Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **55**, p. 301–316, February 2000
Limnology and Lake Management 2000+

Spatial and temporal variation in the standing biomass of emergent macrophytes: effect of water level fluctuations

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with 5 figures and 3 tables

Abstract: We studied the spatial and temporal appearance of emergent macrophytes in the littoral zone of Lake Kinneret, Israel, between 1986-1992. During that period the water level fluctuated 4 m between high and low lake levels. These changes in lake levels resulted in inundation and exposure of large littoral areas. During periods of low lake levels, emergent vegetation developed along exposed shores around the lake. The plants started to develop only during the second year following exposure, and thereafter the vegetation biomass increased exponentially for about two years. The emergent macrophyte community was dominated by *Phragmites australis*, *Cyperus alopecuroides*, *Typha angustata* and *Tamarix jordanensis*. The spatial variability in plant biomass was significantly associated with environmental factors such as littoral slope and substrate quality. Duration of exposure and substrate quality were among the factors affecting macrophyte zonation. During periods of rising lake levels the vegetation was inundated and most of the emergent macrophyte standing biomass was uprooted and decomposed. Decomposition rate of *P. australis*, *C. alopecuroides* and *T. angustata* was similar with ca. 90% of their initial dry weight lost within 130-160 days. The decomposition rate of the woody species, *T. jordanensis*, which is relatively tolerant to complete inundation was significantly slower, losing only ca. 30% of its initial DW in 130 days. The temporal variation in plant development was mainly influenced by water level fluctuation. The standing biomass of the emergent macrophytes that developed during periods of low lake levels (1,000-1500 t organic matter, OM) was two orders of magnitude higher than that found in periods of high lake levels (ca. 20 t OM). Our study suggests that following periods of low lake levels emergent macrophytes constitute a major source of organic matter in the littoral zone of Lake Kinneret.

Introduction

Emergent macrophytes exemplified by the reed *Phragmites* occur on water-saturated soils (0.5 m above the water table) in eulittoral zones and on sediments covered by up to 1.5-2 m of water in the infralittoral zone of lakes (WETZEL 1983, HUTCHINSON 1975). These two permanently, or periodically wetted zones , collectively constitute the littoral zone (WETZEL 1983)

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0071-1128/00/0055-301 $ 4.00
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and are distinguished from the supralittoral zone that is entirely terrestrial. In Lake Kinneret emergent vegetation germinates or develops from runners in exposed regions of the eulittoral that is wetted seasonally, though not in all years. Emergent vegetation can survive flooding but requires occasional exposure of the lake bottom for seedling establishment (SCULLTHORPE 1967, KEDDY & REZNICEK 1986). Unlike submerged macrophytes, emergent macrophytes are less dependent on aquatic resources. For example, they do not depend on the lake's water for nutrients as they take up all the minerals needed for their growth from the soil on which they grow (SPENCE 1967, GRANELI & SOLANDER 1988). During their growth period, emergent macrophytes also release less nutrients to the lake's water than submerged macrophytes (GRANELI & SOLANDER 1988). However, when emergent macrophytes decay, they contribute particulate organic matter (PIECZYNSKA 1972, PIECZYNSKA et al. 1984, POLUNIN 1984) and nutrients (GRANELI & SOLANDER 1988) to the lake ecosystem.

Since the tissues of emergent macrophytes are rich in cellulose and lignin, their decomposition rate is often slower than that of submerged macrophytes (GODSHALK & WETZEL 1977). During the decomposition phase, this particulate detritus serves as a substrate for colonization and as a food source to a wide range of aquatic organisms (MCLACHLAN 1969, 1975) and may also play an important role in the function of the lake ecosystem (RICH et al. 1971, SZCZEPANSKA & SZCZEPANSKI 1973, NEWMAN 1991). In littoral areas lacking submerged vegetation, the presence of emergent macrophytes may increase habitat heterogeneity and structural complexity, providing fish and other organisms with substrate for colonization, protective cover, spawning and foraging grounds.

Lake Kinneret (Israel) is a medium size lake (170 km^2). The lake's littoral zone is characterized by the absence of submerged vegetation (GOPHEN 1982, GAFNY & GASITH 1999). However, submerged macrophytes appear sporadically in certain years and areas, associated with specific sediment composition and lake level (GAFNY & GASITH 1999). For a more detailed description of the lake and its littoral zone see also SERRUYA (1978), GASITH & GAFNY (1990, 1998), GAFNY et al. (1992) and GAFNY & GASITH (1999).

Large annual and inter-annual water level fluctuations, which may reach up to 4 m (between -209 and -213 m altitude), are a major characteristic of Lake Kinneret (Fig. 1) and result in periodic exposures and inundations of littoral areas. Consequently, the entire area that functions as the wetted littoral zone during periods of high water level is exposed when the lake levels drops. Water level fluctuations are followed by changes in the nature of the wetted littoral substrate and slope (GASITH & GAFNY 1990). Emergent macrophytes develop on exposed littoral beds during periods of low lake levels and almost completely disappear during periods of high lake levels.

The emergent vegetation of Lake Kinneret and its watershed were described during the 1930s, 1940s and 1960s (e.g. OPPENHEIMER 1938, EIG 1946, EIG et al. 1948, WAISEL 1967). However, none of these studies reported any information on the standing biomass of the emergent macrophytes nor their importance to Lake Kinneret as a source for organic matter and nutrients.

In a previous paper (GASITH & GAFNY 1990) we included a short description of the massive development of emergent macrophytes around the lake during a low-water phase of 1986/7 (lowest level -212.5 m). Since then, the lake's water level rose in spring 1988 to the maximum permissible level (-208.9 m); declined to a record low during summer 1990 and 1991 (-213 m); and attained the maximum level again following the winter of 1992 (Fig. 1). These changes were followed by the establishment and collapse of emergent vegetation on the lake's shores.

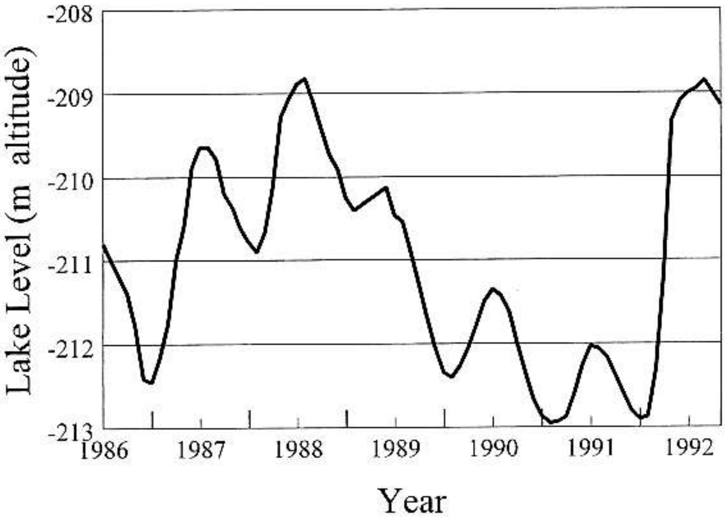

Fig. 1. Water level fluctuations in Lake Kinneret during 1986-1992. Data courtesy of Hydrological Service of Israel.

Since 1973 Lake Kinneret water levels are characterized by a marked increase in variability, including years with record low levels (GASITH et al. 1996, GAFNY & GASITH 1999). Moreover, this trend of increased variability is expected to continue if a decision is made to lower the legal minimum lake level to fulfill the increasing demand for drinking water. We hypothesize that the development of emergent vegetation is strongly influenced by water level fluctuations and would be highest following years of low lake levels. Woody species may get established following consecutive years of low lake levels. Here, we report the biomass buildup and decline of emergent macrophytes in the exposed and inundated littoral zone of Lake Kinneret during 1986-1992 and conclude that emergent macrophytes can be an important source of organic matter for the lake.

Materials and methods

The standing biomass of emergent macrophytes was measured at selected sites around the lake in summer and fall 1986 and during fall the following 5 years. To calculate the total standing biomass in a site TSB, we considered all shore areas around the lake, excluding a 2 km long section of a marshy area in the northern part of the lake (Fig. 2). The shoreline was divided into 76 sections, each approximately 750 m long (hereafter-site). Standing biomass in each site was determined along transects perpendicular to the shoreline. Since emergent macrophytes in the littoral zone of Lake Kinneret are often arranged in belts which may vary from site to site, we first identified these belts and then measured their width perpendicular to the shoreline, recording the substrate type of each belt (rocks, sand, silt and clay), and the average slope of each site (along each transect). The above- ground standing biomass in each belt was estimated using a stratified random sampling design (GERTZ 1984, KREBS 1989) in which 3 quadrats (1 m^2 each) were sampled in each belt. In each quadrat the macrophytes were harvested by cut-

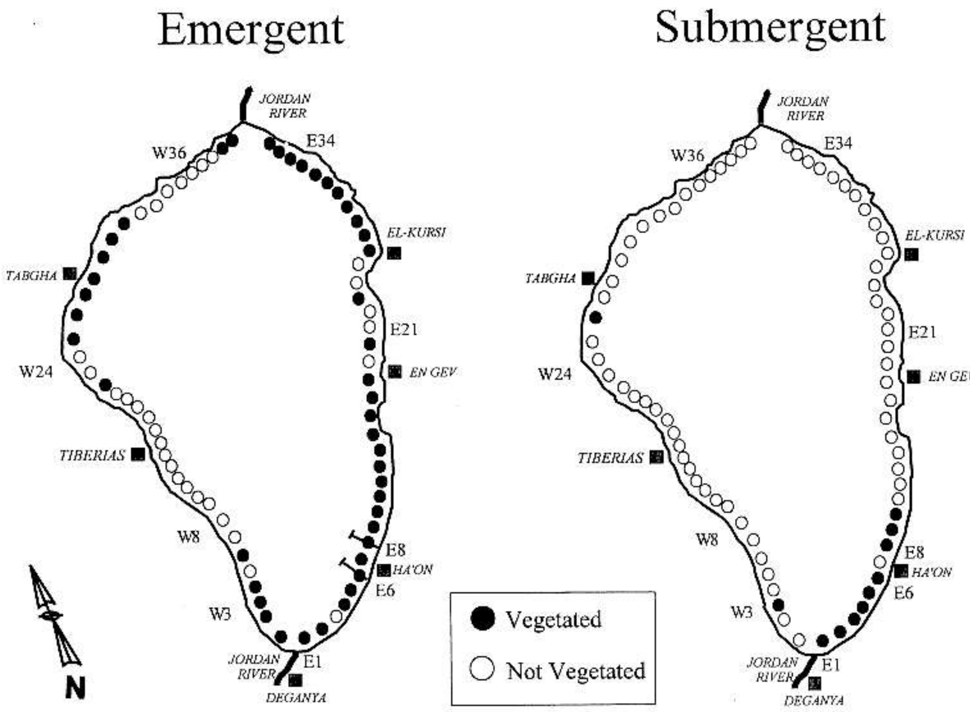

Fig. 2. Comparison of the distribution pattern of emergent (TSB > 0.1 t $_{DW}$ km^{-1}, present study) and submerged macrophytes (GAFNY & GASITH 1999) in the littoral zone of Lake Kinneret.

ting the stems as close as possible to the ground (above-ground production, APHA 1985). The fresh weight (WW) of the vegetation from each quadrat was measured (to the nearest gram) in the field, and subsamples were taken to the laboratory to determine dry weight (DW, at 100 °C for 5 days) and ash free dry weight (OM, 3 hours at 500 °C; to the nearest 0.1 g). The ratio of dry to wet weight was typically 0.33 (± 0.02, n=210), the organic fraction was typically 80% of DW (± 5%, n=74). Organic carbon was assumed to constitute 50% of OM (APHA 1985).

During fall 1987-1991, we revisited all 76 sites and conducted a less detailed survey of the emergent vegetation. We took random quadrat samples from representative sites to obtain estimates of the standing biomass. In addition, we monthly recorded the succession and biomass buildup of the emergent macrophytes in two representative sites (E6 – Tel Qazir and E8 – Ha'On north) at the south-eastern shores (Fig. 2). This part of the study began in 1988, after 2 consecutive years of high lake levels and lasted for 3 years. During that period the lake level declined to a record low and remained so for two years. This allowed us to follow the changes in vegetation development from a point in time when the entire shore was under water to a point in time when maximum shore area was exposed.

The decomposition dynamics of the major species of emergent macrophytes found in the littoral zone of Lake Kinneret (*Phragmites australis*, *Cyperus alopecuroides*, *Typha angustata* and *Tamarix jordanensis*) were studied using litter bags (BENFIELD et al. 1979) containing fresh stems (NELSON et al. 1990) collected in the study sites. Each bag (20x30 cm, 2x2 cm mesh size, protected by 0.5x0.5 mesh screen at each end) contained 3 stem packs of the above plants held together by a narrow ring of duct tape. The bags were introduced into the littoral zone during winter when the lake level was rising. Bags were placed about 50 cm above the bottom to reduce burial by resuspended sediments (GODSHALK & WETZEL 1978).

To examine the effect of exposure to wave action on breakdown rate (WEBSTER & BENFIEL 1986), we introduced the bags on an eastern (E6 – Ha'On 1987) and a western (W29 – Tabgha 1988) shore. The stem packs were removed monthly (triplicate per species), washed with tap water to remove sediments, oven dried (100 °C for 48 h) and weighed (to the nearest 0.1 g) to obtain the percentage remaining dry weight. Water temperature during the incubation period ranged from 14-19 °C. The decay coefficient (k) was calculated using a negative exponential model (PETERSEN & CUMMINS 1974). Percentage loss of initial dry weight was fitted to a linear model and corrected for the effect of temperature by calculating the % loss per degree per day (SHORT et al. 1984). Leaching was not separated from the overall process of weight loss in order to reflect the natural weight loss of inundated vegetation.

Statistical analysis

To assess the relationship between selected environmental conditions and emergent macrophyte development we used the following two approaches: First, using multiple regression analysis (WILKINSON 1990), we tested the effect of littoral slope and sediment composition (grain size of the dominant component) on either macrophyte maximum standing biomass (DW m^{-2}) in each site (MSB) or total standing biomass (DW) in a site (TSB). Second, we examined the linear relationships between a set of selected environmental variables against a set of macrophyte variables using canonical correlation analysis (AFIFI & CLARK 1996). The independent environmental variables we used were: 1. the littoral slope at each site, 2. the width of the exposed shore (i.e., the distance between the shoreline at maximum lake level and the actual waterline at each site at the time of measurement), 3. the exposure to wind expressed as the angle between the mean summer wind direction and the offshore compass direction at each site (GAFNY & GASITH 1999), and 4. the relative proportion of substrate particles (boulders, large cobbles, small cobbles, pebbles, gravel, sand and clay). Data for the independent variables used in the above analyses are presented in GASITH & GAFNY (1990) and GAFNY & GASITH (1999). The dependent macrophyte variables were MSB, TSB and relative biomass of the different macrophyte species.

Results

Spatial distribution

Emergent vegetation (at least 0.1 t_{DW} km^{-1}; Fig. 2) was found along most (60%) of the shores around Lake Kinneret. Among the shores that featured non-significant vegetation growth, nearly half were urban or recreational resorts and the rest were mainly rocky. Thirty percent of the vegetated sites had 5-50 t_{DW} km^{-1} shoreline and only 5% of the sites (mainly at the north-western and south-eastern shores) supported > 100 ton t_{DW} km^{-1}.

Macrophyte biomass (MSB and TSB) for each site was significantly correlated with the site slope (multiple regression analysis, $r = -0.56$, $F = 12.7$, $P<0.001$), but was not significantly correlated with substrate type ($r = 0.24$, $F = 1.8$, $P>0.1$). A similar trend was found for the

Table 1. Canonical r values for the relationship between selected habitat characteristics and biomass per m^2 of each of the dominant emergent macrophyte species found in 76 sites along the shoreline of Lake Kinneret. ♣ = strong correlation ($|r|>0.5$), ^ = weak but meaningful correlation ($0.5>|r|>0.3$), meaningless correlations are without a symbol.

	Shore slope	Angle of wind exposure	Shore width	% Boulders	% Large cobbles	% Small cobbles	% Sand	% Clay
MSB	-0.58♣	0.032	0.65♣	-0.22	-0.36^	-0.44^	0.63♣	0.36^
TSB	-0.49^	0.025	0.82♣	-0.09	-0.34^	-0.43^	0.52♣	0.30
P. australis	-0.24	-0.14	0.04	-0.21	-0.28	-0.30	0.29	0.55♣
T. jordanensis	-0.31^	-0.001	0.42^	-0.05	-0.23	0.18	0.33^	-0.02
C. alopecuroides	-0.41^	0.1	0.48^	-0.22	-0.32^	0.04	0.39^	0.27
C. distachyus	-0.28	0.09	0.17	-0.23	-0.27	-0.25	0.23	0.42^
T. angustata	-0.33^	-0.04	0.53♣	-0.13	-0.12	-0.19	0.38^	0.03

partial correlations of MSB and TSB with slope and substrate type ($b_{slope/MSB} = 0.66$, $P<0.001$; $b_{slope/TSB} = 0.674$, $p<0.001$; $b_{substrate/MSB} = 0.36$, $P> 0.1$; $b_{substrate/TSB} = 0.306$, $p>0.1$). However, as suggested by DUARTE & KALFF (1986) the relationship between substrate characteristics and macrophyte growth is often obscured by the strong correlation between slope and biomass. Indeed canonical analysis revealed that interaction between environmental factors and the development of emergent macrophytes in the littoral zone of Lake Kinneret is probably more complex than suggested by the multiple regression analysis. The combined effect of the selected environmental variables on the macrophyte variables was highly significant (Canonical $r=0.92$, $c^2=228.7$, $df=132$ $p<<0.0001$). Generally, the strongest canonical correlations ($r>0.3$) with either MSB or TSB were found with shore slope and rocky substrate (negative), and with the width of the exposed littoral and fine substrate (positive, Table 1). The correlation between exposure to wind and the above macrophyte variables was weak ($r<0.035$).

The distribution of the dominant emergent species was also correlated with environmental factors. Most species were negatively correlated with slope and rocky substrate (boulders and cobbles). *Phragmites australis* and *Cyperus distachyus* were less strongly correlated ($r< 0.2$) than other species to the width of the exposed littoral; *C. alopecuroides* was not correlated with small cobbles ($r=0.04$); *P. australis* and *C. distachyus* were correlated with clay ($r>0.4$); and *T. jordanensis*, *C. alopecuroides* and *T. angustata* were correlated with sand ($r>0.3$).

In years of low lake levels emergent macrophytes exhibited zonal distribution of several vegetation belts that stretch out in parallel to the shoreline. In 1986/87 such zonation was recorded in ca. 60% of the vegetated shores. The belts often differed in biomass per unit area and the dominant macrophyte species (Fig. 3). Along ca. 75% of the shores the highest biomass was recorded at the highest altitude (-209 to -210 m, hereafter the upper belt) and the lowest biomass near the actual waterline.

Relationship between water level and standing biomass

During 3 consecutive years of low lake levels (1984-1986) the upper region of the littoral zone (from altitude of -209 to -210 m.) was exposed and dense emergent macrophyte beds devel-

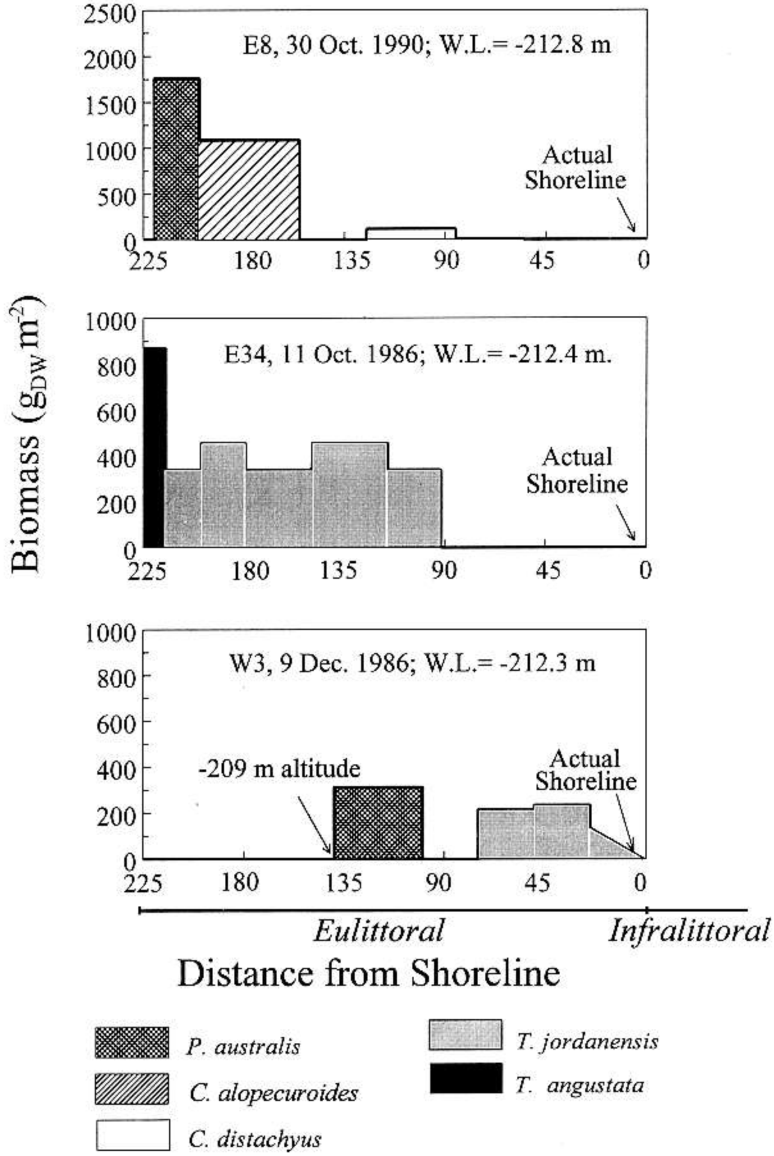

Fig. 3. Typical examples of changes in biomass and in species dominance of emergent macrophytes (zoning) along perpendicular transects from the actual shoreline to the -209 m altitude shoreline in 3 shores of Lake Kinneret (W.L. – water level).

oped. The standing biomass of emergent macrophytes recorded in this zone in fall 1986 ranged from <0.01 to 1.8 kg $_{DW}$ m^{-2} and TSB varied from 0.1 to 135 t km^{-1}. The standing biomass in the entire littoral zone (ΣTSB) in fall 1986 was estimated at 4,000 t_{WW} (GASITH & GAFNY 1990, Table 2) with *C. alopecuroides* and *T. jordanensis* being the dominant species (ca. 60%). Other

Table 2. Maximum standing biomass (MSB) and standing biomass of emergent macrophytes in the entire littoral area (STSB) recorded in the littoral zone of Lake Kinneret during 1986-1992.

Year	lake level	MSB	ΣTSB t			
	m	kg $_{DW}$ m^{-2}	**Wet Wt**	**Dry Wt**	**OM**	**C**
1986/87	-212.45	1.6	4,000	1,200	1,000	500
1987/88	-210.70	0.9	75	25	20	10
1988/89	-210.15	0.8	54	18	14.5	7.3
1989/90	-211.95	0.8	54	18	14.5	7.3
1990/1	-212.95	2.0	4,400	1,450	1,160	580
1991/92	-212.98	2.2	6,000	1,980	1585	790

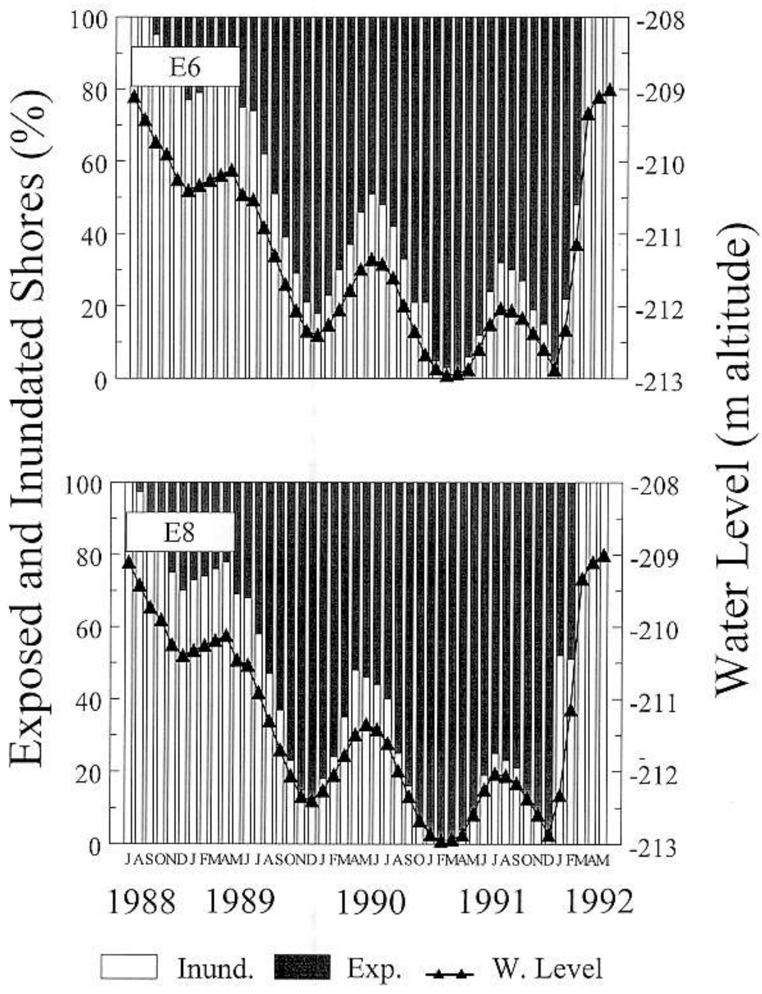

Fig. 4. Changes in the relative proportion of the exposed and inundated shore (1988-1992) in two eastern sites (Ha'On E8 and Tel-Qazir E6) in relation to water level fluctuations

important species were *T. angustata* and *C. distachyus* (formerly mistakenly identified as *Cyperus conglomeratus* – GASITH & GAFNY 1990) which contributed 15-20% each. The common reed *P. australis*, which often locally maintained high biomass, contributed only 7% to the ΣTSB. *Arundo donax* dominated the supralittoral, but was excluded from the biomass calculation because it grows above the maximal lake level.

In the subsequent year (1987), the lake water level rose ca. 3.0 m (Fig. 1) and the ΣTSB decreased to less than 2% of that of the previous year (Table 2). *Phragmites australis* was the dominant species (52%) followed by *T. jordanensis* (39%). *Typha angustata* was scarce (5%) and other species such as *C. alopecuroides* and *C. distachyus* completely disappeared. A 60-cm rise in lake level during winter 1988/89 was followed by a further decrease in ΣTSB. Most of the biomass was contributed by partly inundated stands of *P. australis* and *T. jordanensis*.

Despite a 1.8-m fall in the lake level during 1989/90, and the associated exposure of a large portion of the littoral zone (Fig. 4), ΣTSB remained unchanged. However, starting in the spring of 1990 the emergent macrophyte biomass began to build up rapidly. By the end of 1990, it had exceeded the ΣTSB we measured earlier in the preceding low water level year (1986/7) by about 10%. Subsequently, MSB exceeded 2.2 kg $_{DW}$ m^{-2} and ΣTSB increased by 35%.

Establishment and succession of emergent macrophytes

Most of the biomass accumulation of emergent macrophytes occurred along exposed shores during periods of low lake levels. However, we found that the dynamics of biomass buildup varied in different areas of the exposed shores (Fig. 5). In 1988, the entire eulittoral was inundated (including the upper belt) for 6 months (Mar.-Aug. 1988). Thereafter, following a drop in lake level, the upper belt was exposed and remained uncovered for almost 3 years (until Feb. 1992; Fig. 4). Only one year after exposure (in July 1989) did we record the first macrophyte germination. The pioneer species was *C. distachyus* and the first measurable biomass (>100 g $_{DW}$ m^{-2}) was reached more than 3 months later (Nov. 1989). From this point on, the macrophyte biomass increased exponentially (growth rate coefficient k=0.011, r^2=0.93, F=42.2, P<0.0001) and within a year from germination (July 1990), the average emergent macrophyte biomass in the upper belt had reached 1.9 kg $_{DW}$ m^{-2} (Fig. 5). The dominant species in the upper belt shifted during that period from *C. distachyus* to *P. australis*, which developed vegetatively from invading runners from the supralittoral zone. Thereafter, the average standing biomass in the upper belt remained relatively stable at about 2 kg $_{DW}$ m^{-2} (±15%). Higher biomass (ca. 3 kg $_{DW}$ m^{-2}) was locally found only in stands of *T. angustata*.

The area extending between -210 m and -211 m (hereafter mid belt) remained under water for 18 months (Jan. 1988-June 1989). Germination started in this belt about two months later than in the upper belt. The first measurable biomass was recorded in December 1989 and the first species to develop was also *C. distachyus*. However, after two months, stands of *C. alopecuroides* became established and dominated in this zone. Despite the differences in the dominant species between the upper and mid belts, the growth rate coefficients in these belts were similar (mid belt k=0.13, r^2=0.89, F=20.1, p>0.0001). Later in the season, scattered stands of *P. australis* colonized the mid belt, but unlike the upper belt this species never dominated the community.

Vegetation development dynamics in the area extending below -211 m altitude (lower belt) was different than in the belts above it. The lower belt remained inundated for almost two years

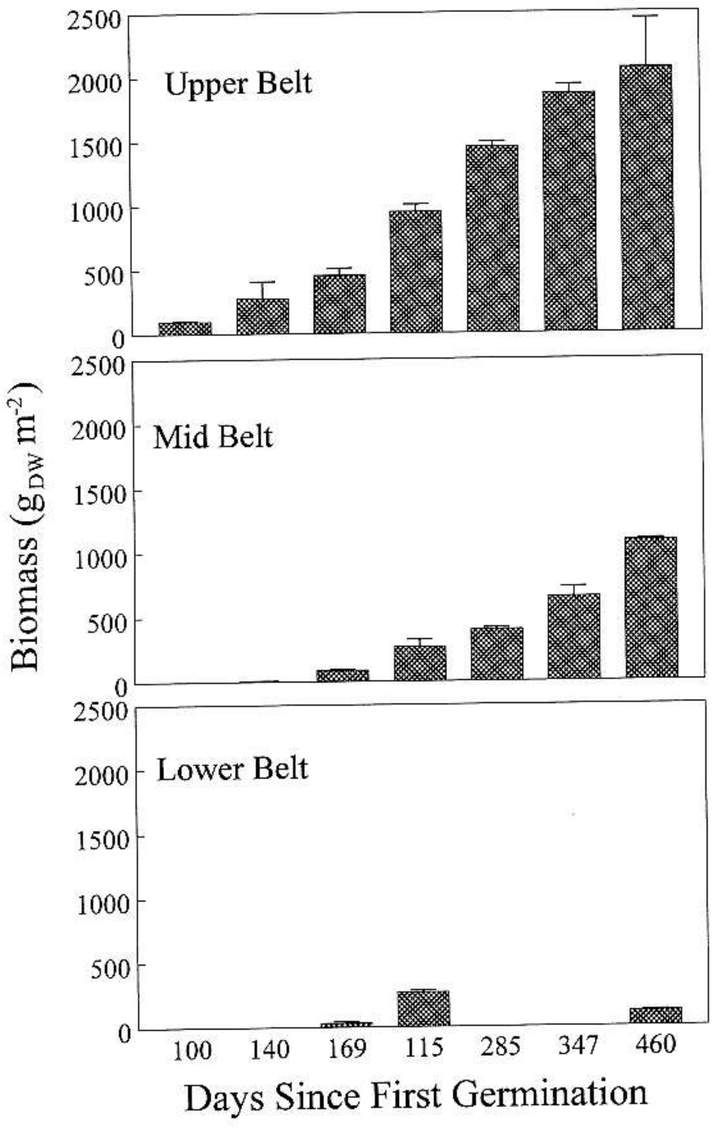

Fig. 5. Comparison of the dynamics of emergent macrophyte biomass accumulation in the upper, mid and lower vegetation belts in an eastern shore (Ha'On – E8, 1989-1990).

and was first exposed in August 1989. Unlike in the upper and mid belts, the period from exposure to first germination in the lower belt was only 3 months. The first species to develop here were *C. alopecuroides* and *T. jordanensis,* while the development of *C. distachyus* was insignificant. The highest biomass recorded in this area was about 300 g_{DW} m^{-2} and 3 month after first germination (March 1990), the lower belt flooded again for six months (Fig. 4, 5). In October 1990, macrophytes (mainly *T. jordanensis*) started to become established again in the lower belt, but the average standing biomass was only <200 g_{DW} m^{-2}, Fig. 5). The lower belt was partly inundated again in January 1991 and January 1992. The area below the lower belt (between -212 and -213 m) had no significant growth of macrophytes throughout the entire study.

Decomposition rates of the dominant emergent macrophyte species

The decomposition dynamics of all the selected emergent macrophyte species fitted equally well a linear or an exponential model ($0.98 > r^2 > 0.87$, $p<0.001$, and $0.96 > r^2 > 0.90$ $p<0.001$, respectively), therefore we used a linear model to compare between the regression lines of the different species (WEBSTER & BENFIELD 1986). The breakdown rates (k) of *C. alopecuroides*, *P. australis* and *T. angustata* were statistically similar ($F=1.18$, $P>0.34$ one way ANCOVA) and ranged from 0.0060 to 0.0074 per day (Table 3). These species loss 50% of the initial weight in 69 to 75 days and 90% in 130 to 160 days (linear model). The decomposition rate of the woody species *T. jordanensis* was less than half that of the other species (calculated $t_{50\%}$=215 days; Table 3). The variability in the decay rate for the non-woody species that were tested both in 1987 (eastern shore) and 1998 (western shore) was slightly reduced (<10%) by correcting for the difference in temperature (% loss per degree-day). The among year variability in the decay rate for the woody species slightly increased (by ca.17%) by correcting for the difference in temperature.

Discussion

Seasonal water level fluctuations are often suggested as an environmental factor that directly alters the growth of aquatic macrophytes (OSBORNE et al. 1987, NICHOLS 1991). Drawdowns are often used as a management tool to control macrophyte growth in lakes and reservoirs (e.g., HESTAND & CARTER 1974, COOKE et al. 1986, NICHOLS 1991) mostly because of their negative effect on the development of submerged macrophytes (e.g. GOLDSBY et al. 1978, GODSHALK & BARKO 1988).

The emergent vegetation in Lake Kinneret typically occupies the region between the highest and lowest interannual fluctuation in water levels. We found that interannual fluctuations in the lake's water level are the major temporal factor affecting the standing biomass of the emer-

Table 3. Linear decomposition rate (k) and summary statistics of fit to a linear decay model of the dominant species of emergent macrophytes in different years. Data on time of 50% dry weight loss ($t_{50\%}$) and temperature adjusted decomposition rate are also given.

species	Year	k	r^2	df	F	P	$t_{50\%}$ days	% loss deg. day^{-1}
P. australis	1987	0.0062	0.88	6	36.2	<0.001	74	0.035
P. australis	1988	0.0074	0.92	5	46.8	<0.001	69	0.039
C. alopecuroides	1987	0.0060	0.95	4	59.0	<0.001	75	0.035
T. angustata	1988	0.0064	0.98	7	335.2	<0.0001	73	0.034
T. jordanensis	1987	0.0025	0.87	4	20.1	<0.001	215	0.014
T. jordanensis	1988	0.0022	0.92	5	49.2	<0.001	227	0.010

gent macrophytes. In contrast to submergent vegetation, the emergent vegetation along the lake shores positively responds to water drawdown (as in marshes: HARRIS & MARSHALL 1963, LYON et al. 1986, COOPS & VAN-DER-VELDE 1996), that exposes shore areas and facilitates the germination and establishment of vegetation beds (HUIJSER et al. 1996).When inundated, the non-woody emergent vegetation around Lake Kinneret decomposes or is uprooted and removed from the area within several months .

HUTCHINSON (1975) and SPENCE (1982) suggested that exposure to wave action limits the distribution and development of emergent macrophytes in lakes. This may result from a direct effect of strong mechanical stress and indirectly by the effect of wind induced currents on sediment distribution (KEDDY 1982, 1983, WEISNER 1987). Correspondingly, in large lakes emergent macrophytes are mostly confined to sheltered areas. In Lake Kinneret, a medium size lake that is relatively poor in sheltered bays (shoreline development index = 1.6), the direct effect of waveaction is weak (weak correlation with the angle of exposure to wind) and the emergent macrophytes are not confined to protected regions. This can be attributed to the fact that the vegetation develops outside the waterline, mostly beyond the range of wave action. Only in periods of rising lake level, when the vegetation is inundated, it becomes sensitive to the direct effect of wave action. There is evidence that fine sediments positively influence the growth of macrophyte on the shores of Lake Kinneret. These sediments support the growth of emergent vegetation in shores with contrasting levels of exposure to wind and wave action around the lake.

Other factors that influence the spatial distribution and development of emergent macrophytes in Lake Kinneret are slope and the width of the exposed littoral zone. These two factors are closely negatively interrelated (Canonical correlation = -0.67) hence, influence the growth of the emergent vegetation in contrasting directions. Shores sloping gently support highest total standing biomass per site, reflecting higher availability of suitable habitat for macrophyte development. The lower MSB typical of steep shores is probably a result of the erosional nature of the habitat that are characterized by coarser, nutrient-poor sediments (SCULTHORPE 1967, DUARTE & KALFF 1986 1990). In many lakes slope is strongly positively correlated with exposure to wind. (DUARTE & KALFF 1986). A weak relation between slope and exposure to wind in Lake Kinneret (Canonical correlation = -0.03) is another possible explanation for the uninhibited growth of emergent macrophytes in wind-exposed shores.

While shore slope is the main attribute of the lake ecosystem determining the availability of suitable habitat for plant growth in each site, water level fluctuations modulate habitat availability temporally. The total exposed area suitable for emergent macrophyte growth around Lake Kinneret is negatively associated with the water level. Indeed, ΣTSB in the littoral zone of Lake Kinneret in years of low lake level is over 100 times greater than that in years of high lake level (Table 2). Many pioneer species of emergent macrophytes are not tolerant to high water levels (HUIJSER et al. 1996). As shown in other lacustrine systems the germination and establishment of emergent macrophytes primarily occurs in exposed shores during periods of low water levels (e.g. VAN DER VALK & DAVIS 1978). NEILL (1990) attributed the better growth of emergent vegetation in years of low water level to a greater efficiency in nutrient utilization in exposed areas. In contrast, inundation reduces the distribution and biomass of emergent macrophytes (LYONS et al. 1986, FROEND & MCCOMB 1994).

The contribution of organic matter from emergent macrophytes to Lake Kinneret organic pool is relatively low. The maximal biomass of emergent vegetation is reached following consecutive years of low lake levels (e.g., 1991/92) and equals about 1.5% of the average annual production of the phytoplankton (SERRUYA 1978). In years of high lake levels the production of emergent macrophytes declines to less than 0.1% of the phytoplankton production. Nevertheless, when inundated the emergent macrophytes may constitute the main source of organic matter in the littoral zone, particularly following years of low lake levels when the contribution of organic matter from alternative sources (e.g. epilithon and submerged macrophytes, GAFNY & GASITH 1999, GAFNY & GASITH, in press) is minimal. Moreover, emergent macrophytes that decompose slowly provide structure for colonization and cover for littoral zone dwellers, which may be important even in years of relatively high lake levels and low emergent biomass.

The emergent vegetation forms distinct zonation of species composition and biomass accumulation perpendicular to the shoreline, reflecting the gradual exposure and inundation of the shore following drawdown in summer and lake rise in winter. Changes in slope and in substrate composition and nutrient content along a lakeward gradient also contribute to the difference in vegetation structure and biomass accumulation (YAMASAKI & TANGE 1981, JOHNSON et al. 1985, COOPS & VAN-DER-VELDE 1996).

In Lake Kinneret, the development of emergent macrophytes starts mostly during the second year following shore exposure, by germination of *C. distachyus*. Pioneering species of emergent macrophytes that develop from seeds (e.g., MARTIN 1953, WELLING et al. 1988) require bare mud-flats to germinate. In a later stage, plants that also reproduce from runners, such as *P. australis*, may take over and dominate the upper belt. The vegetative establishment of *P. australis* is much faster than its recruitment from seeds and this is probably one of the reasons why this species is found mainly in the upper belt in the vicinity of "parent" plants.

Whereas during periods of low lake level the biomass builds up, rising lake level and inundation of the vegetation cause biomass decline by uprooting and decomposition. The duration and extent of inundation determines the intensity of abiotic regulation (e.g. wave action) and biotic interaction (e.g. decomposition, colonization, use of cover, GASITH & HOYER 1998). For example, in years of a limited rise in the lake level (e.g., <1.0 m, in 1989, 1990), most of the inundated plants survive and the contribution of detritus is minimal. Under such conditions the major role of the vegetation is in providing refugia and substrate for colonization.

When the rise in lake level is more significant (e.g., >2 m, 1988, 1992), most of the emergent vegetation is completely inundated and gradually disintegrates. Uprooting and decomposition become the leading processes, and the contributions of the emergent macrophytes to the system is mainly by providing detrital matter. Only the woody species *T. jordanensis* that decomposes slowly and apparently is less sensitive to mechanical stress and of being completely covered by water may survive long periods of inundation (more than 1 year).

In conclusion, emergent macrophytes may constitute an important source of organic matter and provide structure and cover for the biota in the littoral zone of Lake Kinneret. Their spatial distribution is determined by local attributes of the shore such as shore slope and substrate composition and quality, and less by exposure to wind and wave action. Water level fluctuations determine the temporal dynamics of emergent macrophyte development and the extent of biomass accumulation.

Acknowledgements

We wish to thank DEBORAH R. HART and NAOMI PAZ for reviewing the manuscript and their constructive comments and the Lake Kinneret Authorities for providing access to all the study sites around the lake. The study was supported in part by the Israel Oceanographic and Limnological Research Ltd.

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