Hydrobiologia **318:** 103–115, 1996.

Distribution and production of chironomids (Diptera: Chironomidae) in a shallow, alkaline lake (Neusiedler See, Austria)

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Received 18 August 1994; accepted in revised form 17 November 1994

Key words: Chironomidae, shallow lake, horizontal distribution, production

Abstract

From July 1990 to July 1991 the benthic community of the open water zone of Neusiedler See, one of the largest shallow lakes in central Europe, was studied with special reference to the chironomids. Only 16 spp. of chironomids inhabited the sediment of the open water zone. The numerically dominant species were *Tanypus punctipennis, Procladius* cf. *choreus, Microchironomus tener* and *Cladotanytarsus* gr. *mancus*. Most invertebrates showed a distinct horizontal distribution. Species richness and abundance were highest on muddy and organically rich substrates near the reed belt. Chironomid densities in this area reached 54,000 ind m^{-2} and biomass was 2.0 g dw m^{-2}. The two tanypod species accounted for more than 90% of the standing stock of the macrozoobenthos near the reed belt. The sediment of the open lake and of the eastern part of Neusiedler See was composed of compact clay and sand as a result of the erosion of fine material due to strong waves and currents. Individual densities in these areas were much lower. Production of the numerically dominant species *T. punctipennis* was estimated using the increment-summation method, whereas production of the remaining species was estimated using an empirically derived multiple regression. Mean annual production of chironomids exceeded 6 g dw m^{-2} yr^{-1} near the reed belt, but it reached only 0.55 g dw m^{-2} yr^{-1} in the open lake. These values are rather low compared with other lakes and can be explained by unfavourable sediment conditions due to wave action and by physiological stress due to the water chemistry.

Introduction

Neusiedler See and the co called "Seewinkel" east of the lake with its numerous salt pans is one of the largest wetlands in central Europe. In spring 1994 the southern part of the lake was declared a national park by the Austrian government. Limnological research in this area began at the beginning of this century. The first extensive study, however, was initiated during the International Biological Programme in the 1970s and provided the first detailed information about the lake (Löffler, 1979). Since then, studies of phytoplankton and zooplankton have continued (for references see Wolfram, 1993). The benthic community was studied by Schiemer *et al.* (1969), Schiemer (1978a, 1978b, 1979) and Jungwirth (1979b).

The fish fauna, especially its trophic relationships to zooplankton and zoobenthos, was the subject of a thorough project conducted from 1990 to 1993 (Wais, 1993; Herzig *et al.*, 1994). As part of this project, the benthos was studied from 1990 to 1991 (Wolfram, 1993). The current paper presents results on chironomids of the open water zone of Neusiedler See, especially their spatial distribution in relation to abiotic parameters and secondary production. The chironomids of the reed belt have not been studied quantitatively and will be treated in a faunistic survey in a forthcoming paper.

Description of the lake

Neusiedler See (47°82′ N, 16°77′ E, alt. 115 m) is a large (321 km^2), shallow, meso- to eutrophic lake in central Europe, situated on the Austrian-Hungarian border (Fig. 1). It is surrounded by a broad reed belt

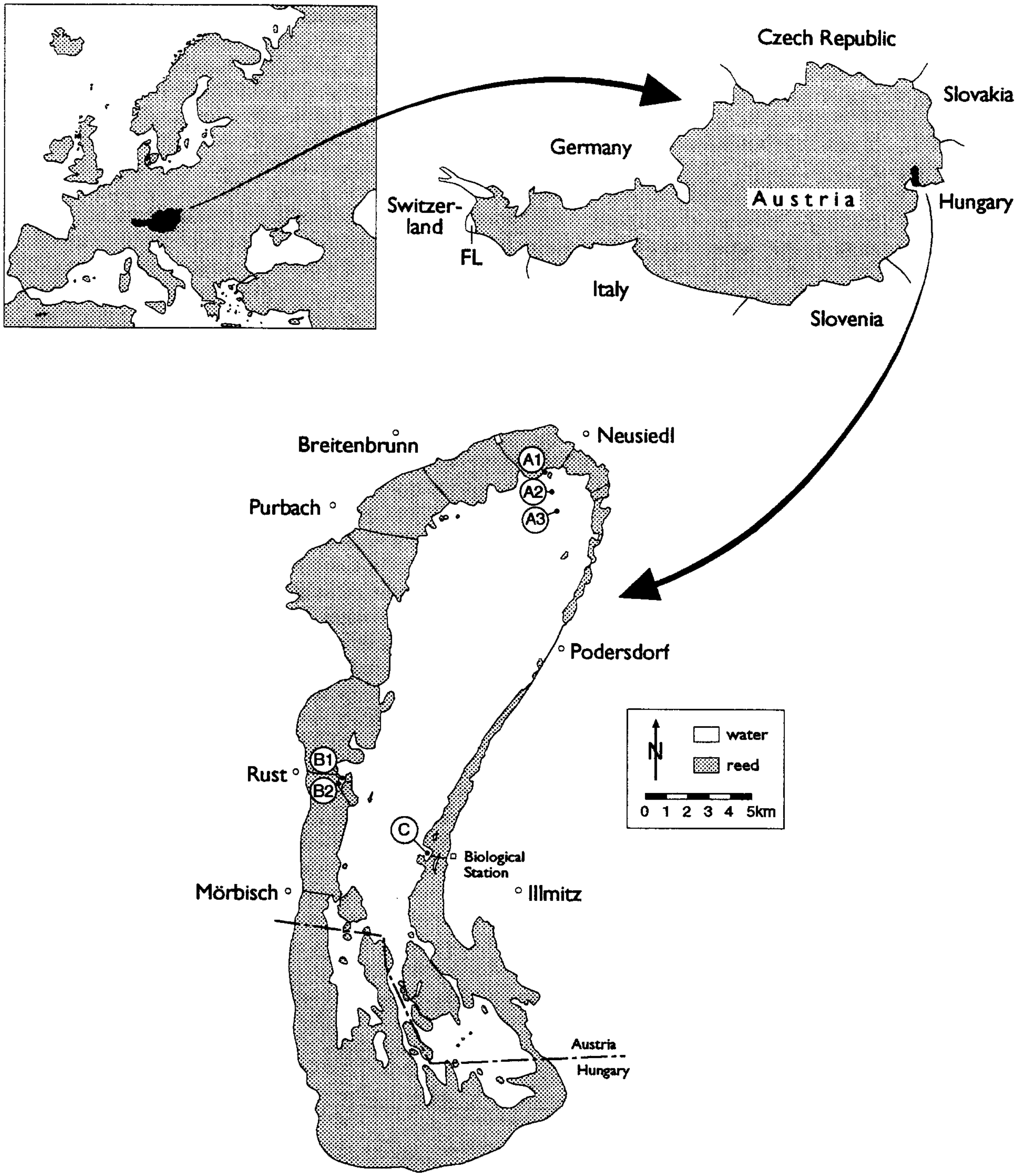

Fig. 1. Map of Neusiedler See. A1, A2, A3, B1, B2, C ... sampling stations. Sampling points in the Bay of Illmitz (C) are given in Fig. 5(B).

(Phragmites australis), which covers more than half of the lake area.

One of the main characteristics of Neusiedler See is its extreme shallowness (Z_{mean} = 1.1 m, Z_{max} = ca. 2 m). In combination with strong and frequent wind events, this leads to erosion of the lake bottom and a high concentration of suspended solids (up to 800 mg dw l^{-1}). Continuous mixing is also responsible for a highly variable temperature regime. In summer, temperatures rise to 28°C, whereas in winter extremely low temperatures (around 1°C) prevail for several weeks. Nevertheless, rapid changes in temperature also can occur within a few hours. Chemically the lake is characterized by high alkalinity (7.5–14.6 meq l^{-1}) and conductivity (1150–2800 μS, 18°C), which also vary throughout the year.

Methods

The benthic community was studied from July 1990 to July 1991. Four stations were sampled regularly at intervals of two to five weeks (Fig. 1, Table 1). Three stations were situated along a transect in the north of the lake: Station A1 was near the reed belt at a distance of 10 m. A2 was 500 m from the reed belt, and A3 represented the open lake at a distance of 2 km to the nearest shore. The fourth station was in the Bay of Illmitz, 10 m from the reed belt, and represented the eastern part of the lake. On 22 and 23 January and on 3 July 1991, a transect in the Bay of Illmitz was sampled for a more detailed investigation of the horizontal distribution and sediment preferences of benthic invertebrates.

Chemical and grain size analyses were conducted on 22 and 23 January and on 17 September 1991. In addition to the northern transect A1–A3 and a number of stations in the Bay of Illmitz at various distances from the reed belt, two stations in the Bay of Rust were sampled. The first one (B1) was situated in the southern part of the bay 10 m from the nearest shore, whereas B2 was located at the edge of the reed belt (distance: 1 m from the reed) (Fig. 1).

Table 1. Sampling schedule for the regularly sampled stations. On sampling dates marked with an asterisk (*) a sieve with a mesh size of 250 μm was used. A plus (+) symbolizes dates on which the material was strained through 150 μm.

Sampling date	A1	A2	A3	C1
03.07.1990	*	*	*	
17.07.1990				*
26/29.07.1990	*	*	*	*
09/12.08.1990	*	*	*	+
04.09.1990	+	+	+	
11.09.1990				+
26.09.1990				+
10.10.1990	+	+	+	
22/25.01.1991		+	+	+
07.02.1991	+			
25.03.1991				+
06/08.04.1991	+	+	+	+
29/30.04.1991	+	+	+	+
14.05.1991				+
03/04.06.1991	+	+	+	+
02/03.07.1991	+	+	+	+

Zoobenthos was sampled using a Gilson-Corer (diameter 6 cm, area 28 cm^2). For chemical and grain size analyses three cores were taken at each sampling station; for animal analyses another five cores were taken. The uppermost 3 cm were analyzed for abiotic parameters. To investigate the vertical distribution of benthic invertebrates, sediment cores were divided into 3 cm sections. The sediment structure did not allow for a finer zonation except at station A1, where on a few sampling dates the core was divided into 1 cm sections.

Sediment was sieved through a 250 μm mesh during July and on the first date of August 1990. A mesh size of 150 μm was used for the remaining sampling periods (Table 1). Samples were preserved in 5% formaldehyde.

The percentage of total nitrogen N_{tot} and organic carbon C_{org} in the sediment was analyzed at the Biological Station Lunz by means of a LECO CHN 600 Analyzer. Total phosphorus P_{tot} was measured photometrically (720 nm) after addition of molybdenum-sulphuric acid-reagent to the sample.

Grain size analyses were conducted by wet sieving using mesh sizes between $-1\ \Phi$ (= 25 μm) and $5.32\ \Phi$ (= 2 mm). Φ units were introduced by Krumbein (1934) and are calculated as follows:

$$\Phi \text{ units} = -\log_2 d$$

(where d is the grain diameter [mm]).

Biomass of chironomids was estimated as follows: The length of a representative number of 3rd and 4th instars of a species was measured. The length of the first and, in the case of small speces, also the second instar was either measured directly or estimated assuming a mean length increase of 160% between subsequent instars (mean for species from Neusiedler See). The length of less common species was estimated according to the length of similarly sized species. The mean length of each instar was then used in a length-weight-regression taken from the literature to calculate a mean biomass. For Chironominae two regressions by Mackey (1977) were used: for small Chironominae and Tanytarsini the regression of *Dicrotendipes modestus* was applied, whereas the biomass of larger species such as *Chironomus* or *Polypedilum nubeculosum* was calculated with a regression originally ascertained for *Glyptotendipes pallens*. A regression for *Procladius bellus* by Sephton & Paterson (1986) was used for the tanypods. Direct and individual weighing of biomass was never carried out. Thus, seasonal changes in biomass within a single instar (especially the fourth instar) could not be detected, and the procedure described must be considered as a rough estimation only (see Wais, 1993).

Production of *Tanypus punctipennis* at station A1 was calculated from smoothed survivorship curves and growth curves by the increment-summation method (Rigler & Downing, 1984) for each cohort. The problems in constructing survivorship curves are discussed in Lindegaard (1992). Plante & Downing (1989) provided an empirically derived formula for calculating secondary production on the basis of mean annual biomass, individual body mass and ambient temperature. A comparative calculation of production by the increment-summation curve method and the formula of Plante & Downing *(loc. cit.)* revealed a negative difference of 13.9%. This may be due to bias in the calculation of biomass. It is also possible that the formula by Plante & Downing does not hold true in shallow lakes such as Neusiedler See with its extreme chemical and physical properties. Nevertheless, the formula was used for a rough calculation of secondary production of species other than *T. punctipennis* at station A1 and of all chironomids at stations A2, A3 and C1, where abundance was too small to calculate secondary production directly. This procedure is considered sufficient to provide "order-of-magnitude production estimates" (Plante & Downing, 1990).

The results of the chemical analyses were calculated as arithmetic means of the three cores. All figures of mean abundance or biomass were calculated after log-transformation of the data. 95% confidence limits are given in most cases. Annual mean abundance was calculated as the arithmetic mean of abundances on individual sampling dates.

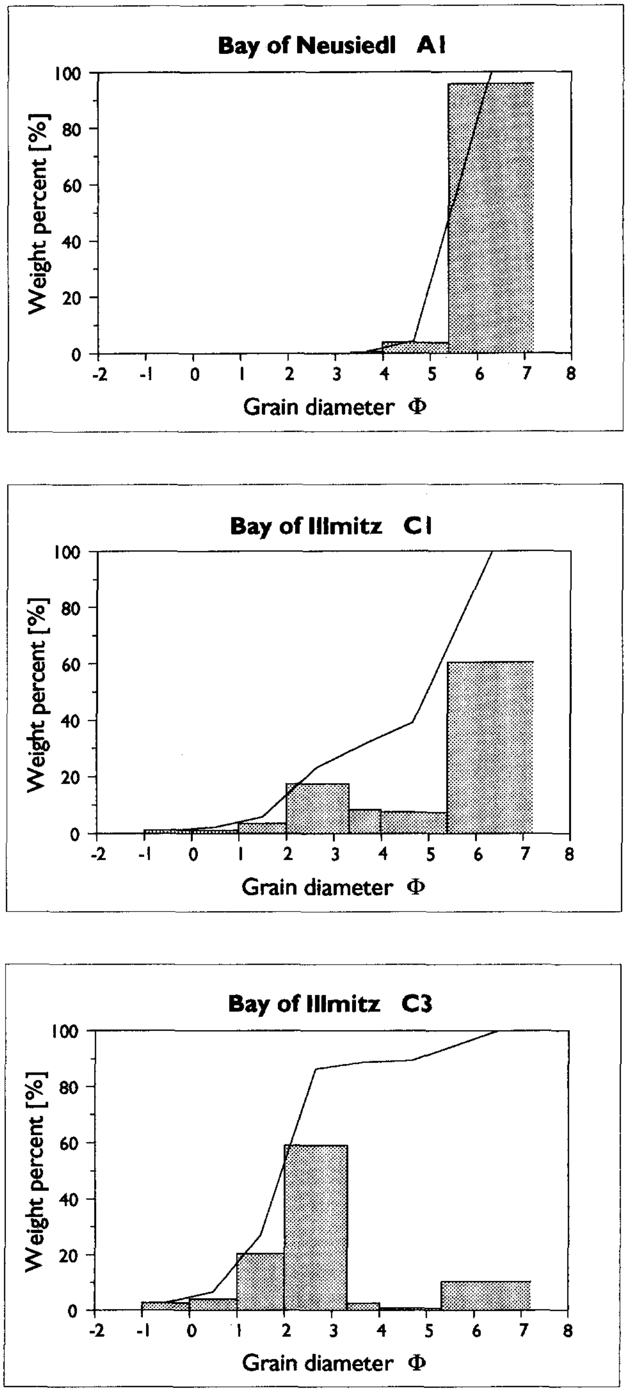

Fig. 2. Histogram (shaded bars) and cumulative plot (solid line) of the grain size distribution at three sampling stations in Neusiedler See. As the mesh size of the finest sieve used in the analysis was 25 μm, silt and clay could not be separated further. To visualize this in the histogram, the bar furthest to the right is drawn with an "open end" to higher Φ units.

Diversity was ascertained by the Shannon-Wiener function (Krebs, 1989) on the basis of natural logarithms. Confidence limits were calculated by the jackknife method (Krebs, 1989). The Spearman correlation coefficient was used as a measure of correlation between diversity and abundance of *Tanypus punctipennis*.

Results

Abiotic parameters

The results of the chemical and grain size analyses are summarized in Table 2. The sediment of Neusiedler See can be devided into three main types: The first type prevailed in the bays of Neusiedl (A1) and Rust (B1, B2) as well as in the sheltered parts of the Bay of Illmitz (e.g. C10, C4, C4*). The lake bottom at these stations was characterized by a very thick layer of soft mud with a grain size greater than 5–6 Φ units, i.e. smaller than 25 μm. This layer became thinner towards the open lake. Sediment at the sampling stations A2 and A3 (sediment type 2) was dominated by compact clay with a low water content. The third sediment type mainly consisted of sand with a grain diameter of predominantly 2–3.3 Φ units (100–250 μm) (Fig. 2). It was restricted to the eastern part of the lake (C1, C11, C3, C5, see Fig. 5B). However, also in the open area, "sand lenses" of variable size can occur within the otherwise homogenous sediment pattern. Thus, at station A3 two different types of grain size (compact clay *vs.* sandy sediment) could be distinguished (station A3a and A3b).

A comparison of the chemical data with the results from the grain size analysis revealed a significant negative correlation between total phosphorus and grain size. Sandy sediment showed low phosphorus content, whereas in muddy sediment and in compact clay (A2, A3) it was much higher.

A similar relationship could be found for total nitrogen and organic carbon. Highest C/N values occurred in muddy sediments, e.g. at station B2 in the Bay of Rust. However, the correlation between grain size and the two parameters was not as clear as for total phosphorus. Obviously a pronounced seasonal variation in chemical parameters obviated a clear relationship. Only when data from the two different sampling dates (January and July) were treated separately, was the correlation significant.

Species richness and composition

The macrobenthic community of Neusiedler See was dominated by crustaceans (17 spp.) and chironomids (16 spp.). Among other insect orders only Trichoptera, represented by a single species *(Ecnomus tenellus)*, occurred sporadically in the benthos. Oligochaeta (5 spp.) were of minor importance and molluscs were lacking.

The chironomids of the open water zone of Neusiedler See were dominated by Chironominae (12 spp.), followed by Tanypodinae (3 spp.) (Table 3). Only one single specimen of Orthocladiinae (a second instar, probably of *Cricotopus* sp.) could be found. Of the 16 species, four species, *viz. Ablabesmyia longistyla, Dicrotendipes nervosus, Parachironomus arcuatus* and *Paratanytarsus inopertus*, are common inhabitants of the periphyton of *Phragmites australis* or live on decomposed reed leaves within the reed belt. They cannot be considered as true sediment dwellers of the open water zone.

If we omit these epiphytic species as well as the unidentified orthoclad, there remain only 11 truly benthic chironomid species.

Abundance, biomass and production

The abundance of chironomids in Neusiedler See (Table 4) generally was low, especially at exposed sampling stations (A2, A3). Considering all sampling dates, only four species have been found in densities of more than 1000 ind m^{-2}. These are *Tanypus punctipennis, Procladius* cf. *choreus, Microchironomus tener* and *Cladotanytarsus* gr. *mancus*. The first two species dominated the benthos of Neusiedler See. Together they attained mean annual densities of 20,000 ind m^{-2}. On individual dates they accounted for more than 95% of total chironomid abundance (maximum: 54,000 ind m^{-2}).

Population dynamics and secondary production were examined in detail for *T. punctipennis* at station A1 (Fig. 3). This species displayed a complex trivoltine phenology with two winter cohorts. The first one began in August and overwintered mainly as third and fourth instar larvae. Emergence began as early as late autumn, but the major part of this cohort emerged in spring after ice-out. The second winter cohort began in late autumn, overwintered as second instar larvae and emerged in May and the beginning of June. In early summer the third cohort appeared and emerged in July and August. A clear distinction between the

Table 2. Results of the chemical and grain size analyses of various sediment types in Neusiedler See. Jan ... sampling date 1 January 1991, Sep ... sampling date 17 September 1991. A1–C11 ... sampling stations (see Figs. 1 and 5B). At station A3 two different types of grain sizes (A3a and A3b) could be distinguished (see text).

	N_{tot} [mg g^{-1}]		P_{tot} [mg g^{-1}]		C_{org} [mg g^{-1}]		C/N-ratio		Percent sand [%]
	Jan	Sep	Jan	Sep	Jan	Sep	Jan	Sep	Jan/Sep
A1	4.183	1.033	0.587	0.607	19.583	14.500	4.739	14.148	0.47
A2	4.203	0.700	0.623	0.470	30.967	8.233	7.457	7.024	12.48
A3 a/b	3.780	1.033	0.660	0.458	31.250	12.258	8.381	9.943	3.79/85.82
B1	4.000	2.133	0.697	0.663	31.733	13.200	7.700	6.265	2.43
B2	6.500		0.863		57.583		8.634		
C1	3.438	1.433	0.573	0.537	24.513	10.833	6.566	8.757	31.69
C2	5.350		0.470		26.310		5.195		
C3	5.867	0.817	0.267	0.280	13.250	2.550	2.341	5.768	88.88
C4	6.883	2.183	0.700	0.643	14.567	16.967	2.644	7.847	6.41
C4*		2.692		0.680		18.867		7.025	2.78
C5	3.067		0.220		3.933		1.268		
C10									4.42
C11		0.883		0.477		5.175		6.081	66.10

Table 3. Species list of chironomids in the open water zone of Neusiedler See. A1, A2, A3, B, C ... sampling stations (see Figs. 1 and 5B). Epiphytic species occasionally collected in the sediment are marked with an asterisk.

	A1	A2	A3	B	C
Tanypodinae					
Ablabesmyia longistyla Fittk.*	+		+		+
Procladius cf. *choreus* (Meig.)	+	+	+	+	+
Tanypus punctipennis (Meig.)	+	+	+	+	+
Orthocladiinae					
?*Cricotopus* sp.*					+
Chironominae – Chironomini					
Chironomus gr. *plumosus*				+	+
Cladopelma virescens (Meig.)	+			+	+
Cryptochironomus sp.	+		+	+	+
Cryptotendipes usmaensis (Pag.)	+				+
Dicrotendipes nervosus (Staeg.)*	+		+	+	+
Harnischia curtilamellata (Mall.)	+	+	+	+	
Microchironomus tener (Kieff.)	+	+	+	+	+
Parachironomus arcuatus (Goetgh.)*	+	+	+		+
Polypedilum nubeculosum (Meig.)				+	+
Chironominae – Tanytarsini					
Cladotanytarsus gr. *mancus*				+	+
Paratanytarsus inopertus (Walk.)*					+
Stempellina almi Brund.		+	+		+

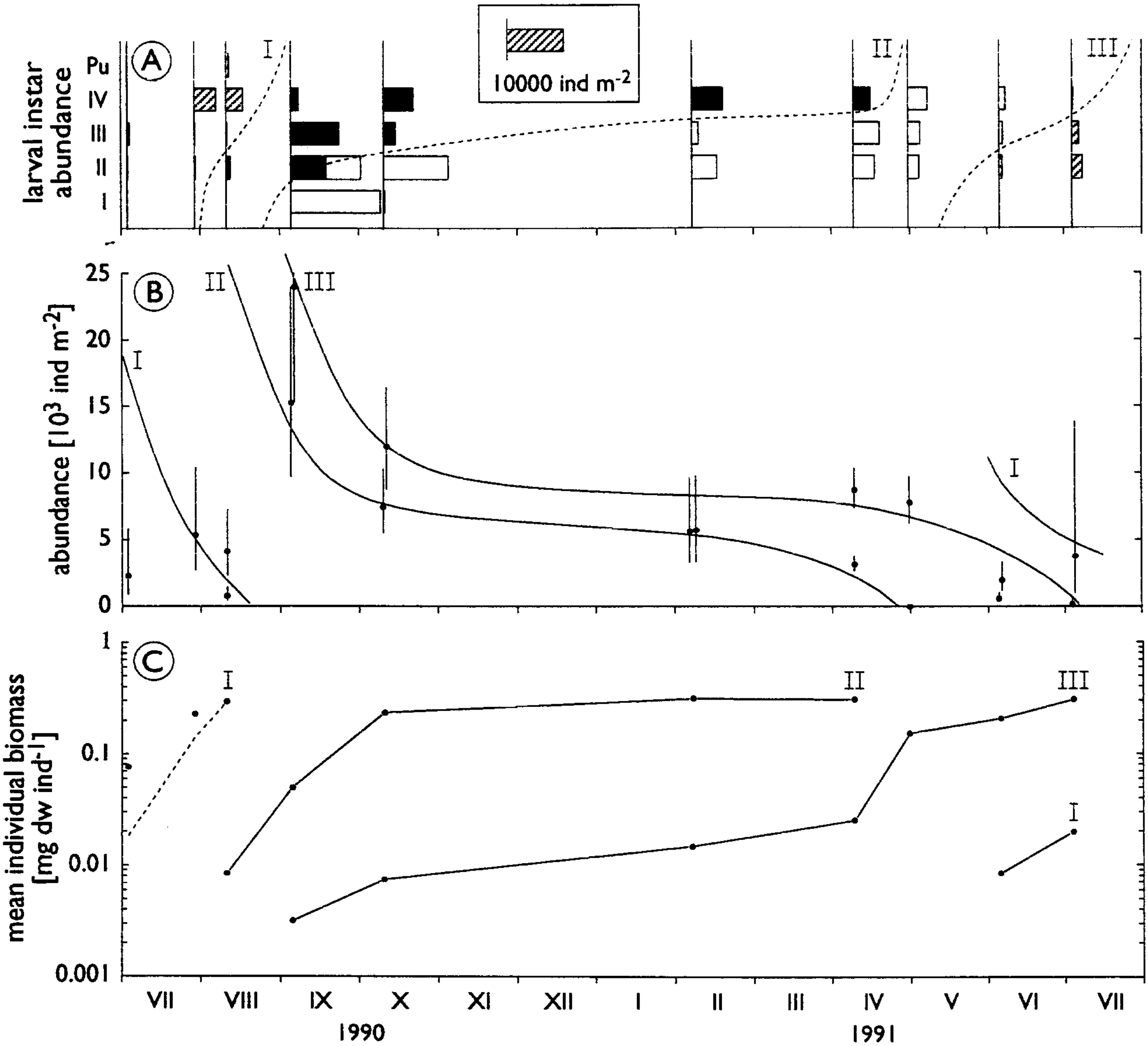

Fig. 3. (A) Life cycle, (B) survivorship curves and (C) growth curves of *Tanypus punctipennis* in the Bay of Neusiedl (sampling station A1). The broken lines in the uppermost diagram separate different generations (white, shaded and black bars). Vertical bars in the second diagram show 95% confidence limits. Emergence occurs in August 1990, March 1991 and June/July 1991.

three cohorts is not always possible (see Schiemer, 1979).

Secondary production of the different cohorts of *T. punctipennis* at station A1 varied between 1.59 g dw m^{-2} yr^{-1} and 2.59 g dw m^{-2} yr^{-1} (Table 5). Annual production was 5.79 g dw m^{-2} yr^{-1}. Cohort P/B ratios also varied, especially between the two winter cohorts. This is because the two winter cohorts overwintered as different larval instars. The high mean individual biomass of larvae in the first winter cohort resulted in a high mean cohort biomass (1.1 g dw m^{-2}) and thus a low P/B ratio. In contrast, the low mean biomass of the second winter cohort (0.25 g dw m^{-2}) was responsible for a high P/B ratio. Nevertheless, the annual P/B ratio of *T. punctipennis* lies within the range suggested by Banse & Mosher (1980).

Total chironomid production was highest in sheltered areas (station A1: 6.64 g dw m^{-2} yr^{-1}) and decreased towards the open lake (station A3: 0.55 g dw m^{-2} yr^{-1}) (Table 6). *T. punctipennis* was responsi-

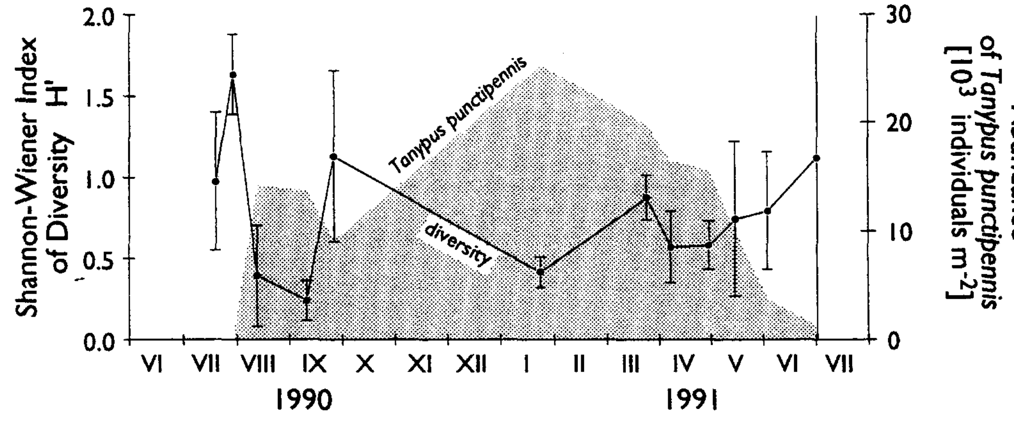

Fig. 4. Shannon-Wiener index of chironomid diversity at sampling station C1 (Bay of Illmitz) in relation to abundance of *Tanypus punctipennis*. Vertical bars indicate 95% confidence limits.

Table 4. Annual mean abundances [individuals m^{-2}] of the most frequent chironomid species in Neusiedler See in relation to other groups and total benthos abundance. Only sampling dates on which a mesh size of 150 μm was used are included.

	A1	A2	A3	C1
Oligochaeta	0	1	7	27
Ostracoda	2944	5793	9053	19692
Cladocera	22223	11004	3011	3735
Chironomidae	22352	6657	1921	15673
Procladius cf. *choreus*	5490	1489	925	657
Tanypus punctipennis	14430	3578	502	13109
Microchironomus tener	1321	670	41	332
Cladotanytarsus gr. *mancus*	0	0	0	385
Total benthos	48548	24507	16699	41119

Table 5. Biomass B [g dw m^{-2}] and production P [g dw m^{-2} yr^{-1}] of the cohorts of *T. punctipennis* in the Bay of Neusiedl (A1).

	B	P	P/B
Summer cohort	0.35	1.61	4.60
1st winter cohort	1.10	2.59	2.35
2nd winter cohort	0.25	1.59	6.24
Annual mean	1.13	5.79	5.13

ble for more than 80% of chironomid production near the reed belt. Combined production of the two tanypods, *Tanypus* and *Procladius*, was never less than 90% of total chironomid production.

Diversity

Diversity of the chironomid community of Neusiedler See was rather low (Table 7). The Shannon-Wiener index of diversity varied between 0.24 and 1.20. The annual median was 0.66 and 0.86 in the Bay of Illmitz (C1) and the Bay of Neusiedl (A1), respectively. In general, chironomid diversity was negatively correlated with *T. punctipennis* abundance ($\rho = -0.65$, $p = 0.0031$). The usually high densities of this species as well as low species richness resulted in low diversity values. Diversity increased and was >1 only when the abundance of *T. punctipennis* was low (e.g. in the open lake or at all stations in early summer) (Fig. 4).

Horizontal distribution

Benthic invertebrates of Neusiedler See showed a distinct horizontal distribution. Species richness and abundance were highest in muddy sediments near the reed belt, whereas species richness and individual numbers sharply declined towards the open lake (A1–A2–A3) and in the sandy sediment in the Bay of Illmitz (Table 4). It should be noted that the area near the reed belt was very small compared to the large extension of the open water zone.

Table 6. Annual mean biomass B [g dw m^{-2}] and annual production P [g dw m^{-2} yr^{-1}] of chironomids in Neusiedler See. All sampling dates (incl. those on which a mesh size of 250 μm was used) are taken into account.

	A1		A2		A3		C1	
	B	P	B	P	B	P	B	P
Tanypus punctipennis	1.13	5.79	0.29	1.73	0.01	0.08	0.45	2.47
Procladius cf. *choreus*	0.09	0.74	0.06	0.50	0.05	0.44	0.03	0.29
Other species	0.01	0.11	<0.01	0.02	<0.01	0.03	0.02	0.23
Chironomidae	1.23	6.64	0.35	2.25	0.05	0.55	0.50	2.99

Table 7. Diversity of Chironomidae at three sampling stations in Neusiedler See. Only data for which a mesh size of 150 μm was used are considered. H‘ ... Shannon-Wiener index of diversity, LC ... lower confidence limit (95%), UC ... upper confidence limit, min ... minimum, max ... maximum, med ... median. C1 is the mean of the two median sampling dates, thus no confidence limits are given. Diversity at station A3 was not calculated because abundances were too low.

	A1			A2			C1		
	H‘	LC	UC	H‘	LC	UC	H‘	LC	UC
Min	0.43	0.19	0.68	0.79	0.28	1.29	0.24	0.12	0.36
Med	0.86	0.75	0.97	1.00	0.81	1.19	0.66		
Max	1.03	0.93	1.13	1.20	1.02	1.39	1.13	0.60	1.65

The horizontal distribution of chironomids was studied in detail in the Bay of Illmitz (Fig. 5) and was similar to that at stations A1 to A3. Five groups could be distinguished:

(1) species dwelling exclusively near the reed belt in sediments with a thick soft mud layer:
Cladopelma virescens, Chironomus gr. *plumosus, Polypedilum nubeculosum*

(2) species dwelling predominantly near the reed belt, but also inhabiting areas with compact sediment:
Tanypus punctipennis

(3) species preferring compact sediment, but also inhabiting areas with soft mud:
Harnischia curtilamellata (mainly compact clay)
Microchironomus tener (mainly compact clay and sand)

(4) species dwelling exclusively on compact sediments:
Stempellina almi, Cladotanytarsus gr. *mancus* (sand)

(5) species without any clear horizontal distribution pattern, inhabiting all types of sediment:
Procladius cf. *choreus*

Vertical distribution in the sediment

Most species preferred the uppermost sediment layer and a penetration into the sediment was restricted to the soft mud areas near the reed belt. Only some chironomid species, such as *Chironomus* gr. *plumosus, Polypedilum nubeculosum* and *Tanypus punctipennis*, occurred in deeper sediment. A clear vertical distribution in the sediment was found only for the fourth instar larvae of *T. punctipennis*: During summer 1990 they were found in the uppermost 3 cm, whereas in winter under ice and in spring they preferred a depth of 3–6 cm. A detailed analysis in February 1991 revealed a peak between 3 and 5 cm below surface with a maximal depth of 12 cm.

Discussion

Neusiedler See is an extreme environment in several respects. It is alkaline, eutrophic and characterized by a highly variable temperature regime. Moreover, in wind-exposed areas in the central and eastern part of the lake continuous mixing disturbs the sediment. Inorganic solids as well as organic matter are eroded,

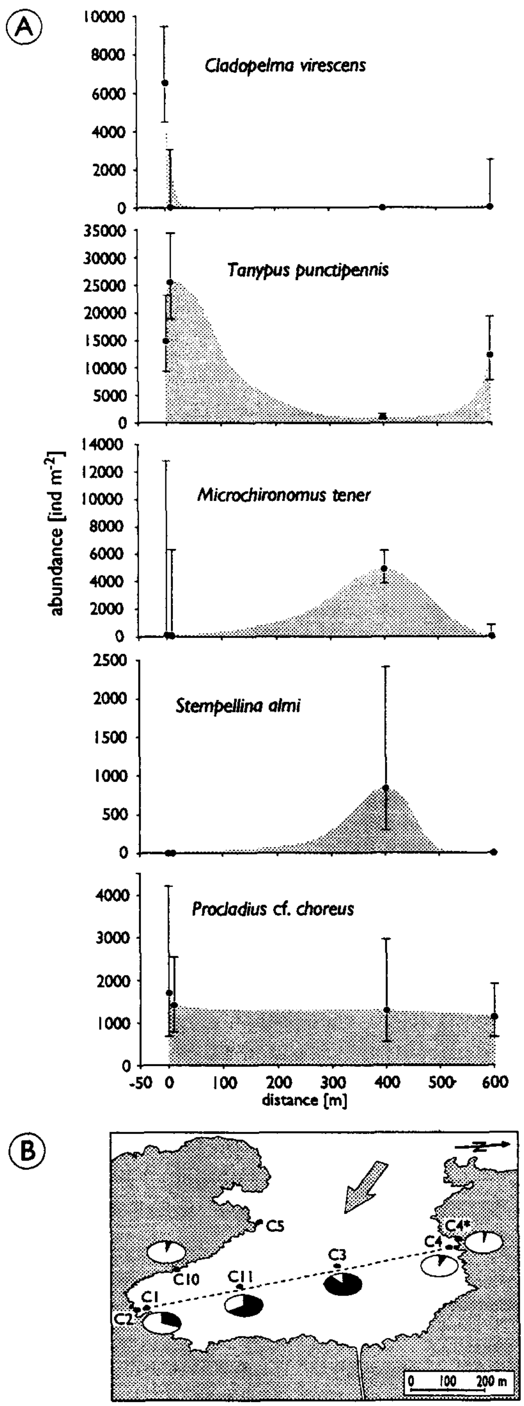

Fig. 5.

Fig. 5. (A) Horizontal distribution of five chironomid species along a transect of four sampling points (C2–C1–C3–C4) in the Bay of Illmitz on 22 and 23 January 1991. The abscissa gives the distance from the reed belt, beginning in the south-east of the bay. Vertical bars show 95% confidence limits. (B) Distribution of grain size in the Bay of Illmitz. Percentage of sand (Ø > 63μm) is shown in pie charts at various sampling points. Black area ... sand, white area ... silt and clay. The broken line indicates the transect from C2 to C4 along which the chironomid abundance (A) was investigated. The grey arrow in the upper part of the diagram shows the main wind direction (NW), which is of major importance for the distribution pattern of the sediment.

transported to the reed belt and deposited in sheltered areas (Jungwirth, 1979a; Preisinger, 1979). Epipelic algae and benthic bacteria are not able to live in the unstable open water zone (Khondker & Dokulil, 1988).

These dynamic conditions likely are the reason for the low number of species in the open water zone of Neusiedler See. Several taxa common in other eutrophic lakes are completely lacking (e.g. molluscs) or represented by only a few species in low densities (e.g. oligochaetes). Among the chironomids, species of the genus *Tanytarsus* are completely lacking in the open water zone. *Chironomus*, often dominant in comparable eutrophic lakes such as Lake Balaton (Dévai, 1988), Tjeukemeer (Beattie, 1982) or Federsee (Frank, 1982) was found only occasionally in low densities.

Obviously, few species can tolerate the chemical and physical stress within the lake. Most benthic invertebrates that can withstand the physical and chemical conditions in Neusiedler See are reported in the literature to be tolerant of organic pollution and oxygen deficiencies (Moller Pillot & Buskens, 1990).

The horizontal distribution pattern appears as a gradient from sheltered soft mud areas with high species richness and abundance to wind-exposed areas with compact sediment and low species richness and abundance (see also Schiemer, 1979). Comparable patterns of sediment distribution have been reported from other shallow lakes (Goulden, 1971; Maitland, 1979; Beattie, 1982). Several factors may influence invertebrate distribution in Neusiedler See. Small animals may be dislodged in the same way that fine inorganic material is eroded. Subsequent transport to areas sheltered from waves and currents could cause a concentration of invertebrates near the reed belt (Jungwirth, 1979b).

A more probable explanation, however, is invertebrate preferences for certain sediment types. The correlation of sediment and invertebrate distribution pattern in standing waters has been documented in numerous papers (McLachlan & Cantrell, 1976; McLachlan, 1976; Maitland, 1979; Jónasson & Lindegaard, 1979; Winnell & Jude, 1984; Winnell & White, 1986; Ferrington, 1992). In Neusiedler See most benthic invertebrates prefer muddy sediments that are rich in organic matter and high in calorific value. *Tanypus punctipennis*, for instance, clearly declines towards the open lake (Table 4) or the central part of the Bay of Illmitz (Fig. 5A). This distribution pattern mirrors the occurrence of epipelic algae, mainly unicellular diatoms (Schiemer, 1979), which are of major importance as a food resource (Titmus & Badcock, 1981). Other chironomids such as *Chironomus* gr. *plumosus* prefer thick layers of soft mud as a substrate for burrowing (McLachlan & Cantrell, 1976).

However, not all species in Neusiedler See live near the reed belt; some also inhabit wind-exposed areas. This may be due to an avoidance of the soft mud areas, where predation pressure by benthivorous fish is much higher than in the open water zone (Herzig *et al.*, 1994). The same is true of interspecific competition among invertebrates. Cantrell & McLachlan (1977) and Smit *et al.* (1992) discuss the possibility of competition as a reason for different distribution patterns of chironomid species. In addition to these direct biotic interactions, deoxygenation processes near the reed belt during night (Schiemer, 1979) may adversely affect benthic invertebrates.

In addition, some species may have a preference for the wind-exposed areas. *Cladotanytarsus* gr. *mancus* and *Stempellina almi* build tubes of fine sand grains and occur in Neusiedler See mainly on sandy sediment. A preference of *Cladotanytarsus* species for sandy sediments or even gravel has also been reported by several authors (Beattie, 1982; Winnell & Jude, 1984; Rae, 1985, 1987; Ten Winkel & Davids, 1987; Kornijow *et al.*, 1990; van de Bund & Davids, 1993). Some species of Chironomini such as *Microchironomus tener, Harnischia curtilamellata, Cryptochironomus* sp. or *Cryptotendipes usmaensis* have also been found mainly on compact sediment. All these species are members of the *Harnischia*-complex, members of which are known to live on the sediment surface. It is clear that compact sediment, where penetration and sinking is impossible, is preferred by these species.

Only one species, *viz. Procladius* cf. *choreus*, was found in high abundance at all sampling stations. Within the Bay of Illmitz (transect C2–C1–C3–C4) this species showed no sediment preference (Fig. 5A). In the north of Neusiedler See along the transect A1 to A3, the highest abundance of *P.* cf. *choreus* was near the reed belt. Although absolute densities of *P.* cf. *choreus* decreased towards the open lake, the relative proportion of this species, especially with respect to *T. punctipennis*, increased. This distribution pattern may be due to the feeding habits of *P.* cf. *choreus*. According to Schiemer (1979), *Procladius* is omnivorous in Neusiedler See, but at least the last two instars are predominantly carnivorous. However, Schiemer *(loc. cit.)* assumed that in the open lake area benthic food (animals or detritus) were too scarce to meet the energy demand of *Procladius* and that precipitating zooplankton play an important role as food for this chironomid species in Neusiedler See. The ability of feeding on a wide range of food items (detritus, algae, precipitating zooplankton) may be one reason why the distribution pattern of *P.* cf. *choreus* was neither clearly correlated with sediment structure nor with the distribution pattern of other benthic invertebrates.

Secondary production estimates of chironomids in standing waters vary widely. In a literature review, Lindegaard (1989) found the lowest chironomid production in Lake Krivoe and Lake Zelewtskoye with 0.10 g dw m^{-2} yr^{-1} (Alimov *et al.*, 1972; Winberg *et al.*, 1973) and the highest in a waste stabilization lagoon, where chironomid production was more than 160 g dw m^{-2} yr^{-1} (Kimerle & Anderson, 1971). In Neusiedler See production was 5–7 g dw m^{-2} yr^{-1} in sheltered bays near the reed belt, which is slightly below the average of the values listed in Lindegaard (1989). However, the open water zone of Neusiedler See revealed a production of 0.6 g dw m^{-2} yr^{-1} and thus clearly lies at the lower end of Lindegaard's production list. Only a few lakes had chironomid production estimates lower than in Neusiedler See.

The basic factor responsible for low zoobenthos production seems to be low primary production (Lindegaard, 1989). This is obvious in oligotrophic lakes with poor food conditions. However, several other factors also can be responsible for low production. These often cause some sort of physiological stress, which reduces growth and development. These stresses include e.g. low temperature (Lindegaard & Mæhl, 1992), oxygen deficiency (Cooper & Knight, 1985), salinity, or low pH (Mori & Jamamoto, 1975). Finally, continuous mixing and resuspension of sediment in shallow, wind-exposed lakes may cause direct physical stress or have an indirect influence by affecting food resources in the sediment. Jónasson & Lindegaard (1979) discussed this problem in detail for Lake Arresø and Lake Myvatn. Low secondary production has also been found in the shallow, wind-exposed lake

Memphremagog (Dermott *et al.*, 1977) and in the open water zone of Tjeukemeer (Beattie, 1982). Secondary production rates in these lakes were highest in the littoral zones, where wind effects are less severe or vegetation stabilizes the sediment.

In Neusiedler See both water chemistry and continuous mixing at wind-exposed sites are likely to have an influence on the distribution, abundance and production of benthic invertebrates. These two stress factors also may be responsible for the strong numerical dominance of chironomids within the zoobenthic community as well as the low invertebrate diversity (Lindegaard, 1989). However, further investigations similar to Schiemer (1979) will be necessary to examine microfaunal production in more detail.

An extrapolation of the results of the present study to the whole lake area should be avoided because of the large chemical and physical differences between the southern and northern areas of Neusiedler See.

Acknowledgements

I am much indebted to Dr A. Herzig for providing optimal working facilities at the Biological Station in Illmitz and for critically evaluating the manuscript. Many thanks are due to Mag. A. Wais for technical assistance in the field. I also wish to thank Dr G. Bretschko for chemical sediment analysis at the Biological Station in Lunz.

References

Alimov, A. F., V. V. Boullion, N. P. Finogenova, M. B. Ivanova, N. K. Kuzmitskaya, V. N. Nikulina, N. G. Ozeretskovskaya & T. V. Zharova, 1973. Biological productivity of Lakes Krivoe and Krugloe. In Z. Kajak & A. Hillbricht-Ilkowska (eds), Productivity Problems of Freshwater, Proceedings of the IBP-UNESCO Symposium, Warsaw: 39–56.

Banse, K. & S. Mosher, 1980. Adult body mass and annual production/biomass relationships of field populations. Ecol. Monogr. 50: 355–379.

Beattie, D. M., 1982. Distribution and production of the larval chironomid populations in Tjeukemeer. Hydrobiologia 95: 287–306.

Cantrell, M. A. & A. J. McLachlan, 1977. Competition and chironomid distribution patterns in a newly flooded lake. Oikos 29: 429–433.

Cooper, C. M. & L. A. Knight, Jr., 1985. Macrozoobenthos-sediment relationships in Ross Barnett Reservoir, Mississippi. Hydrobiologia 126: 193–197.

Dermott, R. M., J. Kalff, W. C. Leggett & J. Spence, 1977. Production of *Chironomus, Procladius* and *Chaoborus* at different levels of phytoplankton biomass in Lake Memphremagog Quebec-Vermont. J. Fish. Res. Bd Can. 34: 2001–2007.

Dévai, G., 1988. Emergence patterns of chironomids in Keszthely-basin of Lake Balaton (Hungary). Spixiana Suppl. 14: 201–211.

Ferrington, L. C., Jr., 1992. Habitat and sediment preferences of *Axarus festivus* larvae. Neth. J. aquat. Ecol. 26: 347–354.

Frank, C., 1982. Ecology, production and anaerobic metabolism of *Chironomus plumosus* L. larvae in a shallow lake. I. Ecology and production. Arch. Hydrobiol. 94: 460–491.

Goulden, C. E., 1971. Environmental control of the abundance and distribution of the chydorid Cladocera. Limnol. Oceanogr. 16: 320–331.

Herzig, A., E. Mikschi, B. Auer, A. Hain, A. Wais & G. Wolfram, 1994. Fischbiologische Untersuchung des Neusiedler See. BFB-Bericht 82: 1–125.

Jónasson, P. M. & C. Lindegaard, 1979. Zoobenthos and its contribution to the metabolism of shallow lakes. Arch. Hydrobiol. Beih. (Ergebn. Limnol.) 13: 162–180.

Jungwirth, M., 1979a. The superficial sediments: their characterization and distribution. In H. Löffler (ed.), Neusiedlersee: The Limnology of a Shallow Lake in Central Europe. Dr W. Junk Publishers, The Hague: 139–143.

Jungwirth, M., 1979b. *Limnocythere inopinata* (Baird) (Cytheridae, Ostracoda): its distribution pattern and relation to the superficial sediments of Neusiedlersee. In H. Löffler (ed.), Neusiedlersee: The Limnology of a Shallow Lake in Central Europe. Dr W. Junk Publishers, The Hague: 385–388.

Khondker, M. & M. Dokulil, 1988. Seasonality, biomass and primary productivity of epipelic algae in a shallow lake (Neusiedlersee, Austria). Acta hydrochim. hydrobiol. 16: 499–515.

Kimerle, R. A. & N. H. Anderson, 1971. Production and bioenergetic role of the midge *Glyptotendipes barbipes* (Staeger) in a waste stabilization lagoon. Limnol. Oceanogr. 16: 646–659.

Kornijów, R., R. D. Gulati & E. van Donk, 1990. Hydrophyte-macroinvertebrate interactions in Zwemlust, a lake undergoing biomanipulation. Hydrobiologia 200/201 (Dev. Hydrobiol. 61): 467–474.

Krebs, C. J., 1989. Ecological Methodology. Harper & Row, N.Y., 654 pp.

Lindegaard, C., 1989. A review of secondary production of zoobenthos in freshwater ecosystems with special reference to Chironomidae (Diptera). In G. Devai (ed.), Advances in Chironomidology. Proceedings of the Xth international symposium on Chironomidae. Acata biol. Debr. Oecol. Hung. 3: 231–240.

Lindegaard, C., 1992. Zoobenthos ecology of Thingvallavatn: vertical distribution abundance, population dynamics and production. Oikos 64: 257–304.

Lindegaard, C. & P. Mæhl, 1992. Abundance, population dynamics and production of Chironomidae (Diptera) in an ultraoligotrophic lake in South Greenland. Neth. J. aquat. Ecol. 26: 297–308.

Löffler, H., 1979. Neusiedlersee, The Limnology of a Shallow Lake in Central Europe. Monogr. Biol. 37: 543 pp.

Mackey, A. P., 1977. Growth and development of larval Chironomidae. Oikos 28: 270–275.

Maitland, P. S., 1979. The distribution of zoobenthos and sediments in Loch Leven, Kinross, Scotland. Arch. Hydrobiol. 85: 98–125.

McLachlan, A. J., 1976. Factors restricting the range of *Glyptotendipes paripes* Edwards (Diptera: Chironomidae) in a bog lake. J. anim. Ecol. 45: 105–113.

McLachlan, A. J. & M. A. Cantrell, 1976. Sediment development and its influence on the distribution and tube structure of *Chironomous plumosus* L. (Chironomidae, Diptera) in a new impoundment. Freshwat. Biol. 6: 437–443.

Moller Pillot, H. K. M. & R. F. M. Buskens, 1990. De larven der Nederlandse Chironomidae (Diptera). Deel C: Autoekologie en verspreiding. Nederlandse Faunistische Mededelingen, 1C: 1–85.

Mori, S. & G. Yamamoto (eds), 1975. Concluding discussion on productivity of communities in Japanese inland water communities, Productivity of communities in Japanese inland waters. JIBP Synthesis 10: 379–419.

Plante, C. & J. A. Downing, 1989. Production of freshwater invertebrate populations in lakes. Can. J. Fish. aquat. Sci. 46: 1489–1498.

Plante, C. & J. A. Downing, 1990. Empirical evidence for differences among methods for calculating secondary production. J. N. Am. benthol. Soc. 9: 9–16.

Preisinger, A., 1979. Sediments. In H. Löffler (ed.), Neusiedlersee: The Limnology of a Shallow Lake in Central Europe. Dr W. Junk Publishers, The Hague: 131–138.

Rae, J. G., 1985. A multivariate study of resource partitioning in soft bottom lotic Chironomidae. Hydrobiologia 126: 275–285.

Rae, J. G., 1987. The effects of flooding and sediments on the structure of a stream midge assemblage. Hydrobiologia 144: 3–10.

Rigler, F. H. & J. A. Downing, 1984. The calculation of secondary productivity. In J. A. Downing & F. H. Rigler (eds), A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook 17: 19–58.

Schiemer, F., 1978a. Verteilung und Systematik der freilebenden Nematoden des Neusiedler See. Hydrobiologia 58: 167–194.

Schiemer, F., 1978b. A contribution to the phenology of chironomids in Neusiedlersee. Acta Univ. Carol. Biologica 1978: 217–226.

Schiemer, F., 1979. The benthic community of the open lake. In H. Löffler (ed.), Neusiedlersee: The Limnology of a Shallow Lake in Central Europe. Dr W. Junk Publishers, The Hague: 337–384.

Schiemer, F., H. Löffler & H. Dollfuss, 1969. The benthic communities of Neusiedlersee (Austria). Verh. int. Ver. Limnol. 17: 201–208.

Sephton, T. W. & C. G. Paterson, 1986. Production of the chironomid *Procladius bellus* in an annual drawdown reservoir. Freshwat. Biol. 16: 721–733.

Smit, H., F. Heinis, R. Bijkerk & F. Kerkum, 1992. *Lipiniella arenicola* (Chironomidae) compared with *Chironomus muratensis* and *Ch. nudiventris*: Distribution patterns related to depth and sediment characteristics, diet, and behavioural response to reduced oxygen concentrations. Neth. J. aquat. Ecol. 26: 431–440.

Ten Winkel, E. H. & C. Davids, 1987. Population dynamic aspects of chironomid larvae of the littoral zone of Lake Maarsseveen I. Hydrobiol. Bull. 21: 81–94.

Titmus, G. & R. M. Badcock, 1981. Distribution and feeding of larval Chironomidae in a gravel-pit lake. Freshwat. Biol. 11: 263–272.

Van de Bund, W. J. & C. Davids, 1993. Complex relations between freshwater macro- and meiobenthos: interactions between *Chironomus riparius* and *Chydorus piger*. Freshwat. Biol. 29: 1–6.

Wais, A., 1993. Ernährungsbiologie des Brachsen (*Abramis brama* (L.)) im Neusiedler See. unpubl. Dipl. Univ. Wien, 69 pp.

Winberg, G. G., A. F. Alimov, V. V. Boullion, M. B. Ivanova, E. V. Korobtzova, N. K. Kuzmitskaya, V. N. Nikulina, N. P. Finogenova & M. V. Fursenko, 1973. Biological productivity of two subarctic lakes. Freshwat. Biol. 3: 177–197.

Winnell, M. H. & D. J. Jude, 1984. Associations among Chironomidae and sandy substrates in nearshore Lake Michigan. Can. J. Fish. aquat. Sci. 41: 174–179.

Winnell, M. H. & D. S. White, 1986. The distribution of *Heterotrissocladius oliveri* Sæther (Diptera: Chironomidae) in lake Michigan. Hydrobiologia 131: 205–214.

Wolfram, G., 1993. Untersuchung der benthischen Lebensgemeinschaft des Neusiedler Sees. unpubl. Dipl. Univ. Wien, 99 pp.

Appendix. The chironomids of the reed belt. List of species found as larvae on periphyton of submerged macrophytes (*Potamogeton pectinatus, Myriophyllum spicatum*) and *Phragmites australis* or as pupal exuviae in channels within the reed belt.

Tanypodinae

Ablabesmyia longistyla Fittk.
Ablabesmyia phatta (Egg.)
Monopelopia tenuicalcar (Kieff.)
Procladius choreus (Meig.)
Tanypus punctipennis (Meig.)
Xenopelopia cf. *falcigera* (Kieff.)

Orthocladiinae

Acricotopus lucens (Zett.)
Corynoneura lacustris Edw.
Cricotopus (s. str.) *flavocinctus* (Kieff.)
Cricotopus (s. str.) *bicinctus* (Meig.)
Cricotopus (s. str.) sp. 3
Cricotopus (Isocladius) intersectus (Staeg.)
Cricotopus (Isocladius) sylvestris (Fabr.)
Hydrobaenus lugubris Fries
Limnophyes pumilio (Holmgr.)
Limnophyes asquamatus Andersen
Nanocladius bicolor (Zett.)
Psectrocladius (s. str.) *barbimanus* (Edw.)
Psectrocladius (s. str.) *limbatellus* (Holmgr.)
Psectrocladius (s. str.) *sordidellus/ventricosus*
Pseudosmittia Pe 2 Langton 1991

Chironominae – Chironomini

Chironomus spp.
Cladopelma virescens (Meig.)
Cryptochironomus obreptans (Walk.)
Cryptochironomus redekei (Krus.)
Cryptotendipes usmaensis (Pag.)
Dicrotendipes nervosus (Staeg.)
Endochironomus albipennis (Meig.)
Glyptotendipes ? glaucus sensu Michailova
Glyptotendipes gripekoveni (Kieff.)
Glyptotendipes imbecillis (Walk.)
Glyptotendipes pallens (Meig.)
Glyptotendipes salinus Michailova
Harnischia curtilamellata (Mall.)
Microchironomus tener (Kieff.)
Parachironomus arcuatus (Goetgh.)
Polypedilum (s. str.) *nubeculosum* (Meig.)
Polypedilum (Pentapedilum) sordens (v.d. Wulp)
Xenochironomus xenolabis Kieff.

Chironominae – Tanytarsini

Cladotanytarsus atridorsum Kieff.
Cladotanytarsus lepidocalcar Krüg.
Cladotanytarsus sp. 3
Paratanytarsus inopertus (Walk.)
Paratanytarsus cf. *intricatus* (Goetgh.)
Stempellina almi Brund.
Tanytarsus mendax Kieff.
Tanytarsus usmaensis Pag.
Tanytarsus verralli Goetgh.