from Ostrovsky et al. 2013 with permission of Wiley)

lets have become the most valuable commercial fish in the lake and account for up to 65 % of the value of the total catch (Snovsky et al. 2010).

16.3 Effect of Water Level Fluctuation on Fish

Since the early 1990s, high rates of water consumption relative to water supply led to three distinct long-term periods of gradual decrease in water level and to a general increase in the amplitude of water-level fluctuations (Fig. 16.1). These changes affect the availability of spawning habitats in the littoral (Chap. 29). At high water levels, the proportion of hard substrates (gravel, boulders, and rocks) in the littoral zone is much higher than at low water levels, when sand and silt become the dominant substrate. Hard-substrate habitats are favorable for the development of diverse periphytic and invertebrate communities, and provide good feeding conditions for herbivore, planktivore, and benthivore fishes and their fingerlings (Gasith and Gafny 1990). The hard substrates also provide refuge and breeding sites for different fishes (Gafny et al. 1992; Chap. 36). Therefore, at high water levels the density of fish and the diversity of their communities in the littoral zone are notably larger than at low water levels (Gasith et al. 1996, 2000; Gasith and Goren 2009).

The long-term decreases in water levels and enlarged seasonal fluctuations favored the development of another ecologically important fish habitat in the littoral—inundated terrestrial plants. These plants proliferated in the exposed shores at the lake circumference when water level dropped below −212 m above mean sea level, i.e., about 3 m below the lake's maximal water level (−209 m; Gasith and Gafny 1990); then, these plants were inundated after subsequent winter–spring floods (Gafny and Gasith 2000). Especially wide areas of inundated plants were observed over 2–3 years following the extreme water level rises of 1991–1992 and 2002–2003. Such well-protected littoral areas served as preferred refuge and spawning habitat for the cichlids and cyprinids, where they could also find plenty of periphyton and invertebrate food. The flooded vegetation also provided protected nursing grounds for fish fry and fingerlings, increasing their survival (Gasith and Gafny 1998; Chap. 29) and eventually leading to increased catches of the commercially valuable species (*S. galilaeus, C. carpio*) after 1–2 years lag time (Chap. 36).

Another species apparently benefits the increased abundance of inundated vegetation was *H. molithrix,* an introduced species whose catch, despite a decline in the rate of its stocking, was greatly increased 2–3 years after the development of the inundated vegetation areas (Chap. 36). This suggests improved survival of the stocked fingerlings, which probably also use the inundated vegetation for feeding and refuge.

Large water-level fluctuations also affect the population dynamics of the bleak *M. terraesanctae*. Gradual declines in the annual mean water level from 1988 to 1991 and again from 1995 to 2002 resulted in reduced availability of suitable spawning substrates (freshly inundated rocks and stones). These gradual water level declines were followed by two extremely rainy winters (1991–1992 and 2002–2003) resulting in a 4–5-m rise in water level within a single season and large increases in the availability of spawning sites for *M. terraesanctae*. These water level rises were highly favorable for bleak reproduction and fingerlings survival (Ostrovsky and Walline 1999; Gafny and Gasith 2000; Zohary and Ostrovsky 2011). Consequently, the density of *M. terraesanctae* fingerlings increased sharply following the years with exceptional water level rise (Fig. 16.1).

The rapid increases in *M. terraesanctae* abundance were followed by increases in fish biomass with 1–2 years lag time (Ostrovsky and Walline 1999, 2001). A misbalance between food requirements of these zooplanktivorous fish and zooplankton productivity (Ostrovsky and Walline 2001; Zohary and Ostrovsky 2011) can explain the collapses of the zooplankton (mainly copepods) observed in 1993–1994 and again in 2004–2005 (Gal and Anderson 2010, Chap. 13). These collapses led to food shortage that affected mainly the post-spawning *M. terraesanctae,* as indicated by lowered body condition index (BCI) in larger-size fish in 1994–1995 (Fig. 16.2) and 2004–2005 (unpublished data) and by increased fish mortality. A huge decline in the proportion of fish with body size exceeding the minimal required for commercial harvest caused a collapse of the bleak fishery in 1994 and again in 2005 (Ostrovsky et al 2013, Chap. 36).

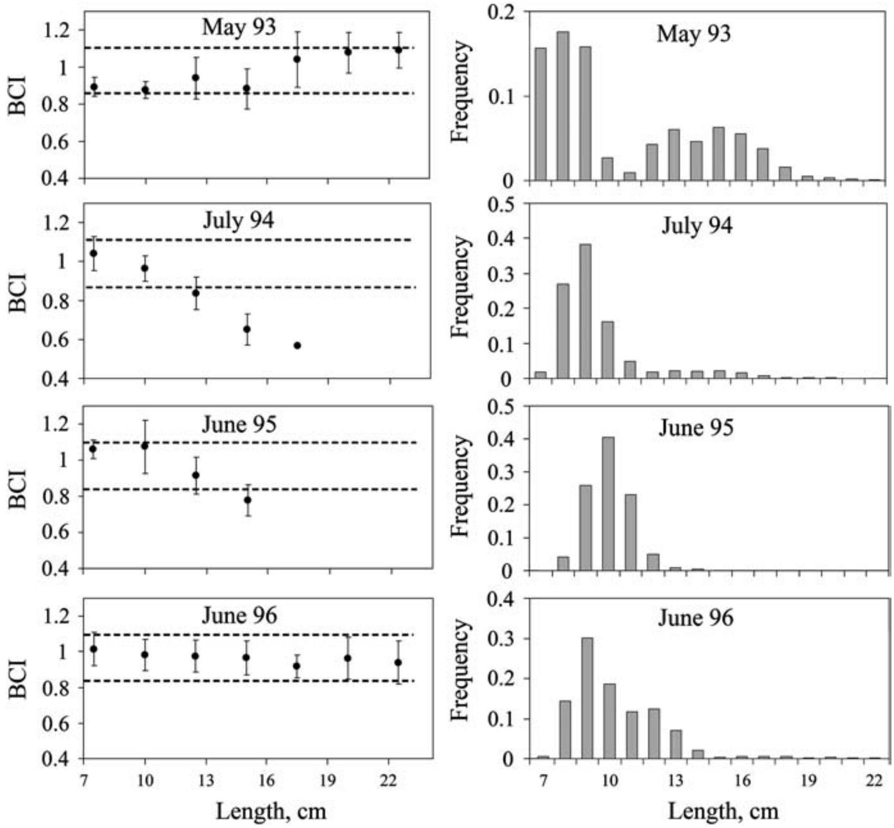

Fig. 16.2 Changes in body condition index (BCI) and length–frequency distribution of Lake Kinneret bleak *M. terraesanctae* in 1993–1996. Sharp decline in the BCI occurred in larger-size (>12 cm) fish in 1994 and 1995, 2–3 years after an unusual increase in abundance of these zooplanktivorous fish and 1–2 years after the lowest-ever record of zooplankton abundance (1993). Disappearance of larger fish from the population co-occurred with the poor BCI of adult individuals, affecting high mortality

16.4 Spatial Variability and Abundance of Pelagic Fish

The abundance and spatial distribution of pelagic fish in Lake Kinneret are being monitored routinely since the late 1980s, along 14 transects, using scientific echo sounders (Walline et al. 1992; 2000; Ostrovsky et al. 2013). Those acoustic surveys indicate that the spatial distribution of fish is highly heterogeneous (Fig. 16.3). In winter and early spring, fish larvae concentrate in the north, where lake productivity is higher than in other areas (Ostrovsky and Sukenik 2008; Ostrovsky and Yacobi 2009) and newly born fish (predominantly *M. terraesanctae*) may have better feeding conditions for growth and survival. During that time, the larvae populate the upper 5–10-m stratum in the pelagic zone (Fig. 16.4a). In summer and fall, when

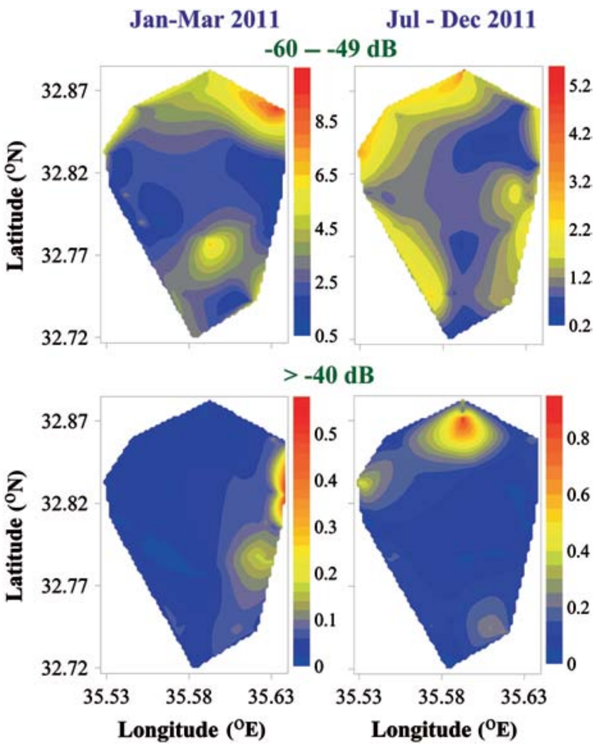

Fig. 16.3 Spatial distribution of depth-integrated fish density in 2011. *Upper panels:* small fish (−60 to −40 dB, mainly *M. terraesanctae)*; *lower panels:* large fish (>−40 dB, mainly commercially valuable species); *left panels:* distributions during the holomixis (averaged from three surveys from January to March), *right panels:* distributions during the stratified period (averaged from five surveys from July to December). *Color bars* show the fish density in ind m^{-2}. Small fish concentrate in the northern section of the lake during holomixis and at the sublittoral areas around the lake during the stratified period. Larger fish migrate all over the lake, but the higher mean density is usually observed near the Jordan inlet zone (northern tip)

the metalimnion and hypolimnion are anoxic, fish are usually concentrated at the lake periphery (Fig. 16.3), where boundary-mixing processes induce sediment re-suspension (Ostrovsky and Yacobi 2010), increase local productivity (Ostrovsky et al. 1996), and thus may improve local feeding conditions. During that time, larger fish (possibly mullets, barbells, carps) concentrated at the upper part of the metalimnion (Fig. 16.4b), where cooler water could be a thermal refuge for these fish as surface water temperatures in Lake Kinneret exceed 30 °C in summer. It is also possible that higher concentration of resuspended particulate matter, sinking detrital particles, and some planktonic organisms in such locations may, in turn, attract the benthos- and plankton-feeding fish. It was shown that the lateral heterogeneity in the distribution of the zooplanktivore *M. terraesanctae* can be associated with the lateral distribution of their prey (Kalikhman et al. 1995). Specifically, these authors found “patchy correlation zones,” i.e., zones where strong positive and/or negative correlations occurred between distribution fields of the fish and the zooplankton in the lake. The formation of such zones can be attributed to *M. terraesanctae*’s foraging behavior and feeding migrations.

The large majority of the total number of fish in the lakes is due to small individuals, mostly fish larvae, which have acoustic size (target strength, TS) of less than −60 dB (<3 cm length). These small fish exhibit highest abundance in winter and early spring, when *M. terraesanctae* larvae are dispersed by currents and appear

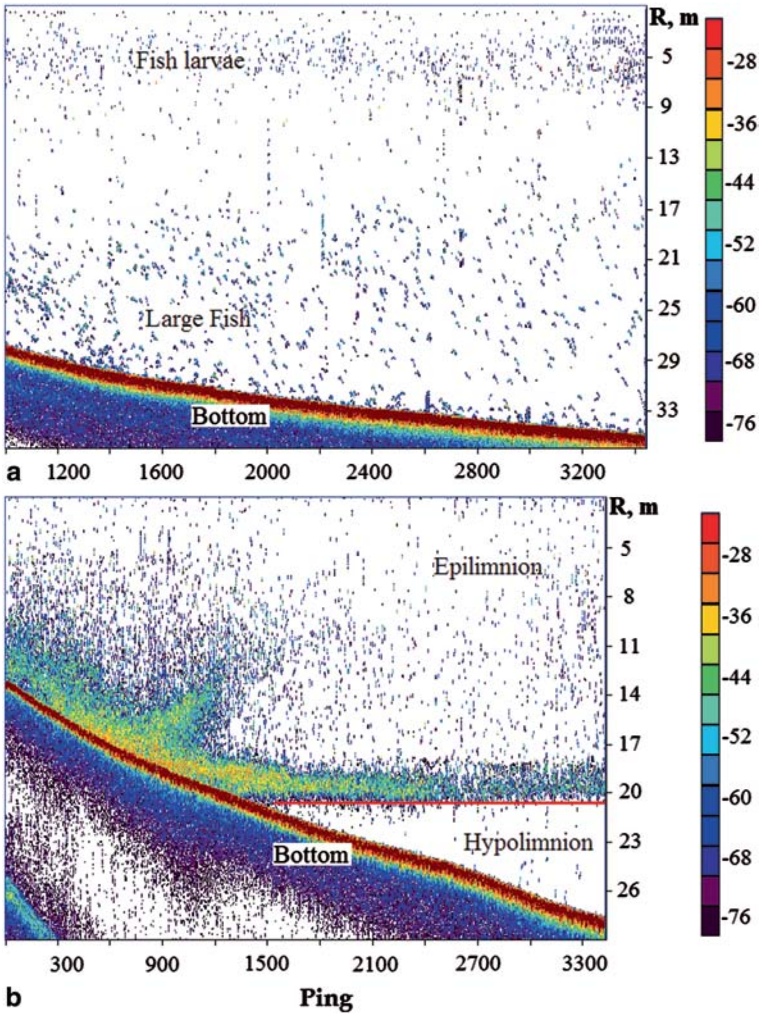

Fig. 16.4 Echograms of fish distributions along two transects. **a** A transect taken during holomixis (February 2011, Gofra). Scattered fish are seen in the entire water column. Clouds of *M. terraesanctae* larvae (<−60 dB) inhabit the upper part of the lake, while larger fish are more dispersed and inhabit the deeper part of the water column. **b** A transect taken during lake stratification (September 2011, Akeb), when anoxia prevailed in the hypolimnion (>18 m water depth). The majority of fish (*reddish, yellow,* and *green* structures) were concentrated at the thermocline-bottom interface, at the top of the sublittoral bottom, and at the top of the metalimnion (16–18 m), while the dispersed fish were seen in the upper and mid-epilimnion. *Horizontal red line* shows the location of the mid-metalimnion. Below this line, targets seen refer to methane bubbles rising from the bottom; bubbles are commonly abundant at low water levels (for more details see Ostrovsky 2009a, b). The data were collected at a rate of five pings per second. Range (*R*) shows the distance from the transducer, which was mounted 0.8 m below the water surface. A legend relates the color of pixels on the echogram to volume backscattering strength (dB re 1 m^{-1})

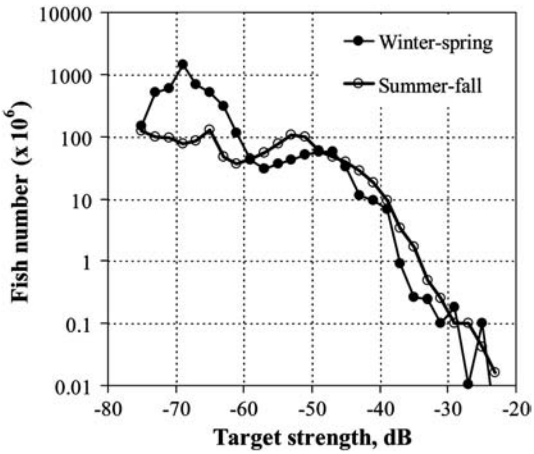

Fig. 16.5 Abundance of fish of different acoustic sizes (target strength, TS) in 2012. Fish abundance was evaluated in the pelagic zonefor winter-spring (February-March) and summer-fall (July-October). The fish abundance data were collected with a 120-kHz Simrad scientific split-beam echo sounder (model EK60). Peripheralareaswith bottom depth < 7–10 m depth were not acoustically surveyed.

in the pelagic zone (Fig. 16.5). Fast growth of the young-of-the-year explains an increase of fingerling (−59 to −49 dB, or 3–5 cm) abundance from winter to summer. In the pelagic zone, the number of larger fish (>−45 dB) also increases from winter to summer. Such an increase can be attributed mainly to seasonal migration of *M. terraesanctae* from the littoral, where these fish are concentrated during the spawning season, to deeper waters.

For assessment of total fish abundance, the minimal TS limit was usually set to −60 dB to disregard the larvae—a highly variable and the most abundant part of the population. Our evaluations of fish number in summer–fall time when most of the fish stay in the pelagic zone and can be accurately quantified with an echo sounder show that the total number of fish in the pelagic zone in 2011 and 2012 was 270 and 590 million, respectively. The last number is higher than the maximal value of 280 million reported for the period of 1987–1994 (Ostrovsky and Walline 2001), which may reflect an increase in the *M. terraesanctae* stock due to a decrease in its landing (cf. Chap. 36).

To approximate fish biomass using the acoustic surveys, we computed the following average TS–length (*L*, cm) relationship, based on the published data for various freshwater fish species (Horn et al. 2000; Rudstam et al. 2003; Mehner et al. 2010):

$$TS = 22.7 \log L - 70.3 \tag{16.1}$$

To evaluate fish biomass, a combined weight (*W*, g)–length (*L*, cm) relationship was calculated for the three most abundant fishes in Lake Kinneret (*M. terraesanctae, L. ramada,* and *M. cephalus*):

$$W = 0.00604 \cdot L^{3.11}. \tag{16.2}$$

The contributions of different size groups to the total fish abundance and biomass are illustrated in Fig. 16.6. The fish of the intermediate-size group of −47 to −33 dB

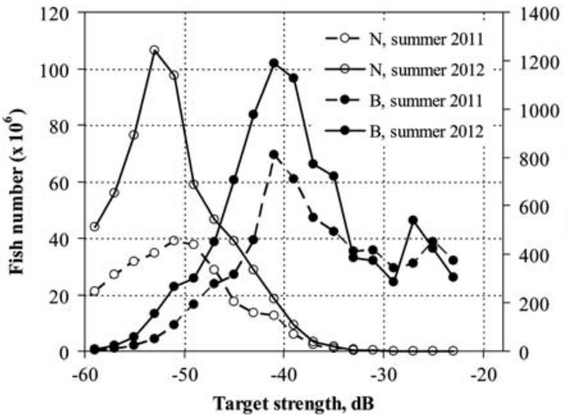

Fig. 16.6 Abundance (*N*) and biomass (*B*) of fish of different acoustic sizes (target strength, TS) in summerfall of 2011 and 2012. Acoustic surveys carried out in that time better represent the abundance and biomass of fish in the lake, because in summer and fall the dominant fish species inhabit the pelagic areas and thus can be properly sampled by the echo sounder. Other explanations as in Fig. 16.5

play an important role in formation of the total fish biomass, while fish smaller than −47 dB largely contribute to the total fish number. The estimated total biomass of pelagic fish in Lake Kinneret was 6,400 and 9,100 t in the summer of 2011 and 2012, respectively. Implementation of the Walline's TS–*L* relationship of bleak (Horne et al. 2000) would lessen the assessed biomass by ~30% and be closer to the previous estimates of 3,500–6,000 t (Walline et al. 1992; Ostrovsky and Walline 1999). Still, the accuracy of the presented values can be considered after detailed experimental measurements of TS–*L* relationships of dominant fishes in Lake Kinneret.

Extreme overfishing of large commercially important fish species (Ostrovsky 2005; Ostrovsky et al. 2013) caused a decrease in their biomass in the lake over the past decade. Concurrently, *M. terraesanctae* biomass increased due to reduced fishing pressure (Chap. 36). Combined, these two trends could substantially shift the fish community in favor of the zooplanktivore bleak. Because *M. terraesanctae* has gained the ability to control zooplankton abundance under some circumstances (see above), these changes could make the pelagic community more vulnerable to external disturbances and extreme events (e.g., water-level fluctuations). One can speculate that the bleak-driven shifts between top-down and bottom-up regulation of zooplankton grazers may also have contributed to destabilization of the phytoplankton community since 1993 (Zohary and Ostrovsky 2011), and thus affect ecosystem integrity.

Overall, the long-term changes in fish community composition in Lake Kinneret were associated with introduction, invasion, and continuous stocking of fishes; changes in fishing intensity; modifications of the littoral; and changes of the lake ecological regime. Water-level fluctuations beyond natural have modified the littoral habitats, which are of specific importance during different life stages of fish (Chap. 29, Ostrovsky et al. 2013), and affected fish reproduction, survival, and recruitment. The destabilization of lake ecological state modified the trophic relationships in the pelagic zone (Zohary and Ostrovsky 2011). Overexploitation of main fishery resources modified the fish community and has led to collapse of certain fisheries (Chap. 36). To protect fish resources and mitigate the negative impact of rapidly altering environmental conditions in the ecosystem, special efforts should be focused on conservation of the native fish species and the lake's natural ecological regime to which the food web components have adapted evolutionarily (Ostrovsky et al. 2013).

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