

Distribution, growth, production, and ecological significance of the clam *Unio terminalis* in Lake Kinneret, Israel

I. Ostrovsky, M. Gophen & I. Kalikhman

Kinneret Limnological Laboratory, Israel Oceanographic and Limnological Research, P.O. Box 345, Tiberias 14102, Israel

Received 12 March 1992; in revised form 2 March 1993; accepted 23 March 1993

Key words: *Unio terminalis*, Lake Kinneret, distribution, growth, production, ecological significance

Abstract

The distribution, body composition, growth rate, and population structure of *Unio terminalis* were measured at different sites of Lake Kinneret (Israel). Maximum clam density was found on the muddy sand between 0.3–6 m depth. Clams were most abundant in the River Jordan inlet zone, where they showed the highest growth rate. This was probably related to both highest food availability and the highest density of fish hosting *Unio* glochidia in this area. *U. terminalis* in Lake Kinneret has a more massive shell and ash content as compared with the European *Unio* species. The annual P/B ratios of *U. terminalis* populations at different sites were similar and ranged within 0.17–0.18. The computed filtration capacity and energetic budget permit the assumption that the *U. terminalis* population plays a substantial role in removal of organic particles from the water in the Kinneret shallow inshore zone (up to 15 m depth), and in nutrient recycling.

Introduction

Unionidae are widespread clams often dominating the zoobenthic biomass in many lakes and reservoirs (Okland, 1963; Mann, 1964; Negus, 1966; Fisher & Tevesz, 1976; Alimov, 1981; Hanson *et al.*, 1988). The adult clams are inaccessible for most fish due to their large and hard valves. The importance of unionid clams in waterbodies is related to the high capacity of their filtration activity, enabling them to purify the water from the suspended matter, and their participation in the nutrient recycling and energy fluxes (Tudorancea, 1972; Stanczykowska, 1975, 1977, 1984; Walz, 1978; Alimov, 1981; Miura & Yamashiro, 1990). Several studies also indicate the possibil-

ity of using the analysis of bivalve shell growth for biological monitoring of environmental conditions (Freeman & Dickie, 1979; Jones, 1981; McGuaig & Green, 1983; Mitchell, 1984; Hanson *et al.*, 1988; Arter, 1989).

Lake Kinneret is the only freshwater lake in Israel, providing about one quarter of the water requirement of the country. Quantitative information on molluscs in Lake Kinneret is scarce. C. Serruya (1978c) reported on the biomass of molluscs (soft part only) in the sublittoral zone (320 tons), calculated from data of two tows carried out in the southern part of the lake (Por & Eitan, 1970). This value is significantly higher than the total biomass of all other benthic animals in the lake (142 tons, Por & Eitan, 1970). The bi-

valve *Unio terminalis* Bourguignat, 1852, which is a common organism in lakes and rivers in the Near East (Dahl, 1956), represents 75% of the molluscan biomass in Lake Kinneret (Por & Eitan, 1970). Paperna (1964) found that larval stages of *Unio* (glochidia) are obligate parasites on the gills of Kinneret fish. The distribution of molluscs in Lake Kinneret was studied by Tchernov (1975), who collected empty shells.

Here we present data on body composition (wet, dry and ash masses), growth, distribution, size structure and production of *U. terminalis* in different parts of Lake Kinneret. Based on these data, the filtration activity and bioenergetic budget were calculated. The potential ecological impact of *U. terminalis* on the lake ecosystem was considered.

Materials and methods

Unionids were collected by SCUBA diving along transects (0.3–15 m depth) in four areas of the lake: Jordan inlet, Tabgha, Ginosar and Poria (Fig. 1) during August–November 1991. A cubic iron bar frame (25 cm length) with one side open, and the others covered by a net with a mesh of 8 mm, was pushed (by a diver) through the bottom sediments at a depth range of 7–15 cm below the substrate surface. In cases where the sediments were very loose (soft mud), and the molluscs occurred deeper than 7–15 cm, the sampling box was pressed down, to a maximum of 20–25 cm below the surface. Each sample was taken from a specified depth and composed of randomly distributed subsamples. Each subsample covered an area of 0.25 m². The number of subsamples was chosen such that the number of organisms in a sample would be from 40 to 150. The total area of a sample was estimated by the number of subsamples and ranged from 2 to 8 m².

The clams were brought to the laboratory, washed carefully, counted, and the total antero-posterior lengths were measured with Vernier calipers (± 0.1 mm). The total wet mass of large individuals was measured with an error within ± 0.1 g, while the total wet mass of small indi-

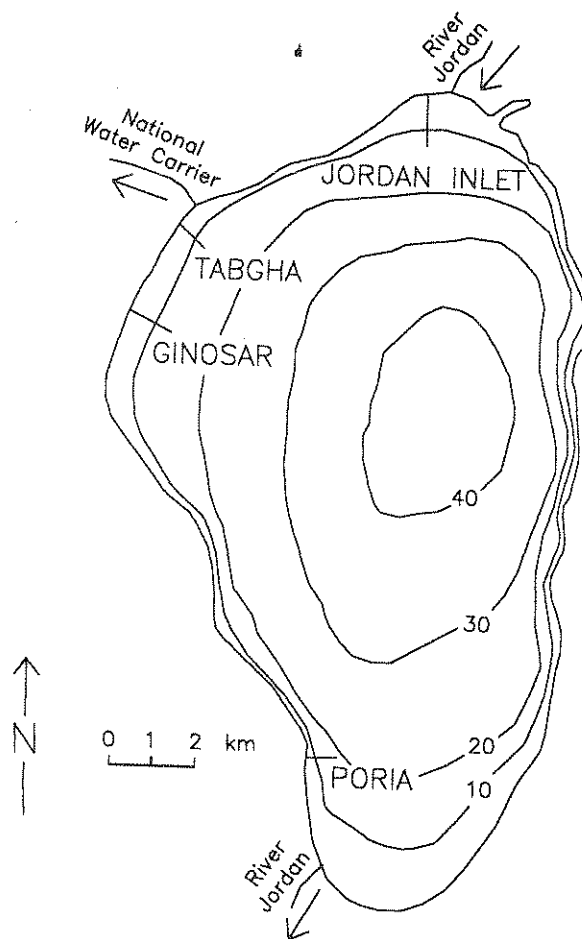


Fig. 1. Map of Lake Kinneret with sampling transects (the lake level was -212.8 m below sea level).

viduals, as well as the wet, dry and ash mass of shells and soft parts were measured with an error within ± 0.1 mg.

The total wet mass (w.m.) was taken after removal of excess water from the shell surface by filter paper. Shells were opened and soft tissues were removed and weighed. The separated shells were also weighed. The interbranchial liquids were collected from 38 organisms. The wet mass of interbranchial liquids (M_1) was calculated for each individual as follows:

$$M_1 = M_t - M_{sb} - M_{sh},$$

where: M_t = total wet mass, M_{sb} = wet mass of soft body (soft tissues), and M_{sh} = wet mass of the shell.

Shells, soft tissues and interbranchial liquids from randomly chosen individuals were dried at 70 °C for 24 hours. Masses were taken before and after drying, and the water content was calculated.

Small portions (0.1–0.3 g) of dry parts (shell, soft tissues and interbranchial liquid) were weighed and burned in a muffle furnace at 520 °C for 24 hours. Ash-free dry mass (organic content) was calculated by subtracting ash mass from dry mass.

Since the content of calories in organic matter of aquatic animals is close to 5 kcal g⁻¹ (Ostapenia, 1968; Winberg, 1971a; Milne & Dunnet, 1972; Dare & Edwards, 1975; Gardner & Thomas, 1987), the body composition data were used to calculate the caloric content of the animal.

For estimating the mass growth rate and calculating the bioenergetic parameters of *U. terminalis*, we used relationships between shell length (L, cm), total wet mass (g), soft tissue wet mass (g) and shell mass (g). Linear regressions were calculated for the logarithmic values of these parameters ($\log y = \log a + b \log x$). The power equation between these characteristics is $y = ax^b$. If in a mass-length equation b is equal to 3, and in a mass-mass equation it is equal to 1, the growth is isometric (Huxley, 1932; Thompson, 1959; Winberg, 1971b).

Growth rate analysis is based on the assumption that shell growth is marked by annual rings. In winter, under low temperatures, the growth rate is lower and a dark ring is formed on the valve external surface, while in summer the growth is faster and rings are light (Negus, 1966; Green, 1973; Ghent *et al.*, 1978; Haukioja & Hakala, 1978; Strayer *et al.*, 1981; McGuaig & Green, 1983; Hochwald & Bauer, 1990). We also considered that sexually mature clams may produce an additional ring during the breeding season (Morton, 1969; Alimov, 1981). The antero-posterior lengths of each consecutive annual dark ring were measured for each individual by Vernier calipers. These values were recorded separately for individuals from different sites to calculate growth curves using Walford's plot method (Ford, 1933; Walford, 1946) which corresponds to von

Bertalanffy's growth model:

$$L(t) = L_{\infty} \cdot [1 - \exp(-kt)], \quad (1)$$

where: $L(t)$ = the shell length (cm) at the age of t (yr), L_{∞} = asymptotic length (cm), and k = growth coefficient (yr⁻¹).

Estimations of annual production (P) of *U. terminalis* populations at the different sites were based on instantaneous mass growth rates, densities and masses of organisms in different length classes (Winberg, 1971a; Zaika, 1983):

$$P = \sum N_i \cdot M_i \cdot G_i, \quad (2)$$

where: N_i = density of individuals in the i -th length class, M_i = mean organism mass in the i -th length class, and G_i = mean instantaneous mass growth rate of organisms in the i -th length class. G_i values were derived as follows (Bayley, 1977):

$$G_i = b \cdot k \cdot (L_{\infty} - L_i) \cdot L_i^{-1}, \quad (3)$$

where: L_i = mean shell length in the i -th length class, and $b = 2.942$ = degree in mass-length relationship (see below).

The respiration (R; mg O₂ h⁻¹) and filtration (F; ml h⁻¹) rates were evaluated by using Alimov's (1981) equations for *Unio* (respiration) and Unionidae (filtration) at 20 °C:

$$R = 0.074 M_i^{0.64},$$

$$F = 85.5 M_i^{0.605}.$$

These equations were transformed because it was found (see Discussion) that the percentage of soft body matter (*i.e.* active tissues) of *U. terminalis* in Lake Kinneret is significantly lower than in European *Unio* spp. (average 60%; Alimov, 1981). The transformed equations for 20 °C are:

$$R = 0.1026 M_{sb}^{0.64},$$

$$F = 116 M_{sb}^{0.605}.$$

The following parameters were used to calculate the annual R and F capacities of the clam communities: densities of *Unio*, length-class frequency, multiannual monthly averages of lake water temperatures at respective depths (S. Seruya, 1978), correcting coefficients for respiration

and filtration in order to convert from 20 °C to relevant temperatures (Alimov, 1981), and caloric equivalents for O₂ (3.4 Kcal/gO₂) and for C (10.6 Kcal/gC) (Ostapenia, 1965; 1968; Winberg, 1971a).

Assimilation energy (A) was calculated as

$$A = P + R.$$

Physiological food consumption (C_{ph}) was computed as

$$C_{ph} = U^{-1} \cdot A,$$

where $U = 0.6$ = the average assimilation efficiency (Tshon-Lukanina, 1987).

Acoustic surveys of Lake Kinneret are carried out routinely to monitor the fish stock and distribution. Fish densities are determined using Simrad equipment – a 70 kHz EY-M Scientific Echo Sounder and a Hydro Acoustic Data Analysis System (HADAS) developed by T. Lindem (Walline *et al.*, 1992). The analysis made in the present study was based on data from surveys undertaken in April and October 1990, and every two months in 1991. The grid of tracks was chosen on the basis of the previous study, using a mathematical model of fish concentrations and acoustic surveys (Kalikhman *et al.*, 1992). This grid resulted in minimization of sampling pattern error and overlap with the *Unio* sampling transects.

Bottom sediments were classified as follows: sand (particles smaller than 2 mm and larger than 20 μ m), mud (silt together with clay, particles smaller than 20 μ m), and muddy sand (the sandy fraction represents more than 50%).

Results

Distribution

The distribution of *U. terminalis* with depth at four locations (Fig. 1) is shown in Fig. 2. This figure indicates that at the Tabgha, Ginosar and Poria transects, the upper boundary of the clam distribution ranges from 1.0 to 1.5 m depth. At

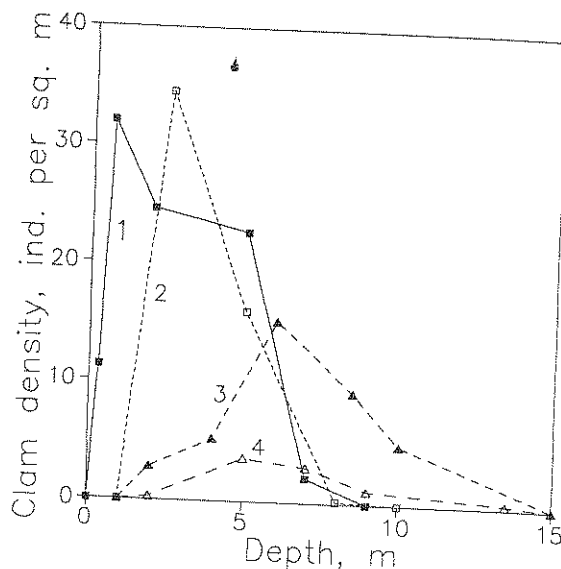


Fig. 2. Bathymetrical distribution of *U. terminalis* at four locations: 1 – Jordan inlet, 2 – Ginosar, 3 – Poria, 4 – Tabgha.

smaller depths, where wave action becomes stronger and the bottom is fully sandy, no molluscs were observed. In the Jordan inlet zone, there is a large area of shallow bottom partially protected from the strong wave action and covered by fine sediments. In this zone the upper boundary of the clam spread almost reached the shoreline.

With increase in depth and simultaneous enhancement of the percentage of the muddy fraction in the sediment, the density of *U. terminalis* rose, reaching a maximum at a depth between 0.3 and 8.0 m where the sand fraction comprised about 40–70% of the sediments. With further increase in depth up to 9–15 m and synchronous augmentation of the muddy fraction up to 90–95%, the clam density decreased at all the locations (Fig. 2).

Based on the data on *Unio* distribution with depth, we calculated the mean density for each transect in the area where the *Unio* were observed. The highest mean density was found in the Jordan inlet zone (16 ind m⁻²) and the lowest one near Tabgha (2 ind m⁻²).

We analysed the clam densities in relation to the fish densities because unionacean glochidia

are obligate parasites on fish, and thus the size of fish host populations can significantly affect the clam reproductive success (McMahon, 1991). The results of the acoustic surveys showed that the distribution of fish in Lake Kinneret changes with time; however, no distinct pattern of seasonal distribution has been revealed. For this reason, the distribution of fish density averaged for all the study period was mapped (Fig. 3) and used in the analysis. The values of fish density on the transects used to collect the clam *U. terminalis* were compared with the corresponding clam densities (Fig. 4). It is clearly indicated that fish and clam densities are positively correlated ($r = 0.81$).

Mass-length relationships and body composition

The data on mass-length and mass-mass relations of whole organisms and their different parts are presented in Figs 5 and 6, and the corresponding equations are given in Table 1. The total mass and soft tissue mass growths are close to isometric, while the shell growth is significantly allometric. However, as the power index in equation 4 is rather close to 1, and in equation 2 it is rather

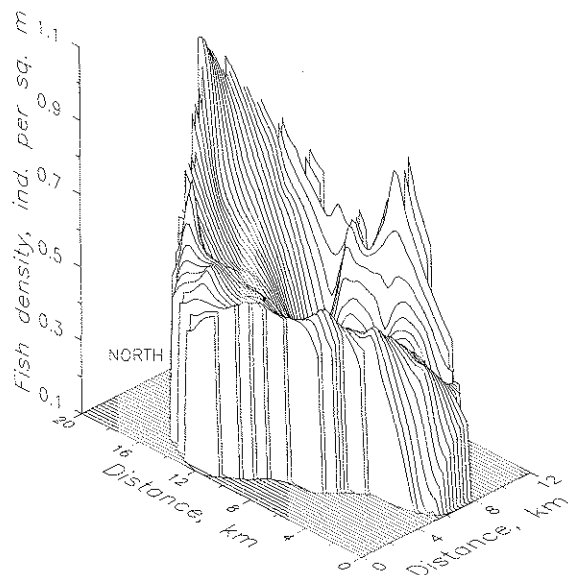


Fig. 3. The distribution of the average density of fish concentrations.

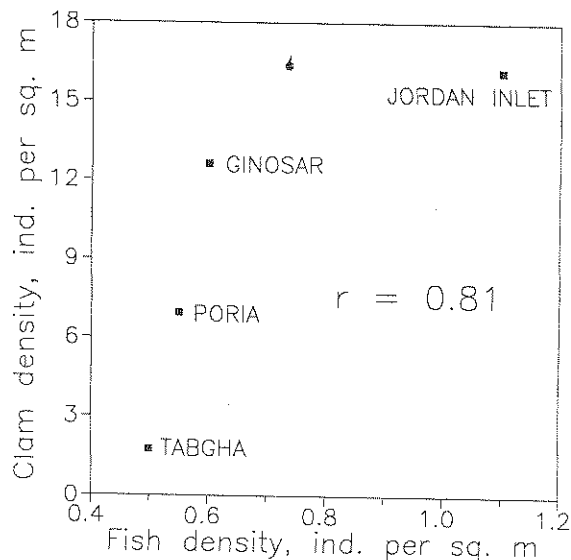


Fig. 4. Field of correlation between *U. terminalis* and fish densities at the sampling locations.

close to 3, the level of shell growth allometry is low. The power index in equation 3 is higher than that in equation 2 ($p < 0.001$), *i.e.* the soft body mass increases with length statistically more than the shell mass.

If the right and left parts of equations 4 and 5 are divided by M_t , the ratios of M_{sh}/M_t and M_{sb}/M_t change only slightly with the clam mass growth. This permits the use of these ratios calculated for the average wet mass of clams in the population (16 g) to evaluate the average body composition and caloric content (Table 2). The results given in Table 2 indicate that the mean water content in the shell and soft tissues is equal to $1.3 \pm 0.4\%$ and $78.1 \pm 2.2\%$, respectively. The average organic content (ash-free matter) in the shell and soft tissues is $2.8 \pm 0.3\%$ and $48.4 \pm 3.9\%$ of their dry masses, respectively.

Growth

In determining clam growth, the distinction between annual and reproductive rings on the external shell surface is important (Alimov, 1981). Our observations indicated that a less dark ring appears after 2–3 clear-cut dark rings. Further-

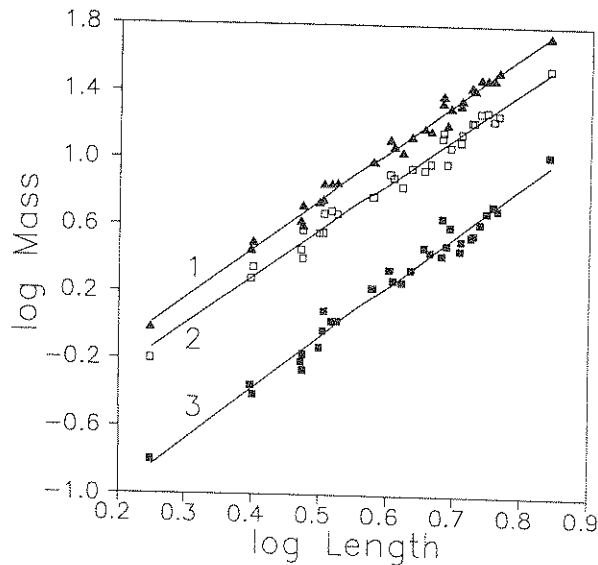


Fig. 5. Linear regressions between logarithmic values of wet mass (g): 1 – total, 2 – shells, 3 – soft tissues, and shell length (cm).

more, the darker and less dark rings alternate. Such a pattern of ring emergence is specific for clams which reproduce from the third or fourth year and typical for many *Unio* species (Tudorancea, 1972; Alimov, 1981). It is reasonable to assume that the less dark rings are reproductive

while the darker ones are annual. Such a pattern was taken into account in determining the *Unio* growth regularities.

The growth of *U. terminalis* was studied at similar depths at two sites (Jordan inlet and Poria) and is given in Fig. 7. The growth rate as indicated from length increments can be expressed by a straight line on Walford's plot, i.e. it fits Bertalanffy's growth model. Both regressions are significant ($P < 0.001$). The coefficients in the equations describing Walford's plot for the two sites (Jordan inlet at 5 m depth and Poria at 6 m depth) are statistically different ($P < 0.01$):

Jordan inlet ($n = 100$; $r = 0.975$):

$$L(t+1) = (0.663 \pm 0.015) \cdot L(t) + (1.77 \pm 0.16); \quad (4)$$

Poria ($n = 146$; $r = 0.959$):

$$L(t+1) = (0.724 \pm 0.018) \cdot L(t) + (1.41 \pm 0.20); \quad (5)$$

where $L(t)$ and $L(t+1)$ are shell lengths (cm) at times t and $t+1$ (yr), respectively.

These formulae can be modified to Bertalanffy's equation as follows:

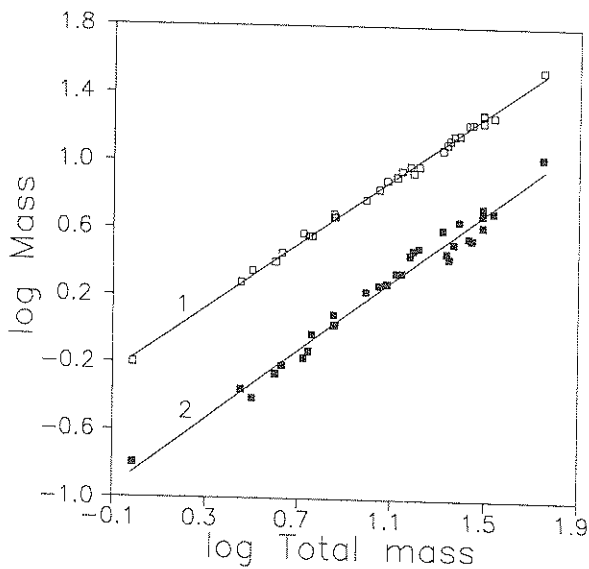


Fig. 6. Linear regressions between logarithmic values of wet masses (g): 1 – shells and total, 2 – soft tissues and total.

Table 1. Coefficients of linear regressions between logarithmic length values (cm) and logarithmic mass values (g)*. The power equations are given. ($n = 31$).

No.	r	Relationship	$\log y = \log a + \log x$		$y = ax^b$	Probability**
			$\log a (\pm SE)$	$b (\pm SE)$		
1	0.994	$\log M_t$ vs $\log L$	$-0.717 (\pm 0.044)$	$2.942 (\pm 0.061)$	$M_t = 0.192 L^{2.942}$	> 0.05 (NS)
2	0.990	$\log M_{sh}$ vs $\log L$	$-0.841 (\pm 0.055)$	$2.816 (\pm 0.075)$	$M_{sh} = 0.144 L^{2.816}$	< 0.05
3	0.986	$\log M_{sb}$ vs $\log L$	$-1.587 (\pm 0.068)$	$3.046 (\pm 0.094)$	$M_{sb} = 0.026 L^{3.046}$	> 0.05 (NS)
4	0.998	$\log M_{sh}$ vs $\log M_t$	$-0.157 (\pm 0.022)$	$0.959 (\pm 0.010)$	$M_{sh} = 0.696 M_t^{0.959}$	< 0.001
5	0.989	$\log M_{sb}$ vs $\log M_t$	$-0.841 (\pm 0.062)$	$1.032 (\pm 0.029)$	$M_{sb} = 0.144 M_t^{1.032}$	> 0.05 (NS)

* All the regressions are significant ($P < 0.001$).

** Significance level of the deviation of b from exponent 3 in equations 1-3 and from exponent 1 in equations 4 and 5.

NS = not significant.

Jordan inlet:

$$L(t) = 5.24 [1 - \exp(-0.412 t)]; \quad (6)$$

Poria:

$$L(t) = 5.30 [1 - \exp(-0.323 t)]. \quad (7)$$

The growth coefficient in the Jordan inlet zone (0.412 yr^{-1}) is higher than that at the Poria site (0.323 yr^{-1}), while the asymptotic lengths in the two zones are rather similar (5.24 and 5.30 cm). These facts indicate a higher growth rate of clams

of the same size in the northern part of the lake than in the southwestern part.

The equations of mass growth were obtained by substituting formulae (6) or (7) into (1):

Jordan inlet:

$$M(t) = 25.2 [1 - \exp(-0.412 t)]^{2.94}; \quad (8)$$

Poria:

$$M(t) = 25.9 [1 - \exp(-0.323 t)]^{2.94}; \quad (9)$$

Table 2. Body composition and calorific content of *U. terminalis* in Lake Kinneret ($\pm SE$).

Parameter	Shell	Soft tissues	Interbranchial liquids	Whole individual
$M_d/M_w, \%$	98.7 (0.4) $n = 24$	21.9 (2.2) $n = 25$	0.34 (0.09) $n = 5$	65.0
$M_a/M_d, \%$	97.2 (0.3) $n = 24$	51.6 (3.9) $n = 25$	37.8 (2.5) $n = 5$	61.5
$M_w, \%$	62.3*	15.6*	22.1**	100.0
$M_d, \%$	94.6	5.3	0.1	100.0
$M_{afd}, \%$	50.5	48.1	1.4	100.0
Caloric content Kcal/g _{dw,m} ***	0.139	0.529	0.011	0.171

n number of measurements

M_w wet mass

M_d dry mass

M_a ash mass

M_{afd} ash-free dry mass

* Calculated for average individual mass in the population (see text)

** Calculated as $M_t - M_{sh} - M_{sb}$

*** Calculated with the assumption that 1 g ash-free dry mass is 5 Kcal (see Materials and methods)

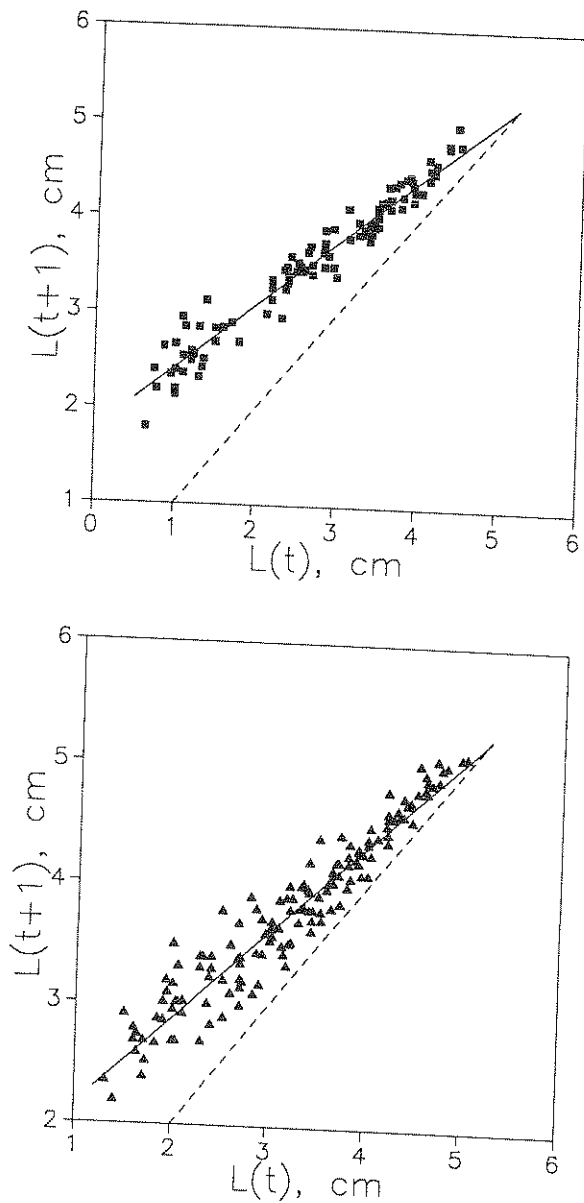


Fig. 7. Walford plots of *U. terminalis*: Jordan inlet zone, 5 m (up) and Poria zone, 6 m (down). The linear regression between the length of two consecutive annual shell rings (cm). The dotted line is the bisector. The coordinates of the point where the regression line crosses the bisector indicate the asymptotic length.

where: $W(t)$ = total wet mass (g) of the clam at time t (yr).

Instantaneous mass growth rate (G , yr^{-1}) can be expressed in terms of L (cm):

$$\text{Jordan inlet: } G = 1.211 \cdot (5.245/L - 1); \quad (10)$$

$$\text{Poria: } G = 0.950 \cdot (5.296/L - 1). \quad (11)$$

Production

The annual production of the population (P) was estimated proceeding from the structure of the population (Fig. 8), mass-length relationship (equation 1 in Table 1) and instantaneous growth rates (equations 10 and 11). The production and biomass of *U. terminalis* in the Jordan inlet and Poria zones are presented in Table 3. In the Jordan inlet zone at 5 m depth, the biomass and production were 1.5–1.7 times higher than in the Poria zone at 6 m depth. Nevertheless the P/B ratios were fairly similar at both sites.

Discussion

Clam distribution

At all locations, the highest *Unio* density was observed in the muddy sand, and thus we can suggest that this kind of substrate is most suitable. Furthermore, the presence of dense *Unio* concen-

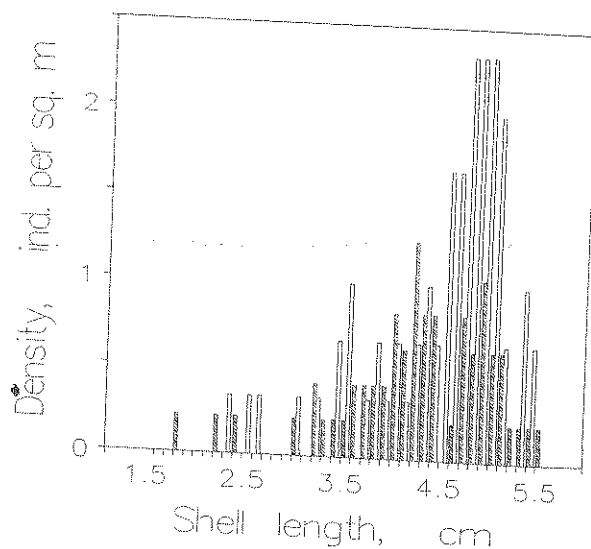


Fig. 8. Size structure of *U. terminalis* population: black bars – in Jordan inlet zone, 5 m; empty bars – in Poria area, 6 m.

Table 3. Biomass and annual energetic budget of *U. terminalis* at two sites in Lake Kinneret.

Site	B		P		P/B yr ⁻¹	R Kcal m ⁻² yr ⁻¹	R/P	A Kcal m ⁻² yr ⁻¹
	g m ⁻²	Kcal m ⁻²	g m ⁻² yr ⁻¹	Kcal m ⁻² yr ⁻¹				
Jordan inlet	371	63	61.8	10.6	0.167	129	12.2	140
Poria	222	38	39.5	6.8	0.178	80	1.8	87

R – metabolic energy (respiration).

A – assimilated energy (= P + R).

trations at intermediate depths where muddy sand was found may also reflect the dependence of the clam upon the wave action and the oxygen regime near the bottom. Thus, the wave action appears to affect negatively the clam density and at the same time it takes part in redeposition of fine sediments to the deeper part of the lake. These phenomena might be the reason for the increase in clam density as well as the percentage of the muddy component in bottom sediments with depth in the upper range of the habitat. On the other hand, in the lower range of the habitat, the decrease of the clam density with depth probably reflects the deterioration of the oxygen regime above the bottom sediments, which occurs during the stratification period. The deterioration consists of an increase in the daily duration of anoxic conditions. This phenomenon can be related to the absence of dissolved oxygen in the hypolimnetic waters (C. Serruya, 1978a) and to the daily seiche movements (up to 10 m) in the inshore zone (S. Serruya, 1978).

The lower boundary of *U. terminalis* distribution in the Jordan inlet zone (9 m) and in other parts of the lake (15 m) coincides with the line below which oxygen is temporarily absent during the stratification period (Tchernov, 1975; C. Serruya, 1978a). It can be suggested that the oxygenation level in the upper layer of the bottom sediments in the Jordan inlet zone is lower than at similar water depths in other parts of the lake, because of the heavy flux of organic matter by the river current. The organic particles fluxed by Jordan waters are sedimented mostly in this inlet area (C. Serruya, 1978b), and their decomposition apparently accelerates oxygen depletion here as compared with the same depth in other parts

of the lake. The coincidence of the lower boundary of the *Unio* habitat with the thermocline-bottom interface indicates that the oxygen regime near the bottom is an important factor controlling the spread of *U. terminalis* to depth.

Recent data indicated that unionid densities are directly related to the densities of fish glochidial hosts (Strayer *et al.*, 1981; Smith, 1985; McMahon, 1991). Moreover, a positive correlation between fish and clam densities might also indirectly go through the level of water productivity, since both fish (Bulion, 1983) and mollusc densities (Alimov, 1979; Strayer *et al.*, 1981) are positively related to the productivity of water bodies. In this respect, the detected correlation between the clam and fish densities in Lake Kinneret suggests that fish glochidial hosts as well as water productivity (food availability) might be significant factors affecting *U. terminalis* distribution in Lake Kinneret. In particular, considerable nutrient influx by Jordan water generating the additional food supply in the inlet zone and the highest fish density both apparently give rise to the highest density of *Unio* in this area.

Body composition

The contributions of the shell and soft tissues to the total *U. terminalis* body mass (Table 2) essentially differ from those obtained by Lewandowska & Stanczykowska (1975) and Alimov (1981) for European *Unio* ($M_{sh}/M_t = 26-43\%$ and $M_{sb}/M_t = 48-69\%$). Thus, *U. terminalis* in Lake Kinneret has a more massive shell and a lower portion of soft tissues as compared with European *Unio*. Green (1972) has shown that the shell mass

); (10)

); (11)

(P) was
of the
relationship
growth
ion and
let and
the Jor-
ss and
n in the
he P/B

was ob-
an sug-
uitable.
concen-



ack bars
rea, 6 m.

and thickness of certain species of unionids is highly dependent on NaCl concentrations, pH and alkalinity. These parameters are high in Lake Kinneret (C. Serruya, 1978a) and therefore could be partially responsible for the massive *U. terminalis* shell.

The percentages of water in the shell and soft tissues of *U. terminalis* are close to those measured in European unionids (3.3% and 84.2% for shell and soft tissues, respectively; Alimov, 1981). The organic contents in the shell and soft tissues of the Kinneret *Unio* are lower than those measured in European *Unio* species (14.5% and 84–94%, respectively; Alimov, 1981).

The lower fraction of organic matter and the high portion of the shell mass in the body of *U. terminalis* resulted in a caloric content (0.171 Kcal/gw.m) which is substantially lower than that obtained for European *Unio* species (0.4–0.7 Kcal/gw.m; Tudorancea & Florescu, 1968; Tudorancea, 1972; Alimov, 1981).

Growth and production

The *U. terminalis* growth rate in the northern part of Lake Kinneret was higher than that in the southwestern zone of the lake. Such a difference can most likely be attributed to enhanced availability of food sources in the Jordan inlet zone (C. Serruya, 1978b). Alimov (1981) documented the lower growth coefficients (0.24–0.28 yr⁻¹) and higher asymptotic shell length (10–13 cm) in European *Unio* species than those computed for the Kinneret unionid.

The average life-span of *U. terminalis* in the Jordan inlet and Poria zones, as estimated by the length frequency distribution data (Fig. 8) and growth equations (6) and (7), varied between 9–11 years which is similar to the range given by Rubbel (1913), Fischer (1950), Wesenberg-Lund (1937), Negus (1966), Tudorancea (1969) and Stadnichenko (1984) for European unionids.

For different species of *Unio* in lakes and rivers in Europe, Canada, and the USA, the annual P/B ratio varied between 0.09 and 0.34 (Negus, 1966; Tudorancea & Florescu, 1968, 1969; Mag-

nin & Stanczykowska, 1971; Tudorancea, 1972; Lewandowski & Stanczykowska, 1975; Nardi, 1978; Strayer *et al.*, 1981; Hanson *et al.*, 1988; Nalepa & Gauvin, 1988). The P/B ratio for the *U. terminalis* population in Lake Kinneret (Table 3) is close to that for other unionid communities in colder waters with similar or even lower levels of productivity. At higher temperatures and better food conditions, the growth rate rises (Winberg, 1971a; Zaika, 1983); therefore it could be expected *a priori* that unionids in Lake Kinneret might have a higher P/B ratio than those in other colder water bodies. The similarity of P/B ratios in populations of unionids in Lake Kinneret and other water bodies probably reflects a higher proportion of longer life-span individuals in Kinneret, since low P/B ratios are appropriate for populations with a high percentage of old-age individuals (Magnin & Stanczykowska, 1971; Zaika, 1983).

Energetic budget and ecological significance

The potential role of *U. terminalis* in Lake Kinneret was assessed by calculating the filtration capacity and the overall bioenergetic budget of the clam population.

Our calculations show that the respired energy was 12 times higher than that used for the secondary production of the *U. terminalis* population at the two examined sites (Table 3). The results given in Table 4 show that in both the Jordan inlet and Poria zones, an average *U. terminalis* specimen can filter about 2 m³ of water per year. The rate of water filtration per unit area by the community of clams is higher in the Jordan inlet zone because of higher clam density.

The similarities of the P/B and R/P ratios as well as the filtration capability of clams at two sites of Lake Kinneret (Table 3 and 4) justify combining them in evaluating the overall bioenergetic budget of the *U. terminalis* population in Lake Kinneret. Thus, these parameters were assumed as: annual P/B ratio = 0.17 yr⁻¹, annual R/P ratio = 12, average filtration rate = 2 m³ ind⁻¹ yr⁻¹. In addition, the following values were

Table 4. Filtration activities of *U. terminalis* populations at two sites in Lake Kinneret.

Site	Depth m	N (ind m ⁻²)	V _f * (m ³ m ⁻² yr ⁻¹)	V _f N (m ³ ind ⁻¹ yr ⁻¹)
Jordan inlet	5	22.7	48.2	2.1
Poria	6	15.3	30.0	2.0

* V_f - annual volume of filtered water by all individuals on m².

accepted for the entire population: depths inhabited by *Unio* = 1–11 m, bottom surface area of inhabited depths = 20 km², and caloric content of total body mass = 2.64 Kcal ind⁻¹. The clam density limits obtained for the chosen locations (2–16 ind m⁻²) were used in our calculations.

Based on the assumed values, the whole population of *U. terminalis* in Lake Kinneret is able to filter from 8×10^7 to 64×10^7 m³ of water per year, that is about 2–17% of the total lake volume, or 60–500% of the water volume above the bottom inhabited by *U. terminalis* (littoral and sublittoral). The ecological significance of the filtration activity of bivalves is attributed to their ability to intensify the sedimentation of suspended matter and in such a way to improve water quality (Alimov, 1981). Moreover, clams may glue and deposit such small particles which are normally not sedimented (Sornin, 1981). Consequently, the clam population forms a belt around Lake Kinneret which may act as a biological filter. Its action is especially important in the shallow zone which supplies the resuspended matter to the pelagic zone.

Taking into account that clams can remove from water almost all particulate organic matter (Kondratev, 1970), and that the annual average concentration of particulate carbon in Kinneret water is 0.9 ppm (Nishri, pers. comm.), it can be computed that the total suspended carbon removed from the water by *U. terminalis* (i.e. ecological consumption) is within a range of 72–580 t C yr⁻¹. Our calculations show that at the same time the physiological food demand of the *Unio* population may comprise about half of the ecological consumption (Fig. 9).

The difference between ecological and physiological consumptions reflects the production of

pseudofeces ejected into the water and sinking to the bottom as pellets. The pseudofeces are produced by clams mainly with excess of food supply when the seston concentration exceeds a certain threshold (Widdows *et al.*, 1979; Alimov, 1981; Deslous-Paoli *et al.*, 1992). For this reason, the concentration of particulate organic matter in general does not limit the food demand of the *Unio* population in Lake Kinneret. However, the concentration of particulate organic matter in the lake seasonally changes about six-fold (Nishri, pers. comm.); therefore food limitation is feasible in some periods.

The fraction of assimilated energy relative to the filtered organic matter of about 31% is similar to that measured for other bivalves (36–49%) in natural waters (Fuji, 1979; Stanczykowska & Planter, 1985; James, 1987; Nalepa *et al.*, 1991).

As shown in Fig. 9, the food demand (physiological consumption) of *U. terminalis* is determined to a great extent (55%) by the metabolic energy expenditure (respiration), because approximately 92% of the assimilated energy is expended to respiration and only 8% to production. The proportion of metabolic energy expenditure versus secondary production energy (12 times) for *U. terminalis* is similar to those presented for three unionid species (9–16 times) by Tudorancea & Florescu (1968) and Tudorancea (1972). This fact confirms their conclusion on the low efficiency of production as a result of the high energy flow to metabolic processes in unionid populations.

Filtration capacities and carbon fluxes (or equivalent energetic values) through the population considered above allow us to draw some preliminary conclusions about the potential impact of clams on the lake ecosystem.

Most of the organic matter filtered by the

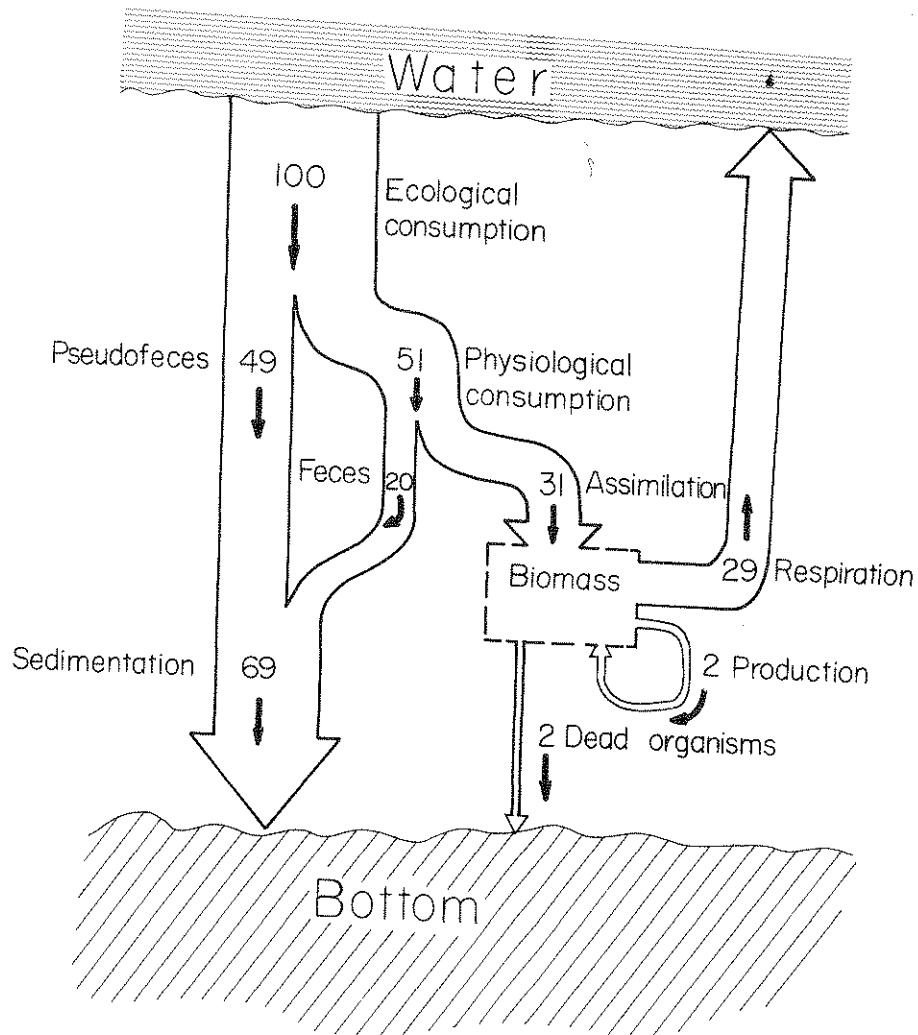


Fig. 9. Annual energetic budget (in percentage of ecological consumption) of the *U. terminalis* population in Lake Kinneret (schematic).

U. terminalis population (ca 70%) is finally deposited to the bottom as feces and pseudofeces. Although the chemical composition and caloric content of feces and pseudofeces are different, their organic matter can serve as fuel for the life activity of other benthic animals (Deslous-Paoli *et al.*, 1992). Consequently, the clams can be considered as organic matter suppliers to the zoobenthic community. About one third of the filtered organic matter are dissipated due to metabolic processes. As known, in the course of the metabolic processes in aquatic organisms, nutri-

ents (such as N and P) are released into the water and in turn are required for the development of primary production. In other words, the clams may also participate in processes of nutrient regeneration in the lake.

Only an insignificant part of the filtered organic matter (ca 2%) is removed from the population by dead organisms (assuming that the annual mortality, in terms of carbon flux, is close to the production of the population).

Although the computed carbon fluxes are tentative and need to be specified, it can be seen

that *U. terminalis* may play a noticeable role in the shallow-water area of Lake Kinneret, in the following ways: a) removal of particulate matter from the water due to biofiltration and sedimentation, b) delivery of organic suspended matter to the littoral and sublittoral benthic communities, c) regeneration and recycling of nutrients as a result of metabolic processes in the clam population.

The activity of *U. terminalis* in Lake Kinneret should be taken into consideration for lake management.

Conclusions

1. The clams inhabit the inshore zone (up to 15 m depth), with a maximum density on the muddy bottom. The highest density was observed in the Jordan inlet area. A positive correlation was found between the densities of *Unio* and fish which might be hosting the clam's glochidia.
2. *U. terminalis* in Lake Kinneret has a massive shell, a high ash component in the total body mass, and therefore a low caloric content as compared with European species of *Unio*.
3. *U. terminalis* growth in Lake Kinneret was found to be close to isometric. Shell growth can be approximated by Bertalanffy's pattern. The growth rate of individuals was higher in the Jordan inlet zone than in the Poria zone. It was assumed that the difference is attributable to food availability.
4. At the same depths, the annual P/B ratios of the clam communities were similar (0.17–0.18) in different parts of the lake.
5. According to our calculations, the water volume above the bottom inhabited by *U. terminalis* might be filtered 0.6–5.0 times a year. The ecological consumption of the *Unio* population ranged from 70–600 t C yr⁻¹. About two thirds of overall organic matter filtered by *U. terminalis* population are deposited to the bottom as feces and pseudofeces; and about one third of its energy is dissipated due to metabolic processes. It can be expected that

U. terminalis 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 of nutrients.

Acknowledgements

We thank two anonymous referees for critical reviews and many valuable suggestions on earlier versions of the manuscript. This work was supported by the Rich Foundation and a grant of the Israel Ministry of Science and Technology.

References

- Alimov, A. F., 1979. Production of freshwater Bivalvia, In G. G. Winberg (ed.), Common Foundations of Water Ecosystem Investigation. Nauka, Leningrad: 177–180. (in Russian).
- Alimov, A. F., 1981. Functional Ecology of Freshwater Bivalvia. Nauka, Leningrad, 248 pp. (in Russian).
- Arter, H. E., 1989. Effect of eutrophication on species composition and growth of freshwater mussels (Mollusca, Unionidae) in Lake Hallwil (Aargau, Switzerland). *Aquat. Sci.* 51: 87–99.
- Bayley, P. B., 1977. A method for finding the limits of application of the von Bertalanffy growth model and statistical estimates of the parameters. *J. Fish. Res. Bd Can.* 34: 1079–1084.
- Bulion, V. V., 1983. Dependence of the fish-productivity of water bodies on the primary production. In G. M. Lavrenteva (ed.), Methods of Study of Food Sources Condition in Fresh Water Bodies. Promrybvod, Leningrad: 3–11 (in Russian).
- Dahl, E., 1956. Ecological salinity boundaries in poikilohaline waters. *Oikos* 7: 1–21.
- Dare, P. J. & D. B. Edwards, 1975. Seasonal changes in flesh weight and biochemical composition of mussels (*Mytilus edulis* L.) in the Conway Estuary, North Wales. *J. exp. mar. Biol. Ecol.* 18: 89–97.
- Deslous-Paoli J. M., A. M. Lannou, P. Geairon, S. Bougrier, O. Raillard & M. Heral, 1992. Effects of the feeding behaviour of *Crassostrea gigas* (Bivalve Molluscs) on biosedimentation of natural particulate matter. *Hydrobiologia* 231: 85–91.
- Fischer, P. H., 1950. Vie et moeurs des Mollusques. Payot, Paris, 312 pp.
- Fisher, J. B. & N. J. S. Tevesz, 1976. Distribution and population density of *Elliptio complanata* in Lake Pocotopaug, Connecticut. *Velliger* 18: 332–338.

- Ford, E., 1933. An account of the herring investigations conducted at Plymouth during the years from 1924-1933. J. mar. Biol. Ass. U.K. 19: 305-384.
- Freeman, K. R. & L. M. Dickie, 1979. Growth and mortality of the blue mussel (*Mytilus edulis*) in relation to environmental indexing. J. Fish. Res. Bd Can. 36: 1238-1249.
- Fuji, A., 1979. Phosphorus budget in natural population of *Corbicula japonica* Prime in poikilohaline lagoon, Zyusan-ko. Bull. Fac. Fish. Hokkaido Univ. 30: 34-49.
- Gardner, J. P. A. & M. L. H. Thomas, 1987. Growth mortality and production of organic matter by a rocky intertidal population of *Mytilus edulis* in the Quoddy Region of the Bay of Fundy. Mar. Ecol. Prog. Ser. 39: 31-36.
- Ghent, A. W., R. Singer & L. Johnson-Singer, 1978. Depth distributions determined with SCUBA and associated studies of the freshwater unionid clams *Elliptio complanata* and *Anodonta grandis* in Lake Bernard, Ontario. Can. J. Zool. 56: 1654-1663.
- Green, R. H., 1972. Distribution and morphological variation of *Lampsilis radiata* (Pelecypoda, Unionidae) in some central Canadian lakes: a multivariate statistical approach. J. Fish. Res. Bd Can. 29: 1565-1570.
- Green, R. H., 1973. Growth and mortality in an Arctic intertidal population of *Macoma balthica* (Pelecypoda, Tellinidae). J. Fish. Res. Bd Can. 30: 1345-1348.
- Hanson, J. M., W. C. Mackay & E. E. Prepas, 1988. Population size, growth and production of a unionid clam *Anodonta grandis simpsoniana* in a small, deep Boreal forest lake in central Alberta. Can. J. Zool. 66: 247-253.
- Haukioja, E. & T. Hakala, 1978. Measuring growth from shell rings in population of *Anodonta piscinalis* (Pelecypoda, Unionidae). Ann. Zool. Fenn. 15: 60-65.
- Hochwald S. & G. Bauer, 1990. Untersuchungen zur Populationsökologie und Fortpflanzungsbiologie der Bachmuschel *U. crassus*. Schriftenreihe des Bayerischen Landesamts für Umweltschutz. 97: 31-49.
- Huxley, I. S., 1932. Problems of Relative Growth, Methuen, London, 276 pp.
- James, M. R., 1987. Ecology of the freshwater mussel *Hyridella menziesi* (Gray) in a small oligotrophic lake. Arch. Hydrobiol. 3: 337-348.
- Jones, D. S., 1981. Annual growth increment on shells of *Spisula solidissima* record marine temperature variability. Science 211: 165-167.
- Kalikhman, I., P. Walline & M. Gophen, 1992. Simultaneous patterns of temperature, oxygen, zooplankton and fish distribution in Lake Kinneret, Israel. Freshwat. Biol., 28: 337-347.
- Kondratev, G. P., 1970. Filtration and mineralization activities of the Bivalvia in Vologradian water body. Ph.D. thesis, Univ. Saratov, Saratov, USSR, 23 pp. (in Russian).
- Lewandowski, K. & A. Stanczykowska, 1975. The occurrence and role of bivalves of the family Unionidae in Mikolajskie Lake. Ecol. Pol. 23: 317-334.
- Magnin, E. & A. Stanczykowska, 1971. Quelques données sur la croissance, la biomasse et la production annuelle de trois mollusques Unionidae de la région de Montreal. Can. J. Zool. 49: 491-497.
- Mann, K. H., 1964. The pattern of energy flow in the fish and invertebrate fauna of the River Thames. Verh. int. Ver. Theor. Angew. Limnol. 15: 485-495.
- McGuaig, J. M. & R. H. Green, 1983. Unionid growth curves derived from annual rings: a baseline model for Long Point Bay, Lake Erie. Can. J. Fish. aquat. Sci. 40: 436-442.
- McMahon, R. F., 1991. Mollusca: Bivalvia. In J. H. Thorp & A. P. Covich (eds), Ecology and Classification of North American Freshwater Invertebrates. Academic Press Inc.: 315-399.
- Milne, H. A. & G. M. Dunnet, 1972. Standing crop, productivity and trophic relations of the fauna of the Ythan estuary. In R. S. K. Barnes & J. Green (eds), The Estuarine Environment. Associated Scientific Publishing, Amsterdam: 85-106.
- Mitchell, H. M., 1984. Investigations of the relationship between unionid clam shell parameters (*Elliptio complanata*) and mean chlorophyll *a* concentrations in lakes. M. Sc. thesis, University of Toronto, Toronto, Ont., 91 pp.
- Miura, T. & T. Yamashiro, 1990. Size selective feeding of *Anodonta calipygos*, a phytoplanktivorous freshwater bivalve and variability of egested algae. Jpn. J. Limnol. 51: 73-78.
- Morton, B. S., 1969. Studies on the biology of *Dreissena polymorpha* Pall. III. Population dynamics. Proc. Malacol. Soc. London 38: 471-482.
- Nalepa, T. F. & J. M. Gauvin, 1988. Distribution, abundance and biomass of freshwater mussels (Bivalvia: Unionidae) in Lake St. Clair. J. Great Lakes Res. 14: 411-419.
- Nalepa, T. F., W. S. Gardner & J. M. Malczyk, 1991. Phosphorus cycling by mussels (Unionidae: Bivalvia) in Lake St. Clair. Hydrobiol. 219: 239-250.
- Nardi, P. R., 1978. Dati sperimentali sulla produttività di *Unio* (Lamellibranchiata). Boll. Mus. Ven. 29 suppl.: 201-202.
- Negus, C. L., 1966. A quantitative study of growth and production of unionid mussels in the River Thames at Reading. J. anim. Ecol. 35: 513-532.
- Okland, J., 1963. Notes on population density, age distribution, growth and habitat of *Anodonta piscinalis* Nilss. (Moll. Lammellibr.) in a eutrophic Norwegian lake. Nytt. Mag. Zool. 11: 19-43.
- Ostapenia, A. P., 1966. Fullness of organic matter oxidation of water invertebrates by dichromate oxidation method. Rep. Acad. Sci. Bel. SSR. 9: 273-276 (in Russian).
- Ostapenia, A. P., 1968. Calculation of caloric value of water organisms dry matter. Hydrobiol. J. 2: 85-89 (in Russian).
- Paperna, J., 1964. The metazoan parasite fauna of Israeli inland water fishes. Bamidgah 16: 3-66.
- Por, F. D. & G. Eitan, 1970. The invertebrate zoobenthos of Lake Tiberias. II. Quantitative data (level bottoms). Isr. J. Zool. 19: 125-134.
- Rubbel, A., 1913. Beobachtungen über das Wachstum von *Margaritana margaritifera*. Zool. Anz. 46: 156-161.

Serr
c)
Ki
lis
40
Serr
La
Pu
Smit
ter
fisl
Inv
Sorn
liés
cyc
Stadi
lus
38:
Stanc
Re
cur
22:
Stanc
(P:
53:
Stanc
anc
98:
Stanc
trie
Lal
moi
Pol
Stray
Bio
Elli
wat
Tcher
lacc

- Serruya, C., 1978a, b, c. a) Water chemistry; b) Sediments; c) Biomass of benthic organisms. In C. Serruya (ed.), Lake Kinneret. Monographiae Biologicae 32. Dr W. Junk Publishers, The Hague: a) 185-204; b) 205-215; c) 395-404.
- Serruya, S., 1978. Water temperature. In C. Serruya (ed.), Lake Kinneret. Monographiae Biologicae 32. Dr W. Junk Publishers, The Hague: 157-166.
- Smith, D. G., 1985. Recent range expansion of the freshwater mussel *Anodonta implicata* and its relationship to clupeid fish restoration in the Connecticut River system. *Freshwat. Invert. Biol.* 4: 105-108.
- Sornin, J. M., 1981. Processus sédimentaires et biodéposition liés à différents modes de conchyliculture. Thèse de 3ème cycle, Université de Nantes: 188 pp.
- Stadnichenko, A. B., 1984. Fauna of Ukrainian. 29. Mollusca. 9. Unionidae, Cycladidae. *Naukova dumka, Kiev*, 383 pp. (in Ukrainian).
- Stanczykowska, A., 1975. Ecosystem of Mikolajskie Lake. Regularities of the *Dreissena polymorpha* Pall. (Bivalvia) occurrence and its function in the lake. *Pol. Arch. Hydrobiol.* 22: 73-78.
- Stanczykowska, A., 1977. Ecology of *Dreissena polymorpha* (Pall.) (Bivalvia) in lakes. *Pol. Arch. Hydrobiol.* 24: 461-530.
- Stanczykowska, A., 1984. Role of bivalves in the phosphorus and nitrogen budget in lakes. *Verh. Int. Ver. Limnol.* 22: 982-985.
- Stanczykowska, A. & M. Planter, 1985. Factors affecting nutrient budget in lakes of the R. Jorka watershed (Masurian Lakeland, Poland). X. Role of the mussel *Dreissena polymorpha* (Pall.) in N and P cycles in a lake ecosystem. *Ecol. Pol.* 33: 345-356.
- Strayer, D. L., J. J. Cole, G. E. Likens & D. C. Buso, 1981. Biomass and annual production of the freshwater mussel *Elliptio complanata* in an oligotrophic soft water lake. *Freshwat. Biol.* 11: 435-440.
- Tchernov, E., 1975. The molluscs of the Sea of Galilee. *Malacologia* 15: 147-184.
- Thompson, D. A. W., 1959. On Growth and Form. Cambridge, 1-2: 793 pp.
- Tsihon-Lucanina, E. A., 1987. Trophology of Water Molluscs. *Nauka, Moscow*: 176 pp. (in Russian).
- Tudorancea, C., 1969. Comparison of the population of *Unio tumidus* Philipsson from the complex of Crapina-Jijila marshes. *Ekol. Pol. Ser. A.* 17: 185-204.
- Tudorancea, C., 1972. Studies on Unionidae populations from the Crapina-Jijila complex of pools (Dunabe zone liable to inundation). *Hydrobiologia* 39: 527-561.
- Tudorancea, C. & M. Florescu, 1968. Considerations concerning the production and energetics of *Unio tumidus* Philipsson population from the Crapina marsh. *Trav. Mus. Hist. Nat. Gr. Antipa.* 8: 395-409.
- Tudorancea, C. & M. Florescu, 1969. Aspecte de productiei si energeticii populatiei de *Anodonta piscinalis* Nilsson din Balta Crapina (zona inundabila a Dunarii). *Studii. Cerc. Biol. Ser. Zool.* 21: 43-55.
- Walford, L. A., 1946. A new graphic method of describing the growth of animals. *Biol. Bull.* 90: 141-147.
- Walline, P. D., S. Pisanty & T. Lindem, 1992. Acoustic assessment of the number of pelagic fish in Lake Kinneret, Israel. *Hydrobiologia* 231: 153-163.
- Walz, N., 1978. The energy balance of the freshwater mussel *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance. I. Pattern of activity, feeding and assimilation efficiency. *Arch. Hydrobiol. Suppl.* 55: 83-105.
- Wesenberg-Lund, C., 1937. *Ferskvandstaunaen, Biologisk belyst. Invertebrata.* Kobenhavn. 1-2: 837 S.
- Widdows, J., P. Fieth & C. M. Worrall, 1979. Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. *Mar. Biol.* 50: 195-207.
- Winberg, G. G., 1971a. Methods for the Estimation of Production of Aquatic Animals. Academic Press, New York-London, 175 pp.
- Winberg, G. G., 1971b. The lean dimensions and body mass of animals. *J. Gen. Biol.* 32: 714-723 (in Russian).
- Zaika, V. E., 1983. The Comparative Productivity of Hydrobionts. *Naukova dumka, Kiev*, 208 pp. (in Russian).