

Productivity and Limnology

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Productivity regimes in Lake Ontario have responded to alterations in phosphorus loading, habitat alteration and more recently the invasion of the lake by exotic invertebrates. Phosphorus was brought under control and the lake had responded by the mid 1980s (Johannsson et al 1998; Mills et al. 2003; Millard et al. 2003). Exotic invertebrates, especially dreissenids (zebra and quagga mussels) and a predatory cladoceran, are further altering nutrient flow, food web structure, and productivity. This report summarizes our knowledge of present day (late 1990s-2002) nutrient levels, and the biomass/abundance, distribution, and productivity of the phytoplankton, zooplankton and macrobenthos in the major habitat zones within the lake: embayments, nearshore (<30 m), an intermediate zone (30-100 m), and offshore (>100 m). This zonation follows temperature and structural-habitat gradients which

strongly influence lower-trophic-level structure and productivity. Although there are as yet no specific fish-community objectives relating to nutrients and lower-trophic-level organisms in Lake Ontario, they are recognized as a major influence on the fish community (Stewart et al. 1999).

Nutrients, Chlorophyll *a* and Phytoplankton

Embayments are the most productive regions of the lake with higher levels of total phosphorus (TP), chlorophyll *a*, and primary production (PP). In the Bay of Quinte, Hamilton Harbour, Chaumont Bay, Sandy Pond, Sodus Bay, and Irondequoit Bay (Fig. 1), after the establishment of dreissenids in the early 1990s, TP levels ranged from 20 to 36 $\mu\text{g}\cdot\text{L}^{-1}$ and chlorophyll *a* concentrations generally averaged 10-16 $\mu\text{g}\cdot\text{L}^{-1}$ during May-October (Klumb et al. 2003; M. Charlton, unpublished data; E.S. Millard unpublished data). Irondequoit Bay had the lowest TP levels and summer chlorophyll *a* was 5 $\mu\text{g}\cdot\text{L}^{-1}$ (Klumb et al. 2003). Chlorophyll *a*/TP ratios ranged from 0.25 to 0.43. May-October primary production (PP) in the upper Bay of Quinte averaged 204 $\text{g C}\cdot\text{m}^{-2}$ over the post-establishment period (1995-2001), whereas at the mouth of the bay (Conway), where the bay and lake waters mix, TP levels were lower (11.6 $\mu\text{g}\cdot\text{L}^{-1}$) and PP averaged 138 $\text{g C}\cdot\text{m}^{-2}$ over the same period (Millard and Burley 2003; E.S. Millard unpublished data).

Embayments are some of the most degraded regions in the lake due to shoreline alteration, high turbidity, and low oxygen in deeper reaches. This degradation altered production, shifting the community from a diverse, benthic-dominated system towards a more pelagic system. Wetlands, both in embayments and along the shore, in the western end of the lake tended to be more degraded than wetlands in the eastern end

of the lake (P. Chow-Fraser, unpublished 1998-2001 data). In some embayments, dreissenids have increased water clarity, promoting the return of macrophyte beds and their associated communities; e.g. the Bay of Quinte (Seifried, 2000).

The nearshore zone (open waters <30 m bottom depth) is a physically and chemically dynamic environment with diverse biological communities. Dreissenids have colonized this region and exert a strong biological influence on these processes. Along the Canadian shoreline, water clarity increased from 3-5 m in 1994 to 6-10 m in 1997, consistent with an increase in dreissenid abundance during this period (E.T. Howell, unpublished data). Phosphorus and chlorophyll *a* exhibited no trend in concentration between 1994 and 2000, but variability increased. Concentrations in the nearshore zone were similar around the lake (Hall et al. 2003; J.C. Makarewicz, unpublished data; V. Richardson, unpublished data). Phosphorus was in the range of 6-17 $\mu\text{g}\cdot\text{L}^{-1}$ and chlorophyll *a* 1-5 $\mu\text{g}\cdot\text{L}^{-1}$. TN/TP ratios were >30 and chlorophyll *a*/TP ratios were <0.5 (J.C. Makarewicz, unpublished data; E.T. Howell, unpublished data). Chlorophyll *a* levels increased towards the offshore; such that, Secchi disc readings at bottom depths <5 m were usually <3 m and ranged from 4.1 m to 17.5 m at bottom depths of 5-30 m. This pattern is likely due to dreissenid filtration. Record low chlorophyll *a* levels occurred in the nearshore zone in spring as algal replacement could not match dreissenid filtration (E.T. Howell, unpublished data). Replacement was depressed by the slow rate of algal growth at cold temperatures and the thermal bar which restricted influx of offshore water. This phenomenon undoubtedly has a major impact on the nearshore food web. A gauntlet of clear, low-productivity water now encircles the lake throughout the year.

Examination of long-term trends suggest that spring TP concentrations in 1998 were lower in all zones in the main lake, while summer, epilimnetic TP concentrations were lower in the intermediate and offshore zone than in the nearshore zone (Fig. 2; Hall et al. 2003; J.C. Makarewicz, unpublished data; V. Richardson, unpublished data).

When dreissenids invade a system, TP levels decline as the expanding mussel populations incorporate phosphorus and/or route it to the sediments. In the eastern and central basins of Lake Erie, TP rose again about six years after the dreisenid invasion (Charlton et al. 1999; M. Charlton, personal communication). The lack of a rise in TP levels in Lake Ontario could be associated with a continued increase and expansion of the mussel population (it now extends beyond 100-m depth), a longer retention time in Lake Ontario (which would slow the re-equilibrium of phosphorus in the lake with inputs), or decreased inputs. Formal loading estimates for phosphorus have not been calculated for Lake Ontario in recent years and this hampers interpretation of water quality findings.

Offshore chlorophyll *a* was higher in the summer surveys in 1998 and 2001 than in surveys during the mid 1980s to early 1990s (Fig. 3; V. Richardson, unpublished data). Phosphorus levels have not increased (Fig. 2), suggesting that grazing pressure on the phytoplankton had decreased through this time period.

Seasonal April-October primary productivity from 1987-1995 averaged $143 \text{ g C}\cdot\text{m}^{-2}$ in the Kingston Basin (Fig. 1, station 81), at the top of the intermediate zone, and $138 \text{ g C}\cdot\text{m}^{-2}$ in the mid-lake south of Cobourg (Fig. 1, Station 41) (Millard et al 1996;

Johannsson et al. 1998). No recent data are available, but PP is likely depressed as it depends on both algal biomass and TP.

Zooplankton:

The predatory cladoceran, *Cercopagis pengoi*, invaded Lake Ontario in 1998, and its impact on the zooplankton community and effects on the food web are not fully understood. *Cercopagis* is small (the size of *Daphnia galeata mendotae*), inhabits all lake zones, and, unlike *Bythotrephes longimanus*, which invaded the lake in 1982, has not been controlled by fish predation. In offshore vertical profiles, *Cercopagis* occurred predominantly at the bottom of the epilimnion and top of the metalimnion, which suggests it may have trouble sustaining itself in clear, shallow waters (Benoit et al., 2002). Peak abundance occurred from mid-July to mid-August. Benoit et al. (2002) and Laxson et al. (2003) suggest that *Cercopagis* predation may reduce the abundance of smaller zooplankters, such as *Bosmina*, *Ceriodaphnia*, copepodids, and nauplii. Slightly higher chlorophyll *a* levels in the summers of 1998, 1999 and 2001 may indicate reduced grazing pressure and support the suggestion that *Cercopagis* can depress the abundance of these smaller herbivorous species.

Summer zooplankton populations develop first in embayments, which warm more rapidly and reach higher temperatures than the lake proper, and are generally more productive. These zooplankters provide an early source of food for small fish, including young-of-the-year of both resident and open-lake species and adult planktivores such as alewife and rainbow smelt. May-October mean zooplankton biomass was similar (0.22-0.26 g dry wt·m⁻³) in the upper Bay of Quinte and three bays on the south shore during 1995-2001 (Johannsson et al., 2003; Hall et al., 2003).

Seasonal mean zooplankton biomass during 1995-1997 in the lower Bay of Quinte ($0.07 \text{ g dry wt}\cdot\text{m}^{-3}$) and southern nearshore zone ($0.10 \text{ g dry wt}\cdot\text{m}^{-3}$) were similar but slightly lower than that at the offshore station 41 ($0.17 \text{ g dry wt}\cdot\text{m}^{-3}$) (Hall et al., 2003; O.E. Johannsson, unpublished data). Zooplankton abundance and biomass normally increase from nearshore to offshore as water depth increases (Johannsson et al. 1991). Individual zooplankters in the offshore zone were larger than in the nearshore or embayment zones, indicative of lower levels of fish predation offshore (Hall et al., 2003).

Following the establishment of dreissenid populations, zooplankton production in the intermediate zone of the Kingston Basin decreased in 1993-1995 to $12.9 \text{ g dry wt}\cdot\text{m}^{-2}$, which was comparable to levels observed in the offshore zone (12.5 to $24.3 \text{ g dry wt}\cdot\text{m}^{-2}$) (Kuns and Sprules 2000; Johannsson 2003). Epilimnetic zooplankton production accounted for approximately 80% of total water column production (Johannsson, 2003). The production of veliger larvae of dreissenids in the Kingston Basin is normally only a small percentage of epilimnetic production in the main lake (<3%), but was more variable and could be as high as 39% (Johannsson, 2003). No production data are available for 1995-2002.

The distribution, abundance, biomass, size-structure, and production of *Mysis relicta* were well-documented for Lake Ontario in 1990 (Johannsson, 1995) and additional population data were obtained in 1995-96 (O.E. Johannsson, unpublished data). Abundance and biomass increased rapidly with depth through the intermediate zone and maximum densities were observed offshore. The whole-lake October survey in 1995 and a restricted survey in October 1999 off Oswego, New York (Fig. 1),

detected no decrease in mysid abundance with the onset of the dreissenid expansion. However, reports of the absence or low abundance of mysids along the south shore of the lake in the spring of 2002 (Robert O'Gorman, U.S. Geological Survey, 17 lake St., Oswego, New York 13126, personal communication) prompted a whole-lake survey in early November 2002. Mysid abundance at bottom depths >100 m was 49% lower in 2002 than in the early 1990s. Mysid whole-lake production in 1990 and 1995-96 was 507×10^8 and 540×10^8 g dry wt, respectively (Johannsson 1995; Johannsson, unpublished data). If the decline in abundance in 2002 is real and not transitory, whole-lake mysid production also will have decreased.

Macrobenthos

Since their discovery in the lake in 1989, the zebra mussel (*Dreissena polymorpha*) has had profound effects in embayments, especially on the Bay of Quinte ecosystem. The most notable effect has been increased water quality and increased rate of expansion of macrophyte beds, particularly in the furthest reach between Trenton and Belleville, Ontario (Fig. 1; Seifried 2000). In high-macrophyte regions of the upper Bay of Quinte (Big Bay) in 2001, biomass of non-dreissenid benthic invertebrates was twice as high as in low-macrophyte areas, and six times as high as in open-mud areas (Bowen et al. 2003). Zebra mussels were most abundant (highest biomass) on the cobbled shores of the low-macrophyte areas and negligible in the open-mud areas. Each habitat supported a different benthic community; communities on the macrophytes, themselves, were not sampled (Dermott, 2003). Oligochaete worms and chironomids composed most of the open-mud assemblage. Amphipods, caddisflies (Trichoptera) and snails (Gastropoda) were important in both high- and low-macrophyte communities, while flatworms (Turbellaria) and isopods (Isopoda) also

contributed a significant amount to the biomass in the high-macrophyte areas. Increased water clarity, expansion of macrophyte beds, and increased biomass of macroinvertebrates has likely occurred in other embayments, but, with the exception of the Bay of Quinte, Sodus Bay, and Toronto Harbour, information is lacking or limited. Further changes to the habitats and macroinvertebrate communities in embayments can be expected with the expansion of round goby populations and colonization of the open-mud areas by quagga mussels (*Dreissena bugensis*).

As of 1995, information has been obtained for the nearshore, benthic community on soft sediments and reefs near Olcott, New York (Hayes et al., 1999) and on soft sediments at the mouth of the Bay of Quinte (Dermott and Legner, 2002) (Fig. 1). The benthic community at the 10-m depth off Olcott was primarily zebra mussels, and secondarily the amphipod *Gammarus fasciatus* and oligochaete worms. The diversity of this community was similar to that in 1983 at the same locations, although the abundance of individual taxa was lower. How much change is normal in these sparse, long-term comparisons and how much is related to changes in nutrient levels and the presence of zebra mussels is unknown.

Dense mats of the bacterium, *Thioploca ingrlica*, developed at the mouth of the Bay of Quinte and in the Kingston Basin after the disappearance of the burrowing amphipod, *Diporeia* (Dermott and Legner 2002). As a consequence, benthic invertebrate biomass and species richness have decreased. The invertebrate community in these areas is now predominantly oligochaete worms, and the biomass of oligochaetes at the Kingston basin site was 1.6 g dry wt·m⁻² in 2000 compared to 3.6 g dry wt·m⁻² for *Diporeia* at this site in 1991. *Thioploca* has been observed at depths between 28 m

and 146 m in Lake Ontario. However, since *Thioploca* appears to be successful only on very fine soft sediments, it is unlikely to spread over large areas of the lake or come into competition with dreissenids.

By 2002, dreissenids had colonized most hard substrate out to the 100-m depth off the north and south shores and had started to increase in abundance on softer sediments in the nearshore zone (Mills et al., 2003; M. Keir, Fisheries and Oceans, Canada, 867 Lakeshore Rd., Burlington, ON L7R 4A6, personal communication; E.T. Howell, unpublished data). U.S. Environmental Protection Agency (USEPA) surveys in 1997 and 1999 indicated that the loss of *Diporeia*, which began in eastern Lake Ontario during 1995, was expanding further offshore and westward. By 1997, *Diporeia* had disappeared from much of the bottom at depths less than 80 m (Lozano et al., 2001). Abundance of *Diporeia* at a 70-m deep site off the Niagara River decreased from about $16,000\cdot\text{m}^{-2}$ in 1990 to 0 in 1997, and remained nil in December 2002 (Dermott 2003; R.M. Dermott unpublished data). The abundance of *Diporeia* at the 125-m depth at the mid-lake station (41) south of Cobourg declined from more than $5000\cdot\text{m}^{-2}$ in 1996 to $100\cdot\text{m}^{-2}$ in October 1999, but increased to $1800\cdot\text{m}^{-2}$ by November 2002 (Fig. 4). This increase represents a return of this population to levels more typical of the deep profundal zone, albeit their lower levels.

Wet-weight biomass of non-dreissenid macroinvertebrates in the lower Bay of Quinte and eastern Lake Ontario at the 30-m depth has decreased progressively since 1986 (R.M. Dermott, unpublished data; Fig. 5). This gradual decrease reflects the loss of *Diporeia*, which disappeared in the Kingston Basin in 1995, and the loss of the fingernail clams *Sphaerium* and *Pisidium*. Decreased biomass of native

macroinvertebrates was evident prior to the arrival of zebra mussels, indicating a response to decreased nutrients. Limited information on non-dreissenid macroinvertebrates is available for other regions of the lake between 1996 and 2002.

Questions for the Future

Given that increased loadings, especially phosphorus, can be expected in the future due to increases in the human population in the basin, to what degree will dreissenids buffer this increase through filtering activity? What are the consequences of the continuous increases in organic matter and shells on the bottom associated with dreissenid activity? Will other native invertebrates, besides *Diporeia*, be lost from the ecosystem?

With the continuing expansion of dreissenids into deeper water and the consequent changes in the macroinvertebrate community, including loss of *Diporeia* and the decrease in mysids, what is the prognosis for the deepwater fish community?

Climate change could have serious repercussions on productivity of the present food web. How will disturbances to the hypolimnion temperature/oxygen regime (as predicted by some climate-change models) or alterations in the production of diatoms in the spring due to development of thermal stratification before the diatom bloom has developed, alter the production of zooplankton, *Mysis* and *Diporeia*?

Recommendations

Energy flow/production in ecosystems is generally envisaged in much too static a fashion. Processes such as production occur along gradients and these are rarely

incorporated into our thoughts or models: we need to change how we view, monitor and model these systems. Gradients in benthic species composition, abundance and biomass, mysid density and productivity, and areal zooplankton biomass and productivity from nearshore to offshore are present in Lake Ontario (Table 1). Energy gradients also exist—in the offshore zone less energy is incorporated into the hypolimnetic benthic food web due to a decrease in allocthanous inputs and a greater use of energy in the overlying water, and more biomass accumulates in larger organisms. These hypolimnetic species have lower rates of production per unit of biomass than similar-sized species in warmer regions.

Overlaid on these gradients are distributional mechanisms—organisms or forces that move energy from one part of the gradient to another. The movement of energy and storage of energy in time and space are important mechanisms in dispersing energy to all habitats within the system. For instance, mysids capture summer epilimnetic production that they make available to fish over the winter in the hypolimnion.

The current bio-monitoring programs on Lake Ontario do not adequately address questions of productivity. Managers and researchers need a coordinated productivity monitoring program that is sensitive to existing pressures (nutrient loading, exotic species) and expected new pressures (human population expansion, climate change) and can detect and assess change expeditiously. Surveys should be designed to account for seasonal and inter-annual variability. Benthos and mysids should be sampled once or twice a year on a broad spatial pattern, whereas zooplankton, phytoplankton, and water chemistry should be sampled every 1-2 weeks at a few representative sites.

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Table 1. Physical and lower trophic-level characteristics and gradients associated with the embayment, nearshore, and offshore habitat zones in Lake Ontario.

Physical characteristics

- earlier warming and community development in nearshore and embayments than in the offshore
- partially stratified or unstratified nearshore to thermally stratified in summer offshore
- decrease in variability of habitat conditions (substrate type, nutrient levels, temperature, currents, upwellings) from nearshore to offshore

Biological trends and nearshore to offshore gradients before the dreissenid mussel invasion and expansion—prior to 1994:

- TP and chlorophyll *a* higher in the nearshore than offshore
- TP/chlorophyll *a* ratio predicted from Mazumder's (1994) northern temperate lake equation
- decrease in benthic biomass
- decrease in benthic species richness and composition
- greatest density and biomass of zooplankton in the embayments
- zooplankton densities ($\cdot\text{m}^{-3}$) similar in nearshore and offshore surface waters
- increase in areal abundance ($\cdot\text{m}^{-2}$) of zooplankton
- decrease in species richness of zooplankton
- decrease in variability of abundance and biomass of zooplankton and benthos
- increase in the abundance and biomass of mysids

Changes in biological trends after the dreissenid mussel invasion—since 1994, generally:

- TP highest in the embayments and similar in the nearshore and offshore (1995-1997)
 - chlorophyll *a* highest in the embayments, and lowest in the nearshore (1995-1997)
 - chlorophyll *a*/TP low in the nearshore, and as predicted by Mazumder's (1994) equations, low in the embayments and offshore (1995-1997)
 - benthic biomass highest in the nearshore
 - richness of non-dreissenid benthic species in the nearshore zone increased then returned to pre-mussel levels, but remained lower offshore
 - *Diporeia* abundance much lower to absent in the areas above 80 m bottom depth
 - mysids rarer in the nearshore and densities lower offshore in 2002 than in the mid 1990s
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Lake Ontario

Survey Sites

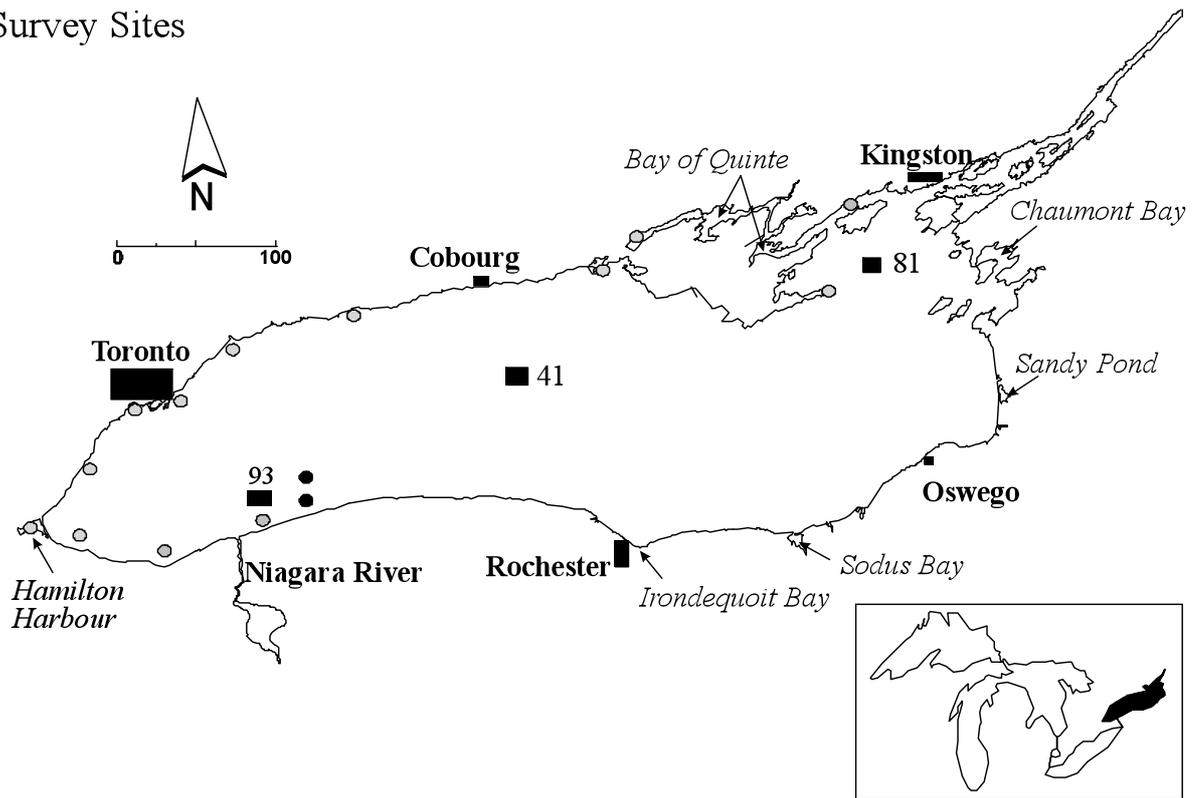


Figure 1. Map of Lake Ontario referencing sampling locations. Light gray circles – OMNR nearshore program; black circles – Makarewicz – SUNY Brockport sampling program; black rectangles (41, 81, 93) DFO Bioindex sampling sites.

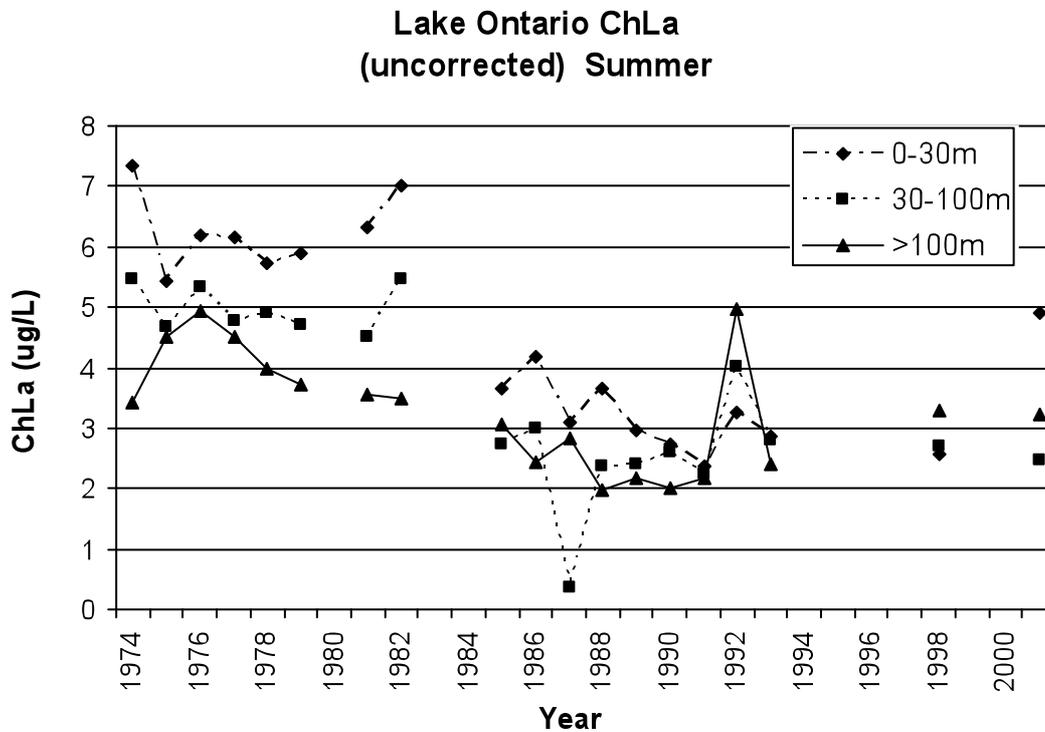


Figure 2. Long-term trends (1968-2002) in summer and spring total phosphorus levels in Lake Ontario. Data are from the Environment Canada Surveillance Program. Samples collected at the 1-m depth in August and April from the three open-water habitat zones: nearshore (\blacktriangle ; <30 m), intermediate (\blacksquare ; 30-100 m), and offshore (\blacklozenge ; >100 m).

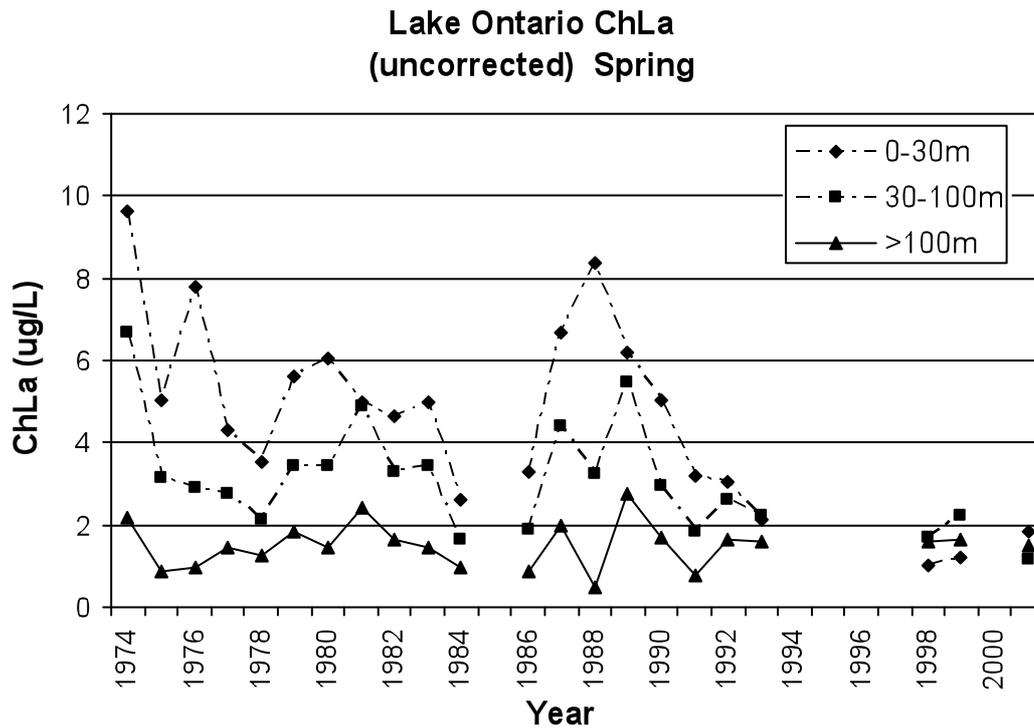


Figure 3. Long-term trends (1974-2002) in summer and spring chlorophyll *a* levels in Lake Ontario. Data are from the Environment Canada Surveillance Program. Samples collected from the 0-20-m depth range in August and April from the three open-water habitat zones: nearshore (\blacktriangle ; <30 m), intermediate (\blacksquare ; 30-100 m), and offshore (\blacklozenge ; >100 m).

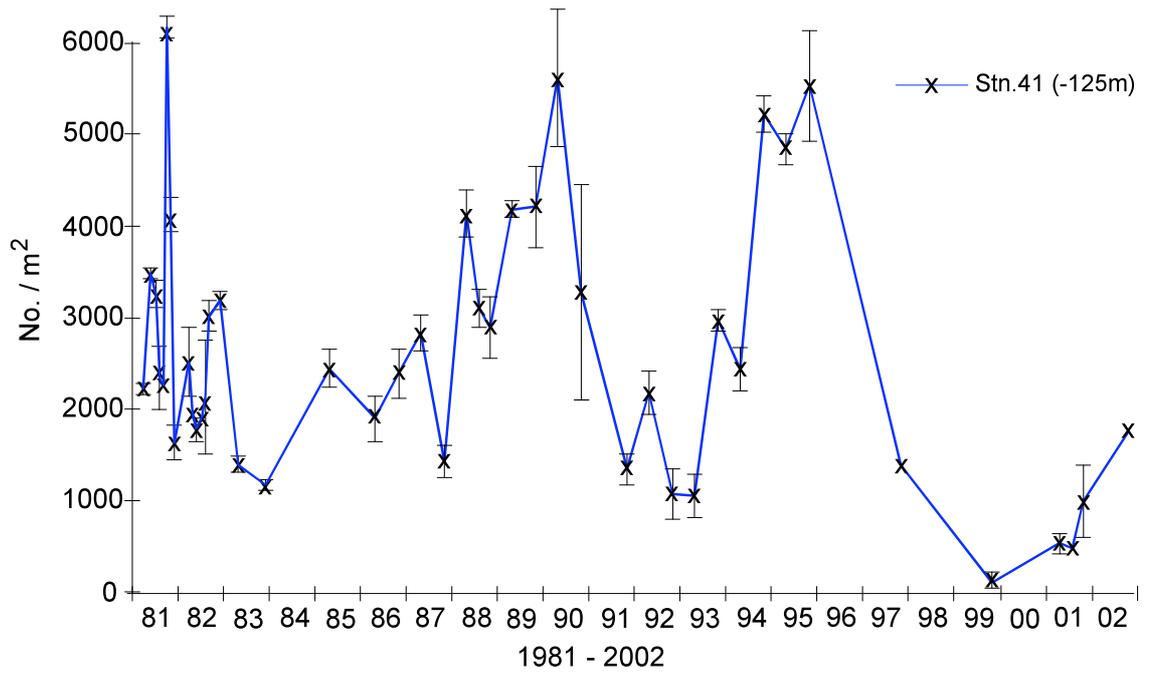


Figure 4. Density of *Diporeia* in Lake Ontario, 1981-2002, at a depth of 125 m at the mid-lake station 41 (Fig. 1).

Figure 5

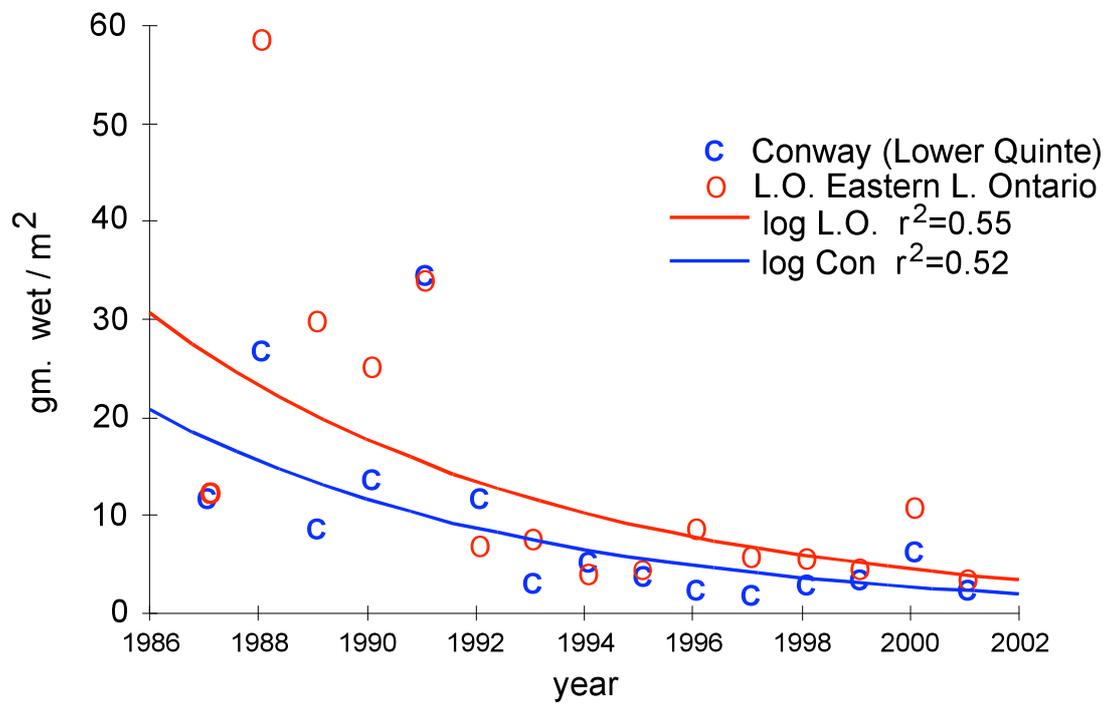


Figure 5. Non-*Dreissena* biomass ($\text{g}\cdot\text{m}^2$ +shells, wet weight) in the lower Bay of Quinte (Conway) and eastern Lake Ontario (Kingston Basin), 1986-2001.