Erik Jeppesen Martin Søndergaard
Morten Søndergaard Kirsten Christoffersen
Editors

The Structuring Role of Submerged Macrophytes in Lakes

With 117 illustrations

Springer

Erik Jeppesen
Department of Lake and Estuarine Ecology
National Environmental Research Institute
DK-8600 Silkeborg
Denmark

Martin Søndergaard
Department of Lake and Estuarine Ecology
National Environmental Research Institute
DK-8600 Silkeborg
Denmark

Morten Søndergaard
Freshwater Biological Laboratory
University of Copenhagen
DK-3400 Hillerød
Denmark

Kirsten Christoffersen
Freshwater Biological Laboratory
University of Copenhagen
DK-3400 Hillerød
Denmark

Cover illustration: As it will appear from this book, submerged macrophytes may have an important impact on the nutrient dynamics, trophic structure, and trophic interactions of shallow lakes. Within certain nutrient limits, submerged macrophytes may via a number of feedback mechanisms maintain a clearwater state despite increased nutrient supply. Drawing by Bjørn Bachmann and Erik Jeppesen.

Library of Congress Cataloging-in-Publication Data
The structuring role of submerged macrophytes in lakes/Erik Jeppesen
... [et al.].
p. cm.—(Ecological studies; v. 131)
Includes bibliographical references and index.
ISBN 0-387-98284-1 (hc: alk. paper)
1. Lake ecology. 2. Lake plants—Ecology. I. Jeppesen, Erik.
II. Series.
QH541.5.L3S77 1997
577.63—dc21 97-22884

Printed on acid-free paper.

Production coordinated by Princeton Editorial Associates and managed by Francine McNeill; manufacturing supervised by Jeffrey Taub.
Typeset by Princeton Editorial Associates, Princeton, NJ.
Printed and bound by Maple-Vail Book Manufacturing Group, York, PA.
Printed in the United States of America.

9 8 7 6 5 4 3 2 1

ISBN 0-387-98284-1 Springer-Verlag New York Berlin Heidelberg SPIN 10632906
ISSN 0070-8356

24. Importance of Physical Structures in Lakes: The Case of Lake Kinneret and General Implications

Avital Gasith and Sarig Gafny

Introduction

Rock formations, plants, and woody debris are typical sources of physical structure in lakes. They determine physical complexity of littoral habitats, form the basis for the heterogeneous nature of the nearshore environment, and support metabolic (organic matter and nutrient dynamic) and nonmetabolic (structure) related functions (Wetzel and Hough, 1973; Lodge et al., 1988). Physical structures are often colonized by a diverse assemblage of microorganisms, algae, and invertebrates and attract predators (mostly fish and macroinvertebrates), which exploit this rich food resource (e.g., Lodge et al., 1988; Heck and Crowder, 1991; Diehl, 1993). Structured habitats also provide refugia for prey organisms (Heck and Crowder, 1991) and are favored as spawning sites (e.g., Goodyear et al., 1982; Gafny et al., 1992). Lake Kinneret (Israel) undergoes relatively wide water-level fluctuations, providing an opportunity to examine biotic responses to changes in littoral habitat structure in a relatively large (170 km^2), deep (43 m) lake. Here, we present selected results of our study on the effects of water-level fluctuation on habitat structure and availability, fish breeding, and community structure and discuss the importance of physical structures in lakes of different morphometry.

Results and Discussion

Effect of Water Level on Habitat Structure and Availability

Lake Kinneret water level normally fluctuates within 1.5–2 m. After drought years, the lake level may fall by 4 m (Gasith and Gafny, 1990). As water levels rise and fall, large areas along the shoreline are inundated or exposed, changing the location and structure of the littoral zone. The proportion of shores with rocky substrate declines from greater than 60% at the highest lake level to less than 10% as the water level falls by 3.5 m (Gasith and Gafny, 1990). The belt of submerged rocks also narrows markedly with falling lake level (Fig. 24.1), and stone size usually becomes smaller. Submerged macrophytes (e.g., *Potamogeton pectinatus, Myriophyllum spicatum*) develop sporadically in Lake Kinneret (e.g., Gasith and Gafny, 1990; Gafny, 1993). Emergent vegetation (mostly *Cyperus alopecuroides, Tamarix jordanensis, Typha angustata,* and *Phragmites australis*) is restricted to the supralittoral zone during periods of high lake levels. However, dense macrophyte stands develop (up to mean biomass of 1.3 kg dry weight/m^2; total lake shore biomass of ca. 1,000 metric tons ash-free dry weight) in sandy shores exposed after lake drawdown (Gasith and Gafny, 1990). Rising lake level inundates the newly developed vegetation and provides highly structured habitats for a period of a few months until the plants are uprooted or senesce and decompose (Gasith and Gafny, 1990; Gafny, 1993). In addition to affecting habitat complexity, water-level fluctuation markedly changes the availability of substrate colonized by periphyton, which, in the absence of macrophytes, form the main source of organic matter in the littoral zone (Gafny, 1993).

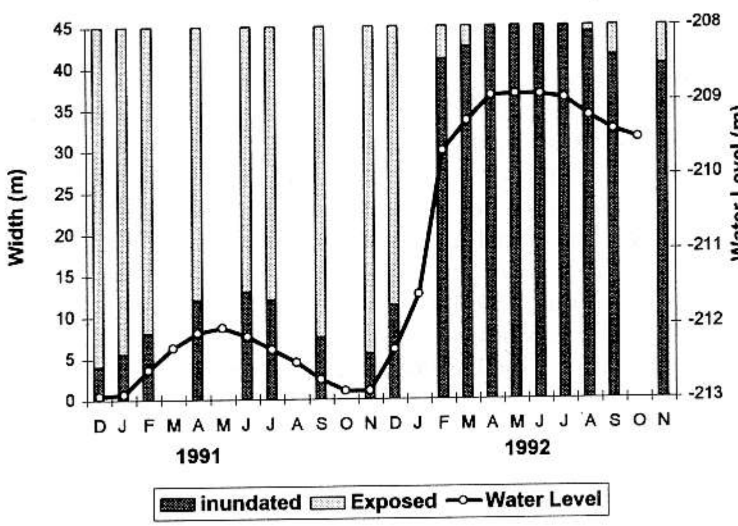

Figure 24.1. Change of the width of submerged rocky habitats in a selected littoral site (E-21) of Lake Kinneret during years of low (1991) and high (1992) lake levels.

Effect of Water-Level Fluctuation on Fish–Habitat Interaction

Of the 24 fish species extant in the lake, 15 may be found during the daytime in the shallow littoral zone (m), all at sites with boulders. Eight of these species may also be found at sites where the substrate is dominated by cobbles, and only four at sites with structurally simple, sandy substrate (Gafny, 1993). Most of these fish are small (<80 mm), either small-bodied species or juveniles of larger fish. Under conditions of high lake level, fish biomass over boulders is often an order of magnitude higher (80 g/m^2 wet weight) than over cobbles, reflecting preference of more structurally complex habitats over simple ones. During periods of low lake levels, fish biomass at both habitat types is similar and relatively low (<40 g/m^2). This reflects a decline in fish biomass over boulders and an increase over cobbles. Apparently, under low water-level conditions the fish have no choice but to use any structured habitat available (Gasith and Goren, 1995). Forcing the fish out of their preferred habitats can reduce fish survival, partly due to greater predation mortality.

Water-level fluctuation may also affect fish breeding success. During winter (November–May), large schools of the "lavnun" (*Mirogrex terraesanctae,* a keystone zooplanktivorous cyprinid) move inshore at night to spawn over rocks in very shallow waters (<50 cm). Only eggs that stick firmly to the substrate develop (Gafny et al., 1992). Winter is also the peak period of epilithon growth in Lake Kinneret (Gafny, 1993), and algae such as diatoms (e.g., *Cymbella* sp., *Gomphonema* sp., *Navicula* sp.) form a slimy covering on the stones' surface, making the substrate unsuitable for egg attachment. During periods of low lake levels, the lavnun uses the "window of opportunity" provided by the rising lake level to spawn over freshly inundated, temporarily (7–10 days) algae-free rocks found along the shoreline (Fig. 24.2). A minimal rise in lake level (ca. 30 cm) in the winter of 1988/89 produced unusual conditions in the littoral zone, and submerged rocks were overgrown by epilithon throughout most of the littoral zone. We estimated that more than 90% of the lavnun eggs were lost that winter and concluded that water-level fluctuation can strongly influence breeding success and, ultimately, recruitment of young of year (YOY) of the lavnun (Gasith and Gafny, 1990; Gafny et al., 1992; Gasith et al., 1996). This association between water level, the availability of spawning substrate, and YOY recruitment has been corroborated by findings from hydroacustic studies of fish abundance in the lake (Walline et al., 1992; Walline et al., 1994).

Water level also influences the availability of preferred spawning substrate for a blenny *(Salaria [Blennius] fluviatilis),* an important zoobenthivorous fish that spawns on rocks in the littoral zone of Lake Kinneret. Spawn density and size drop under low lake levels (Aidliñ, 1995). However, the same conditions of low lake levels that deleteriously affected the above species enhance emergent macrophyte development in exposed shores. When inundated, this vegetation provides excellent breeding sites for certain cichlids (nest densities >0.8/m^2) as well as refugia and feeding grounds for the larvae and YOY. We can therefore predict higher recruitment of cichlids in littoral sites around the lake in a rainy year that follows years of low lake levels.

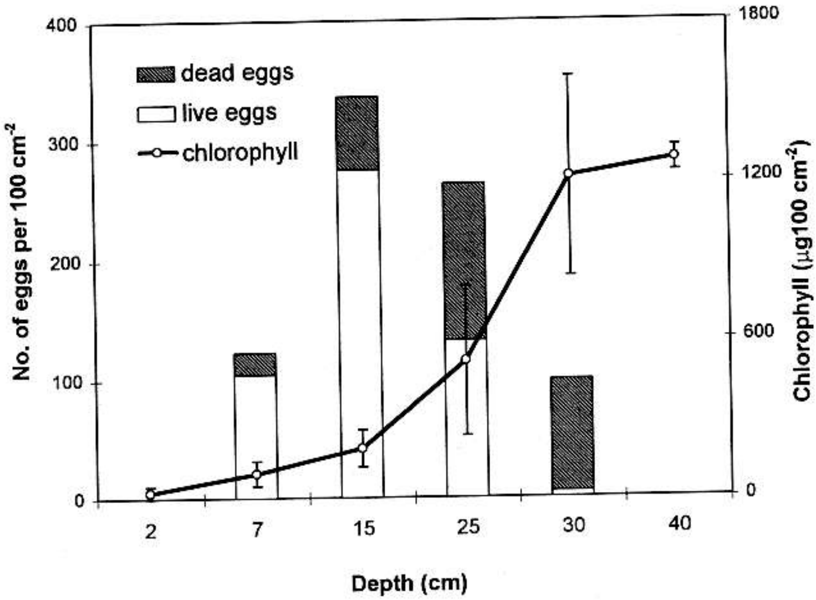

Figure 24.2. Typical relationship between lavnun (*Mirogrex terraesanctae*, Cyprinidae) egg density (mean ± SD) and survival (live and dead eggs), depth, and epilithon biomass (chlorophyll *a*) in the littoral zone of Lake Kinneret. (From Gafny et al., 1992.)

General Implications: The Role of Vegetative Versus Abiotic Formations and Effect of Lake Morphometry

Most of the knowledge on the structure and function of littoral zones comes from studies of small vegetated lakes, where the littoral region occupies a relatively large portion of the lake. In such lakes, both metabolic and structural features of the littoral zone are important and have been well recognized (e.g., Wetzel and Hough, 1973; Lodge et al., 1988). However, the role of the littoral zone in large deep lakes is less well understood (Danehy et al., 1991; Gasith, 1991). The availability of vegetated habitats in lakes is influenced by physical (e.g., wave action, light), water and sediment quality, and biotic controls (e.g., Carpenter and Lodge, 1986; Gasith and Hoyer, this volume, Chapter 29). In small and shallow lakes, temporal variability in habitat structure usually follows the seasonal cycle of macrophyte development. Macrophyte importance in lakes generally declines with increasing lake size. Duarte et al. (1986) concluded that, on average, the percentage of lake area colonized by submerged macrophytes declines with increasing lake size from about 50% in lakes of about 10 ha to about 10% in lakes of 10^4 ha and to less than 10% in larger lakes. They attributed the relatively higher importance of emergent vegetation in large lakes to a greater proportion of sheltered bays and floodplains. Large deep lakes often derive physical complexity from abiotic formations (e.g., Gasith and Gafny, 1990; Danehy et al., 1991;

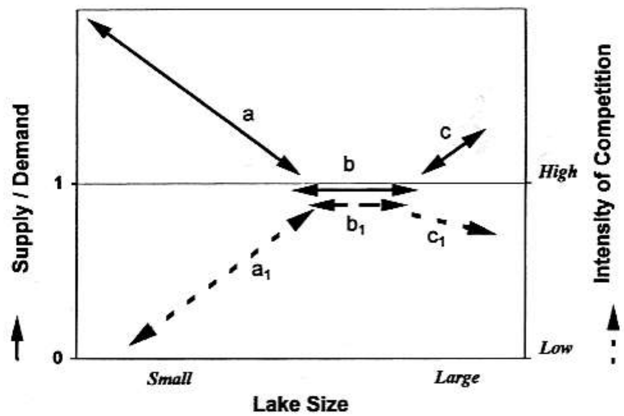

Figure 24.3. Relationship between lake size and the ratio of supply to demand of littoral resources and the corresponding intensity of competition over these resources among consumers that move into the littoral zone (for further details, see text).

Beauchamp et al., 1994). The size and form of these structures is mostly independent of water-quality conditions but is affected by wave action that sorts for the larger and heavier particles in the high-energy, nearshore zone and for finer ones in deeper water (e.g., Walter, 1985). Like plants, the surface of abiotic substrates is often seasonally modified by growth of periphyton. The availability of littoral habitats with vegetative or abiotic structure may be altered by water-level fluctuations.

The portion of the lake occupied by the littoral zone is inversely related to basin slope (Duarte and Kalff, 1986) and to the degree of shoreline regularity, being smallest in large deep lakes with low shoreline development index. Gasith (1991) proposed that physical structures and habitat complexity are unique littoral zone features, and thus littoral resources can be limiting, particularly in large and deep lakes where the littoral zone occupies a small proportion of the lake area. Similarly, Danehy et al. (1991) stated that "the relatively few regions of highly structured habitats [in the Great Lakes] may be more important to the ecology of fish populations than has been previously recognized." If this is true, we can predict that in small lakes, where the supply-to-demand ratio of littoral resources is high (Fig. 24.3, a), the intensity of competitive interactions among consumers that move from the pelagic zone to use littoral resources should be relatively low (Fig. 24.3, a_1). The cross boundary movers are typically adult or large fish that move between deep and shallow water for feeding, for cover (e.g., at night time; Gasith, Goren, and Gafny, unpublished data), and seasonally, for breeding. These fish may use different littoral resources than those used by the "resident," mostly young or small-bodied littoral species. Higher intensity of competition over littoral resources may be expected in larger deeper lakes (Fig. 24.3, b_1), where littoral resources are relatively limited (Fig. 24.3, b). The underlying assumption is that, other factors being equal, larger lakes with larger pelagic region can sustain larger consumer populations, some of which at times or at some part of their life history move back and forth between the pelagic and littoral zones. Beyond a certain size of a water body, the dependency on littoral resources is expected to diminish due to increased cost of energy expenditure in moving large distances across habitat boundary, and interhabitat links weaken (Lodge et al., 1988). For example, most lacustrine fish use nearshore habitats for spawning and nursery, whereas open-water spawning is usually typical to large deep lakes (Goodyear et al., 1982) and is characteristic of ocean-breeding fish. In such a situation, supply of littoral resources may again exceed the demand (Fig. 24.3, c), lowering the intensity of competition among cross-boundary movers over these resources (Fig. 24.3, c_1). Competition for food among resident littoral populations may be as intense in large and small lakes, depending on the availability of cover, which reduces predation mortality and increases density-dependent food limitation. High competition for food has been reported in small lakes (Mittelbach, 1988), mostly under excessive growth of foliated plants species such as milfoil (Heck and Crowder, 1991; Carpenter et al., this volume, Chapter 11).

Conclusions

Water-level fluctuations markedly modify the structure and availability of littoral zone habitats in Lake Kinneret and can influence fish community structure in a multiple mechanistic way. During periods of low lake levels, the littoral zone of Lake Kinneret supports fewer fish. Small fish and YOY are probably most affected by a reduction in the availability of structured habitats. Low water level is detrimental for fish breeding over rocky substrate but may be beneficial for other species that exploit the increased availability of vegetated habitats. Two hypotheses on the role of the littoral zone in lakes, and of physical structure in particular, are evoked from Lake Kinneret study. (1) Structural complexity is unique to littoral zones making it a potentially limiting factor, particularly in large deep lakes. In small shallow lakes, the availability of littoral resources may exceed the demand placed on them by interhabitat consumers. Thus, intensity of competitive interactions over littoral zone resources is expected to increase with increasing lake size and diminishing proportion of littoral zone area. (2) Under constant lake levels, abiotic formations may constitute a stable source of structural complexity of littoral habitats, allowing more temporal leeway in resource utilization. In vegetated lakes, littoral structure and complexity are amenable to biological feedback and usually follow seasonal plant cycle. The organisms using these resources are forced to synchronize with the window of opportunity provided by macrophyte growth. Competitive interactions over vegetative resources is expected to be highest where the period of plant growth is shortest.

In conclusion, the case of Lake Kinneret underscores the importance of water level fluctuation as a major environmental factor that can strongly influence habitat structure and related interactions. Due to global climate changes, this factor may become relevant in lakes that presently exhibit stable water levels.

Acknowledgments. We thank Larry B. Crowder for constructive remarks and Merav Bing and Susan Gilman for assistance in manuscript preparation. The study was supported by the German-Israel Research and Development Fund (BMFT-DISUM 00016-GR 00984) and the Kurt Lion Fund for Scientific Cooperation between the University of Konstanz (Germany) and Tel-Aviv University.

References

Aidlin, M. Biological and ecological aspects of *Salaria fluviatilis* in the littoral zone of Lake Kinneret. M.Sc. thesis, Tel-Aviv Univ., Israel (Hebrew, English summary); 1995.

Beauchamp, D.A.; Byron, E.R.; Wurtsbaug, W.A. Summer habitat use by littoral-zone fishes in Lake Tahoe and the effects of shoreline structures. North Am. J. Fish. Manage. 14:385–394; 1994.

Carpenter, S.R.; Lodge, D.M. Effects of submersed macrophytes on ecosystem processes. Aquat. Bot. 26:341–370; 1986.

Danehy, R.J.; Ringler, N.H.; Gannon, J.E. Influence of nearshore structure on growth and diets of yellow perch *(Perca flavescens)* and white perch *(Morone americana)* in Mexico Bay, Lake Ontario. J. Great Lakes Res. 17:183–193; 1991.

Diehl, S. Effects of habitat structure on resource availability, diet and growth of benthivorous perch, *Perca fluviatilis*. Oikos 67:403–414; 1993.

Duarte, C.M.; Kalff, J. Littoral slope as predictor of the maximum biomass of submerged macrophyte communities. Limnol. Oceanogr. 31:1072–1080; 1986.

Duarte, C.M.; Kalff, J.; Peters, R.H. Pattern in biomass and cover of aquatic macrophytes in lakes. Can. J. Fish. Aquat. Sci. 43:1900–1908; 1986.

Gafny, S. The effect of substrate type on the structure and function of the littoral zone in Lake Kinneret, Israel. Ph.D. dissertation. Tel-Aviv Univ., Israel (Hebrew, English summary); 1993.

Gafny, S.; Gasith, A.; Goren, M. Effect of water level fluctuation on shore spawning of *Mirogrex terraesanctae* (Steinitz), (Cyprinidae) in Lake Kinneret, Israel. J. Fish Biol. 41:863–871; 1992.

Gasith, A. Can littoral resources influence ecosystem processes in large, deep lakes? Verh. Int. Verein. Limnol. 24:1073–1076; 1991.

Gasith, A.; Gafny, S. Effects of water level fluctuation on the structure and function of the littoral zone. In: Tilzer, M.M.; Serruya, C., eds. Large lakes, ecological structure and function. New York: Springer-Verlag; 1990:156–171.

Gasith, A.; Goren, M. Fish community of the littoral zone of large lakes: the Lake Kinneret and Lake Conctance experience. Part I—Lake Kinneret. Joint German-Israeli Research Projects. Final report INCR Tel-Aviv Univ., Israel; 1995.

Gasith, A.; Goren, M.; Gafny, S. Ecological consequences of lowering Lake Kinneret water level: effect on breeding success of the "Kinneret sardine." In: Steinberger, Y., ed. Preservation of our world in the wake of change. Jerusalem: ISEEQS VIB:569–573; 1996.

Goodyear, C.D.; Edsall, T.A.; Ormsby Dempsey, D.M.; Moss, G.D.; Polanski, P.E. Atlas of the spawning and nursery areas of Great Lakes fishes. Washington, DC: Fish and Wildlife Service, U.S. Department of the Interior; 1982.

Heck, K.L.; Crowder, L.B. Habitat structure and predator-prey interactions in vegetated aquatic systems. In: Bell, S.S.; McCoy, E.D.; Mushinsky, H.R., eds. Habitat structure, the physical arrangement of objects in space. London: Chapman & Hall; 1991:281–299.

Lodge, D.M.; Barko, J.W.; Strayer, D.; Melack, J.M.; Mittlebach, G.G.; Howarty, R.W.; Menge, B.; Titus, J.E. Spatial heterogeneity and habitat interactions in lake communities. In: Carpenter, S.R., ed. Complex interactions in lake communities. New York: Springer-Verlag; 1988:181–208.

Mittelbach, G.G. Competition among refuging sunfishes and effect of fish density on littoral zone invertebrates. Ecology 68:614–623; 1988.

Walline, P.; Pisanty, S.; Lindem, T. Acoustic assessment of the number of pelagic fish in Lake Kinneret, Israel. Hydrobiologia 232:153–163; 1992.

Walline, P.; Kalichman, Y.; Ostrovsky, I. Effect of water level fluctuation on the increase of the "lavnun" population size. In: Zohary, T.; Hambright, K.D., eds. Preliminary assessment of potential impacts of lowering Lake Kinneret water levels to –214 altitude. Kinneret Limnol. Lab: Special Report T24/94 ILOR (Hebrew); 1994:42–45.

Walter, R.A. Benthic macroinvertebrates. In: Likens, G.E., ed. An ecosystem approach to aquatic ecology: Mirror Lake and its environment. New York: Springer-Verlag; 1985: 280–288.

Wetzel, R.G.; Hough, R.A. Productivity and the role of aquatic macrophytes. An assessment. Pol. Arch. Hydrobiol. 20:9–19; 1973.