

Environment Canada

Water Science and
Technology Directorate

Direction générale des sciences
et de la technologie, eau

Environnement Canada

Production at the Bottom of the Food Chain (i.e. below
fish): What we know about present conditions and future
developments

By:

O. Johannsson, M. Charlton, P. Fraser, R. Dermott...

TD
226
N87
no.
03-189

03-189

Production at the Bottom of the Food Chain (i.e. below fish):

What we know about present conditions and future developments.

Ora E. Johannsson¹, Murray Charlton², Pat Chow-Fraser³, Ron M. Dermott¹, E. Todd Howell⁴,
Joseph C. Makarewicz⁵, E. Scott Millard¹, Ed L. Mills⁶, and Violeta Richardson⁷

NWRI Cont. #03-189

¹Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada,
867 Lakeshore Rd., Burlington, ON L7R 4A6

²National Water Research Institute, Environment Canada,
867 Lakeshore Rd., Burlington, ON L7R 4A6

³Department of Biology, McMaster University
1280 Main St. W. Hamilton, ON L8S 4K1

⁴Environmental Monitoring and Reporting Branch, Ontario Ministry of the Environment,
125 Resources Rd., Toronto, ON M9P 3V6

⁵Department of Biological Sciences, SUNY College at Brockport
Brockport, N.Y. 14420

⁶Cornell Biological Field Station, University of Cornell
900 Shackleton Point Rd. Bridgeport, N.Y. 13030

⁷Environmental Conservation Branch-Ontario Region, Environment Canada
867 Lakeshore Rd., Burlington, ON L7R 4A6

Production at the Bottom of the Food Chain (i.e. below fish):

What we know about present conditions and future developments.

Ora E. Johannsson, Murray Charlton, Pat Chow-Fraser, Ron M. Dermott,
Todd Howell, Joseph C. Makarewicz, E. Scott Millard, Ed L. Mills, and
Violeta Richardson

Abstract

Lake Ontario is in a continuous state of flux at this point in time (2003) as it suffers from wave after wave of exotic invasions. In the past 25 years, *Bythotrephes longimanus* (predatory cladoceran 1982), *Dreissena polymorpha* (mussel 1989), *Dreissena bugensis* (mussel 1990), *Echinogammarus* (amphipod 1997), *Potamopyrgus antipodarum* (snail 1991), and *Cercopagis pengoi* (predatory cladoceran 1998) have established themselves. At the same time, management initiatives had lowered the phosphorus loading to the lake and a strong salmonid stocking program had changed the dynamics of the fish community in the main body of the lake. Two syntheses of the impacts of these changes in forcing variables on food-web structure and function were undertaken in the late 1990s. The first is a book, 'State of Lake Ontario: past, present and future' published by Backhuys Publishers and edited by M. Munawar, with chapters addressing each component of the ecosystem from nutrients and bacteria to fish and birds. The second is a product of the SCOL 2 (Salmonid Communities in Oligotrophic Lakes) process initiated by the Great Lakes Fishery Commission: a primary publication 'Lake Ontario: Food web dynamics in a changing ecosystem (1970-2000)' in the Canadian Journal of Fisheries and Aquatic Sciences. Both publications are scheduled to appear in the late spring of 2003. The present report on lower trophic level production in Lake Ontario was requested by the Lake Ontario Committee to bridge the gap between these publications and conditions in 2002. Therefore, although we may mention impacts of these forcing variables on present conditions, this report is not a review of their impacts. We have attempted to provide the latest information on biomass/abundance, distribution, and productivity and to contrast it with conditions in the mid-1990s. However, for many estimates, the latest data come from the mid-1990s. Most of the recent data has not yet been published. Therefore, to protect contributors' ability to publish their findings in the primary literature we have at times presented qualitative summaries of findings and not the actual data.

The ultimate goal of this review by the Lake Committee is to better understand the production base which supports the fish communities in the Lake Ontario ecosystem. The ecosystem encompasses embayments, the nearshore, an intermediate zone between the nearshore and offshore, and the truly offshore environment. This zonation generally follows both temperature and structural-habitat gradients. We have roughly assigned bottom-depth ranges to the last three zones of <30m, 30-100m and >100m. The depth limit of the nearshore zone will actually vary seasonally and with location around the lake

because the depth of the thermocline sets this zone and it deepens seasonally and along a north-west, south-east gradient across the lake. In the nearshore, maximum temperatures also occur along the southeast shoreline and minimal temperatures, along the northwest shoreline. These gradients are structured by the predominantly north-west winds which blow through the summer period. Warm water builds up along the southeast shore which forces deeper water to move northwest along the bottom and well up along the northwest shoreline. Thus, a temperature gradient is established around the circumference of the lake. The physical habitat in the nearshore zone is more diverse than in the other zones. Substrates range from clay to sand to cobbles and rocks, to dreissenid beds and submerged macrophytes and coastal wetlands. Allocthanous inputs and dreissenid pseudofaeces increase the organic content of the sediments. Currents and wind-related turbulence make life more difficult for many organisms. The complexity of the nearshore habitat diminishes through the intermediate depth zone and into the offshore where mud and sand form the bottom substrate and bottom temperatures range from $<1^{\circ}\text{C}$ in April to just over 4°C in December. Lower-trophic level structure and productivity change across these different environments and we have attempted to provide general information for each of these regions.

In the conclusions, we have addressed concerns about present monitoring efforts on the lake, and areas of needed research both immediate and long-term.

Productivité à la base de la chaîne alimentaire (au niveau inférieur à celui des poissons) :

conditions actuelles et évolution prévisible

Ora E. Johannsson, Murray Charlton, Pat Chow-Fraser, Ron M. Dermott,
Todd Howell, Joseph C. Makarewicz, E. xScott Millard, Ed L. Mills et
Violeta Richardson

Résumé

Le lac Ontario est actuellement (2003) dans un état de déséquilibre continué puisqu'il subit des vagues d'invasions d'organismes exotiques. Au cours des 25 dernières années, *Bythotrephes longimanus* (cladocère prédateur, apparu en 1982), *Dreissena polymorpha* (moule, apparue en 1989), *Dreissena bugensis* (moule, apparue en 1990), *Echinogammarus* (amphipode, apparu en 1997), *Potamopyrgus antipodarum* (gastéropode, apparu en 1991) et *Cercopagis pengoi* (cladocère prédateur, apparu en 1998) se sont établis. Pendant la même période, des interventions de gestion ont permis d'abaisser la charge en phosphore du lac, et un bon programme d'ensemencement de salmonidés a modifié la dynamique de la communauté ichthyenne dans la partie centrale du lac. On a entrepris, à la fin des années 1990, la rédaction de deux synthèses sur les effets qu'ont eu les modifications de ces variables de forçage sur la structure et les fonctions du réseau trophique. La monographie sur l'état passé, présent et futur du lac Ontario (*State of Lake Ontario: past, present and future*), publiée par Backhuys Publishers sous la direction de M. Munawar, dont les chapitres portent sur chacun des constituants de l'écosystème (des nutriments et des bactéries aux poissons et aux oiseaux), présente la première synthèse. La seconde est exposée dans un article sur la dynamique du réseau trophique dans l'écosystème en évolution du lac Ontario (*Lake Ontario: Food web dynamics in a changing ecosystem [1970-2000]*) à paraître dans une revue scientifique primaire, le *Journal canadien des sciences halieutiques et aquatiques*; c'est le résultat du processus d'étude des communautés de salmonidés dans les lacs oligotrophes (Salmonid Communities in Oligotrophic Lakes [SCOL 2]) entrepris par la Commission des pêcheries des Grands Lacs. La parution des deux synthèses est prévue pour la fin du printemps de 2003. Nous avons rédigé le présent rapport sur la production trophique inférieure du lac Ontario à la demande du Comité du lac Ontario pour établir un pont entre ces publications et les conditions en 2002. Par conséquent, quoique l'on fasse mention des effets que les variables de forçage peuvent avoir sur les conditions actuelles, le présent rapport n'est pas une recension de ces effets. Nous nous sommes efforcés de présenter les plus récentes informations sur la biomasse/abondance, la distribution et la productivité, et de les comparer avec les conditions du milieu des années 1990. Toutefois, pour un bon nombre d'estimations, les dernières données datent du milieu des années 1990. La plupart des données récentes n'ont pas encore été publiées. Cependant,

afin de ne pas nuire aux auteurs publient leurs résultats dans une revue primaire, nous présentons parfois des résumés qualitatifs des résultats (et non les données réelles).

L'objectif ultime du rapport commandé par le Comité du lac Ontario est de mieux comprendre les bases de la production qui soutient les communautés halieutiques de l'écosystème du lac Ontario. L'écosystème comprend les baies, le littoral, le large et la zone entre le littoral et le large. La zonation suit habituellement les gradients de température et d'habitat physique. On a grossièrement attribué aux trois dernières zones des intervalles de profondeur : < 30 m, 30-100 m et > 100 m. La limite de profondeur de la zone littorale variera effectivement selon la saison et la région du lac à cause de la profondeur de la thermocline qui établit la limite de la zone et qui s'enfonce selon la saison et selon un gradient allant du nord-ouest au sud-est du lac. De façon similaire, dans le littoral, les températures maximales se trouvent dans la région sud-est alors que les températures minimales se trouvent dans la région nord-ouest. Les gradients sont occasionnés par les vents prédominants du nord-ouest qui soufflent pendant l'été. L'eau chaude s'accumule sur la rive sud-est, ce qui pousse les eaux plus profondes à se déplacer vers le nord-ouest sur le fond jusqu'à ce qu'elles remontent le long du littoral nord-ouest. Un gradient de température est ainsi formé à la circonférence du lac. L'habitat physique de la zone littorale est plus diversifié que celui des autres zones. Les substrats sont variés : argile, sable, galets, roches, gisements de moules, macrophytes submergés et terres humides du littoral. Les apports allochtones et la présence de pseudofèces de moules entraînent une augmentation du contenu organique des sédiments. Les courants et la turbulence liée aux vents rend la vie plus difficile à de nombreux organismes. La complexité de l'habitat littoral décroît dans la zone de profondeur intermédiaire jusqu'au large, où le substrat de fond est constitué de boue et de sable et où les températures varient de $< 1^{\circ}\text{C}$ en avril à un peu plus de 4°C en décembre. Comme la structure et la productivité du plus bas niveau trophique varient avec les divers environnements, on a voulu donner de l'information générale sur chacune de ces zones.

En conclusion, nous nous sommes penchés sur les activités actuelles de surveillance du lac et sur les aspects qui nécessitent des recherches immédiates et à long terme.

NWRI RESEARCH SUMMARY

Plain language title

Productivity at the base of Lake Ontario's food chain

What is the problem and what do scientists already know about it?

Alien species have invaded Lake Ontario. Some of these species are fish which are now main food items for sport fish. These alien species and other that have arrived alter the productivity of the system and yet expectations of fishery yield remain undiminished.

Why did NWRI do this study?

NWRI contributed to this review study to help clarify expectations of the Lake Ontario ecosystem

What were the results?

Biomonitoring programs do not address questions of productivity therefore our understanding of how to manage the lake is limited. Productivity interacts strongly with habitat and changes along gradients. These gradients are not well sampled.

How will these results be used?

To recommend more sophisticated and coordinated food chain research and monitoring.

Who were our main partners in the study?

Dept of Fisheries and Oceans, Ontario Ministry of the Environment, McMaster University

Sommaire des recherches de l'INRE

Titre en langage clair

Productivité à la base de la chaîne alimentaire du lac Ontario

Quel est le problème et que savent les chercheurs à ce sujet?

Des espèces exotiques ont envahi le lac Ontario. Certaines de ces espèces sont des poissons qui sont maintenant des proies principales des poissons de pêche sportive. Ces espèces exotiques et d'autres altèrent la productivité de l'écosystème mais les attentes sur la production halieutique demeurent inchangées.

Pourquoi l'INRE a-t-il effectué cette étude?

L'Institut national de recherche sur les eaux (INRE) a contribué à cette étude en aidant à rendre plus claires les attentes visant l'écosystème du lac Ontario.

Quels sont les résultats?

Les programmes de biosurveillance ne s'occupant pas des questions de productivité, nous sommes peu au fait du mode de gestion à appliquer au lac. La productivité est fortement reliée à l'habitat et elle varie avec les gradients. De plus, les gradients ne sont pas bien échantillonnés.

Comment ces résultats seront-ils utilisés?

Les résultats serviront à recommander des études plus pointues et mieux coordonnées sur la chaîne alimentaire.

Quels étaient nos principaux partenaires dans cette étude?

Le ministère des Pêches et des Océans, le ministère de l'Environnement de l'Ontario, l'Université McMaster

Lake Ontario is in a continuous state of flux at this point in time (2003) as it suffers from wave after wave of exotic invasions. In the past 25 years, *Bythotrephes longimanus* (predatory cladoceran 1982), *Dreissena polymorpha* (mussel 1989), *Dreissena bugensis* (mussel 1990), *Echinogammarus* (amphipod 1997), *Potamopyrgus antipodarum* (snail 1991), and *Cercopagis pengoi* (predatory cladoceran 1998) have established themselves. At the same time, management initiatives had lowered the phosphorus loading to the lake and a strong salmonid stocking program had changed the dynamics of the fish community in the main body of the lake. Two syntheses of the impacts of these changes in forcing variables on food-web structure and function were undertaken in the late 1990s. The first is a book, 'State of Lake Ontario: past, present and future' published by Backhuys Publishers and edited by M. Munawar, with chapters addressing each component of the ecosystem from nutrients and bacteria to fish and birds. The second is a product of the SCOL 2 (Salmonid Communities in Oligotrophic Lakes) process initiated by the Great Lakes Fishery Commission: a primary publication 'Lake Ontario: Food web dynamics in a changing ecosystem (1970-2000)' in the Canadian Journal of Fisheries and Aquatic Sciences. Both publications are scheduled to appear in the late spring of 2003. The present report on lower trophic level production in Lake Ontario was requested by the Lake Ontario Committee to bridge the gap between these publications and conditions in 2002. Therefore, although we may mention impacts of these forcing variables on present conditions, this report is not a review of their impacts. We have attempted to provide the latest information on biomass/abundance, distribution, and productivity and to contrast it with conditions in the mid-1990s. However, for many estimates, the latest data come from the mid-1990s. Most of the recent data has not yet been published. Therefore, to protect contributors' ability to publish their findings in the primary literature we have at times presented qualitative summaries of findings and not the actual data.

The ultimate goal of this review by the Lake Committee is to better understand the production base which supports the fish communities in the Lake Ontario ecosystem. The ecosystem encompasses embayments, the nearshore, an intermediate zone between the nearshore and offshore, and the truly offshore environment. This zonation generally follows both temperature and structural-habitat gradients. We have roughly assigned bottom-depth ranges to the last three zones of <30m, 30-100m and >100m. The depth limit of the nearshore zone will actually vary seasonally and with location around the lake because the depth of the thermocline sets this zone

and it deepens seasonally and along a north-west, south-east gradient across the lake. In the nearshore, maximum temperatures also occur along the southeast shoreline and minimal temperatures, along the northwest shoreline. These gradients are structured by the predominantly north-west winds which blow through the summer period. Warm water builds up along the southeast shore which forces deeper water to move northwest along the bottom and well up along the northwest shoreline. Thus, a temperature gradient is established around the circumference of the lake. The physical habitat in the nearshore zone is more diverse than in the other zones. Substrates range from clay to sand to cobbles and rocks, to dreissenid beds and submerged macrophytes and coastal wetlands. Allocthanous inputs and dreissenid pseudofaeces increase the organic content of the sediments. Currents and wind-related turbulence make life more difficult for many organisms. The complexity of the nearshore habitat diminishes through the intermediate depth zone and into the offshore where mud and sand form the bottom substrate and bottom temperatures range from $<1^{\circ}\text{C}$ in April to just over 4°C in December. Lower-trophic level structure and productivity change across these different environments and we have attempted to provide general information for each of these regions.

In the conclusions, we have addressed concerns about present monitoring efforts on the lake, and areas of needed research both immediate and long-term.

Base of the Food-Web: Nutrients, Chlorophyll *a* and Phytoplankton

Embayments:

Embayments are the more productive regions around the lake with higher levels of total phosphorus (TP), chlorophyll *a* and primary production (PP) (Table 1). Recent conditions have been studied in the Bay of Quinte, Hamilton Harbour, Chaumont Bay, Sandy Pond, Sodus Bay, and Irondequoit Bay. Total phosphorus levels were in the range of 20 to 36 ug.L^{-1} , chlorophyll *a* concentrations during the summer were near 5 ug.L^{-1} in Irondequoit Bay, but averaged 10-16 ug.L^{-1} in the other Bays over the May-October season. Irondequoit Bay had the lowest phosphorous levels of the embayments. Primary production was measured in the Bay of Quinte:

upper bay May-October PP averaged 204 g C m^{-2} over the post-dreissenid period (1995-2001), while at the mouth of the bay, which is highly influenced by water from the lake, TP levels had dropped to 11.6 ug.L^{-1} and PP averaged 138 g C m^{-2} over the same period (Table 2). This value was similar to that in the main lake in the 1987-1995 period.

Embayments are also some of the more degraded regions with shoreline alteration, high turbidity, and low oxygen in deeper reaches. All these factors alter the type and decrease the amount of production, shifting it towards a more pelagic system and away from a benthic-oriented system with a diverse community of large macroinvertebrates. Macrophyte beds and their diverse and productive assemblages are returning in some areas due to the clearing of the water by dreissenids. This is particularly true in the Bay of Quinte (Seifried, 2000) and will be discussed in the section on benthos.

Nearshore:

The nearshore is a very dynamic environment physically and chemically. It is also biologically diverse due to the range of habitat types. A strong biological influence is now superimposed on these processes by dreissenids which have colonized suitable habitat around the entire circumference of the lake. The Ontario Ministry of the Environment (OME) established a nearshore, soft-sediment, monitoring program along the Canadian shoreline in 1994 in order to quantify and track changes in the nearshore with the invasion of exotics. Samples were collected at seven sites, three times a year in 1994, 1997 and 2000. Water clarity increased between 1994 and 1997 (Fig. 2), consistent with an increase in the influence of dreissenids. The possible role of upwellings in these increases in water clarity has not been ruled out at this time. Phosphorus and chlorophyll *a* exhibited no trend in concentration across time, but variability increased. Phosphorus and chlorophyll *a* concentrations were similar to those observed along the south shore by Hall et al. (in press) and by the Environment Canada Surveillance stations at <30 m depth (Tables 3, 4). Phosphorus is in the range of $6\text{-}13 \text{ ug.L}^{-1}$ and chlorophyll *a* $1\text{-}5 \text{ ug.L}^{-1}$. TN/TP ratios were > 30 in all areas.

As part of their surveillance strategy, OME also characterized the range and patterns of conventional water quality in the nearshore zone including tributary and harbour mouths (Fig. 3). Inputs from land sources were traced with conductivity and associated with elevated phosphorus and chlorophyll *a* concentrations. Chlorophyll *a* levels increased either linearly or quadratically towards the offshore (Fig. 4). Water quality conditions in the nearshore have become patchier: periodically areas of very clear water and low chlorophyll *a* levels were observed. These observations support the conclusion of increased variability encountered in the discrete site study. Between 2 and 5 km offshore, TP concentrations blended with offshore concentrations. Secchi Depth at bottom depths < 5m were usually < 3m, while at greater bottom depths it was 4.1-17.5 m. The relative areal extent of chlorophyll *a* was greatest for low concentrations, usually 0.5-2.0 $\mu\text{g.L}^{-1}$.

Spring-time, spatial surveys captured the effects of the thermal bar. Very low levels of chlorophyll *a* were observed within the nearshore regions. It is suspected that dreissenid impacts on nearshore waters were particularly strong at this time due both to the slower rate of algal growth at relatively cold temperatures and the restricted volume of entrapped water. This is likely a general phenomenon and could be having a major impact on the pelagic food-chain in the nearshore.

There now appears to be a gauntlet of clear, low productivity water encircling the lake through out the year.

Intermediate Zone:

We see distinct gradients in benthic species composition, abundance and biomass, mysid densities and productivity, and areal zooplankton abundance and biomass between the outer edge of the nearshore and bottom depths of 100m. Distinct gradients also used to occur in the past for chlorophyll *a* and TP. Now Chlorophyll *a* and TP concentrations are similar in both regions in

the spring while chlorophyll *a* but not TP is slightly higher in the summer offshore (Tables 3, 4). Normally, surface water zooplankton concentrations are also similar in the two regions although no data for Lake Ontario have been published since the full establishment of *Dreissena* and *Cercopagis*.

Offshore:

Inspection of long-term trends in spring and summer TP suggest that spring TP concentrations were lower in all regions of the lake in surveys conducted as of 1998 (Fig. 5). No surveys were conducted from 1994 to 1997. In the summer, epilimnetic TP concentrations were lower in the intermediate and offshore regions as of 1998 (Fig. 5). In the nearshore the data were variable and without trend. Therefore, generally TP concentrations appear to be lower now than they were in the early 1990s when dreissenids invaded the lake. When dreissenids first invade a system, TP levels decline as the expanding mussel populations incorporate and keep phosphorus and route phosphorus to the sediments. In other systems, such as the eastern and central basins of Erie, phosphorus levels rose again after several years (Charlton et al. 1999; Charlton, pers. com.). The lack of rise in Lake Ontario could be associated with a continued increase in the mussel population - it now extends to 100-m depth on the north shore as well as the south shore, a longer retention time in Lake Ontario which would slow the re-equilibrium of phosphorus concentrations 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 the previous surveys which ended in the early 1990s (Fig. 6). As phosphorus levels have not increased it suggests that grazing pressure on the phytoplankton has decreased. Have *Cercopagis* had a sufficiently large impact on the grazing zooplankton populations that the phytoplankton populations have been released to some extent? This would likely mean a less efficient transfer of energy into higher trophic levels.

Zooplankton:

Cercopagis pengoi invaded Lake Ontario in 1998. We are still trying to sort out the impacts of this species on the zooplankton community and its effects on production in the food-web. Like *Bythotrephes*, it is a predatory cladoceran from the Ponto Caspian region. Unlike *Bythotrephes*, it is small - the size of *Daphnia galeata mendotae* - and has not been controlled by fish predation in the lake. *Cercopagis* inhabits all regions in the lake: embayments, the nearshore, intermediate zone and the offshore. In offshore vertical profiles, it occurred predominantly at the bottom of the epi- and top of the metalimnion which suggests that its population may have trouble sustaining itself in clear shallow waters (Benoit et al., 2002). The population starts to develop at temperatures of 12-14°C and it has been observed in Lake Ontario in abundance in November (Makarewicz et al., 2001; Bowen and Gerlofsma, GLLFAS, Fisheries and Oceans Canada, pers. comm.). Peak populations occur in the mid-July to mid-August period. Benoit et al. (2001) suggested that *Cercopagis* predation may impact the population size of smaller zooplanktors, such as *Bosmina*, *Ceriodaphnia*, copepodids and nauplii. *Cercopagis* also appears to alter the vertical distribution of young copepods: the immature forms were most abundant at 25 -30 m depth. In these cold waters their rate of production would be depressed. At the mouth of the Bay of Quinte (Conway), *Cercopagis* are abundant for several weeks in the summer and depress small zooplankton during this period. There are suggestions in the data that this is sufficient to depress the seasonal population abundances of some species; however, we need a rigorous analysis of a larger data base to tease out the impacts of *Cercopagis* from other factors. However, the slightly higher chlorophyll a levels present in the summers of 1998, 1999 and 2001 also support this suggestion. Dave Warner at Cornell is presently working on this problem with a long-term data set for the main body of the lake. Other work on *Cercopagis* life history and production is also occurring in Dr. J. Makarewicz's laboratory.

Embayments:

Embayments warm and cool more rapidly than the main body of the lake and reach higher temperatures. Summer zooplankton populations develop first in the embayments, providing an early source of food for small fish and spawners, such as, alewife and smelt. The ability to utilize different regions of the lake when they are warm prolongs the growing season for mobile species, such as alewife, which come into the embayments and nearshore regions in the spring and stay in the open lake in the autumn. Embayments with their warm temperatures and higher levels of productivity than the open lake, are also valued nursery areas for a number of species which live in the open lake as adults, e.g. alewife, whitefish, walleye. Thus, embayment production serves not only the resident fish species but also the fish populations in the main lake.

Seasonal changes in biomass and composition of zooplankton have been studied recently in Chaumont Bay, Sandy Pond and Sodus Bay (1995-1997, Hall et al. in press), Irondequoit Bay, (1996-1997, Klumb et al., in press), the Bay of Quinte (1976-present, Johannsson and Bowen) and Hamilton Harbour (1997, 2000-2002, Chow-Fraser, Evans, Johannsson and Bowen). Zooplankton production has been calculated for the Bay of Quinte but not the other bays. Zooplankton samples from Hamilton Harbour are presently being counted and are not yet ready to be included in this report.

Seasonal (May-October) mean biomass was similar in the upper Bay of Quinte and the three bays studied by Hall et al. (in press): $0.26 \text{ g dry wt m}^{-3}$ averaged over the post-dreissenid period (1995-2001) compared with $0.22 \text{ g dry wt m}^{-3}$ averaged over the three bays for the 1995-1997 period. In the lower Bay of Quinte, seasonal biomass averaged $0.07 \text{ g dry wt m}^{-3}$ over the post-dreissenid period. These corresponded to mean seasonal abundances of $84 \text{ to } 95 \times 10^3 \text{ m}^{-3}$ in the first set of bays and $19 \times 10^3 \text{ m}^{-3}$ in the lower Bay of Quinte. In Hall et al.'s study, nearshore sites and offshore August and October surveys were included for comparison. The seasonal biomass at these sites was more in line with the lower Bay of Quinte: $0.10 \text{ g dry wt.m}^{-3}$ nearshore and $0.17 \text{ g dry wt.m}^{-3}$ offshore in August. Hall et al. (in press) noted that the zooplankton were larger offshore than at either the nearshore or embayment sites, indicative of higher levels of predation in these latter regions. In the Bay of Quinte, zooplankton and cladoceran mean lengths are slightly longer in the upper bay than at the mouth (Johannsson, pers. comm.), suggesting that in the Bay of Quinte predation on zooplankton was less intense in the upper bay.

Nearshore and Offshore:

Information on nearshore zooplankton conditions can be found in three studies: the DFO Bioindex Program with long-term monitoring sites in the main lake (station 41) and Kingston Basin (station 81), the whole-water column production study of Kuns and Sprules (2000), and the nearshore sites in the study of Hall et al. (in press) mentioned above (Table 5). By 1993-1995, zooplankton production in the Kingston Basin had decreased to levels observed in the main lake (Johannsson et al., 1998). Whole-water column production in 1993 and 1994 ranged from 12.5 to 24.3 g dry wt .m⁻² in the main lake and was stable at 12.9 g dry wt .m⁻² in the Kingston Basin (Kuns and Sprules, 2000). Epilimnetic zooplankton production accounted for approximately 80% of total water column production (Johannsson, 2003). The production of veliger larvae of dreissenids 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% in the Kingston Basin (Johannsson, 2003). No other seasonal biomass or production estimates have been published. Other information does exist on species composition and biomass in August (USEPA biomonitoring program, OMNR-NYSDEC-Cornell biomonitoring program) and April (USEPA biomonitoring program). The USGS-Cornell group also collect monthly samples at a set of nearshore and one offshore site, while Dr. Joe Makarewicz collects zooplankton samples at a 30 m and a 100 m deep site near Brockport. These data have not been published and are presently being analyzed as part of several graduate theses.

Mysids:

The distribution, abundance, biomass, size-structure and production of *Mysis relicta* were well documented for Lake Ontario in 1990 and 1995-96 (Johannsson, 1995; Johannsson and Perkins pers. comm.). With the association between the expansion of *D. bugensis* and the loss of *Diporeia* from areas of the lake, the question was raised whether the mysid population might also be affected. A whole-lake survey in 1995-1996 and two restricted surveys in October 1999 and

May 2000, along a transect off of Oswego, detected no decrease in mysid abundance. Reports of the absence or low abundance of mysids along the south shore of the lake in the spring of 2002 (O'Gorman, USGS Oswego, pers. comm.), prompted a whole-lake survey in early November 2002. Mysid abundance was lower over much of the lake (Fig 7). Along the south shore, there was some indication of movement of mysids inshore from depths > 100 m. These movements were most likely related to mass water movements in the lake. Additional analyses are examining the size structure, essential fatty acid composition and indices of growth potential (RNA/DNA and RNA/protein) of mysids from the 2002 survey. It is suspected that the decline in Mysis may be real and may be related to the predatory impact of *Cercopagis* on zooplankton populations during the summer as described above.

Mysid whole-lake production in 1995-96 was 539.52×10^8 g dry wt (Table 6). With the recent decline in mysid abundance, biomass and production should also be decreased proportionately. The proportionality of the decrease will depend on the relative survivorship of the large individuals between the two time periods. The larger individuals contribute significantly to both biomass and production.

Benthos:

Embayments:

Limited information on the benthic community exists for embayments in Lake Ontario, with the exception of the Bay of Quinte, Sodus Bay, and Toronto Harbour. The only recent data for Hamilton Harbour were collected in the summer of 2002 and are presently being analyzed.

The Bay of Quinte data has captured the changes that have occurred with decreasing nutrient loads, invasion of dreissenids and changes in the fish community. Over the past eight years, *Dreissena polymorpha* has had a profound effect on the Bay of Quinte ecosystem. The most important environmental changes, associated with the dreissenid invasion, are the increase in water clarity and expansion of macrophyte beds, particularly in the region between Trenton and

Belleville (Seifried 2000). A comparison of benthic biomass and composition amongst high macrophyte, low macrophyte and 'offshore' open mud regions in Big Bay in the upper Bay of Quinte in 2001, found (1) that the biomass of non-dreissenid benthic invertebrates was 2-fold higher in the high macrophyte than in the low macrophyte regions, and 6-fold higher in the high macrophyte than in the open mud areas, (2) that dreissenids were most abundant (highest biomass) on the cobbled shores of the low macrophyte region and negligible in the open-mud, and (3) that each habitat supported a different benthic community (Dermott, 2003). Oligochaete worms and chironomids composed most of the open-mud assemblage. Amphipods, caddisflies and snails were important in both nearshore communities, while flatworms and isopods also contributed a significant amount to the biomass in the high macrophyte regions. It should be noted that all sampling in this comparison was done with a Ponar sampler which would not sample macroinvertebrates associated with the macrophytes, themselves. Therefore the differences in benthic biomass amongst the different types of habitat is underestimated. Similar types of changes would be expected in the other embayments, but would differ in the areal extent to which macrophytes could recolonize shoreline and bottom substrate. From a fisheries perspective, the resurgence of macrophyte beds has increased not only total benthic production but also diversity and size composition of food resources.

Further changes can be expected with the expansion of round goby into the bay. Also waiting in the wings is *Dreissena bugensis* which could colonize the open-mud regions of the bay and further depress pelagic productivity.

Nearshore:

The nearshore is a complex environment bounded by open shoreline, wetlands, tributary mouths and harbours. Coastal wetlands are a key component of this region, providing a variety of important ecological functions. Wetlands are areas of exceptional biodiversity and as noted above provide higher benthic biomass per unit area, equivalent or higher zooplankton biomass per unit water volume, and a wider range of prey types and sizes than open-substrate areas (Bowen et al., 2003). They are particularly important spawning and nursery habitat for the Great

Lakes fish community not only for the cover they provide but also for the range of planktonic and substrate-oriented prey available.

An index of wetland health has been developed by Dr. Chow-Fraser at McMaster University, based on physical and chemical water-quality conditions as well as a measure of pelagic production (chlorophyll *a*). Examination of wetlands around the shores of Lake Ontario between 1998 and 2001 indicated that wetlands in the western end of the lake tended to be degraded while wetlands in the eastern end of the lake ranged from excellent to degraded. There is obviously a lot of scope for improvement in the food supply and production in these nearshore habitats.

Open-water benthic community composition and biomass have been examined recently (as of 1995) in two different regions of the lake: one on soft sediments and reefs at 10 m bottom depth in the south-western region of the lake near Olcott (Hayes et al., 1999), and the other on soft sediments at the mouth of the Bay of Quinte (Dermott and Legner, 2002) (Table 6). The benthic communities in the two areas could not be more different.

In 1995, the benthic community at the western basin sites was dominated by dreissenids and secondarily by 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. No estimates of biomass were given, but were likely lower if abundance was lower over all. Kilgour et al. (2000) found that the benthic community at 5 m depth had changed greatly in response to reduced nutrient levels since 1981. Therefore, we do not know how much change is normal interannual variability in these sparse long-term comparisons and how much is directional and related to changes in nutrient levels and the presence of dreissenids.

At the mouth of the Bay of Quinte and in the Kingston Basin, dense mats of the bacterium, *Thioploca ingrica*, have developed after the disappearance of the burrowing amphipod, *Diporeia*. Benthic invertebrate biomass and species richness have decreased in areas taken over by *Thioploca*. The invertebrate community is composed predominantly of oligochaete worms. The biomass of oligochaetes, coexisting with *Thioploca* at the Kingston basin site, was 1.6 g dry

wt.m⁻² in 2000 compared with 3.6 g dry wt.m⁻² for *Diporeia* at this site in 1991. Although *Thioploca* mats are densest at 32 m, the bacterium has been observed between 28 m and 146 m in Lake Ontario. The deeper sites examined were off the south shore of the lake near Oswego. *Thioploca* appears to be successful on very fine soft sediments, and therefore, is unlikely to spread over large areas of the lake or come into competition with dreissenids.

Intermediate Zone and Offshore:

By 2002, dreissenids had colonized most hard substrate out to 100 m depth on both the north and south shores and started to increase in abundance on softer sediments in the nearshore region (Mr. M. Keir, Fisheries and Oceans Burlington, pers. comm.; Mills et al., 2003; OME Surveillance data).

Limited data are available on other offshore benthic fauna of Lake Ontario since 1995. The most complete data set collected in recent years is that of the US EPA surveys of 1997 and 1999. That data had shown that the loss of the deepwater amphipod *Diporeia*, which began in eastern Lake Ontario during 1995, had expanded further offshore and westward. By 1997, the amphipod had disappeared from much of the bottom of Lake Ontario at depths less than 80 m (Lozano et al., 2001). The exception was along the north shore and near Toronto. (Fig. 9)

Limited data for the long term biomonitoring site off the Niagara River (station 93 at 70 m depth) indicated that the amphipods had decreased from about 16,000 m² in 1990 to 0 in 1997, and remained absent in December 2002. No data were available at the site between 1984 and 1990 (Fig. 10). The population of *Diporeia* at the mid-lake station 41 in 125 m of water, had dropped to 100 m² in October 1999, but has again increased to 1800 m² by November 2002. This increase has returned the population in mid-lake to levels more typical of the deep profundal zone of Lake Ontario, albeit their lower levels (Fig. 11).

Data from the lower Bay of Quinte and eastern Lake Ontario at 30 m depth has shown a progressive decrease in non-*Dreissena* wet biomass (shells included). This reflects the loss of the

deepwater amphipods which disappeared in the Kingston Basin in 1995, and also the gradual loss of the fingernail clams *Sphaerium* and *Pisidium*. The decreasing trend in benthic biomass was evident between 1986 and 1991 prior to the arrival of zebra mussels indicating that the biomass of benthic fauna was responding to decreasing nutrient levels in the Bay of Quinte (Fig. 12).

Specific and General Questions:

Specific

Is *Mysis* really declining - and if it is - why?

Is *Diporeia* still declining - why - what areas have and will have depressed densities? Which areas will continue to support *Diporeia* and at what level?

Has efficiency of the transfer of energy through the zooplankton in the offshore decreased through the activities of *Cercopagis* ? (depletion of grazers, addition of a trophic level, redistribution of groups to colder water)

Cladophora - how to control it with dreissenids creating conditions that favour its growth?

Can fish feed in or on *Thioploca* mats? What is the value of this food source?

Will *D. bugenesis* get into the upper Bay of Quinte?

General

Nutrient levels are appropriate or a bit low except in some embayments, based on lake and RAP goals. However, we expect increases in loadings in the future with projected increases in the human population. To what degree will dreissenids buffer this increase through nearshore filtering activity? Besides the known impacts of increasing phosphorus loads to the lake, what are the consequences of the continuous increases in organic matter and shells on the bottom associated with dreissenid activity? More botulism? Loss of other invertebrates?

With the problems with benthos in the nearshore (switch to dreissenids - movement of fish offshore) and the decline in *Diporeia*, and perhaps *Mysis*, what is the prognosis for introducing deepwater sculpin and bloaters? On the other hand, if the very deep waters of the lake do not lose their fauna, perhaps these species are two of the few which could survive on their own.

Climate change could have serious repercussions on productivity of the present foodweb. If climate change disturbed the hypolimnion temperature/oxygen regime or alter the production of diatoms in the spring that might well alter the production of zooplankton, *Mysis* and *Diporeia*. This could occur if the thermocline formed while diatom growth was still highly limited by light over much of the lake. Offshore, diatom population growth was usually maximal in May (1981-1995) before the formation of the thermocline in mid-June. With formation of the thermocline, diatoms tend to sink to the bottom. The 'normal' spring populations would never have time to develop. The short mixed depth with higher light levels and warmer temperatures would favour other species including some summer diatoms. These would tend to be eaten by summer zooplankton. It is unlikely that they could replace the spring diatom bloom as a food source for *Diporeia*.

Conclusions:

- 1) Government Bioimonitoring Programs on the Lake do not Address Questions of Productivity.

With the closure of the DFO Bioindex Program in 1995 which sampled 2 fixed sites on a weekly basis, we no longer have estimates of offshore and eastern basin:

- production of any of the lower trophic levels
- a record of changes in the seasonal cycle of any components of these lower trophic levels
- an adequate ability to ask questions linking the lower trophic levels to other variables such as fish, climate change, exotic invasions etc.

Present data are snap shots in time which means they can not easily be corrected for position in the seasonal cycle for comparisons across years or with other variables.

There is an overwhelming lack of data by which to characterize the status of the lake at the present time, or to try to understand how the changes occurring in the Lake Ontario ecosystem are inter-related. There is some nearshore work for water quality and benthos on the Canadian side. Those surveys are conducted every three years. Similarly, a spring and summer whole-lake survey is conducted every three years for nutrients, physical conditions and chlorophyll *a* by Environment Canada. There is an annual survey for water quality, phytoplankton and zooplankton in the open lake in April and again in August conducted by the USEPA. They have collected benthos for Dr. Steve Lozano (GLERL-NOAA) in 1997 and 1999.

Seasonal and inter-annual variability are sufficiently high in Lake Ontario that surveys which do not take these two sources of variation into account can not detect change for many years unless it is dramatic (Johannsson et al. 1998). In order to detect changes at the lower trophic levels, annual sampling is needed for all lower trophic levels. Benthos could be sampled once or twice a year, but the zooplankton, phytoplankton and water chemistry need to be sampled every week or two. Mysids production is more sensitive to change than mysid abundance, especially changes in predation. In order to estimate production, mysids should be monitored monthly if only a few monitoring sites are surveyed or three times a year if whole lake surveys are conducted in spring summer and late fall.

Two university-based programs do sample temporally for phosphorus, chlorophyll *a* and zooplankton and thus could provide some of the needed information. Joe Makarewicz at

Brockport samples a pair of stations in the western end of the lake weekly, and Ed Mills at Cornell together with the USGS out of Oswego sample a set of nearshore and an offshore station monthly (in most years). These data sets are often incorporated into graduate student projects. Special arrangements would have to be made to access these data for monitoring purposes and still protect the graduate students' rights to analyze and publish the data. The governments and their agencies need to develop a co-ordinated monitoring program which is sensitive to expected pressures, such as climate change, and can detect and assess change within a reasonable period of time.

The Great Lakes community needs to work towards a co-ordinated monitoring program, based on the goals of the LaMP and GLFC, and hopefully including land-use planners. These goals are going to have to be reconciled amongst the various interest groups. The Lake Erie LaMP has made good progress in this direction. They developed ecosystem scenarios based on a fuzzy-logic ecosystem model of Lake Erie and then chose the scenario most acceptable to everyone. In this way, the goals had to be internally compatible with the ecosystem structure, and not a list of individual desires. The Lake Committees themselves have set an excellent example of the process needed to integrate information and co-operation from numerous agencies when there is commitment towards common goals. The overarching role and independence of the Great Lakes Fishery Commission is perhaps one of the key reasons for the success of the Lake Committee structure. The other is the dedication of the fisheries biologists working in the many agencies around the Great Lakes. Similar dedication exists amongst other scientists working on the Great Lakes and could be harnessed towards a common set of goals. Perhaps what is needed is the binational, overarching, dedicated structure.

2) Productivity Interacts Strongly with Habitat and Changes along Gradients

We have much too static a view of energy/production. We are not good at incorporating gradients into our thoughts or models. We constantly try to measure processes; such as, production, which occur along gradients, and assign them to areas (Table 8). These gradients change depending on the scale we use - species, trophic level, volumetric, areal. In addition to

gradients, we have mixers -organisms or forces which move energy from one part of the gradient to another.

Transitions exist from the nearshore to the offshore: As you move offshore, (1) less energy is incorporated into the benthic food-web due to a decrease in allocthanous inputs and a greater use of energy in the overlying water, and (2) more biomass accumulates in larger organisms in the cool waters of the hypolimnion. These hypolimnetic species have lower rates of production per unit of biomass than similr-sized species in warmer regions. If we were to sum gross production for each m^2 of surface area along the nearshore-offshore transect we would expect it to peak in the nearshore zone beyond the depth of physical disturbance because in this region there are both anthropogenic and other allocthanous inputs as well as warmer temperatures. Gross production should then decrease towards the offshore, as inputs settled out or were diluted, and then reach a plateau across the mid-lake region.

Movement of energy and storage of energy in time and space are also important concepts. Mysids capture summer epilimnetic production that they make available to fish over the winter in the hypolimnion or even in more nearshore areas. Areas of high production also move around the lake with time. Embayments warm and develop zooplankton populations earlier in the spring than other lake regions. Spring then moves to the nearshore with its thermal bar and higher productivity (at least prior to dreissenids), and finally to the offshore which warms last and cools down last. This allows zooplankton and algal production to continue late into the fall. Some fish could capitalize on these shifting patterns in temperature and production to extend their growth/reproductive period. Alewife did this prior to the colonization of the nearshore and intermediate area by dreissenids.

Acknowledgements:

We wish to thank the US EPA for allowing collection of samples from the Lake Guardian in 2001, and data on the *Diporeia* distribution in 1997 from the paper by Steve Lozano et al. (2001) in Can. J. Fish. Aquat.Sci. 58:518-529.

References:

- Benoit, H.P., Johannsson, O.E., Warner, D.M., Sprules, W.G. and Rudstam, L.G. 2002. Assessing the impact of a recent predatory invader: The population dynamics, vertical distribution and potential prey of *Cercopagis pengoi* in Lake Ontario. *Limnol. Oceanogr.* 47: 626-635.
- Bowen, K., Millard, E.S., Dermott, R.M., Johannsson, O.E. and Munawar, M. 2003. Lower Trophic Level Comparison of Nearshore and Offshore Habitats in the Bay of Quinte, Lake Ontario. Report #12. Project Quinte Annual Report 2001. Kingston, ON, Bay of Quinte Remedial Action Plan.
- Charlton, M.N., Le Sage, R., and Milne, J.E. 1999. Lake Erie in transition: the 1990's. In: State of Lake Erie (SOLE): past, present and future. Ed. M. Munawar, T. Edsall and I.F. Munawar, Leiden, The Netherlands, Backhuys Publishers.
- Dermott, R. 2003. *Diporeia* in Lake Ontario. In: State of Lake Ontario (SOLO): past, present and future. Ed. M. Munawar. Leiden, The Netherlands, Backhuys Publishers.
- Dermott, R. 2003. Report on the Benthic Fauna, Bay of Quinte - 2001. Report #12. Project Quinte Annual Report 2001. Kingston, ON, Bay of Quinte Remedial Action Plan.
- Dermott, R.M. and Geminiuc, M. 2003. Changes in the benthic fauna of Lake Ontario 1990-1995, with local trends after 1981. In: State of Lake Ontario (SOLO): past, present and future. Ed. M. Munawar. Leiden, The Netherlands, Backhuys Publishers.
- Dermott, R.M. and Legner, M. 2002. Dense mat-forming bacterium *Thioploca ingrica* (Beggiatoaceae) in eastern Lake Ontario: implications to the benthic food web. *J. Great Lakes Res.* 28:688-697.
- Dermott, R.M. and Munawar, M. 2003. Influence of Dreissena on the benthos and primary production in Lakes Ontario and Erie. In: State of Lake Ontario (SOLO): past, present and future. Ed. M. Munawar. Leiden, The Netherlands, Backhuys Publishers.
- Hall, R.H., Pauliukonis, N.K., Mills, E.L., Rudstam, L.G., Schneider, C.P., Lary, S.J. and Arrhenius, F. in press. A comparison of total phosphorus, chlorophyll a and zooplankton

- in embayment, nearshore and offshore habitats of Lake Ontario. J. Great Lakes Res. 29:: 54-69.
- Hayes, J.M., Stewart, T.W. and Cook, G.E. 1999. Benthic macroinvertebrate communities in southwestern Lake Ontario following invasion of *Dreissena*: continuing change. J. Great Lakes Res. 25: 828-838.
- Johannsson, O.E. 1995. The response of *Mysis relicta* population dynamics and productivity to spatial and temporal gradients in Lake Ontario. Can. J. Fish. Aquat. Sci. 52: 1509-1522.
- Johannsson, O.E. 2003. Lake Ontario zooplankton: Role in energy transfer and response to management actions. State of Lake Ontario: Past Present and Future. M. Munawar. Leiden, The Netherlands, Backhuys Publishers.
- Johannsson, O.E., Millard, E.S., Ralph, K.M., Myles, D.D., Graham, D.M., Taylor, W.D., Giles, B.G. and Allen, R.E. 1998. The changing pelagia of Lake Ontario (1981 to 1995): A report of the DFO Long-term Biomonitoring (Bioindex) Program. Can. Tech. Rep. Fish. Aquat. Sci. No. 2243:: i-ix + 278 pp.
- Johannsson, O.E., Rudstam, L.G., Gal, G. and Leggett, M.F. 2003. *Mysis relicta* in Lake Ontario: Population dynamics, trophic linkages and further questions. In: State of Lake Ontario (SOLO): Past, Present and Future. Ed. M. Munawar. Leiden, The Netherlands, Backhuys Publishers.
- Kilgour, B.W., Bailey, R.C. and Howell, E.T. 2000. Factors influencing the changes in nearshore benthic communities on the Canadian side of Lake Ontario. J. Great Lakes Res. 26: 272-286.
- Klumb, R.A., Bunch, K.L., Mills, E.L., Rudstam, L.G., Brown, G., Knauf, C., Burton, R. and Arrhenius, F. in press. Establishment of a metalimnetic oxygen refuge for zooplankton in a productive Lake Ontario embayment. Ecological Applications.
- Kuns, M.M. and Sprules, W.G. 2000. Zooplankton production in Lake Ontario: a multistrata approach. Can. J. Fish. Aquat. Sci. 57: 2240-2247.
- Lozano, S.J., Scharold, J.V. and Nalepa, T.F. 2001. Recent declines in benthic macroinvertebrate densities in Lake Ontario. Can. J. Fish. Aquat. Sci. 58: 518-529.
- Makarewicz, J.C., Grigorovich, I.A., Mills, E.L., Damaske, E., Cristescu, M.E., Pearsall, W., LaVoie, M.J., Keats, R., Rudstam, L.G., Hebert, P. and Halbritter, T.K., C. Matkovich,

- and H. J. MacIsaac. 2001. Distribution, fecundity, and genetics of *Cercopagis pengoi* (Ostroumov) (Crustacea, Cladocera) in Lake Ontario. J. Great Lakes Res. 27: 19-32.
- Millard, E.S. and Burley, M. 2003. Photosynthesis, Chlorophyll *a* and Light Attenuation. Report #12. Project Quinte Annual Report 2001. Kingston, ON, Bay of Quinte Remedial Action Plan.
- Millard, E.S., Myles, D.D., Johannsson, O.E. and Ralph, K.M. 1996. Phytoplankton photosynthesis at two index stations in Lake Ontario 1987-92: Assessment of the long-term response to phosphorus control. Can. J. Fish. Aquat. Sci. 53: 1092-1111.
- Mills, E.L., Casselman, J.M., Dermott, R., Fitzsimons, J.D., Gal, G., Hoyle, J.A., Johannsson, O.E., Lantry, B.F., Makarewicz, J.C., Millard, E.S., Munawar, M., Munawar, I.F., O'Gorman, R., Owens, R.W., Rudstam, L.G., Schaner, T. and Stewart, T.J. 2003. Lake Ontario: Food web dynamics in a changing ecosystem (1970-2000). Can. J. Fish. Aquat. Sci. in press.
- Seifried, K.E. 2000. Submerged Macrophytes in the Bay of Quinte: 1972 - 2000. Department of Zoology. Toronto, ON, University of Toronto: 125.
- Zaranko, D.T., Farara, D.G. and Thompson, F.G. 1997. Another exotic mollusc in the Laurentian Great lakes: the New Zealand native *Potamopyrgus antipodarum* (Gray 18430 (Gastropoda, Hydrobiidae). Can. J. Fish. Aquat. Sci. 54: 809-814.

Table 1. Water quality conditions in several embayments of Lake Ontario: temperature, oxygen in bottom waters, total phosphorus (TP) and Chlorophyll *a* (Chla).

Location	Date	Season	Temperature (°C)	Temperature Maximum	Oxygen (mg.L ⁻¹)	TP (ug.L ⁻¹)	Chla/ TP	Chlorophyll (ug.L ⁻¹)	References*
Irondequoit Bay	1996-1997	Epi	21.8 ± 1.0	24 -25	-	20	0.25	6.1, 4.6	Klumb et al. (in press)
	June-early	Meta	16.4, 15.3		3.8, 1.8				
	Aug	Hypo	6-13		0.5				
Hamilton Harbour	1998-2000	Epi	22.1***	24.2	-	37.0	0.43	16.1	Charlton (pc) Millard (pc)
		Meta	17.7		-	-	-	-	
		Hypo	13.2		<1	-	-	-	
		May-Oct.	14.8			33.5	0.36	12.3	
Bay of Quinte Belleville	1995-2001	Jun-Sep**	22.9	23.6-25.8		-	-	-	(Millard and Burley, 2003, pc)
		May-Oct.	19.0			36.5	0.38	13.4	
Bay of Quinte Conway	1995-2001	Epi	19.2	22.3-23.3		-	-	-	Millard and Burley (2003, pc)
		May-Oct.	15.4			11.6	0.31	3.5	

* pc = personal communication, **samples from mid- June until mid-September, ***temperature and oxygen data from 2002 only

Table 2. Phytoplankton production, composition and biomass in different geographic regions of Lake Ontario. Old data come from prior to 1996 in the lake. New data were collected in the post-dreissenid period in the Bay of Quinte (1995-2001). No new data are available for the main body of the lake.

	Offshore-old >100 m	Offshore-new >100 m	Nearshore-old 30 m	Nearshore-new 30 m	Embayments	References
Bioindex - DFO						
Primary Production (g C m ⁻²)	ML: 138 (1987-1995) (Apr-Oct)		KB: 143 (1987-1995) (Apr-Oct)		BoQ: 138 - 204 (1995-2001) (May-Oct.)	(Millard et al., 1996) Millard and Burley (2003)
Biomass	ML: 0.8487 (1993-1995) (Apr-Oct)		KB: 0.8567 (1993-1995) (Apr-Oct)			Johannsson et al. (1998)
Composition (Apr.-Oct.)	ML: 24.0%, 1.2% (1993-1995) (Apr-Oct)		KB: 20.1%, 2.5% (1993-1995) (Apr-Oct)			Johannsson et al. (1998)
% Diatoms,						
% Cyanophytes						

ML = mid-lake, KB = Kingston Basin, BoQ = Bay of Quinte

Table 3. Total phosphorus (TP) concentrations in three bottom depth zones of Lake Ontario. New refers to data collected after 1997 while old refers to data collected before 1998.

	Offshore:old >100 m	Offshore:new >100 m	Mid-Depth: old 30-100 m	Mid-depth: new 30-100 m	Nearshore:old <30 m	Nearshore:new <30 m	References
TP (ug.L ⁻¹) whole lake	9.8 (spr) 10.1 (sum) (1987-1992)	7.4-8.0 (spr) 7.9-8.4 (sum) (98,99,2001)	10.6 (spr) 10.9 (sum) (1987-1992)	7.2-7.6 (spr) 8.4 (sum-01) (98,99,2001)	16.0 (spr) 13.2 (sum) (1987-1992)	8.0-10.4 (spr) 9.6-16.9 (sum) (98,99,2001)	Richardson: Surveillance Program EC
TP (ug.L ⁻¹) SS -west (US)		10.5, 5.5 (2000,2001) (Jul-Oct)		6.3, 8.8 (2000,2001) (Jul-Oct)			Makarewicz: a 100m and 30m site
TP (ug.L ⁻¹) south shore				≈ 8 (1995-1997) Aug,Oct		10-11 (1995-1997) Aug,Oct	Hall et al. (in press)
TP (ug.L ⁻¹) Canadian shore						6-10 (SW) 7-11 (NW) 8-13 (N, NE) (94,97,2000)	Howell: Surveillance Programs OMEE
Total Nitrogen/TP						>30, and often >40, along the Canadian shoreline	Howell: Surveillance Programs OMEE

Spr = spring, sum = summer, SS = south shore

EC = Environment Canada, OME = Ontario Ministry of the Environment

Table 4. Chlorophyll *a* concentrations in three bottom depth zones of Lake Ontario. New refers to data collected after 1997 while old refers to data collected before 1998. Values of chlorophyll *a* for the south shore were taken from graphs in Hall et al. (in press)

	Offshore:old >100 m	Offshore:new >100 m	Mid-Depth: old 30-100 m	Mid-depth: new 30-100 m	Nearshore:old <30 m	Nearshore:new <30 m	References
Chlorophyll <i>a</i> (ug.L ⁻¹) whole lake	0.5-2.7 (spr) 1.9-2.8 (sum) (1987-1991)	1.5-1.7 (spr) 3.3-3.3 (sum) (98,99,2001)	1.7-5.5 (spr) 2.2-2.7 (sum) (1987-1991)	1.2-2.3 (spr) 2.5-2.7 (sum) (98,99,2001)	3.2-8.4 (spr) 2.4-3.7 (sum) (1987-1991)	1.0-1.8 (spr) 2.6-4.9 (sum) (98,99,2001)	Richardson: Surveillance Program EC
Chlorophyll <i>a</i> (ug.L ⁻¹) SS -west (US)		3.2-4.2 (2000,2001) (Jul-Oct)		3.6-4.3 (2000,2001) (Jul-Oct)			Makarewicz: a 100m and 30m site
Chlorophyll <i>a</i> (ug.L ⁻¹) south shore				≈ 2.0-3.5 (1995-1997) Aug,Oct		1-2 (1995-1997) Aug,Oct	Hall et al. (in press)
Chlorophyll <i>a</i> (ug.L ⁻¹) Canadian shore						2-5,7 (SW) 1.5-5 (NW) 1-3 (N, NE) (94,97,2000)	Howell: Surveillance Programs OMEE
Chlorophyll/TP		SW: 0.4-0.6 (2000-2001)		SW: 0.5 (2000-2001)		SS: 0.1-0.2 W: 0.2-0.4 NS: 0.1-0.3 NE: 0.2-0.3 (1994-2000)	Makarewicz: Howell: Surveillance Programs

Table 5. Properties of the zooplankton communities within three geographic regions of Lake Ontario. 'New' refers to data collected after 1997, while 'old' refers to data collected before 1998.

	Offshore-old >100 m	Offshore-new >100 m	Nearshore-old 10-30 m	Nearshore-new 10-30m	Embayments	References
Water-Column Production April- Oct. (g dry wt.m ⁻²)	ML: 12.5 - 24.3 (1993-1994)		KB: 12.9 (1993-1994)		BoQ: 27.2 - 56.4 (1995-2001)**	Kuns & Sprules (2000)* Johannsson (2003)
Veliger Production (%vel/vel+zoopl)	ML: <3% (1993-1995)		KB: 4% - 39% (1993-1995)		BoQ: 2% - 11% (1995-2001)	Johannsson (2003, unpubl. data)
Epilimnetic Biomass & Density, Stratified Period (g dry wt m ⁻³) & (no x 10 ³ .m ⁻³)	ML: 0.139 & 98 (1987-1995)		KB: 0.153 & 85 (1987-1995)			Johannsson (2003)
Epilimnetic Biomass & Density, May-October (g dry wt m ⁻³) & (no x 10 ³ .m ⁻³)	ML: ≈ 0.17 & ? (1995-1997)		SS: ≈ 0.10 & 30 (1995-1997)		SS bays: ≈ .22 & 95 (1995-1997) BoQ: 0.07- 0.26 & 19 ^a - 84 (1995-2001)**	Hall et al. (in press) Johannsson & Nicholls (unpubl data)
Zooplankton Size (mm)	Greatest offshore: but still high planktivory (1995-1997)		Small: high planktivory (1995-1997)		Small: high planktivory (1995-1997)	Hall et al. (in press)

Species	Small species, <i>Epischura</i> and <i>Limnocalanus</i>	Similar + <i>Cercopagis</i> June-Nov.	Small species, <i>Epischura</i>	Similar + <i>Cercopagis</i> June- Nov	Small and medium species + littoral + <i>Cercopagis</i> July- Aug. HH, BoQ, IB	Johannson (2003), pers comm. Vogel, pers. comm. Klumb et al. (in press)
Low Oxygen Refuge (1-2 mg.L ⁻¹ in meta)					IB: Increase in large <i>Daphnia</i> in meta refuge HH: low O ₂ refuge below epilimnion	Klumb et al. (in press) DFO (unpubl. data)

*after removing mysids and converting wet to dry weight: I assumed a 10% conversion

**2000 unusually low year and was removed from average

ML = mid-lake, KB = Kingston Basin, SS = south shore, BoQ = Bay of Quinte, IB = Irondiquoi Bay, HH = Hamilton Harbour

Table 6. Properties of the *Mysis relicta* population in Lake Ontario. 'New' refers to data collected after 1997, while 'old' refers to data collected before 1998.

	Offshore-old >100 m	Offshore-new >100 m	Intermediate-old 30-100 m	Intermediate-new 30-100 m	References
Annual Production (g dry wt.m ⁻²)	Stn 41: 130 m 3.5 - 4.8 (1988 -1995 : no 1992)		50-99m 1.77 (1995)		Johannsson et al., (2003) Johannsson & Perkins (pc)
Annual Production Whole Lake (g dry wt.m ⁻²)	539.52 x 10 ⁸ (1995-1996)				
Abundance - Oct. Deep Hole (no.m ⁻²)	408 - 1125 (1990-1997)	393±105 (SD) (2002)			Johannsson et al. (2003) Johannsson, Bowen, Gerlofsma (pc)
Abundance - Oct. 50-100 m* (no.m ⁻²)			54, 59 (1991,1995)	29 (2002)	Johannsson, Perkins, Bowen, Gerlofsma (pc)
Abundance April-October Stn 41: 130 m (no.m ⁻²)	354 (range 196- 535) (1984-1995)				Johannsson et al. (2003)

*numbers estimated for a bottom depth of 75 m from regression equations based on 0-99m data.

Table 7. Properties of the benthic community in different geographic regions of Lake Ontario. 'New' refers to data collected after 1997, while 'old' refers to data collected before 1998.

	Offshore-old >100 m	Offshore-new >100 m	Nearshore-old 0-100 m	Nearshore-new 0-100 m	Embayments	References
Dreissenid Abundance	0	-	Quaggas out to 100 m on south shore - but rare in soft muds of Eastern Lake Ontario	Out to 100 m on northshore (Cobourg)	patchy	Dermott and Munawar (2003) Keir (pers. comm.) Dermott (pers. comm.)
<i>Diporeia</i> Abundance	Generally low (1997)	Stn 41 (125 m water depth) back to 'normal' 1800.m ⁻² (2002)	Gone from most of eastern end of lake and at depths < 80 m (1997) - but not north shore or near Toronto	none off of Niagara (2000, 2002)		Lozano et al. (2001) Dermott & Munawar (2003) Dermott (pers. comm.)
Other Inverts	-Oligochaete and sphaeriid densities low (1997) - <i>Pisidium</i> biomass ok: 2.2 mg.m ⁻² (1995)		-Sphaeriid densities low (1997) east of Niagara - <i>Echinogammarus</i> common at rocky and shallow sites - <i>Potamopyrgus</i> <i>antipodarum</i> found (1991)	- <i>Potamopyrgus</i> <i>antipodarum</i> has replaced <i>Ammnicola</i> and <i>Valvata</i>	- <i>Echinogammarus</i> present (e.g. HH, BoQ, Sodus Bay) -Large increases in macrophytes have increased macroinvertebrate biomass (BoQ, HH, others?)	Lozano et al. (2001) Mills et al. (2003) Zaranko et al. (1997)
Benthic Biomass Dry wt. (no mussels)			3.6 g dry wt.m ⁻² <i>Diporeia</i> (1991 eastern basin)	1.6 g dry wt.m ⁻² Oligochaetes in <i>Thioploca</i> mats (2002 eastern basin)		Hayes et al. (1999) Dermott & Legner (2002)
Benthic biomass Wet wt (no shells)	10.8 g.m ⁻² (1990 >90 m) 3.96 g.m ⁻² (1995 >90 m)		28.8 g wet wt.m ⁻² <i>Diporeia</i> (1991 eastern basin)	10.3 g wet wt.m ⁻² Oligochaetes	27.2 g.m ⁻² high macrophyte density; 4.1 g.m ⁻² open mud (2001)	Dermott & Legner (2002) Dermott, (2003) Dermott and Geminiuc (2003)

Table 8. Gradients in physical and lower trophic level characteristics from the nearshore to offshore environments.

Physical characteristics

- earlier warming and community development nearshore and in 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) towards the offshore

Biological trends before the dreissenid invasion:

- TP, Chla were higher in the nearshore than offshore
- TP/Cha ratio predicted from Mazumder's 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 density (.m^{-3}) in surface waters was similar from nearshore to offshore -
- increase in areal abundance (.m^{-2}) of zooplankton towards offshore,
- decrease in species richness of zooplankton towards offshore
- 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 invasion-1994 and on, generally

- TP was highest in the embayments, lower in the nearshore and offshore which were similar (1995-1997)
 - Chla was highest in the embayments, and lowest in the nearshore (1995-1997)
 - Chla/TP was low in the nearshore, and as predicted by Mazumder's equations, in the embayments and offshore (1995-1997)
 - Benthic biomass was highest in the nearshore with the addition of dreissenids - it also tends to increase when dreissenids invade
 - Richness of non dreissenid benthic species increased then returned to pre-mussel levels in nearshore: still lower offshore
 - Diporeia abundance much lower to absent in the areas above 80 m bottom depth
 - Mysids are rarer in the nearshore and at lower densities in 2002 than in mid-1990s
-

Figure 1. Map of Lake Ontario referencing locations mentioned in the manuscript.

Figure 2. Mean and range of secchi depths at stations in 1994, 1997 and 2000. Stations were visited 3 times in 1997 and 2000 and 4 times in 1994. B- secchi visible on bottom.

Figure 3. Diagram of transect run at Oshawa when characterizing the new shore environment shows the field conductivity (coloured track) and concentration of total phosphorus in discrete water samples (numerical values). Conductivity is temperature compensated to 25° C. Ontario Ministry of the Environment Surveillance Program.

Figure 4. Mean concentration of chlorophyll *a* as estimated from fluorescence (closed circle) and surface temperature (open circle) over 1m intervals of lake depth on August 25, 1997 over the Cobourg study area. Square symbols indicate chlorophyll *a* concentration in discrete water samples analyzed using lab methods.

Figure 5. Long-term trends in summer and spring total phosphorus levels in Lake Ontario from the Environment Canada Surveillance Program. Samples collected from 1m depth in August and April from three bottom-depth ranges: nearshore <30 m water depth, intermediate zone 30-100 m water depth, offshore >100 m water depth. nearshore (⊗), intermediate zone (⌈), offshore (⌈)

Figure 6. Long-term trends in summer chlorophyll *a* levels in Lake Ontario from the Environment Canada Surveillance Program. Samples collected from 0-20 m depth in August and April from three bottom depth ranges: nearshore <30 m water depth, intermediate zone 30-100 m water depth, offshore >100 m water depth. nearshore (⊗), intermediate zone (⌈), offshore (⌈)

Figure 7. The relationship between *Mysis* abundance in late October-November and bottom depth in Lake Ontario between 1990 and 2002.

Figure 8. Figure taken courtesy of Bowen et al. (2003). Mean wet shell-free biomass and standard errors of *Dreissena* and other benthic invertbrate groups, inshore-offshore study, Bay of Quinte 2001.

Figure 9. Distribution of *Diporeia* in Lake Ontario taken from the LOTT cruises of 1990 and 1995, and EPA data in Lozano et al. 2001.

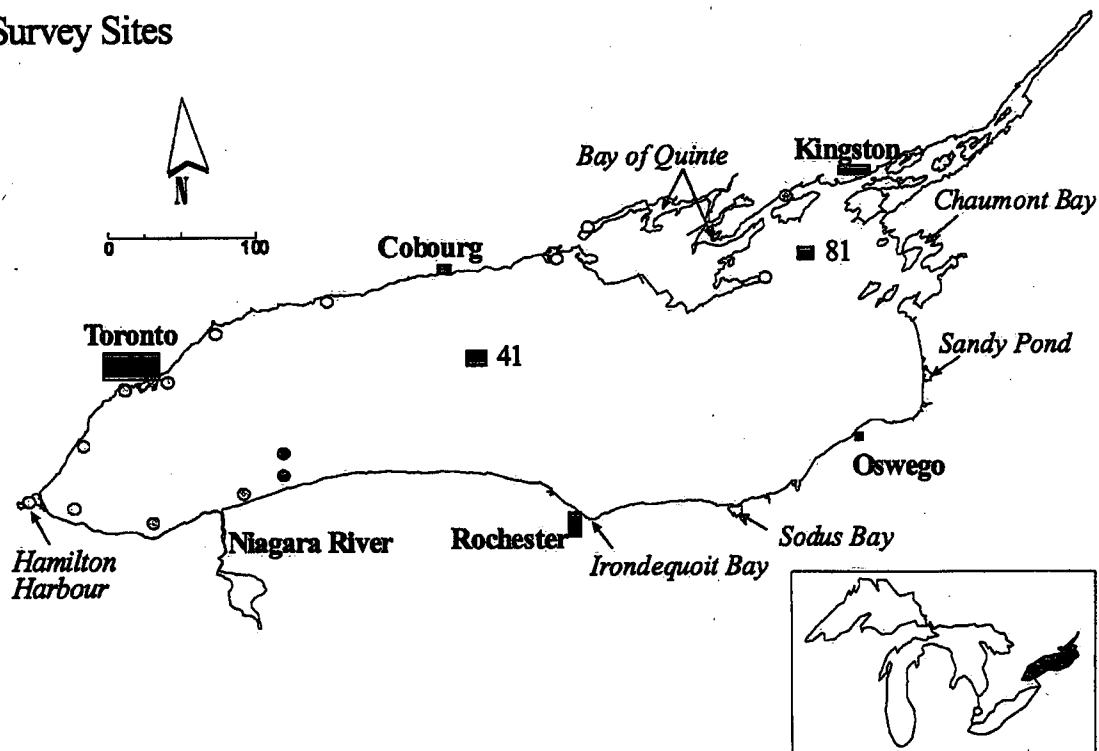
Figure 10. Density of *Diporeia* at 70 m depth in western Lake Ontario station 93 near the Niagara River.

Figure 11. Density of *Diporeia* at mid lake station 41 in 125 m depth.

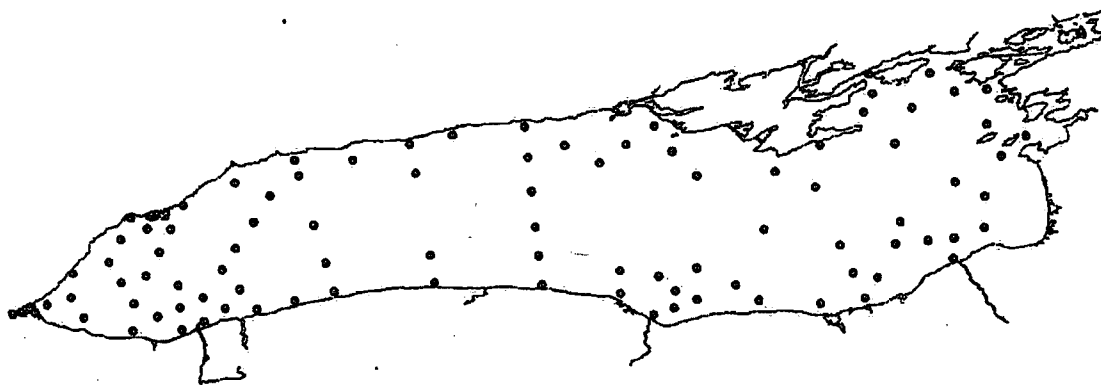
Figure 12. Wet non-*Dreissena* biomass (g/m^2 +shells) in the lower Bay of Quinte (Conway) and eastern Lake Ontario (Upper Gap) between 1986 and 2001.

Lake Ontario

Survey Sites



Environment Canada Monitoring Sites



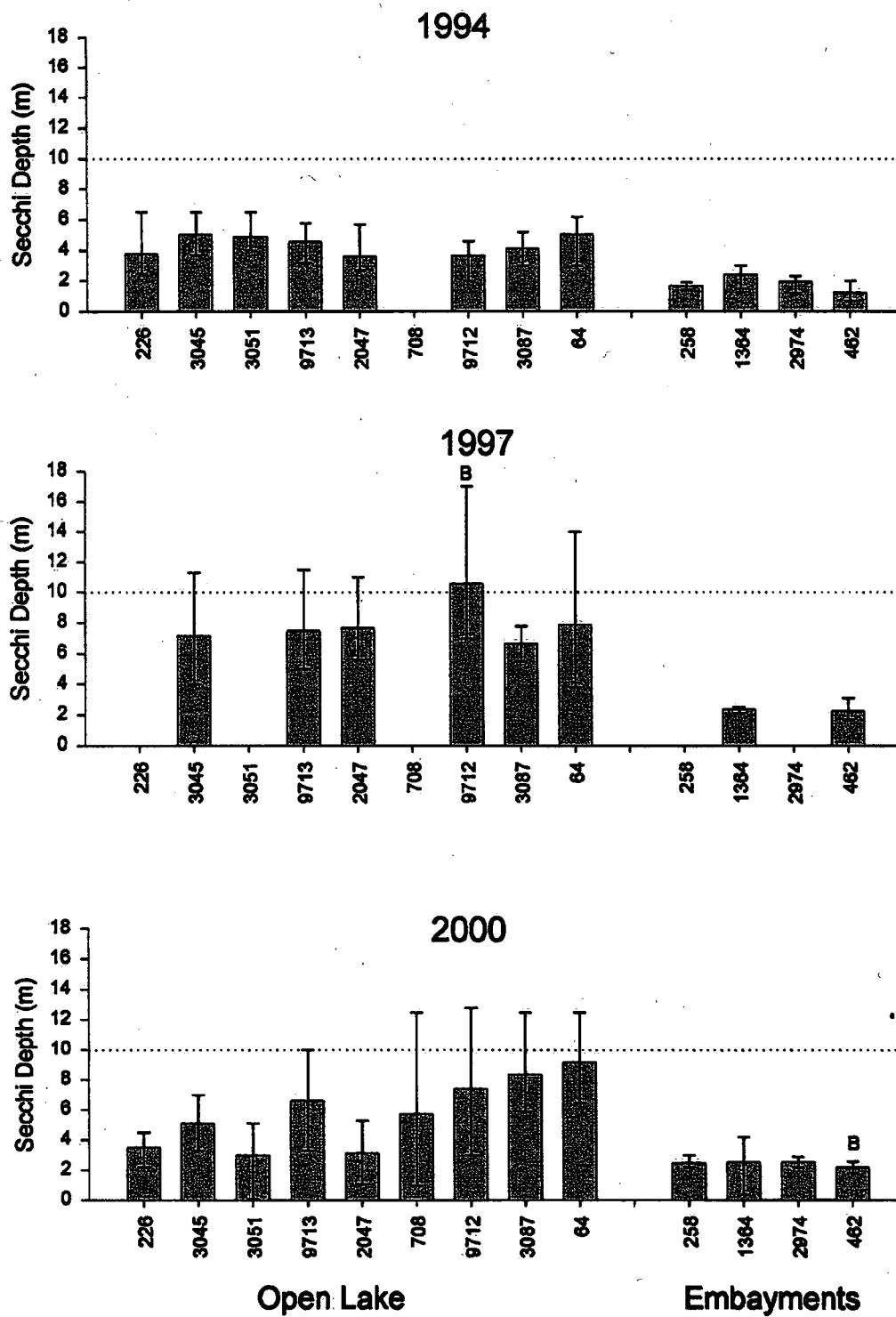


Fig.2

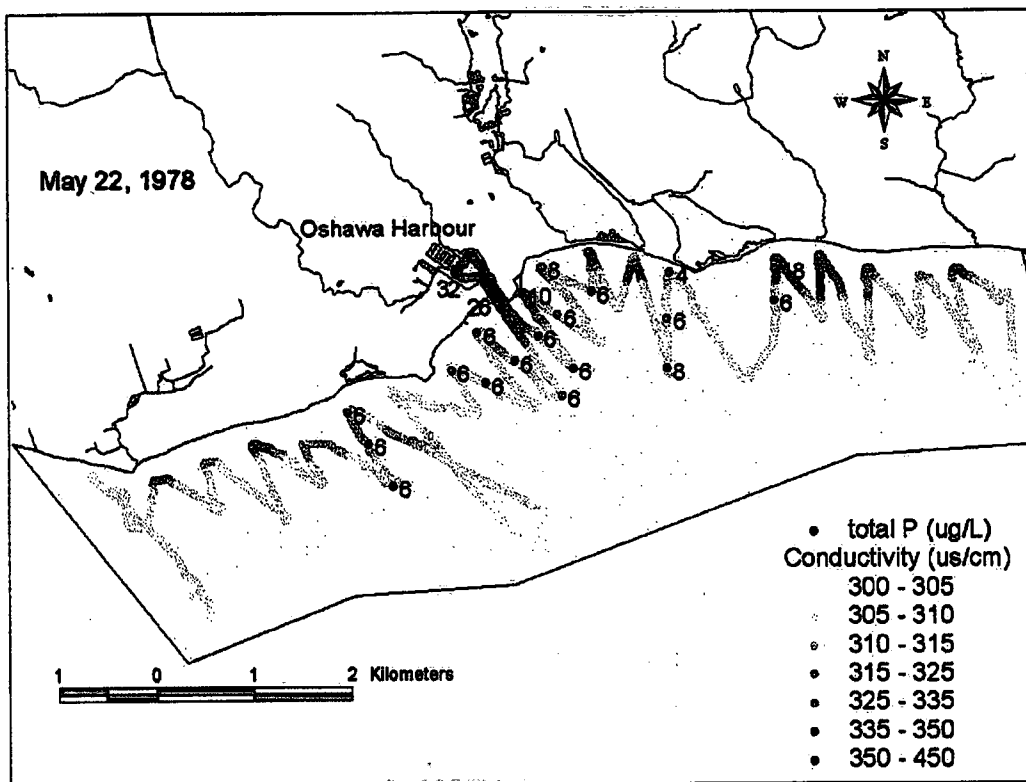
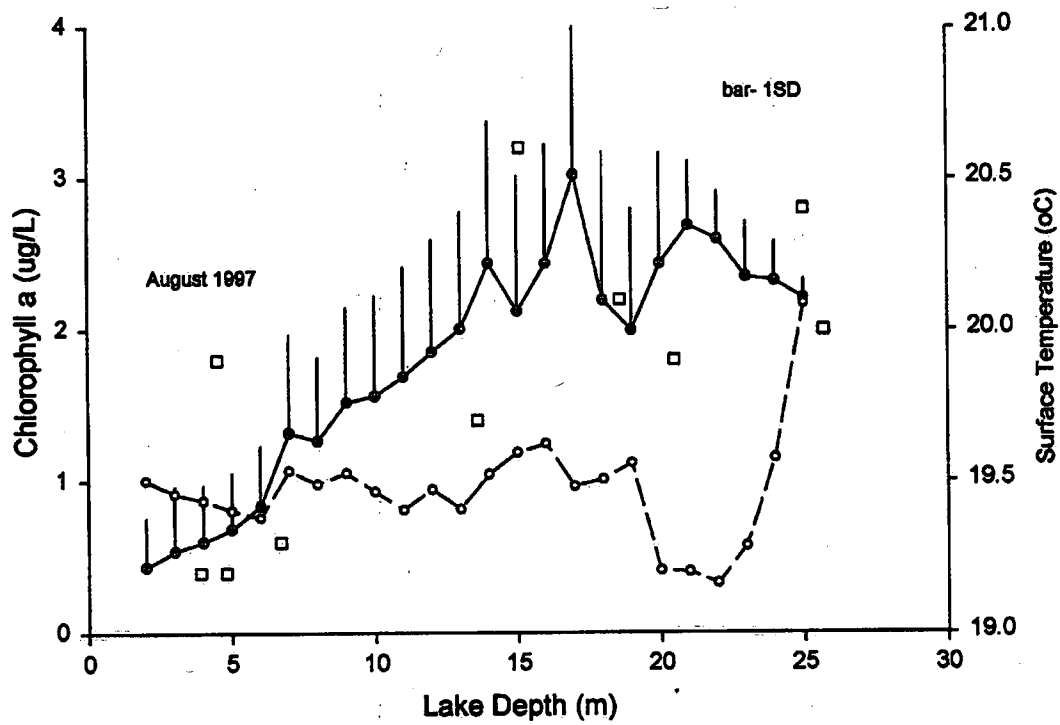


fig 3

fig 4



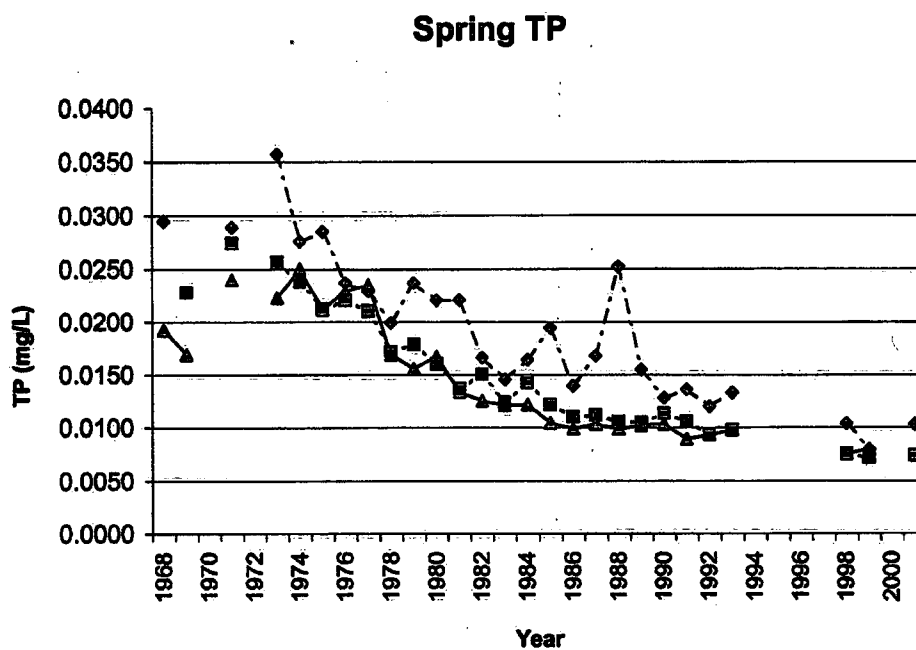
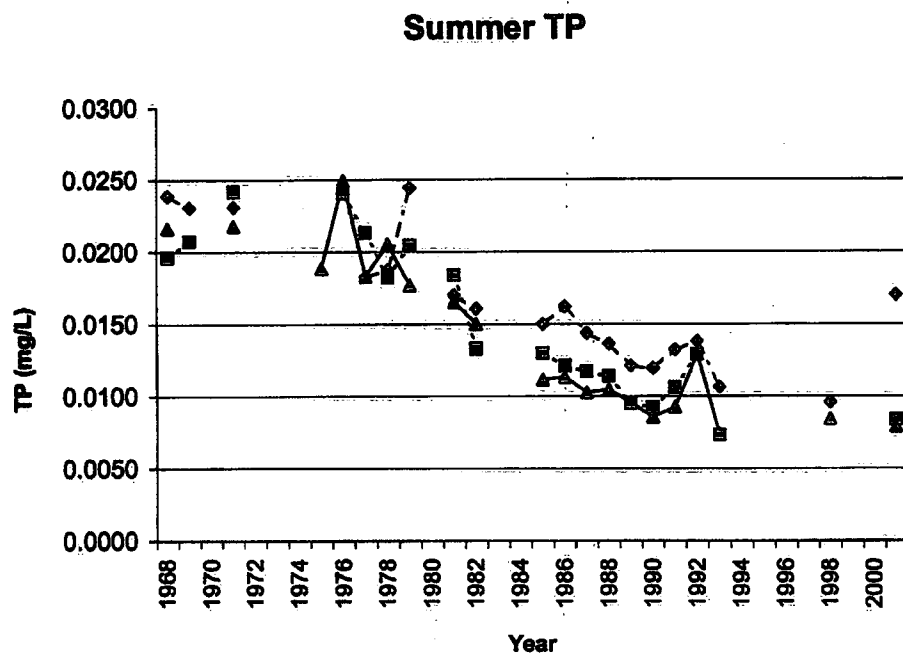
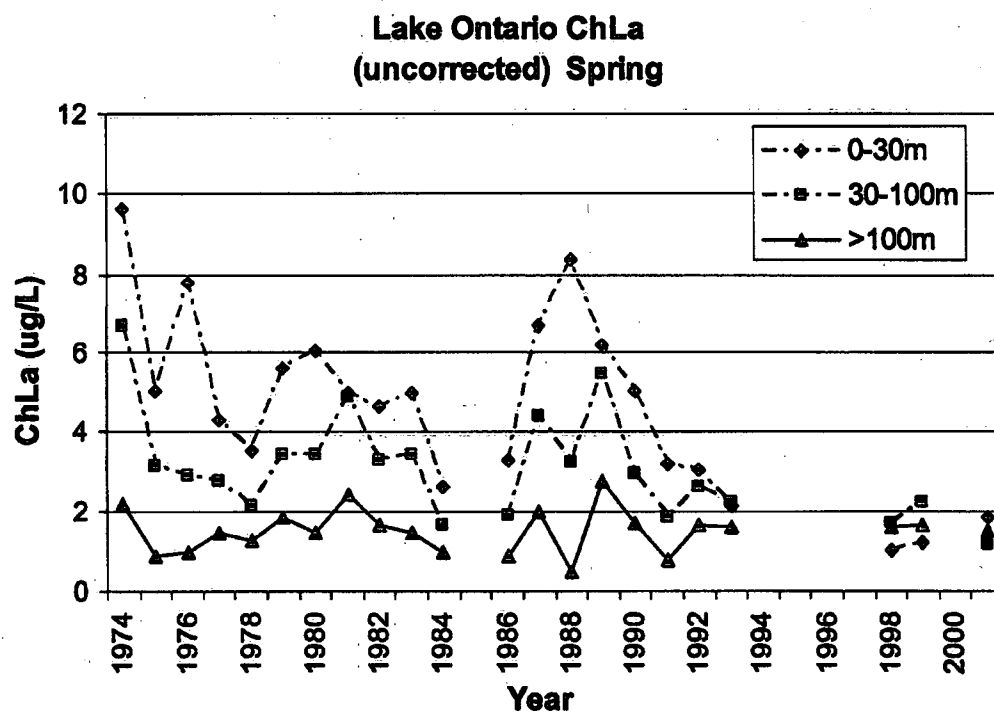
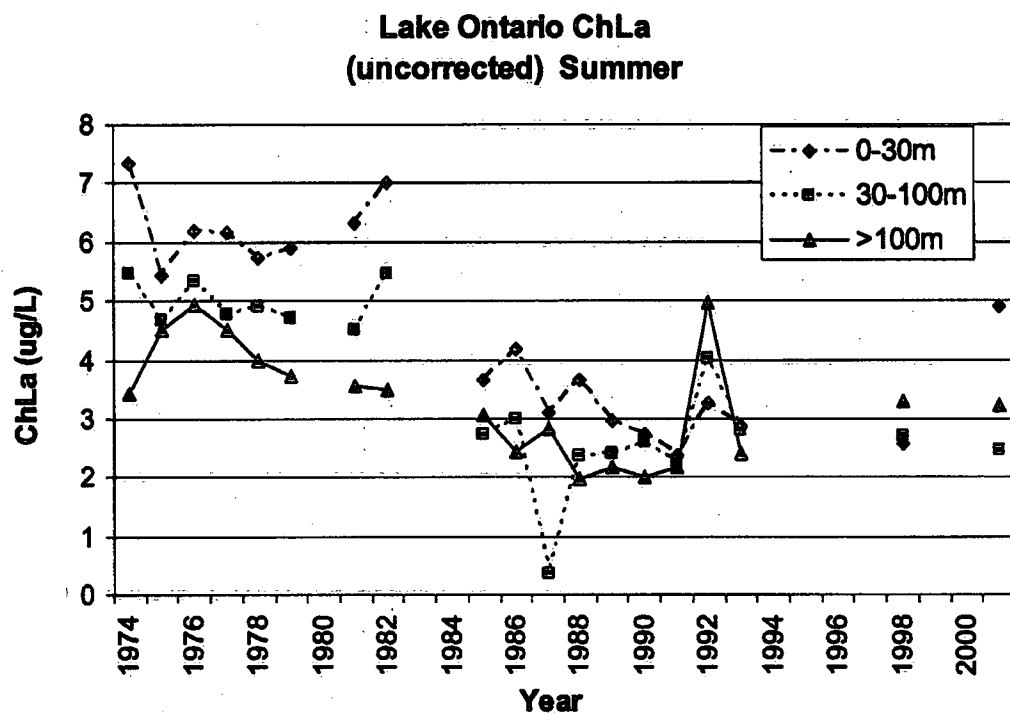


Fig 5

Fig 6 for chl a



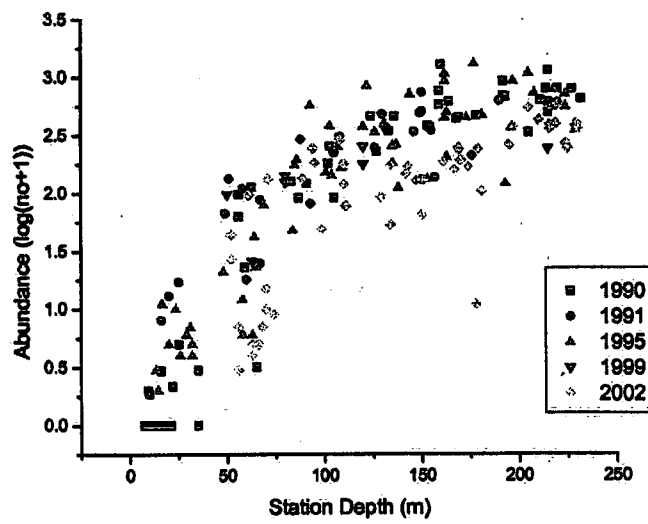


Fig. 7.

Fig 8

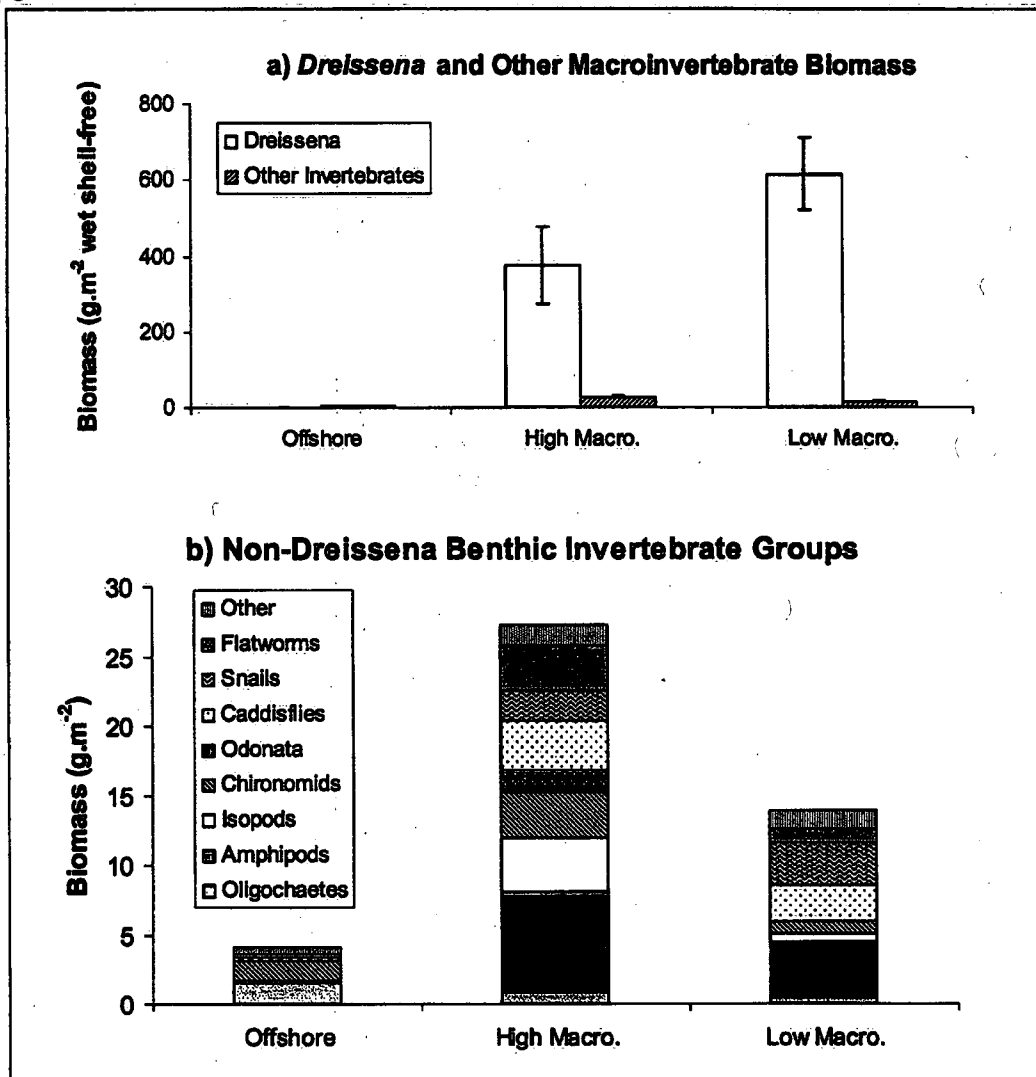


Fig 9

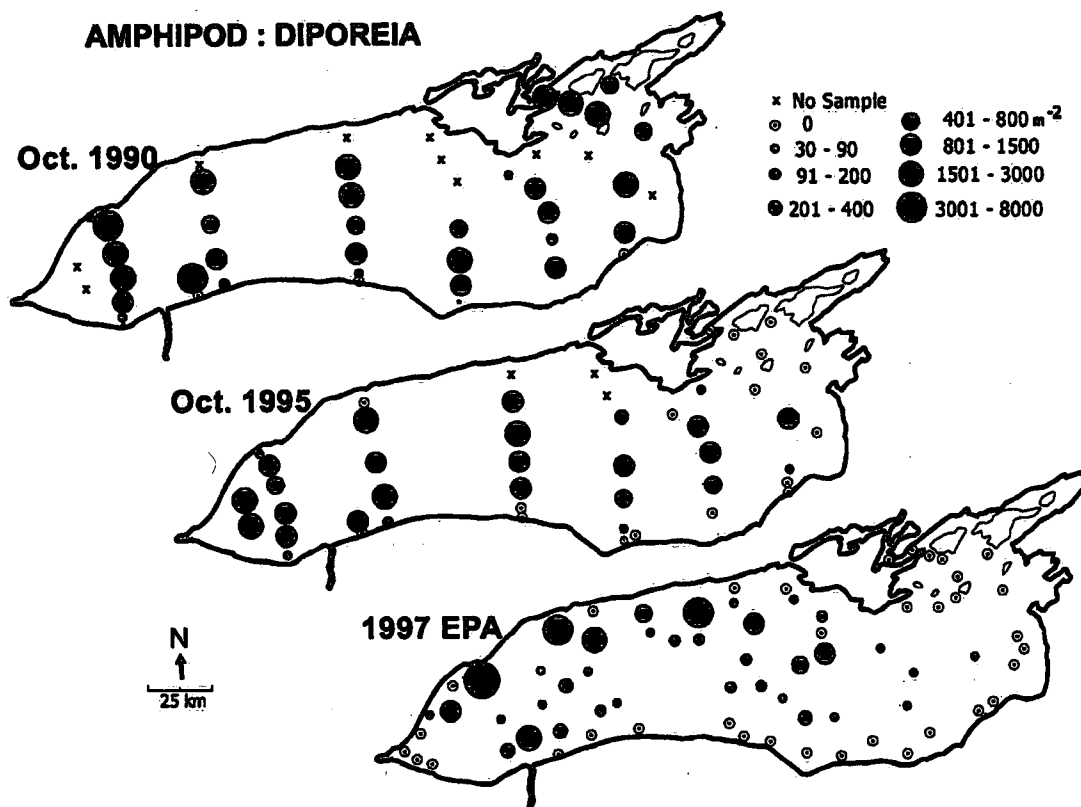


Fig 10

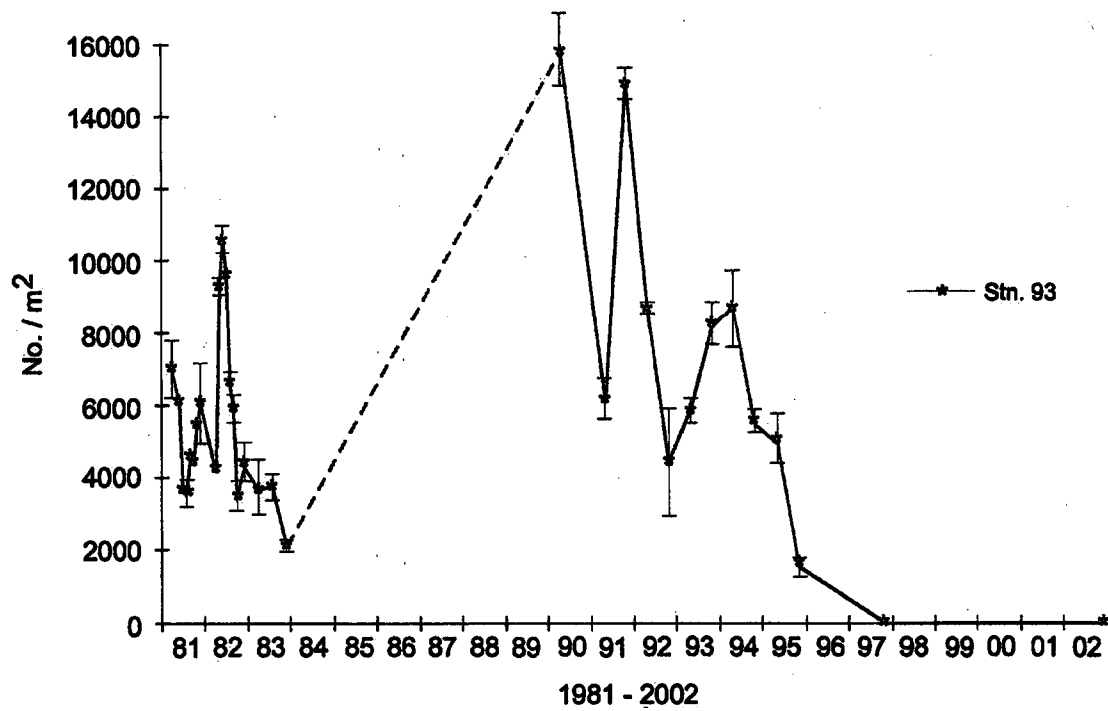


Fig 11

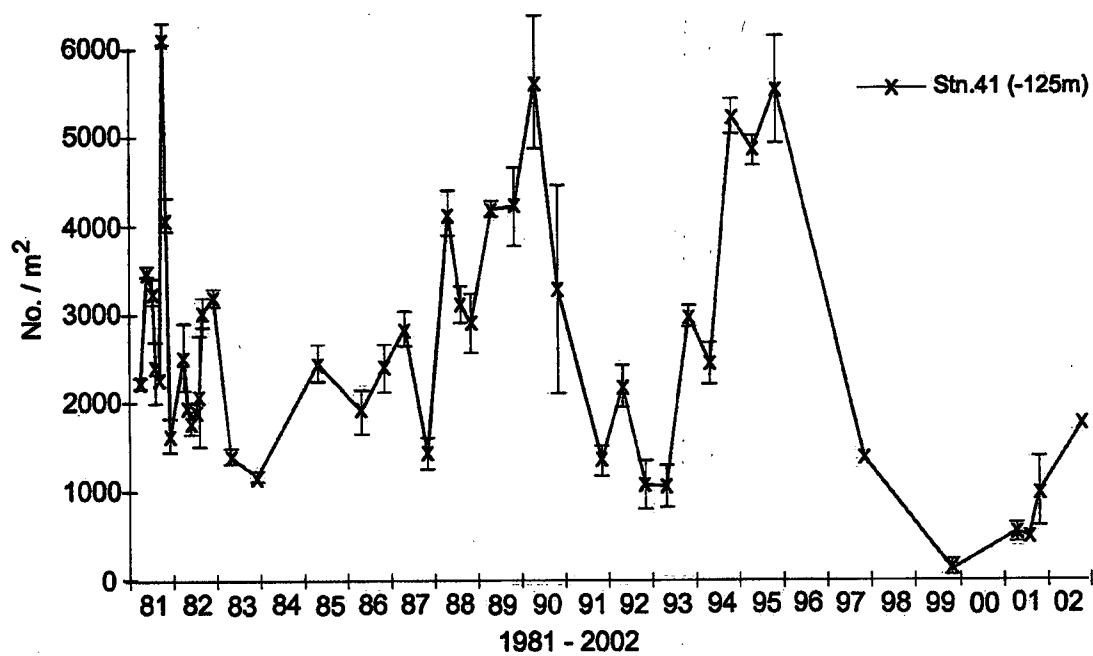
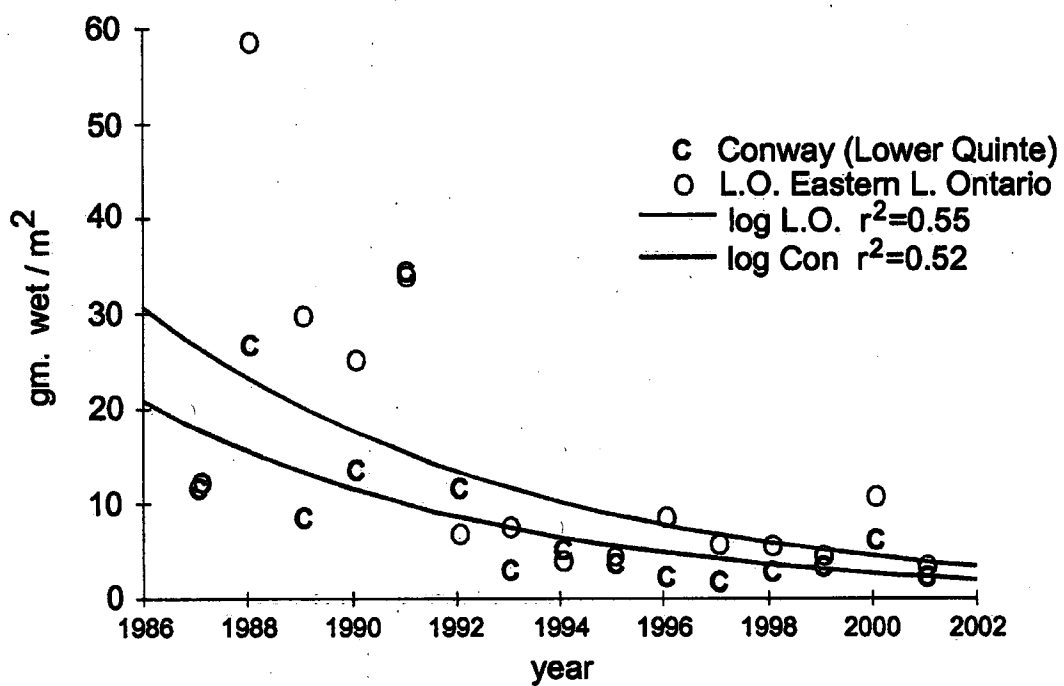


Fig 12



Environment Canada Library, Burlington



3 9055 1018 1268 2



Environment
Canada

Environnement
Canada

Canada

Canada Centre for Inland Waters

P.O. Box 5050
867 Lakeshore Road
Burlington, Ontario
L7R 4A6 Canada

National Hydrology Research Centre

11 Innovation Boulevard
Saskatoon, Saskatchewan
S7N 3H5 Canada

St. Lawrence Centre

105 McGill Street
Montreal, Quebec
H2Y 2E7 Canada

Place Vincent Massey

351 St. Joseph Boulevard
Gatineau, Quebec
K1A 0H3 Canada

Centre canadien des eaux intérieures

Case postale 5050
867 chemin Lakeshore
Burlington (Ontario)
L7R 4A6 Canada

Centre national de recherche en hydrologie

11 boul. Innovation
Saskatoon (Saskatchewan)
S7N 3H5 Canada

Gentre Saint-Laurent

105, rue McGill
Montreal (Québec)
H2Y 2E7 Canada

Place Vincent-Massey

351 boul. St-Joseph
Gatineau (Québec)
K1A 0H3 Canada