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Limnol. Oceanogr., 46(3), 2001, 689–692
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Langmuir circulations disturb the low-oxygen refuge of phantom midge larvae

Abstract—The previously unknown effects of wind-induced Langmuir circulations on the distribution of phantom midge larvae (*Chaoborus flavicans*) were studied by echosounding. The study was carried out in the eutrophic Lake Hiidenvesi, where chaoborids use a metalimnetic oxygen minimum as a daytime refuge against fish predation. At a wind velocity of 8–9 m s⁻¹, the upwelling water circulations snatched clouds of chaoborids from the metalimnion (12–15 m depth) to the more oxygenated epilimnion. The average density of *C. flavicans* in the clouds was 790 ind. m⁻², whereas, elsewhere in the epilimnion, it was 380 ind. m⁻². Planktivorous fish (smelt *Osmerus eperlanus*) were actively aggregated in the upwellings. When the wind velocity decreased to 3 m s⁻¹, chaoborids disappeared from the epilimnion. The results suggest that Langmuir circulations may affect the abundance of chaoborids by disturbing their low-oxygen refuges.

Langmuir circulations, which are wind-induced vertical motions of water, are common in large water bodies at wind velocities above 2–3 m s⁻¹ (Langmuir 1938; Barstow 1983). They are often marked by streaks of surface materials such as foam or tree leaves oriented parallel to the wind (Barstow 1983). Beneath the streaks the water has a downward movement, whereas between streaks there is upwelling (George and Edwards 1973). Algae and zooplankton are often concentrated into patches between the streaks (Reynolds and Walby 1975; Barstow 1983; Kingsfjord et al. 1991). Langmuir circulations may also increase the predation pressure on zooplankton, since fish actively aggregate in the areas of high prey densities (McNaught and Hasler 1961; Kingsfjord et al. 1991).

In spite of the wide literature on Langmuir circulations, their effects on the distribution of pelagic invertebrate predators have never been studied. However, invertebrate predators are important regulators of zooplankton communities (Lane 1978; Brabrand et al. 1986; Lair 1990) and have contributed in the failure of biomanipulation trials aiming to enhance the filtration capacity of zooplankton through reduction of planktivorous fish (Benndorf 1995; Wissel and Benndorf 1998). In the present article, we study the effects of Langmuir circulations on the distribution of phantom midge larvae (Diptera, Chaoboridae) and on the predator-prey interactions between chaoborids and planktivorous fish.

Chaoborids form high biomasses in many eutrophic lakes. They are known as voracious predators on small cladocerans and copepods and may substantially regulate zooplankton communities (Vanni 1988; Lair 1990). Chaoborids can co-exist in relatively high densities with fish if they can find refuges against predation. They tend to spend the hours of daylight in the hypolimnion or burrowed into the sediment

and migrate during the darkness into the epilimnion to forage on zooplankton (Malueg and Hasler 1966; Parma 1971; Sæther 1997). In Lake Hiidenvesi (southwestern Finland, area 30.3 km²), *Chaoborus flavicans* (Meigen) exists in densities up to 10,000 ind. m⁻² (Horppila et al. 2000). The majority of the population stays in the metalimnion and hypolimnion during the daytime, thus decreasing predation threat by smelt (*Osmerus eperlanus* L.), which is the dominant planktivorous fish species in the area. However, occasionally even during the daytime, considerable quantities of chaoborids can be captured by net hauls taken from the upper 10 m. In order to find out the possible role of water currents behind this phenomenon, we carried out echosounding trials. Here we present data from 7–8 October 1999, when, because of variable wind velocities, the effects of fluctuating water circulations could be detected.

Methods—Water temperature and the concentration of dissolved oxygen were measured with a YSI meter. Echosoundings were conducted in the deepest area of the lake (maximum depth 33 m) with a SIMRAD EY-500 echosounder that was equipped with a split-beam transducer 120–7F (operating frequency 120 kHz and beam opening angle 7° at –3 dB level). Usually, to minimize the instability caused by wave action, echosounding is carried out parallel to the

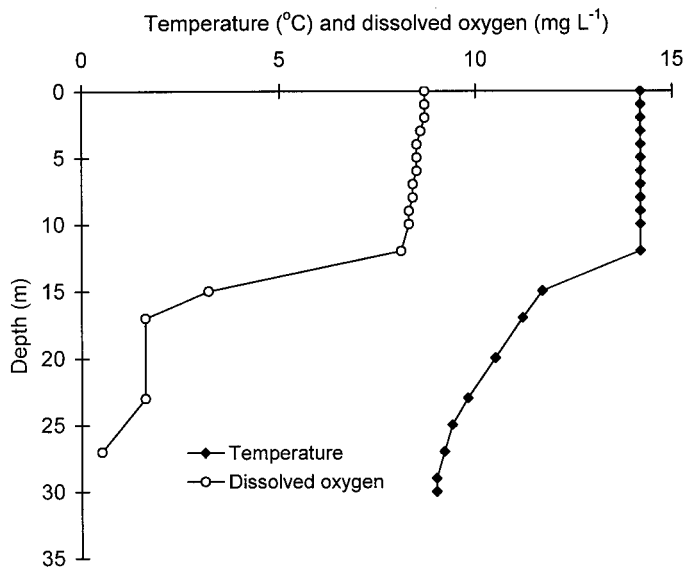


Fig. 1. Vertical profile of water temperature and concentration of dissolved oxygen in Lake Hiidenvesi on 7 October at 1800 h (water depth 33 m).

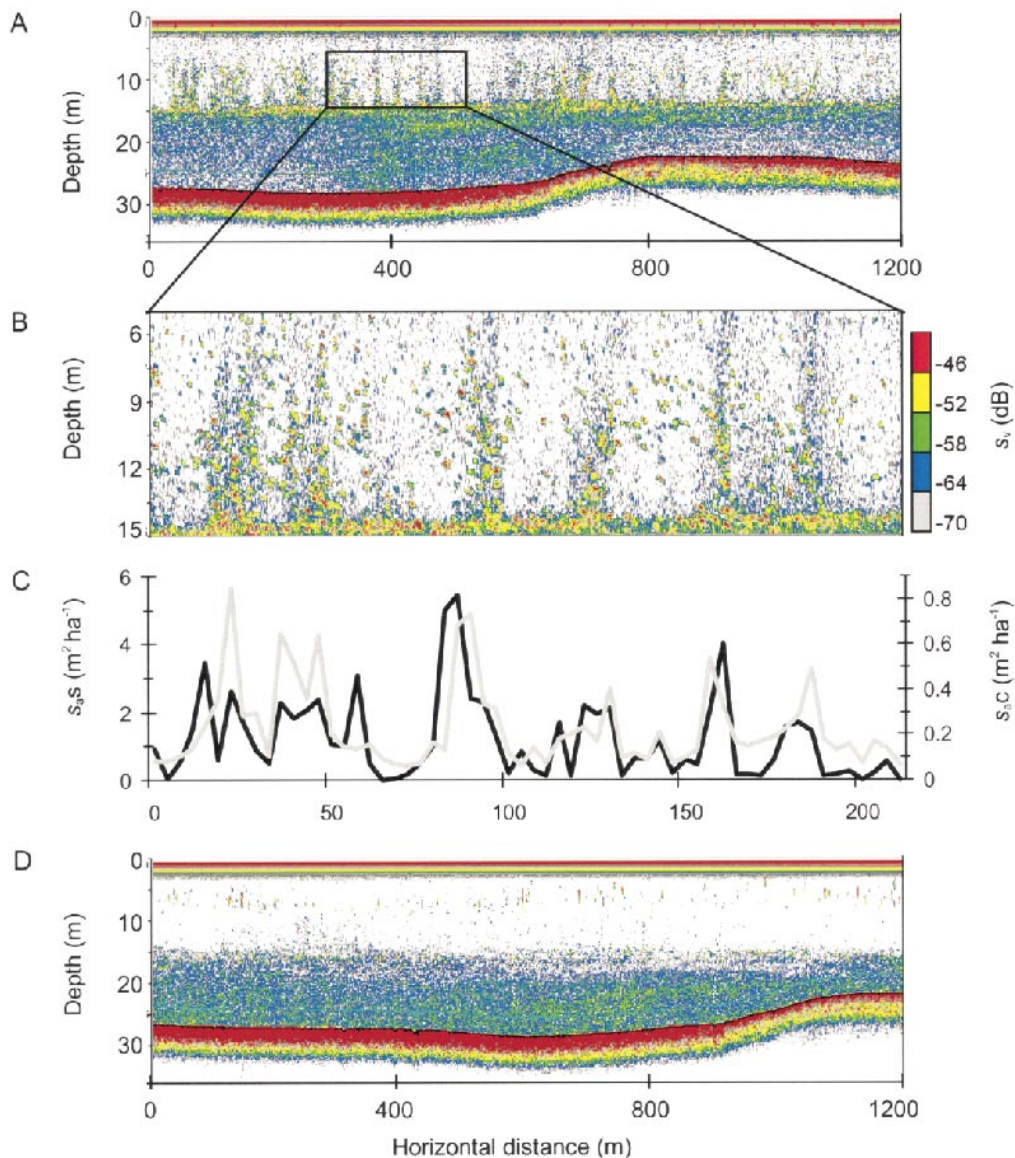


Fig. 2. Echograms and their analysis from the study transect in Lake Hiidenvesi on 7 October 1999 at 2030 h, when wind velocity was 9 m s^{-1} . The colors represent different dB values of the volume backscattering strength (s_v)—i.e., the echo integral from a small volume of water. (A) Echogram from the whole study transect (horizontal distance 1,200 m). The majority of the *C. flavicans* population is situated below 14 m depth, the highest density (yellow) taking place in the 14–15 m layer in the metalimnion. The upwelling clouds of *C. flavicans* in the epilimnion can be clearly detected. (B) A magnification (horizontal distance 250 m) showing that smelts (separate large spots) are concentrated in the upwelling clouds and at the edge of the *C. flavicans* population. (C) Echo integrals ($s_a s$, $\text{m}^2 \text{ ha}^{-1}$) from smelts (black) and from *C. flavicans* (gray) calculated in 4-m horizontal sections (depth 5–13 m) confirming that the peaks of both integrals took place at the same locations. (B) and (C) present the same section of the study transect. (D) Echogram from the study transect on 8 October 1999 at 1215 h, (horizontal distance 1,200 m) when wind velocity was 3 m s^{-1} .

wind. In this study, however, to detect Langmuir circulations, we echosounded perpendicular to the wind. The data were analyzed with EP 500 software with time-varied gain $20 \log R$. At first, the echo integral (area backscattering coefficient, s_a) from smelts ($s_a s$) and from *Chaoborus* ($s_a c$) were computed in sections of 10 pulses ($\sim 4 \text{ m}$) with the method presented by Eckmann (1998), in which the data are analyzed

with several integration thresholds. The relationship between $s_a s$ and $s_a c$ was studied with Spearman rank correlation analysis. Then the $s_a s$ values in the upwelling clouds of *Chaoborus* and in areas between the clouds were computed with the integration threshold of -60 dB . This threshold value was chosen because it gives equal $s_a s$ values, compared with Eckmann's method. The $s_a c$ values in the clouds and in areas

between them were computed by subtracting the s_{as} value from the total integral (threshold = -100 dB). The smelt density in each section was computed by dividing the s_{as} value of section with the mean backscattering cross-section (σ_{bs}) of single-target echoes in the whole transect (horizontal distance, 1,200 m). The *Chaoborus* density was calculated by use of a regression between *Chaoborus* counts from net hauls (unpubl. data) and echo integral values (Eckmann 1998). Confidence limits were calculated on the basis of Poisson distribution for smelt density (Jolly and Hampton 1990) and normal distribution for chaoborids.

Results and discussion—The thermocline was situated in 12–15 m depth, where the water temperature decreased from 14 to 11°C (Fig. 1). The concentration of dissolved oxygen was 8–9 mg L⁻¹ in the epilimnion but <3 mg L⁻¹ from the 15 m depth downward (Fig. 1). Echosounding was started on 7 October at 1800 h (1.5 h before sunset). The wind was blowing from the southwest (open fetch 3 km) with a velocity of 7–8 m s⁻¹. A dense swarm of *C. flavicans* from 14 m depth to the bottom was observed, the density averaging 2,000 ind. m⁻².

Between the 14 m depth and the surface, upwelling clouds of *C. flavicans* could be detected. During the evening, the wind velocity increased to 8–9 m s⁻¹, and the frequency of the upwelling clouds increased. At 2030 h, the clouds were situated in average 30 m from each other and reached the uppermost 5 m layer (Fig. 2 A,B). The highest *C. flavicans* density (yellow) was situated at 15 m depth (Fig. 2A). The average density of *C. flavicans* in the clouds was 790 ind. m⁻² (95% confidence interval 690–880 ind. m⁻²), whereas, elsewhere in the epilimnion, it was 380 ind. m⁻² (95% confidence interval 300–470 ind. m⁻²). In the center parts of the clouds, the density frequently exceeded 2,000 ind. m⁻². Smelts (separate large spots) were aggregated in the upwelling clouds and at the edge of the *C. flavicans* population. When the echo integrals from fish and those from *C. flavicans* were calculated in short (4 m) sections, it was found that the peaks of both integrals took place almost exactly at the same locations (Fig. 2C). The densities of smelts and *C. flavicans* were strongly positively correlated (Spearman rank correlation coefficient = 0.72, $P < 0.001$, $n = 324$). In the upwelling areas, the average smelt density was 19,000 ind. ha⁻¹ (95% confidence interval 12,000–27,800 ind. ha⁻¹), whereas between them it was 7,400 ind. ha⁻¹ (95% confidence interval 4,700–10,800 ind. ha⁻¹).

During the following night, the wind velocity decreased to 5–6 m s⁻¹, and the upwelling clouds of *C. flavicans* gradually disappeared. By noon on 8 October, the wind velocity had decreased to 3 m s⁻¹, and the clouds could no longer be detected (Fig. 2D). The density of *C. flavicans* in the epilimnion was undetectable with the echosounder, and the population was concentrated from the 14 m depth downward. Smelt inhabited the uppermost 10 m layer.

The occurrence of Langmuir circulations in relation to wind speed was in accordance with earlier observations (Langmuir 1938; Scott et al. 1969): circulations ceased when the wind velocity decreased below 3 m s⁻¹. The velocity of the upwelling currents often exceeds 1 cm s⁻¹ (Langmuir 1938). Since the swimming speed of chaoborids remains

clearly below this value (Franke 1987), the aggregations of *C. flavicans* were obviously due to passive gathering. Active diel vertical migration was not an important factor behind the observed phenomenon, since the upwelling clouds occurred in daylight as well as during the night. In Lake Hiidenvesi, active migrations by *C. flavicans* take place during high summer but usually cease during September (Horppila et al. 2000 and unpubl. data).

The majority of the *C. flavicans* population inhabited the 14–16 m depth, a layer having a steep decreasing oxygen gradient (Figs. 1, 2), thus avoiding predation by fish, the downward migrations of which are restricted by oxygen concentrations of ~3 mg L⁻¹ (Wright and Shapiro 1990). Obviously, in Lake Hiidenvesi, as well as in many other lakes, chaoborids use low oxygen concentrations as a refuge against fish predation (Saunders and Lewis 1983; Hanazato 1992; Horppila et al. 2000). Our results demonstrated, however, that Langmuir circulations throw parts of the population to upper, more-oxygenated water layers, where they are hunted by fish. In the present study, approximately one fifth of the limnetic *C. flavicans* population was snatched from the low-oxygen refuge by the circulations. The implications of the phenomenon on the *Chaoborus* population depend on the frequency and timing of the circulations. During May–October 1999, the wind velocity exceeded 3 m s⁻¹ in 48% of the wind recordings, suggesting that Langmuir circulations are a frequent phenomenon in Lake Hiidenvesi and thus forming an important avenue of future research.

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Acknowledgments

We thank Jyrki Lappalainen and Risto Lignell for helpful comments on the manuscript. The study was financially supported by the University of Helsinki.

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Received: 10 August 2000

Amended: 4 December 2000

Accepted: 21 December 2000

Rapid estimation of in situ growth rates of *Caridina nilotica* (Crustacea: Decapoda) in Lake Victoria: Description and pilot application of a simple, field-compatible technique

Abstract—A simple rapid approach to estimating in situ growth rates of *Caridina nilotica* (Roux), a small shrimp that plays a pivotal role in Lake Victoria's food web, is described. The approach, potentially applicable to many arthropods, is based on moulting intervals (MI) and per moult size increments (PMI) determined during brief experimental confinements. Physiological justification of its reliability as a measure of in situ rates is given. *Caridina* moults at night. Feral animals collected shortly (≤ 2 h) before dusk were sorted into one of five arbitrary size classes and held around 27°C overnight without food. MI, the inverse proportion of a batch moulting overnight, increased from 2 d in small shrimps (carapace length [CL] ≤ 1.8 mm) to >9 d in larger animals (CL ≥ 4.3 mm)—a value comparable to egg development time (10.3 d) at the corresponding temperature. PMI was measured from differences in CL of postecdysal shrimps (CL_{*i*+1}) and corresponding cast exuviae (CL_{*i*}). In absolute terms, PMI, surprisingly, was constant (0.284 ± 0.027 mm moult⁻¹) over the size range of shrimps tested, although relative growth (PMI as a percentage of CL_{*i*}) declined with size. Growth trajectories modeled with regressions fitted to the data (MI = $1.573 \times \text{CL}_i^{0.999}$ and CL_{*i*+1} = $0.284 + 0.977 \times \text{CL}_i$) show that *C. nilotica* grows significantly faster (by at least 20%) in L. Victoria than previously estimated (Ignatow et al.), with corresponding implications to other evaluations of lake productivity. Prospective refinements and future uses for this simple technique are outlined.

Caridina nilotica (Roux) is a small decapod shrimp (carapace length up to 7 mm and dry weight up to 50 mg; Hart 1980, 1981) that is widely distributed in African inland waters. It is a dominant macroinvertebrate in tropical L. Victoria, where it abounds in deep open offshore waters, in inshore bays, and in littoral margins (Fryer 1960; Branstrator et al. 1996; Lehman et al. 1996). Functioning primarily as a benthic detritivore (Fryer 1960), it replaced the detritivorous haplochromines of L. Victoria following their decimation by introduced Nile perch—*Lates niloticus* (Ligtvoet and Witte 1991; Goldschmidt et al. 1993). However, *C. nilotica* is additionally recognized as a pelagic component in this and other African great lakes (Lehman 1996). Recent studies indicate that it constitutes up to 20% of zooplankton standing stock in deep offshore waters of L. Victoria (Lehman et al. 1996; Ignatow et al. 1996).

Caridina nilotica plays a key role in the contemporary lake's food web. It is a dominant food item for *L. niloticus*, L. Victoria's major vertebrate predator (Ogari and Dadzie 1988; Ligtvoet and Witte 1991; Hughes 1992; Mkumbo and Ligtvoet 1992; Goldschmidt et al. 1993). And it presumably serves as a major trophic intermediary between decomposing mats of the prolific invasive water hyacinth, *Eichhornia crassipes* (Twongo 1996), and other secondary producers. Despite this functional significance, its population dynamics