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Factors Affecting Population Fluctuations of the Glacial Relict Amphipod *Monoporeia affinis* (Lindström) in Sweden's Largest Lakes

Factors affecting long-term (1982–2000) population densities of the glacial relict amphipod *Monoporeia affinis* were studied in Sweden's three largest lakes. *Monoporeia* showed large population fluctuations in all three lakes, with conspicuous peaks in density occurring in Lakes Vänern and Mälaren. In Lake Vänern, amphipod densities showed highly significant relationships with spring maximum diatom biovolume at a 1-yr lag. The lack of relationship between diatom biovolumes and *Monoporeia* densities in L. Vättern is likely due to the larger depth and the lower nutrient content of this lake. In eutrophic L. Mälaren, summer hypoxia (< 4 mg O_2 L^{-1}) is likely an important regulating factor. Hypolimnetic temperature showed a clear periodicity with relatively warm deep water occurring between 1989 and 1994. Hypolimnetic temperatures in Vänern and Vättern were correlated with total solar irradiance. However, neither hypolimnetic water temperature nor diatom biovolumes correlated with the North Atlantic Oscillation winter index. We speculate that variations in temperature and near-bottom oxygen concentrations negatively affect population densities by acting on recruitment success (reproduction) and juvenile (young-of-the-year) survival.

INTRODUCTION

Oxygen concentrations and food availability are important structuring factors for the profundal zoobenthos of lakes (1). Also species interactions may strongly affect invertebrate population densities and community structure, either directly through interference competition and/or predation (2), or indirectly through the exploitation of a common food resource (3). Food availability in profundal sediments is strongly dependent on sedimentation events of primarily diatoms (4, 5). Because of their high sedimentation rates, diatoms generally reach the deep sediments in a relatively fresh state within days, thereby supplying profundal invertebrates with pulses of high-quality food (6, 7). Diatoms constitute a high-quality food resource for both pelagic and benthic invertebrates due to the lack of cellulose cell walls and high concentrations of long-chain polyunsaturated fatty acids (8, 9). Hence variations in the magnitude of spring diatom blooms may have strong repercussions on populations of profundal benthic invertebrates.

The glacial relict amphipod *Monoporeia affinis* (Lindström) is an ecologically important species of the profundal benthic communities of relatively large and deep lakes below the highest coast line in Sweden and in the brackish water Baltic Sea. In Vänern, Vättern, and the deeper eastern basins of Mälaren *Monoporeia* typically comprises more than 70% of the total macroinvertebrate abundance, with chironomids, oligocheates, and sphaerids making up the remaining fauna (10). Johnson and Wiederholm (11) showed that population densities of the amphipod *Monoporeia affinis* in L. Vänern were positively correlated with biovolumes of the diatom *Aulacoseira* spp. (predominantly *A. islandica*) between 1973 and 1989. These findings suggest that the magnitude of diatom blooms is important for the recruitment success of *Monoporeia affinis* in L. Vänern. Also experimental studies using radiotracers have shown that *Monoporeia* rapidly assimilates the energy/nutrients in diatoms (12, 13) and thereby constitutes a highly efficient trophic link to fish (6). Besides diatom sedimentation events, profundal oxygen concentrations (14) and temperature (15) are important factors governing *Monoporeia* population dynamics and distribution patterns. For example, Johansson (14) showed that swimming activity of the amphipods at 5°C decreased when oxygen saturation levels dropped below 33%.

During the 20th century lakes and rivers in the Northern Hemisphere have become warmer as a consequence of long-term fluctuations in weather patterns and/or global warming (16). Weyhenmeyer and coworkers (17) showed, for example, that ice-out and spring bloom maxima in the Swedish Lake Erken occurred approximately one month earlier during the 1990s compared with the 1960s, although the onset of summer stratification was not affected. Variation in the duration of water column mixing events and thermal stratification of lakes may have strong repercussions on hypolimnetic oxygen concentrations and subsequently on important biological processes such as the rates of production and decomposition of organic matter, nutrient regeneration, and species compositions (18). Long periods of mixing during spring will transport more heat to the deep profundal of the lake, increase oxygen consumption rates in hypolimnetic water during summer stratification and, thereby, increase the risk and deleterious effects of hypoxia. Furthermore, if diatom blooms are affected by long-term fluctuations in weather patterns and/or climate change, also diatom-sedimentation events, and thus indirectly the population densities of deposit-feeding invertebrates, may be affected.

In this study, we present long-term population densities of *Monoporeia affinis* in Vänern, Vättern, and Mälaren and address the questions of how different environmental factors affect the amphipods' population fluctuations. In particular, we were interested to determine if *Monoporeia* population densities were correlated with food availability (diatoms), oxygen concentrations, and the observed changes in weather patterns during the 1980s and 1990s. To do this we used 2 climate proxis commonly used to describe these long-term fluctuations in weather patterns, the North Atlantic Oscillation (19) and total solar irradiance (20, 21). We hypothesized that amphipods would be affected negatively either directly through temperature or hypoxia or indirectly through effects of these environmental variables on the magnitude of diatom blooms.

METHODS

Benthic macroinvertebrate and phytoplankton samples, as well as water column samples for physicochemical variables were collected from 2 sampling stations in Vänern, Vättern, and Mälaren as part of a long-term ecological monitoring program. Some morphometric and chemical characteristics for these lakes are given in Table 1. Macroinvertebrate samples were collected

Figure 1. Map of southern Sweden showing the sampling stations Megrundet (A) and Tärnan (B) in L. Vänern, Visingsö (C), and Omberg (D) in L. Vättern, and Södra Björkfjärden (E) and Görväln (F) in L. Mälaren.
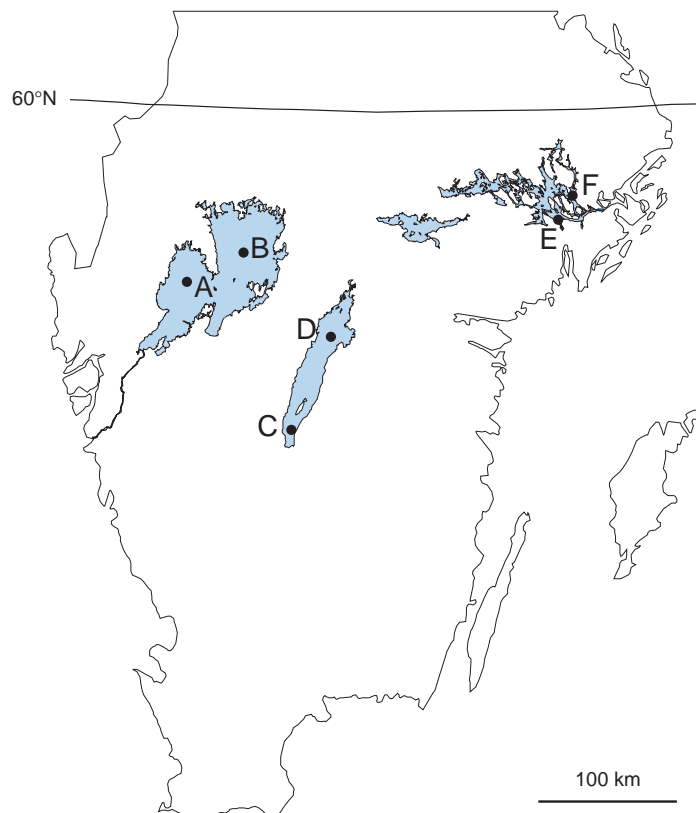
at 2 stations in each lake (Fig. 1). Samples for analyses of water chemistry, temperature and phytoplankton were collected at the same (Tärnan SSO, Megrundet N, and Görväln) or a nearby sampling station in the same basin (Södra Björkfjärden and both stations in L. Vättern). Exact positions for all sampling stations are given in Table 2.

Data for spring phytoplankton were obtained from monthly water column samples (April/May–June) collected at 0–8 m (Vänern and Mälaren) or 0–25 m depths (L. Vättern). Phytoplankton samples were preserved in the field with Lugol's solution supplemented with acetic acid and counted in the laboratory according to the Utermöhl technique (22). Determination of diatom biovolumes followed the methods described in *Handbook of Environmental Monitoring* (http://www.environ.se/index.php3?main=/dokument/lagar/hbmo/hbstart.htm). We included data from 1982–2000 in our analyses, since sampling and analysis techniques were consistent during this period. Spring bloom diatom maxima were defined as the maximum biovolume occurring during April, May or June. We used spring-bloom data since spring-bloom sedimentation events are generally regarded

Table 1. Morphometric and chemical characteristics for Vänern, Vättern, and Mälaren.

Lake		Area km^2	Volume km^3	Mean depth m	Max. depth m	WRT* year	Tot-P** µg L^{-1}
Vänern		5650	153	27	106	8.8	
	Eastern basin	2099	44	21	89	9.3	6.8–10.7
	Western basin	3794	109	30	106	2.8	8.2–10.0
Vättern		1856	74	40	128	58	5.2–11
Mälaren		1096	14.3	13	63	2.8	
	Görväln	96.5	1.3	14	63	0.4	22–31
	Södra Björkfjädern SO	94.6	1.7	18	60	1.8	17–26

*WRT = Water Renewal Time.
**Range for annual means (surface samples, monthly observations May–October) between 1986 and 1995.

Table 2. Sampling depth and geographical positions for sampling stations of benthic macroinvertebrates and phytoplankton in Vänern, Vättern, and Mälaren. Note that for Omberg, Visingsö, and Södra Björkfjärden phytoplankton data were used from a nearby, alternative sampling station.

Lake	Basin/site	Depth m	Sampling station latitude	Sampling station longitude	Alternative sampling station latitude	Alternative sampling station longitude
Vänern	Tärnan SSO	70–80	59°05.50	13°28.00		
	Megrundet N	63–78	58°50.80	12°49.00		
Vättern	Omberg	85–106	58°14.70	14°34.70	58°30.05	14°40.70
	Visingsö SV	106–116	57°56.70	14°15.30	57°54.45	14°13.75
Mälaren	Görväln	50	59°25.40	17°44.30		
	Södra Björkfjärden	47–50	59°18.00	17°30.70	59°17.44	17°31.40

as the major annual supply of fresh organic material to the profundal communities (5, 6).

Water column temperature profiles were recorded (thermistometer) at regular depth intervals (usually 2 m down to 30 or 40 m and 10 m in deeper water strata). Oxygen samples were collected a few meters above the sediment surface, fixed in the field, and analyzed in the lab using the Winkler method. Five or ten replicate macroinvertebrate samples were collected in the autumn (August or September) at each site with an Ekman sampler (ca 240 cm^2), sieved (0.5 μm), and preserved in 70% ethanol. In the laboratory, fauna samples were sorted against a black background using 10x magnification, and macroinvertebrates were determined to the lowest possible taxonomic unit and counted. Data on total solar irradiance (http://www.pmodwrc.ch) and NAO (http://www.cgd.ucar.edu/cas/) were obtained from the Internet.

Statistical analyses were run using the statistical software JMP®-package (version 3.2.2) for Macintosh (23). Trends were analyzed using linear regressions with α set at 5%.

RESULTS

Populations of *Monoporeia affinis* showed large interannual fluctuations in all three lakes, with conspicuous peaks in density occurring in Vänern and Mälaren (Fig. 2). In L. Vänern, *Monoporeia* densities at Megrundet peaked in 1984 and 1998 at 5091 ± 254 and 6797 ± 617 ind m^{-2} (mean ± se, used throughout), respectively. Indeed, both stations in L. Vänern showed almost identical density trends over time, with a peak in 1984 and a gradual increase during the 1990s (Fig. 2A). *Monoporeia* densities in L. Vättern were generally much lower, ranging from less than 100 ind m^{-2} (Visingsö, 1978–1982) to slightly more than 2000 ind m^{-2} (Fig. 2B). Even for L. Vättern, *Monoporeia* population density trends for both sampling stations show good temporal correspondence. *Monoporeia* densities at both stations in L. Mälaren also showed large interannual variability. For example, densities at Södra Björkfjärden exceeded 15 000 ind m^{-2} in 1971 and 1980, but were less than 100 ind m^{-2} during 1973–1976 and 1992–1997. At Görväln, *Monoporeia* densities showed drastic declines on several occasions (e.g. 1973–1974, 1984–1985, 1990–1991), but populations generally showed a more rapid recovery than those at Södra Björkfjärden did.

For both basins of L. Vänern, *Monoporeia* densities showed highly significant relationships with spring maximum diatom biovolume at a 1-yr lag (i.e. strong relationships were found between *Monoporeia* population densities and the magnitude of spring diatom blooms during the previous year) (P ≤ 0.019) (Fig. 3). For Tärnan, the interannual variation in diatom biovolume could explain nearly 73% of the variation in *Monoporeia* population densities. No significant relationships were found between diatom biovolume and *Monoporeia* densities in L. Vättern or L. Mälaren (linear regression, P ≥ 0.163).

In Vänern and Vättern, hypolimnetic oxygen concentrations consistently exceeded 8.9 mg O$_2$ L^{-1}, except on 2 occasions when oxygen concentrations of 6.1 mg L^{-1} (Tärnan, L. Vänern, October 1985) and 6.9 mg O$_2$ L^{-1} (Jungfrun, L. Vättern, October 1986) were recorded (data not shown). In eutrophic L. Mälaren, however, occasional low-oxygen concentrations occurred in the deep hypolimnetic water (Fig. 4). The risk for hypoxia is especially high during years when a stable thermal stratification exists until October. For example, data on hypolimnetic oxygen concentrations in Görväln, collected at a depth of 40 m, showed values less than 4 mg O$_2$ L^{-1} during late stratification (mid-October) in 1989, 1990, and 1991. In Södra Björkfjärden, summer-low oxygen concentrations were almost consistently higher than those in Görväln. In Södra Björkfjärden, at 40 m, summer-low hypolimnetic oxygen concentrations between 4.0 and 4.5 mg O$_2$ L^{-1} were recorded in 1982, 1989, and 2000. Despite these relatively low deep-water oxygen concentrations, *Monoporeia* den-

Figure 2. Temporal trends in population densities (ind m^{-2}) of *Monoporeia affinis* at 2 sampling stations each for the sampling stations Tärnan (white) and Megrundet (black) in L. Vänern (A), Visingsö (white) and Omberg (black) in L. Vättern (B), and Södra Björkfjärden (white) and Görväln (black) in L. Mälaren (C). Error bars denote the standard error of 5 (Vänern and Mälaren) or 10 replicate samples (L. Vättern). Note the differences in scale.
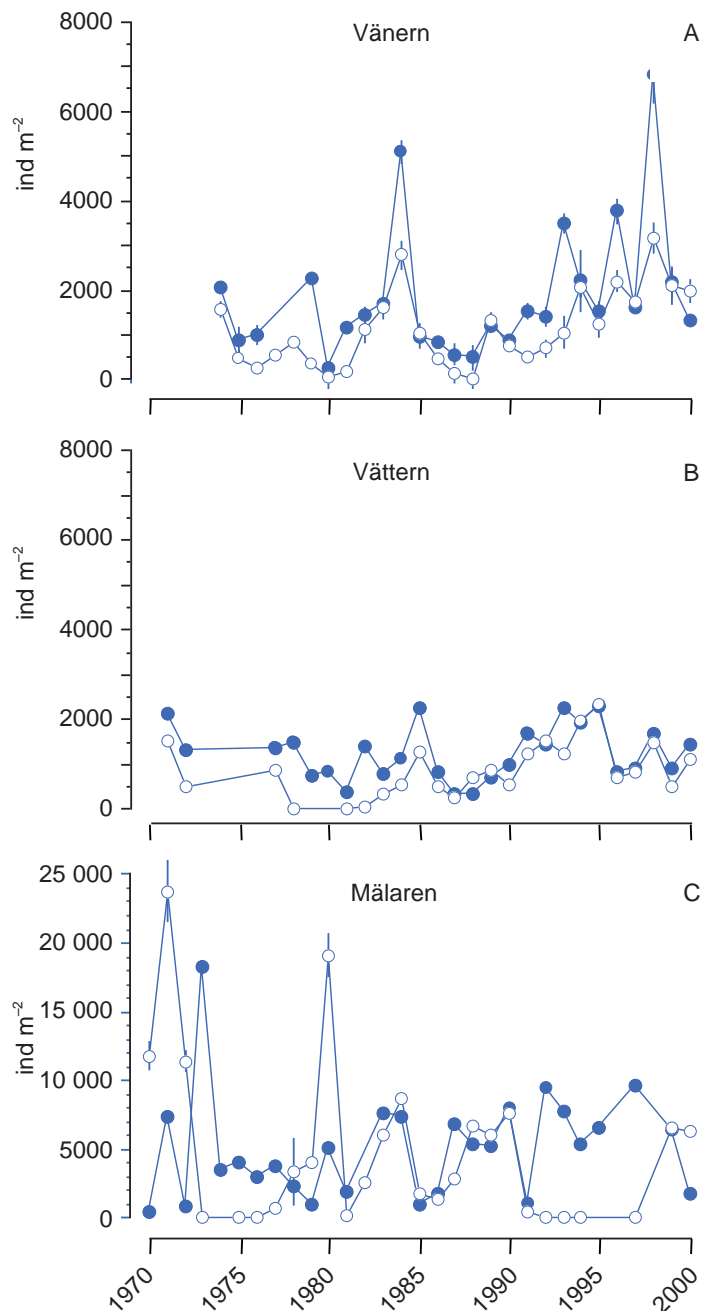
sity-declines were not correlated with the oxygen concentrations.

Hypolimnetic temperature, i.e. the deepest temperature reading in water-column profiles (a few meters above the sediment-water interface), showed a clear periodicity of alternating colder and warmer deep water (Fig. 5). The years 1989–1994, in particular, appear to be warmer, whereas 1982–1988 and 1996–2000 were colder than the long-term average. This trend was most pronounced for the stations in Lake Vättern, but the patterns were also clearly visible in the data from the other lakes. Relationships between summer hypolimnetic temperature (mean July–August or July–September) and annual total solar irradiance were significant for the stations in Vänern and Vättern (linear regression, $P \leq 0.048$), but not for the basins in L. Mälaren. Neither spring-bloom diatom maxima nor summer hypolimnetic temperature were correlated with another frequently used climate proxy, the North Atlantic Oscillation between December and March (NAO$_{winter}$). *Monoporeia* densities showed no relationship with hypolimnetic temperature during summer or in October, respectively.

Temporal trends (1982–2000) for spring maximum diatom volumes showed a significant increase at Tärnan ($P = 0.026$) (Fig. 6A) and close to significant increase at Megrundet ($P = 0.081$). Also at Jungfrun in L. Vättern, spring maximum diatom volumes increased during this time interval ($P = 0.003$) (Fig. 6B). At the station Edeskvarna in L. Vättern and both basins of L. Mälaren, however, no temporal trends in spring maximum diatom biovolumes were found ($P \geq 0.831$).

DISCUSSION

The large interannual population fluctuations of *Monoporeia affinis* observed in Vänern, Vättern and Mälaren could not be explained by one single factor. Different mechanisms presumably act concurrently and may vary in their relative importance within and among years. Interannual variations in diatom biovolume were found to be important for *Monoporeia* population densities in L. Vänern, whereas no significant relationships were found between diatom biovolumes and *Monoporeia* densities in the other two lakes. We suggest that also occasional hypoxia (L. Mälaren) and food quality aspects are important regulatory mechanisms (L. Vättern).

The highly significant relationships between spring-bloom maximum diatom biovolume and *Monoporeia* densities (at a 1-yr lag) in L. Vänern stress the importance of pelagic primary production for profundal benthic secondary production in this lake. The significant relationships for both basins of L. Vänern confirm the results reported by Johnson and Wiederholm (11) for a combination of different sampling stations over the period 1973–1989. Diatoms are rich in polyunsaturated fatty acids, in particular eicosapentaonoic acid and arachidonic acid. These fatty acids are precursors of prostaglandins and other hormones that are involved in sexual maturation and reproduction (24, 25). Hence, the finding that pelagic-benthic coupling is an important process in Lake Vänern was not unexpected.

The lack of correlation between *Monoporeia* densities and diatom biovolumes in L. Vättern suggests a weaker coupling between pelagic primary and benthic secondary production. This may be due to the larger depth (mean depth 39 m, maximum depth 128 m) and the lower nutrient content of L. Vättern (cf. Table 1) compared with L. Vänern (mean depth 27 m, maximum depth 106 m). Consequently, sedimenting diatoms will, to a larger extent, be decomposed in the water column, resulting in less fresh material reaching the profundal zoobenthos. Additionally, spring phytoplankton in L. Vättern occasionally shows a strong dominance of *Asterionella formosa* Hass., a species that does not settle as readily as the heavier *Aulacoseira* species do, and chrysophytes that are entirely decomposed in the water column. Hence, during "*Asterionella* years" there should be a

Figure 3. Relationships between diatom biovolume (mm³ L⁻¹) and densities of *Monoporeia affinis* (ind m⁻²) at 1-yr lag for Tärnan (A) and Megrundet (B) in L. Vänern.
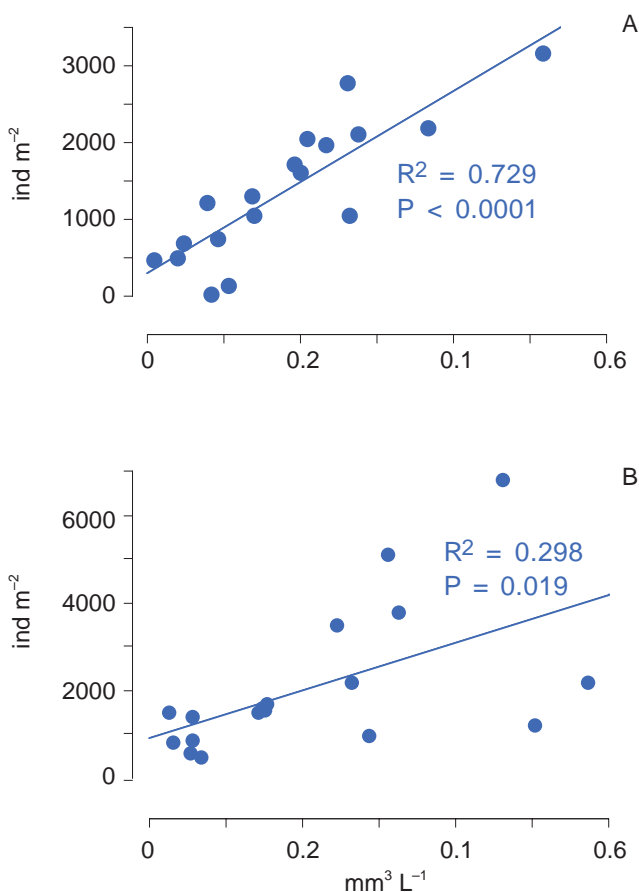
Figure 4. Summer-low oxygen concentrations (mg O₂ L⁻¹) in hypolimnetic water (40 m) in L. Mälaren between 1982 and 2000 – Björkfjärden (A) and Görväln (B).
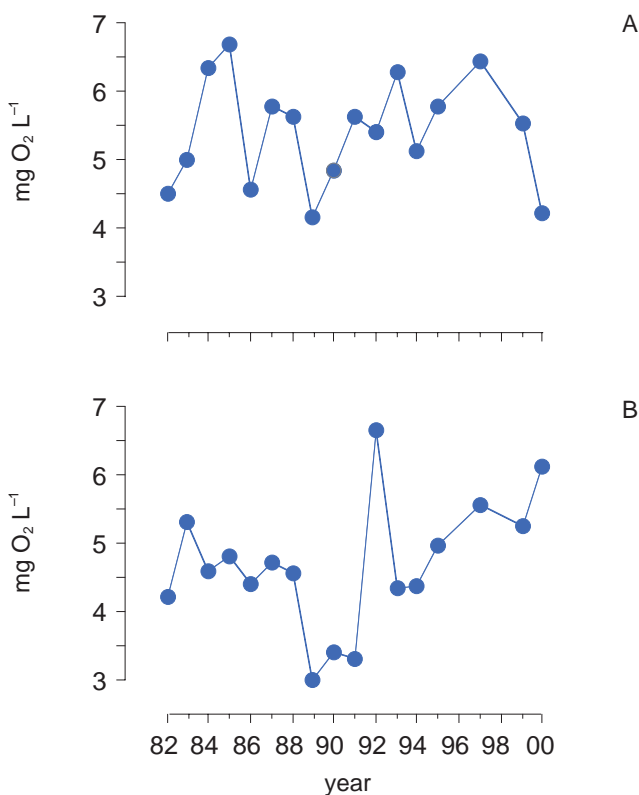
decoupling between phytoplankton production and that of the profundal zoobenthos. Typical "*Asterionella* years" were 1987 (Edeskvarna 0.02 mm^3 L^{-1}, 32% of total phytoplankton biovolume; Jungfrun 0.027 mm^3 L^{-1}, 58%), and 1988 (Edeskvarna 0.065 mm^3 L^{-1}, 60%; Jungfrun 0.029 mm^3 L^{-1}, 42%). Relatively low *Monoporeia* densities were observed during these years (Fig. 2), lending some support to this conjecture.

Further evidence of food limitation in L. Vättern is provided by the observed low fecundity of *Monoporeia* compared with L. Vänern (26). In L. Vänern, *Monoporeia* fecundity generally exceeded 30 eggs per female (mean for 4 stations), whereas *Monoporeia* fecundity in L. Vättern was substantially lower, on average 12 eggs per female (mean for 5 stations) (Fig. 7). Furthermore, analyses of fatty acids in *Monoporeia* for both lakes showed that animals from L. Vänern were substantially higher both in total fatty acids and the ω3-fatty acids eicosapentaenoic acid and docosahexaenoic acid (unpubl. data). Hence, we surmise that food limitation is the single most important factor regulating *Monoporeia* populations in L. Vättern.

Lake Mälaren is relatively shallow (mean depth 13 m, maximum depth 63 m) and the most eutrophic of the three lakes studied here. *Monoporeia* populations in L. Mälaren were, however, not correlated with spring maximum diatom biovolume. This may seem surprising, considering that diatoms heavily dominate the spring phytoplankton and that the two basins studied are relatively shallow (50 m). Possibly, any relationship between *Monoporeia* densities and spring diatom biovolumes was masked by the negative effects of low oxygen concentrations during summer stratification. *Monoporeia* may experience environmental stress from low oxygen concentrations in combination with relatively high profundal temperatures. Unfortunately, we could not adequately test this conjecture using our data set. The lack of relationship between summer-low oxygen concentrations and *Monoporeia* densities in the two basins of L. Mälaren may be due to the fact that oxygen measurements were made 5–10 m above the sediment surface. Hence, the oxygen concentrations reported here (lows of 3–4 mg O$_2$ L^{-1}) undoubtedly overestimate the ambient oxygen concentrations at the sediment-water interface. However, even oxygen concentrations of 3–4 mg O$_2$ L^{-1} are known to inhibit the amphipods' activity in experiments performed at 5°C (14). In an experimental study using Baltic populations, Eriksson-Wiklund and Sundelin (27) showed that the number of fertilized *Monoporeia* females was reduced at moderate hypoxia (2–4.5 mg O$_2$ L^{-1}). In L. Mälaren, late summer profundal temperature usually exceeds 5°C. Also, a late break-up of summer stratification may be accompanied by low oxygen concentrations in deep water. Hence, the observed combination of low oxygen concentrations, high temperature, and long exposure in hypolimnetic water may well have detrimental effects on or induce migration in *Monoporeia* populations.

Hypoxia in the deep water of both basins of L. Mälaren likely occurs during years when summer stratification is unusually long, extending into October. The lower oxygen concentrations at Görväln compared with Södra Björkfjärden are a consequence of more stable water-column stratification and the deep intrusion of organic-rich water of higher salinity from the Ekoln basin in the north into the hypolimnion of Görväln (28). Events like these may well be the cause of the observed drastic declines in *Monoporeia* population densities observed in

Figure 5. Temporal trends (1982–2000) for hypolimnetic temperature (monthly observations April/May–October, °C) for
A) Tärnan, L. Vänern (depth 70 m)
B) Megrundet, L. Vänern (70 m)
C) Jungfrun, Lake Vättern (70–75 m)
D) Edeskvarna, L. Vättern (110–115 m).
E) Görväln, L. Mälaren (40 m) and
F) Södra Björkfjärden, L. Mälaren (40 m).
Data are shown as deviations from the long-term average (1982–2000), given adjacent to the horizontal axis.
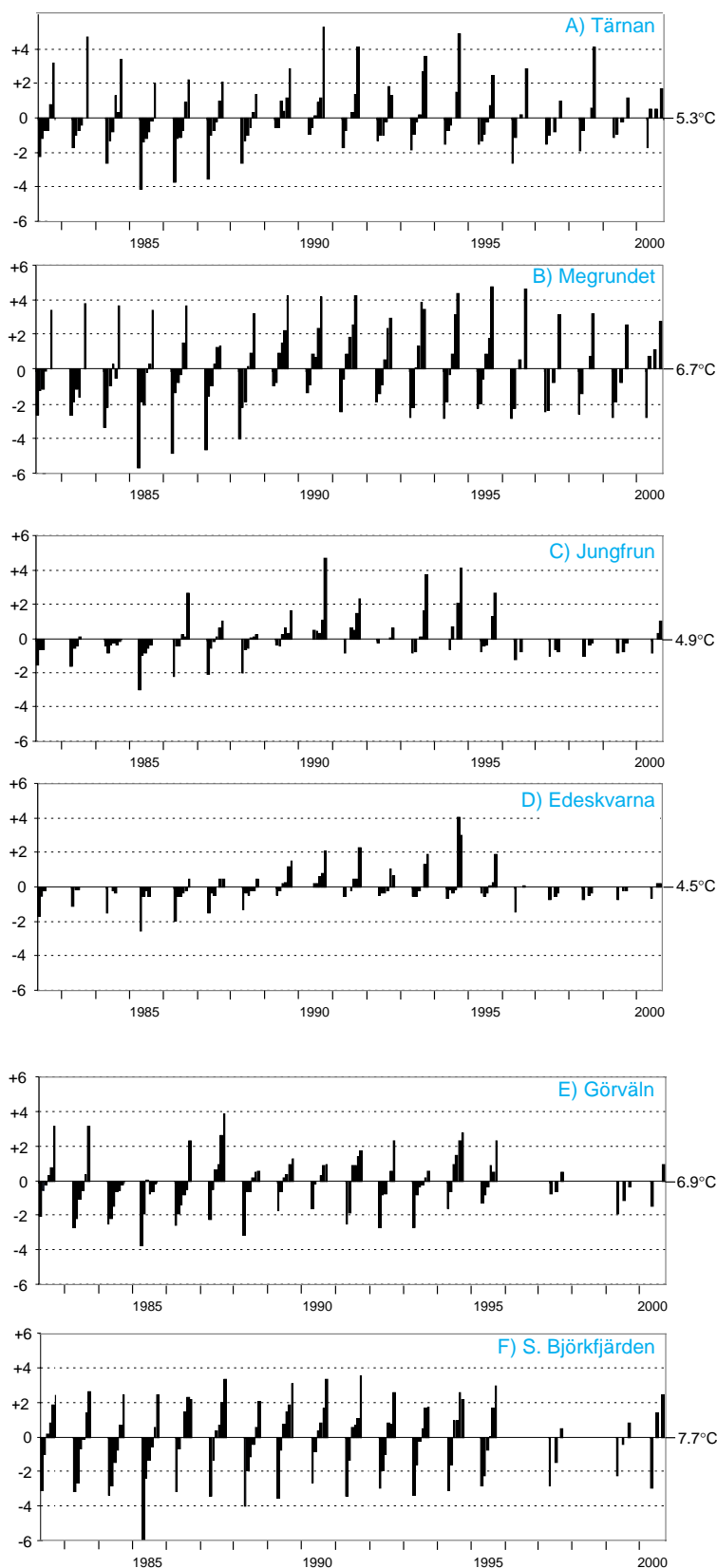
L. Mälaren. Therefore, we believe that low oxygen concentrations are a plausible explanation for the low population densities in Södra Björkfjärden between 1991 and 1994 and in Görväln between 1985 and 1991.

The observed long-term variability in hypolimnetic temperature may also affect internal lake processes such as the metabolic rates of benthic invertebrates and decomposers, and subsequently nutrient regeneration rates. The sinusoid fluctuations of hypolimnetic temperature deviations from the long-term average (Fig. 5) show a periodicity of 5–6 years, i.e. approximately one half solar cycle (20). The observed significant relationships between deep-water temperature and total solar irradiance show that natural fluctuations in weather patterns may affect the environmental conditions of invertebrate populations at large depths in lakes. Stress caused by increasing hypolimnetic temperature is likely to act first on cold-stenotherms and will possibly be amplified by global warming. Hence, if global warming is occurring, populations of cold-stenotherms may suffer from high temperatures during future periods of high total solar irradiance. Although *Monoporeia affinis* occasionally has been found in shallow waters at temperatures exceeding 18°C (29), these amphipods are sensitive to long-term exposure to temperatures exceeding 11°C (30). Eriksson-Wiklund and Sundelin (27) recently showed that a moderate increase (3.2–5.4°C) of temperature over *in situ* conditions (3.9–6.6°C) negatively affected the number of fertilized *Monoporeia* females and their fecundity under long-term incubations. The authors claim that moderate increases in temperature or decreases in oxygen concentrations may have deleterious effects on the gonadal and embryonic development in *Monoporeia* long before adult amphipods are affected (27). These results suggest that even relatively small changes in the heat budgets of lakes due to global warming may have marked effects on populations of benthic cold-stenotherms.

Top-down effects were not considered in this study, but it is likely that they are important as a population regulating mechanism in *Monoporeia*. Johnson and Wiederholm (11) found that *Monoporeia* densities in L. Vänern were not correlated with catches of important commercial fish species. However, it is well known that the amphipods are readily consumed by fish (6, 31). Also biotic interactions with other benthic invertebrates may affect *Monoporeia* population densities (10, 32). The rapid declines in population densities of the closely related amphipod *Diporeia* in the Great Laurentian Lakes (3, 33, 34) have been attributed to competition for settling phytoplankton with the invasive bivalves *Dreissena polymorpha* Pallas and *Dreissena bugensis* Andrussow. *Dreissena* are highly efficient in actively filtering phytoplankton from the water column, thereby intercepting the food supply to deposit-feeding invertebrates. This may result in a general degradation of the sediment nutritional quality (35) and induce migration and/or mortality of *Monoporeia*. *Dreissena* is common in L. Mälaren, but has hitherto not been recorded in Vänern and Vättern. Unfortunately, little is known of the chemical and biological effects of *Dreissena* populations in Swedish lakes.

Lastly, the possible occurrence of pathogenic diseases may drastically minimize population densities of *Monoporeia* and other benthic invertebrate taxa. Although our knowledge about the role of pathogens under *in situ* conditions is poor, considerable knowledge is gained from commercially important crustaceans and mollusks (36). One example of pathogen effects under *in situ* conditions is the drastic, large-scale effects on Swedish crayfish populations (37, 38). Also Segerstråle (39) speculates about pathogen infections as a possible cause of the observed drastic population declines of the amphipod *Corophium volutator* Pallas in the Baltic Sea. Possibly, pathogenic diseases may provide an alternative explanation to the observed drastic declines in amphipod populations in Swedish and North American large lakes.

Figure 6. Temporal trends (1982–2000) for maximum spring diatom volumes (mm³ L⁻¹) for Tärnan, L. Vänern (A) and Jungfrun, L. Vättern (B).
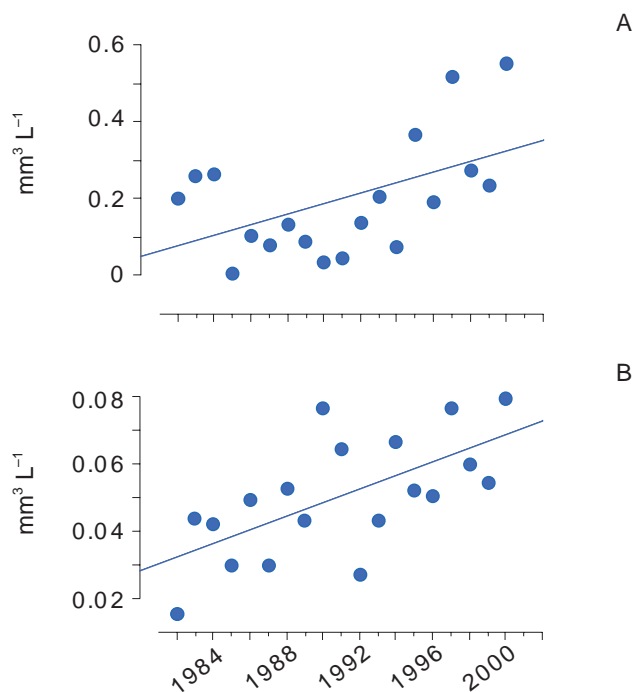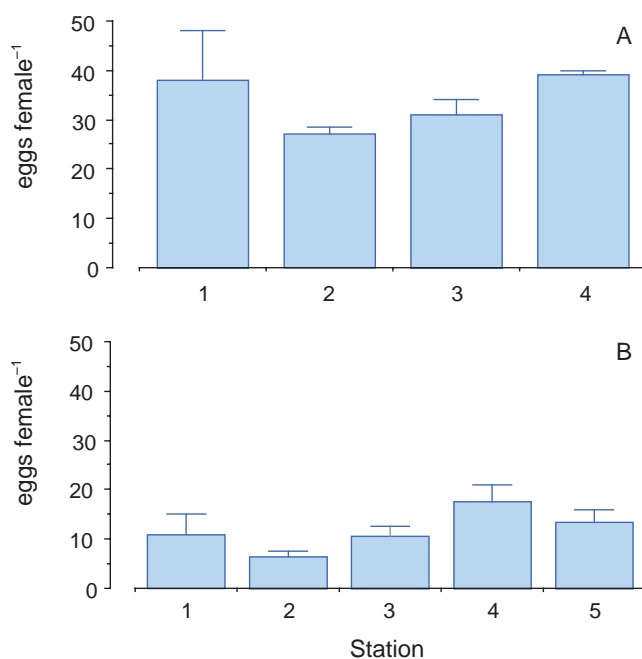

Figure 7. Fecundity (eggs per female ± 95% CL) for *Monoporeia affinis* in A) L. Vänern and B) L. Vättern. Re-plotted from Sundelin et al. (26).

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