The Littoral Zone

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2 authors:

Tamar Zohary
Israel Oceanographic and Limnological Research Institute (IOLR)

Avital Gasith
Tel Aviv University

Chapter 29
The Littoral Zone

Tamar Zohary and Avital Gasith

Abstract The littoral zone of Lake Kinneret is characterized by high diversity of both abiotic (sand, stone) and biotic (vegetation) substrates, forming habitats of varying complexity that change markedly on both spatial and temporal scales. Most Kinneret fish and macro-invertebrates use littoral habitats for at least part of their life cycle. Many use littoral resources (substrate for attachment, refuge, food) for reproduction and growth. Higher species diversity and fish abundance and biomass are associated with higher degree of habitat complexity. Water level fluctuations (WLFs) influence the availability of littoral resources, with impacts not only on the littoral fauna and flora but indirectly also on the pelagic populations. Consecutive years of drought and a negative water balance for Lake Kinneret result in low lake levels and exposure of continuously increasing shore areas on which shore vegetation develops. The shore vegetation is inundated in high-rainfall winters, presenting a window of opportunity for the littoral zone biota that takes advantage of the temporarily augmented vegetative resources (e.g., enhanced reproduction of cichlids; refuge for young of the year of many fish species). Upon drawdown of the lake water levels, the proportion of rocky littoral declines, limiting the biota that dwell in this habitat. Correspondingly, littoral biota flourish on years of high water levels when rocky habitats are abundant. For example, fluctuation of population size of the endemic cyprinid *Mirogrex* (syn: *Acanthobrama*) *terraesanctae,* a major planktivore, was directly influenced by the availability of freshly inundated rocky substrate used for spawning. In a cascading effect, the pelagic zooplankton populations were impacted by the resulting fluctuations in *Mirogrex* population size and in their predation pressure. The case of Lake Kinneret underscores the importance of WLFs that can act as a major environmental factor influencing littoral habitat structure and resources, and resulting populations dynamic. Intensification of these fluctuations beyond their natural amplitude is likely to markedly impact the lake ecosystem structure and function.

T. Zohary (✉)
The Yigal Allon Kinneret Limnological Laboratory, Israel Oceanographic
& Limnological Research, P.O. Box 447, 14950 Migdal, Israel
e-mail: tamarz@ocean.org.il

A. Gasith
George S. Wise Faculty of Life Sciences, Department of Zoology,
Tel-Aviv University, 69978 Tel-Aviv, Israel
e-mail: avitalg@tauex.tau.ac.il

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29.1 Littoral Zones: General Overview

Lake shores are transitional zones, or ecotones, that provide habitats for both terrestrial and aquatic organisms. The littoral zone is the shallow-water, near-shore region of the lake, interfacing between land and water, extending to the lower limit of the euphotic zone, where light reaching the bottom is sufficient to support plant growth (Wetzel 2001). The littoral zone depth varies from one lake to another, often extending 1–5 m. Habitat diversity in the littoral zone is higher than that found in the pelagic zone. It emanates from the variety of bottom substrates and the mosaic of macrophytes, as well as the diverse biotic conditions resulting from the interaction between substrate and water and between water and air in this shallow-water environment (Schmieder 2004).

Littoral zones tend to be more productive than pelagic zones (Wetzel 2001), and have richer species diversity of both micro- and macro-organisms. The microbiota of the littoral zone includes bacteria, algae, fungi, and small invertebrates. The macrobiota includes macroinvertebrates, fish, birds, and submerged, floating and emergent plants. The structured substrate, whether abiotic (e.g., rocks) or biotic (e.g., plants), provides surface for attachment for algae and invertebrates, refuge for prey organisms, sites for fish spawning, and nursery grounds for young fish (Gafny et al. 1992; Schmieder 2004). Most fish in lakes inhabit the littoral zone and use its resources during at least part of their life cycle.

Gasith and Gafny (1990) pointed out the importance of littoral habitat complexity. Niche availability increases with "particle" size: Small particles such as sand and silt provide relatively low structural complexity, suitable only for small organisms, whereas larger particles such as stones and boulders provide refuge for both small and large organisms. Macrophytes, tree stems, and roots further increase habitat complexity (Gasith and Gafny 1998; Gasith and Hoyer 1998; Meerhoff et al. 2007; Brauns et al. 2008). Different macrophyte species provide habitats varying in food, cover, and structure for the aquatic biota (Wilcox and Meeker 1992). In contrast, man-made structures along lakeshores, such as walls, piers, and paved surfaces, usually reduce habitat complexity.

Littoral zones shift their position with changes in water level that exposes or inundates shore areas. Correspondingly, habitat complexity (physical structure provided by rocks and vegetation) varies with the regime of water level fluctuations (WLFs) and lake bathymetry. Wave action is another factor influencing structure and habitat conditions in the littoral zone. Wave action in interaction with changing water levels facilitates transport of small particles to deeper water, leaving rocks at higher water level marks (Hofmann et al. 2008). While rocky substrates are stable over time, the physical structure provided by plants is often seasonal, with large interannual variability; both types of substrates change with water depth and are influenced by WLFs (Gasith and Hoyer 1998).

Shallow lakes have extensive littoral area. In contrast, the littoral of deep lakes is limited to a narrow belt around the lake perimeter, often occupying $<10\,\%$ of the lake surface area (Gasith 1991; Beauchamp et al. 1994). As the size and depth of the lake increase, the source of autochthonous organic matter shifts from that of macrophytes in the littoral zone to that of phytoplankton in the pelagic zone. Concomitantly, non-metabolic littoral structural resources such as stones or macrophytes, used by the biota for colonization, refuge, and spawning, become increasingly scarce. Based on this consideration, Gasith (1991) hypothesized that littoral resources become increasingly limiting with increasing lake size and depth. In deep lakes, macrophytes are restricted to near shore areas of the littoral zone; therefore, the structure and food that they provide may result in short supply (Gasith 1991; Beauchamp et al. 1994; Gasith and Gafny 1998).

Species inhabiting lakes undergoing natural WLFs are adapted to the seasonal changes in habitat structure and conditions. However, accentuated WLFs produced by man can reduce species survival as their resilience is surpassed (Smith et al. 1987). As a result, the diversity of the littoral fauna and flora declines; in extreme cases, macrophytes are lost altogether and the fauna consists of only short-lived ephemeral species (e.g., insect larvae).

29.2 The Littoral Zone of Lake Kinneret

The following section will address the diversity of littoral habitats, the factors impacting the characteristics of those habitats, the biota that inhabit them, and the interactions between habitat type and the biota.

29.2.1 Physical Factors

Physical factors such as wave action, WLFs , and substrate particle size are important drivers that determine the nature and conditions (including lake bathymetry as reflected in shoreline development and basin slope) of littoral habitats in Lake Kinneret.

Bathymetry of the littoral zone: The 56-km-long shoreline of Lake Kinneret is mostly regular, with a shoreline development index of 1.14; it includes only one region of natural lagoons, in the north of the lake (Beteha lagoons). This region is dry during periods of low water levels (below ~-213 m). The slope of the Kinneret shoreline ranges from being gentle (1–2 %) in the Beteha lagoons in the south (Tzemach) and in the Ginnosar Valley on the west, and to being much steeper ($>5\,\%$) in the vicinity of Tiberias, at the north-east shore of the lake (Amnun, Kefar Nahum), and along much of the eastern side of the lake (details in Chap. 4). As water levels fluctuate between -214 and -209 m, the position of the littoral area of gentle-sloping shores is shifted by hundreds of meters whereas in steep-sloping shores it may shift only a few tens of meters. Correspondingly, the extent of shoreline vegetation that gets inundated varies markedly between gentle-sloping and steep-sloping shores (see below).

Wave action: In summer, westerly winds blow nearly every afternoon, causing strong wave action along the eastern shores. The winter period is less windy but with occasional exceptionally high-velocity easterly winds, known as “Sharakiya,” causing strong waves action on the western shores (details in Chap. 6). The absence of continuous growth of macrophytic vegetation in the littoral zone of Lake Kinneret may be attributed in part to the strong wave action that is capable of uprooting young shoots.

WLFs: Natural WLFs in Lake Kinneret are ~1.5 m, fluctuating between a maximum in spring (March–May) and a minimum in autumn (November–December). However, since the late 1960s, the lake supplies 25–30% of the country’s demand of potable water, which increased the multiannual amplitude of Kinneret WLFs up to 6 m, substantially impacting littoral zone habitats and resources (Zohary and Ostrovsky 2011).

Abiotic substrates: The lake bottom in the littoral zone is made of particles of variable sizes, ranging from fine clays, silt, and sand to gravel, pebbles, stones, and boulders. Rocky substrate including boulders is more prevalent in shores with a steep slope, whereas the gentle slopes tend to be sandy or silty.

The proportion of shores with fine substrates increases with declining water levels, whereas that of rocky substrate respectively declines. Gasith and Gafny (1990) reported that the overall percent of littoral bottom covered by fine substrates increased from 6% at −209.5 m to 49% when the water level was 3 m lower (−212.5 m). The change in the proportion of rocky littoral area in a selected site in a year of low lake level followed by high lake levels is demonstrated for example in Fig. 29.1. Using fluorescently dyed Kinneret sand particles, Shteinman and Parparov (1997) demonstrated that wave action transports small-grain sediments, and that the extent of the transport was correlated with the strength of the wave action. Currents transport the sediment along the shoreline. The sediment particles segregate by size, moving towards or away from the shore, depending on basin slope.

29.2.2 Biotic Substrates: Macrophytic Vegetation

Inundated emergent vegetation provides biotic substrates that contribute to habitat complexity of the littoral zone. Submerged macrophytes (*Myriophyllum spicatum* and *Potamogeton pectinatus*) were sporadically abundant in the past (Gophen 1982) but have become extremely rare in Lake Kinneret of recent years, both spatially and temporally (Gafny and Gasith 1999b; Gasith, unpublished data). Waisel (1967) attributed the limited growth of submerged vegetation to an increase in the magnitude of the lake’s WLFs and to unfavorable light conditions. An additional contributing factor operating in Lake Kinneret may be the destructive effect of high wave action, which uproots germinating rooted plants. For the same reasons, emergent macrophytes do not germinate and develop in the littoral zone. Emergent macrophytes seen in the lake are plants that germinated and started to develop

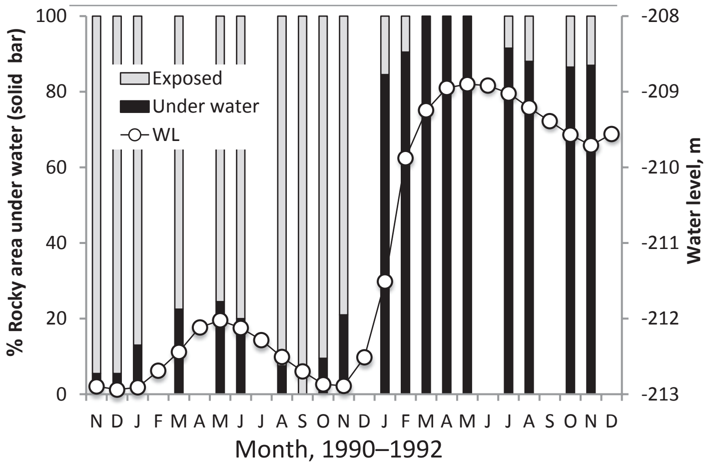

Fig. 29.1 Temporal changes in the availability of rocky area in the littoral zone of Lake Kinneret in an eastern beach on a dry year (1991) followed by a rainy year (1992). *Solid line* indicates changes in water level. *Solid* and *open bars* indicate the proportion of rocky area under and above the water level, respectively. (Reproduced from Gasith and Gafny (1998) with permission from Springer)

on shores, and become part of the littoral zone when inundated by the rising lake level (Fig. 29.2a). The community of emergent macrophytes is composed mostly of *Phragmites australis* (common reed), *Typha angustata* (cattail or bulrush), *Cyperus alopecuroides* (sedge), and the tree *Tamarix jordanis* (tamarisk). When inundated, this vegetation contributes structure and reduces wave action and the strength of currents among the plants.

Plant growth on exposed shores responds positively to declining basin slope (highest growth rates and biomass attained on gentle slopes) and inversely to sediment particle size (lowest on rocky shores). Moreover, the extent of growth of the shore vegetation is positively influenced by the duration of shore exposure (Gafny and Gasith 2000). Following three consecutive years of low lake levels (1984–1986), when the upper region of the littoral zone (altitude −209 to −210 m) was exposed, Gafny and Gasith (2000) estimated the total standing biomass of the shore vegetation around the lake in fall, 1986, at 4,000 t wet weight (ranging from <0.01 to 1.8 kg dry weight m^{-2}). *Cyperus alopecuroides* and *Tamarix jordanis* contributed about 60 % of the biomass. Similar estimates were made in other years of low water levels (e.g., 1990/1991). In years of high lake levels (e.g., 1987–1989), the estimated standing biomass of shore vegetation was <2 % of that recorded on years of low lake level, mostly because the belt of exposed shores was narrower, leaving smaller areas suitable for plant germination and growth.

In years of low water level, typically with massive shore vegetation, the littoral zone is mostly devoid of inundated vegetation, whereas in years of high water levels that follow years of low lake level, the extent of inundated vegetation can be massive (Fig. 29.2b). Thus, the extent of vegetative cover in the littoral zone varies spatially and temporally, depending on the extent of WLFs and the recent history

Fig. 29.2 **a** Recently inundated young *Phragmites* reeds that germinated and grew when the same site was exposed due to lower water levels (photo: Gasith A). **b** Dense shoreline vegetation (mostly tamarisk trees) that developed during consecutive years of below-average rainfall and low water levels, Ginnosar region (photo: Gasith A). **c** Periphyton-covered stones in the shallow water of Lake Kinneret (photo: Gasith A). **d** Shore aggregation of Kinneret snail shells. Native species: *Melanopsis costata; Melanoides tuberculata*; invasive species: *Pseudoplotia scabra* (photo: Zohary T)

of those fluctuations. An analysis of a series of >300 air photographs of the lake perimeter taken in May 2009 when lake level was low (−213.37 m) shows that >90 % of the littoral zone had no emergent macrophytes (Fig. 29.3a). In contrast, in May 2012, following a rise in water level by 2.35 m in a single winter (−211.32 m; i.e., ~2 m higher than in May 2009), only 39 % of the littoral zone had no vegetation, the rest was covered by either dense (45 %) or sparse (16 %) inundated vegetation (e.g., Fig. 29.3b).

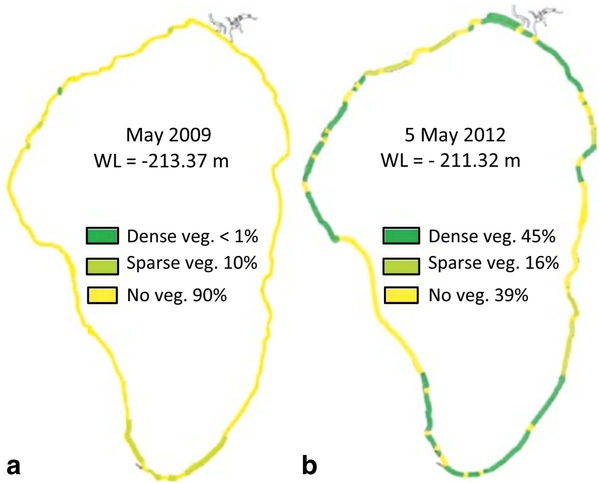

Fig. 29.3 Maps showing the locations of inundated vegetation in the littoral zone in May, the time of the year when water level is at or near its annual maximum. **a** In 2009, a low-water-level year that followed three drought years with declining water levels. **b** In 2012, a year of a major water level rise that followed six consecutive below-average rainfall years. Areas of thick, sparse, or no vegetation are indicated. The hand-drawn maps (by David Cummings) are each based on a series of >300 aerial photographs, on 1 May 2009, by Idan Shaked and on 5 May, 2012, by Asaf Dori, Israel Nature Parks Authority. Only inundated vegetation was mapped, shore vegetation outside the water was ignored

Following six consecutive years of below-average rainfall starting in 2005, dense shore vegetation developed, covering not only the sandy shores but also rocky regions. Moreover, we observed that when the shores were exposed continuously for more than 3–4 years, the tree *Tamarix jordanensis* replaced the common reed *Phragmites australis* as the dominant plant, forming dense, forest-like vegetation (Fig. 29.2b). In certain shore areas, alien invasive trees including *Acacia saligna, Eucalyptus* sp., *Parkinsonia aculeate,* and *Washingtonia* palms also got established. However, after inundation by the rising water levels, most of the vegetation died or was uprooted by wave action and decomposed within several months. Exceptional were large *Tamarix* trees with much of their canopy extending above the water; these trees may apparently survive long periods of inundation (possibly years).

The rise of the lake level is associated with periodic high accumulation of organic debris. In years of massive accumulation of plant litter (at times of shore inundation after several years of continuous low lake levels), puddles within piles of debris may be formed on the shore with potential development of short-term nuisances of foul smell and mosquitoes. In 2011/2012, such nuisances raised a debate whether the vegetation should be massively removed to alleviate related inconveniences but at the same time risking the integrity of the lake ecosystem. Most scientists argued that the nuisances can be treated and their effect can be drastically reduced which was proved true. Until relevant information will be obtained, the precautionary principle should be followed. Accordingly, vegetation will be completely removed from bathing beaches; partly removed (up to 30 %) from nearby shores and fronts of the local kibbutzim; and removed elsewhere to form access corridors, where needed.

29.2.3 Benthic Algae and Heterotrophic Bacteria

Phytobenthos: The benthic algae of the littoral zone (Fig. 29.2c) comprise an important food source for higher trophic levels inhabiting this region. Nevertheless, so far the phytobenthos was studied only sporadically. Dor (1971, 1974) reported that benthic diatoms comprised a low-diversity, high-abundance assemblage, whereas benthic cyanobacteria were highly diverse but of low abundance. According to Round (1978), the phytobenthos is richly developed on all available substrates in the littoral zone, extending to the limit of light penetration. Diatoms dominate, often covering the substratum by a brown mucilaginous "blanket" and contribute most (~ 90 %) of the primary production. Filamentous and coccoid cyanobacteria, filamentous green algae, and occasionally euglenoids, cryptomonds, and some desmids, are also abundant. Unlike the pattern typical of temperate lakes, highest biomass and species richness of epilithon in the littoral zone of Lake Kinneret was recorded in winter, and was lowest in the summer (Gafny and Gasith 1999a). As the water level rises in winter and spring, newly inundated rocky areas are colonized by epilithon. The organic matter produced by the epilithon is more labile than that produced by macrophytes, and is probably a better quality food for the littoral biota. According to Gafny and Gasith (1999a, 2000), benthic primary production may amount to only a fraction of 1 % of the annual phytoplankton production in the lake, but is higher by an order of magnitude than that of inundated vegetation. They further showed that epilithon production declines drastically with falling water levels, and warned that if the water level is further reduced, littoral benthic grazers may be deprived of an important food source. Yehoshua et al. (2008) showed that epilithon growth rates in the Kinneret littoral were higher on limestone than on basalt and flint, and that different assemblages inhabited the different kinds of stones.

Heterotrophic bacteria: Little is known on heterotrophic bacteria and their activity in the littoral zone of Lake Kinneret. Ora Hadas (unpublished) recorded considerably higher rates of microbial production and glucose uptake rates in the littoral zone compared with that measured in the pelagic waters of Lake Kinneret. Similarly, Sala and Güde (2006) concluded that the overall contribution of the littoral zone to degradation of organic matter in Lake Constance was comparable to that of the total pelagic water body although the littoral comprised less than 10 % of the lake surface area.

Sukenik and Parparov (2008) conducted laboratory experiments and showed that *Phragmites australis* and *Tamarix jordanensis* decomposed rapidly in Kinneret water, with loss rates of 2–3 % of dry weight per day. The loss rates of nitrogen and phosphorus were twice as high (6.0 and 5.3 % day^{-1}, respectively). However, Gafny and Gasith (2000) recorded much slower rates of in situ decomposition rates, of ~0.6 % day^{-1} for *P. australis,* and half of that rate for *T. jordanensis*. Part of the difference in the rates recorded in these two studies may be attributed to the lower temperatures in the in situ experiments.

29.2.4 Invertebrates

The first encompassing report on the benthic invertebrates in the littoral zone of Lake Kinneret was that of Por (1968) and Por and Eitan (1970). An additional study of the invertebrates in the shallow littoral zone (<2 m) was conducted by Tamir and Gasith during 1999–2001 (Tamir 2002). Taxa richness in rocky and soft sediment substrates was similar (19 and 17 species, respectively) but species composition was different. On rocky substrates, the amphipod *Echinogammarus veneris* was dominant (64–75 % of total organisms) whereas on soft sediments chironomid larvae and oligochaetes were most prevalent. Seven taxa were found exclusively on rocks (sponges, bryophytes, leeches, mayflies, and three species of caddisflies; Trichoptera; Gasith 1969) as well as the invasive snail *Radix natalensis*. Four taxa were found exclusively in soft sediment (oligochaetes, bivalves). Native gastropods had representatives on both types of substrate. A seasonal succession was apparent with dominance of mollusca in the summer and that of *Echinogammarus* and the snail *Bithynia phialensis* in winter.

The native snail fauna of Lake Kinneret consists of three main freshwater species, *Melanopsis costata, Melanoides tuberculata*, and *Theodoxus jordani,* species that were reported to occur in the Jordan Valley for the last 1.5 million years (Heller 2010), long before Lake Kinneret existed in its current form. The abundance of the native molluscs declined dramatically after an unusually large water level rise of winter 2002/2003. This decline coincided with the establishment of an invasive snail *Pseudoplotia scabra,* first reported in the lake (as *Thiara scabra*) in 2007 by Mienis and Mienis (2008). By summer 2010 and throughout 2011, *P. scabra* was the dominant mollusc around the entire lake, with all the native species seen only rarely (Fig. 29.2d; Heller et al. 2014). However, by December 2012, the abundance of *P. scabra* has declined and that of the native species increased. The consequences of this recent invasion for the fauna and flora of Lake Kinneret and the impact on the functioning of the ecosystem are still unknown.

Three native species of bivalve molluscs are known in Lake Kinneret, two unionid mussels *Unio terminalis terminalis* and *Potamida (previously Unio) semirugatus* and a clam *Corbicula fluminalis*. Of those, *U. t. terminalis* is the most abundant species, *C. fluminais* is common, and *P. semirugatus* is rare. Cohen (1993) found high density of *U.t. terminalis* on relatively steep-sloping, sandy bottom on the east side of the lake where relatively strong lateral currents prevail. Ostrovsky et al. (1993) reported highest densities of *Unio t. terminalis* in muddy sands at 0.3–6-m depth, and especially near the Jordan River inflow. They concluded that this bivalve plays a substantial role in removing particulate matter from the water in the shallow inshore area, supplying suspended organic matter to the benthic community and regenerating nutrients. Its larval stage (glochidium) is an obligatory parasite on fish and was recorded on the Kinneret bleak (*Acanthobrama terraesanctae*; Cohen 1993). Like the snails, the abundance of *U. t. terminalis* has declined dramatically over the last decade, but no studies were conducted to highlight any aspects of this decline.

Fig. 29.4 **a** Leeches (*Helobdella stagnalis*) attached to foot after standing for 3 min in the shallow water, May 2012 (photo Beny Sulimany). **b** A regular nest of tilapia (*Oreochromis aureus*) among inundated plants (photo: David Cummings). **c** A single nest of *Oreochromis aureus,* found in a wide sandy area bare of vegetation. It was dug next to the only physical structure present (photo A Gasith)

The stony shores of Lake Kinneret are inhabited by three species of leeches, *Helobdella stagnalis, Dina lineata,* and *Batracobdelloides tricarinatus* (Bromley 1994). They are usually found, in low numbers, adhering to the bottom side of pebbles or stones in shallow waters. Dolev et al. (2012) examined these three species in the field and in the laboratory and reported that *B. tricarinatus* fed on small fish, sucking their blood, *H. stagnalis* fed on snails, and *D. lineata* fed on snails, with preference for the invasive snail *Pseudoplotia scabra.* Gasith (unpublished) recorded that *D. lineata* fed also on chironomid larvae. Several outbreak events of *Helobdella stagnalis,* in summer 2005 and again in summer 2012, attracted attention to this group of invertebrates. Swimmers complained that after standing in the shallow water for a few minutes their feet got covered by tens of leeches (Fig. 29.4a). The leeches do not suck human blood, and are not pathogenic to humans; however, finding them stuck to one's feet was a cause for public complaints. The leech outbreaks were limited in time (few days to weeks) and space (focal

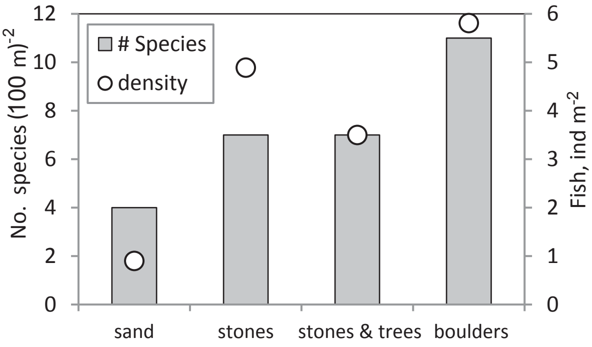

Fig. 29.5 Relationship between fish species richness and abundance and habitat type in the littoral zone of Lake Kinneret. (Source of data: Gafny 1992)

points of several tens of square meters). They occurred at a few man-modified sites, where the bottom substrate was covered by gravel to make wading in the water easier for vacationers.

29.2.5 Fish

Nineteen native fish are present in Lake Kinneret, including an endemic species (the Kinneret bleak, *Mirogrex* (syn. *Acanthobrama*) *terraesanctae,* cyprinidae; Goren and Ortal 1999) and additional alien species (Chap. 16). Most of the fish of Lake Kinneret spend at least part of their life in the littoral zone (Gasith et al. 2000). As shown by Gafny (1992) and Gasith et al. (2000), the nature of the littoral substrate affects fish distribution, richness, density, and biomass. These attributes of the fish community increase with increasing habitat complexity that is influenced by substrate size. Higher richness, density, and biomass (including larger fish) were recorded in littoral zone areas with large stone and boulders than in sandy areas (Fig. 29.5). Thus, WLFs that influence littoral zone structure and habitat complexity have an indirect effect on the fish community. In the following sections, we address some of the fish species individually.

The Kinneret bleak is the most abundant fish in Lake Kinneret, comprising more than 80% of all pelagic fish (Chap. 16). Being a zooplanktivore, this fish plays a central role in the lake's food–web interactions. This fish depends on littoral resources to complete its life cycle. It spawns in winter when the water level rises and inundates rocky areas, where the fish sheds its eggs that adhere to the freshly inundated (i.e., epiphyton-free) stones, in shallow (<50 cm) water (Fig. 29.6; Gafny et al. 1992; Gasith et al. 1996). As the water level rises, there is a short window of opportunity of several days for the bleak to successfully spawn on the algae-free stony surface. Algae may completely cover the stones within a week. Once the algae (e.g., diatoms such as *Navicula* and *Gomphonema*) cover the stone surface, they prevent the eggs from adhering to the stone's surface; the eggs fall to the ground and are infested by the fungus *Saprolegnia* (Gasith, unpublished). Preference of epiphyton-free substrates for adhering eggs was reported for other fish species in other

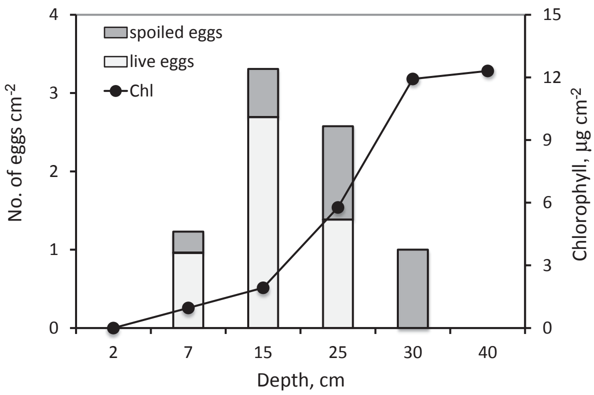

Fig. 29.6 The relationship between water depth, epilithon development (Chlorophyll-a concentration, Chl) and egg density on stones of the Kinneret bleak (*Mirogrex terraesanctae*) in the Kinneret littoral zone. (Reproduced from Gafny et al. 1992, with permission from John Wiley and Sons)

lakes, e.g., *Abramis brama* (cyprinid), (Probst et al. 2009), yellow perch (Fisher et al. 1996), and American smelt (Rupp 1965).

Gafny et al. (1992) and Gasith et al. (1996) showed that the availability of stony substrate suitable for spawning of *M. terraesanctae* increases with increasing rise of the lake level and vice versa. They therefore hypothesized that reproductive success of the bleak is directly influenced by the extent and rate of change of the lake level. Ostrovsky and Walline (2000) and Zohary and Ostrovsky (2011) later corroborated this hypothesis: Based on data from hydroacoustic fish surveys, they showed that indeed years of exceptional rise of the water level were followed by population explosion of *M. terraesanctae*. They too attributed the marked population increase to the increase in the availability of suitable spawning substrate relative to years of natural WLFs. Furthermore, Gasith and Gafny (1998) and Zohary and Ostrovsky (2011) argued that the newly inundated vegetation in years of high water level provide the young of the year with ample food, shelter from predators, and refuge from strong currents thus increasing their survivorship.

Among the fish species that require littoral habitats stands out a small blenny *Salaria fluviatillis* that besides a short pelagic larval stage spends the rest of its life in the shallow water in rocky habitats. It spawns under rocks with preference of rocks of a certain size (Aidlin et al. 1994); therefore, its breeding success is predicted to be affected by WLFs that determine the availability of rocky habitats (Gasith and Goren 2009). Another strictly littoral species is the small cichlid *Astatotilapia (Haplochromis) flaviijosephi* (Spataru and Gophen 1985).

The native cichlids of Lake Kinneret, and particularly *Sarotherodon galilaeus, Tilapia zilli,* and *Oreochromis aureus,* utilize sandy littoral habitats for nesting and spawning, preferably near or among inundated vegetation (Gasith and Goren, unpublished; Fig. 29.4b). Some cichlids may also spawn in sandy areas with no vegetation (Gophen and Bruton 1989). The preference of nesting in sheltered sites is demonstrated, for example, in choosing to nest by a single rock that was available and not nearby in barren sandy area (Fig. 29.4c). Gasith and Goren (unpublished) found that when inundated vegetation is available, *Oreochromis aureus* and *Tilapia zilli* favor the vegetation over bare sand substrate for nesting (Fig. 29.4b). This was corroborated in a recent survey of cichlid reproduction (spring–summer 2012), which clearly indicated that cichlids used the window of opportunity when structured habitat was available, and favored nesting near or among the inundated vegetation. Between mid-April and mid-September 2012, 11 different sites around the lake were visited regularly and nesting of cichlids was recorded along transects perpendicular to the shoreline. Nesting activity was recorded at all but one site (Gofra) where the substrate is rocky. Of the total of ~6,000 squares of 1 m^2 each surveyed, about 50 % were covered by inundated vegetation and 50 % were without vegetation (although plants may have been close by, even in the adjacent square). The density of nests in the vegetated sites was on average 28 nests per 100 m^2, double the density of nests in areas with no vegetation (14 nests per 100 m^2). Most of the nests were of *Tilapia zilli* and *Oreochromis aureus,* those of *S. galilaeus* were seen infrequently. The latter was seen breeding in shallow littoral sites near vegetation after only minimal nest-building activity.

The common carp *Cyprinus carpio* as well as the catfish *Clarias gariepinus* also reproduce in the spring, among inundated vegetation. Furthermore, the littoral zone is the main nursing ground for fingerlings of most fish species. Fingerlings of the Kinneret bleak and other cyprinids and of cichlids were observed in the littoral zone during spring and summer, mostly among inundated vegetation (Gasith and Goren, unpublished).

29.3 Impacts of Processes in the Littoral Zone on Ecosystem Functioning and Services

Processes occurring in the littoral zone may have a cascading impact on the entire ecosystem and the services it provides. Some examples are given here:

a. The Kinneret bleak reproduces in the littoral but lives most of its life and feeds on zooplankton in the pelagic zone. Its reproduction success has direct impact on the zooplankton populations. Years of exceptional reproduction success of the bleak (e.g., 1992 and 2003, years of high rise of the water level) were followed by the bleak's population explosion and a collapse of the zooplankton—that is attributed to high predation pressure (Gal and Anderson 2010; Zohary and Ostrovsky 2011).
b. Sukenik and Parparov (2008) estimated that the maximal nutrient addition due to inundated macrophyte decomposition occurred in April and May, comprising 17 % of the externally loaded total phosphorus during these months. They concluded that there is a potential for enhanced biological activity (extended bloom) during the spring and early summer following a flooding event of massive shoreline vegetation areas, but that the impact would not extend further in time. Their conclusion was supported in spring 2012 that followed a wet winter with 2.35-m rise in water level and inundation of massive areas with dense shoreline vegetation. An intensive bloom of the dinoflagellate *Peridinium gatunense* developed

that spring, a bloom that persisted longer and reached higher peak biomass than in most other years (see Chap. 11). Thus, the lake's major pelagic foodweb structure was impacted.

c. Following consecutive years of low lake levels, rising of the water levels in 2012 with improved conditions for cichlid reproduction and survivorship, the commercial harvest of *S. galilaeus* has also improved, from an all-time minimum of 8 t in 2008 to 166 t in 2012 (Jamie Shapiro, Dept. of Fisheries, pers. comm.).

29.4 Conclusions

Littoral zones of large lakes naturally occupy relatively small proportion of the lake surface area (<10%) but have a disproportionately important role, by providing resources that are available nowhere else in the lacustrine ecosystem (Gasith 1991; Gasith and Gafny 1998; Wantzen et al. 2008).

Shoreline vegetation is an integral part of the lake ecosystem and when inundated provides a "window of opportunity" for the fish to reproduce, feed, and find refuge.

Changes in the structure of the littoral zone and its resource availability are expected to cascade to the pelagic zone, eventually influencing ecosystem processes and water quality (Gasith 1991; Gal and Anderson 2010; Zohary and Ostrovsky 2011).

Management of the lake's hydrology in a way that reduces extreme WLFs will prevent excessive growth of shoreline vegetation and associated short-term environmental nuisances when inundated. Less variable amplitude of WLFs is also expected to support a healthier Lake Kinneret ecosystem.

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