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By:

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**Historic changes in populations of
burrowing mayflies (*Hexagenia limbata*) from
Lake Erie based on sediment tusk profiles.**

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Management Perspective

There has been some controversy regarding the historic status of the central basin of Lake Erie and whether anoxic events have always occurred or are a relatively recent phenomenon arising from cultural eutrophication. The burrowing mayfly, *Hexagenia*, is particularly sensitive to oxygen depletion and a decline in mayfly numbers in the central basin was first noted in 1949, though they recovered in 1950 and were reported annually until 1957. They were not reported after 1958 (IJC 1969). These reports of mayfly emergence in the central basin suggest that populations of *Hexagenia* may have been present. If these were widely distributed throughout the deeper areas of the central basin, this would support the view that the central basin was oxygenated throughout the summer period and that recovery to this state would be an appropriate management objective. Furthermore, *H. limbata* would be an appropriate ecosystem objective for central as well as western Lake Erie (Edwards and Ryder 1990, Reynoldson et al. 1989). On the other hand, if *Hexagenia* was never present offshore in the central basin this would suggest that intermittent anoxia may be an inherent property of the basin and that management to achieve a state where anoxia does not occur is not a realistic goal for lake managers.

This study supports the view that the deeper waters of the central basin exhibited periodic anoxia prior to European colonization. However, these data suggest that there were significant populations of *Hexagenia* in the central basin probably limited to an area above the thermocline (< 20 m) and in suitable substrate. It is likely these nearshore areas that, as a result of enrichment, supported the nuisance emergences recorded by shoreline communities in the early part of the 20th century. It is from these same areas that mayflies were subsequently eliminated either by the extension of the anoxic area and its duration or possibly in combination with other contaminants.

Finally, the fact that the numbers of tusks observed in the lower parts of cores from both the central and western basins are similar suggests that *Hexagenia* can be used as an ecosystem objective for those areas of the central basin where it was historically present.

ABSTRACT

One of the most dramatic recorded changes in benthic invertebrate community structure due to eutrophication was the elimination of the burrowing mayfly, *Hexagenia limbata*, from the western basin of Lake Erie. This was a catastrophic event occurring as a result of two periods of anoxia in the summers of 1953 and 1955. From the examination of sediment cores the changes in historic populations of *Hexagenia* have been reconstructed from enumeration of mandibular tusks. The changes in the numbers of tusks found in the sediment cores from the western basin of Lake Erie agree well with known historic events but suggest that numbers found in the earliest field samples represent a considerable increase over historic populations. Cores taken from the central basin suggest that *Hexagenia* was formerly only found in a band around the shore and populations never occurred in the offshore waters. It is suggested that this is strong evidence for the occurrence of brief periods of anoxia in the central basin of Lake Erie prior to cultural eutrophication.

Keywords: Lake Erie, *Hexagenia limbata*, pseudo-fossils, anoxia

INTRODUCTION

The disappearance of the burrowing mayfly, *Hexagenia limbata* (Serville), from the western basin of Lake Erie has been one of the most dramatic and best documented responses of benthic communities to environmental stress in the Great Lakes. Prior to 1953 *H. limbata* was the most abundant species in the benthic community of the western basin of L. Erie (Reynoldson et al. 1989), and during adult emergence attained nuisance proportions in many shoreline communities. However, two particularly long warm calm spells in both 1953 and 1955 produced anoxic conditions in the western basin (Britt 1955a, 1955b). *Hexagenia* is particularly sensitive to oxygen depletion and since 1955 the species has been essentially absent from the western basin, although a few individuals have been found near the mouth of the Detroit River, and oligochaetes have been numerically dominant in the benthic community (Reynoldson et al. 1989).

Much of the central basin of Lake Erie undergoes thermal stratification each year, and hypolimnetic anoxia has been an ongoing issue of concern. This anoxia is a result of both high sediment oxygen demand, which has been enhanced by cultural eutrophication, and a small hypolimnetic volume. In recent years, and after great efforts, inputs of phosphorus to Lake Erie have been dramatically reduced (Fraser 1987) and the lake has responded in terms of reduced levels of phosphorus and chlorophyll a (El-

Shaarawi 1987, Rosa 1987). However, the benthic community of the central basin remains dominated by oligochaetes and hypolimnetic anoxia still occurs each year.

There has been some controversy regarding the historic status of the central basin of Lake Erie and whether anoxic events have always occurred or are a relatively recent phenomenon arising from cultural eutrophication. Newspaper reports (IJC 1969) from as early as 1927 describe "immense swarms" of mayflies blown into the City of Cleveland. A decline in mayfly numbers was first noted in 1949, though they recovered in 1950 and were reported annually until 1957. They were not reported after 1958 (IJC 1969). These reports of mayfly emergence in the central basin suggest that populations of *Hexagenia* may have been present. If these were widely distributed throughout the deeper areas of the central basin, this would support the view that the central basin was oxygenated throughout the summer period and that recovery to this state would be an appropriate management objective. Furthermore, *H. limbata* would be an appropriate ecosystem objective for central as well as western Lake Erie (Edwards and Ryder 1990, Reynoldson et al. 1989). On the other hand, if *Hexagenia* was never present offshore in the central basin this would suggest that intermittent anoxia may be an inherent property of the basin and that management to achieve a state where anoxia does not occur is not a realistic goal for lake managers.

Unfortunately, we know little about the pre-enrichment benthic communities of central Lake Erie (IJC 1969, Cook and Johnson 1974, Burns 1985). The earliest data with which we are familiar are the 1963 and 1964 surveys conducted by the United States Public Health Service (1965) and in 1963 by the University of Toronto (Brinkhurst et al. 1968). These data were all collected after the onset of anoxia, and after the last mayfly emergence, based on newspaper reports. As an alternative to historic data we have investigated the use of sub-fossil material to provide an indication of temporal changes in *Hexagenia* populations in Lake Erie.

Hexagenia limbata has a burrowing lifestyle. The nymphs construct a U-shaped burrow in consolidated fine grained sediments. They are then able to remain in the burrow through which they pump water and feed on particulate material carried on the current. As an adaptation to their burrowing life style they have modified mandibles with heavily sclerotized tusks (Hunt 1954).

One of the authors (Hamilton) had earlier observed an abundance of mayfly tusks during a preliminary scan of a sediment core from the western basin of Lake Erie. That core was examined in conjunction with a review of chironomid populations in the lower Great Lakes and Georgian Bay (Brinkhurst et al. 1968). From this observation it seemed that these tusks remain preserved in the sediment. As a consequence of this observation we have investigated whether or not the distribution and abundance of the tusks in sediment cores can be used to indicate changes in populations over time.

In this study we attempted to address the following issues: first, to determine whether *Hexagenia* tusk profiles can be obtained and replicated in the sediments; second, to relate profiles to populations from contemporary sampling; and finally, to establish the spatial pattern of tusk distribution in the central basin.

MATERIALS AND METHODS

Thirty two cores were obtained from 45 stations in four sampling years (Table 1). The stations were located in all three basins of the lake (Fig. 1). In 1988 a large box core (0.5 x 0.5 m) was used for sampling four sites and single cores were removed from the box core by slowly inserting a large diameter (i.d. 10 cm) plexiglass core tube into the box core. The core was capped and removed for subsequent slicing in 2 cm horizons. Four sites (Fig. 1) were sampled in 1988, to establish whether or not tusks could be identified from sediment profiles. The sites included a station from western L. Erie (357) where large populations existed prior to the 1953 disappearance (Britt, 1955a, 1955b) and three stations in the central basin. All subsequent cores were taken using a Benthos Corer using a smaller diameter core tube (i.d. 6.6 cm) as it permits longer (up to 1 m) cores to be obtained. Three replicate cores were taken at one station (357) to establish small scale variability. The longer Benthos cores were sliced in 4 cm horizons. The core sections were placed in individual Whirlpak® plastic bags and stored at 4°C prior to processing. Each core slice was sieved through 250 μ mesh to remove the excess material,

and the residue was stored in 4% formalin for preservation and sorting. Tusks were counted in individual core horizons using a low power (25 x) stereo microscope.

RESULTS

1. Are tusks present?

Results from the 1988 cores (Fig. 2) showed that the tusks do provide a core record where known historic populations existed in the western basin (357) and furthermore that a pattern exists in the tusk profile. In core 357 there were no tusks from the core surface to a depth of 6 cm. From 6 - 14 cm the number of tusks were variable, followed by a large increase in numbers between 16 and 22 cm, below which the numbers were lower and showed little variation, to the bottom of the core at 36 cm. From two of the central basin cores few (815) or no (84) tusks were found, and from site 817 tusks only occurred regularly below 22 cm (Fig. 2).

We believed these data were sufficiently encouraging to support further investigation of the use of tusk profiles for interpreting historic patterns in the population dynamics of *Hexagenia*.

2. Do profiles exist and do they represent past events?

The argument for the existence of tusk profiles and their historical interpretation is based on data from cores taken from site 357 in the western basin. The core taken in 1988 clearly showed a distinct vertical profile. Three replicate cores taken in

1990 from the same site using a benthos corer (i.d. 6.6 cm) showed a similar profile over a greater length (Fig. 3). We consider these cores to provide an interpretable record of historic patterns in abundance of *Hexagenia* that is consistent both with early benthic surveys and with historical events in the basin. The cores show historic populations, represented by the deeper portions of the core from 33 cm to over 70 cm, have been stable with little fluctuation in numbers. This was followed by two periods of increasing numbers (33 - 25 cm and 17 - 9 cm), and a period of decline and then eventual disappearance (7 - 0 cm). While the precise depth at which these events occur in the replicate cores is variable (Fig. 3) and also offset from the 1988 core (Fig. 2), possibly because of different core tube diameters and amount of compression, the sequence is the same in both.

Historic data assembled from field sampling (Fig. 3) of the western basin were compiled in a previous publication (Reynoldson et al. 1989) and show the decline and disappearance of the population of *Hexagenia* in the mid 1950's. The disappearance was preceded by a period of decline and instability in the late 1940's. The field data also indicate periodic declines in the population in the late 1930's. However, the populations of *Hexagenia* in the early 1930's and 1940's were extremely large. These field data are consistent with the two cores and describe similar trends. However, as there are no simple mechanisms for dating the core profiles it is not possible to match the two data sets chronologically.

True sedimentation rates are extremely difficult to obtain for the western basin of Lake Erie because of frequent resuspension events. However, accumulation rates have been proposed by various authors ranging up to 7 mm yr⁻¹ (Kemp et al., 1977). In a recent survey Carter and Hites (1992) sampled 10 stations in the western basin and using ¹³⁷Cs profiles and maxima suggested linear sedimentation rates between 2.8 and 7.2 mm yr⁻¹, with an average of 3.9 mm yr⁻¹. Burns (1985) suggested an average accumulation rate of 3.1 mm yr⁻¹. The use of an average sedimentation rate is possibly misleading as sedimentation rates have undoubtedly varied due to both climatic and cultural changes. We would anticipate rates to have been lower than the average prior to the draining of the Black Swamp, to be higher than average during the draining of the swamp, to have then likely declined immediately after the swamp was drained but to have subsequently increased with more intense agricultural and urban development in the basin. Despite these considerations an average rate is considered the most appropriate to use. Dates derived from a sediment accumulation rate of 3.1 mm yr⁻¹ have been applied to the two cores taken from the western basin. The profiles show remarkable corroboration with historic events. The peak in abundance in the late 19th century occurs just after the clearing of the Black Swamp, an area of over 3900 km², which was part of the Maumee, Portage and Sandusky River watersheds. A second increase in numbers appears coincidental with rising human population in the basin and may be a response to general enrichment of the lake. Large populations of *Hexagenia* were sustained until the mid 1950's.

We believe the core profiles are consistent enough with historic events to provide a chronological record of the overall pattern of abundance of *Hexagenia* populations in western Lake Erie and thus may be indicative of populations in the central basin of Lake Erie.

3. Distribution of Tusk Profiles in the Central Basin

Forty sites were visited in the central basin of L. Erie between 1989 and 1991 (Table 1). Of these 16 had a substrate that was unsuitable for coring consisting either of sand, stone or clay (Fig. 4). As *Hexagenia*, requires fine silt for burrow construction such areas would be less suitable habitat for *Hexagenia* which would likely be absent or found in low numbers in such areas. Data from the remaining 24 sites have been summarised by compositing the number of tusks at various sediment depths. The sediment depths were selected to represent approximate 50 year time intervals using an average sediment accumulation rate for the basin of 1.5 mm yr^{-1} (Burns 1985), which is similar to the rate of 1.3 mm yr^{-1} that was presented by Carter and Hites (1992). While such a rate is arguably inappropriate for all parts of the basin, it serves as a useful general indicator for the purposes of summarizing the data. From these 50 year accumulations of tusks we have developed distribution contours that represent the potential distribution of *Hexagenia* in the central basin for three 50 year time intervals (Fig. 4).

In the deepest core sections (40-48 cm) tusks were found on both

south and north shores but were essentially absent from almost all the deeper waters (>20 m) of the central basin. In the middle sections of the cores (16-24 cm) a similar pattern was observed with some loss on the south shore and little change in the deeper waters of the north shore. The most striking differences are in the most recent sediments (0-8 cm). No tusks were found in the more modern material on the south shore, except on the western extremity of the basin and no tusks were found on the north shore west of Rondeau Pt (Fig. 1).

DISCUSSION

The results from this study demonstrate the value of palaeo-ecological data in addressing environmental management issues. We believe these tusk data do provide a true chronology of the basic changes and distribution of *Hexagenia* populations in Lake Erie. The observed sequence of tusks in the sediment matches the available chronological pattern based on sediment accumulation rates. It also coincides with both contemporary sampling of the benthic community and the known history of *Hexagenia*. This is illustrated in the profiles obtained from the western basin. These profiles shows historic populations that fluctuated only slightly in numbers, based on numbers of tusks, from an estimated date of 1740 (bottom of core) to the late 1890's. This was followed by a large increase in tusks co-incident with the completion of the clearing of the Black Swamp, which formed a large part of the watershed of the western basin. It is reasonable to presume that

the result of this clearance was an increase in nutrient supply and primary production in the western basin, and thus a response of increased production in the benthic community, including *Hexagenia*. This appears to have been followed by a second period of stability until the 1930's when the number of tusks increased. This high number of tusks occurred in the core from 17-9 cm, which represents, based on sediment accumulation rates, a period during which record numbers of mayflies occurred in the western basin (Manny, 1991). Numbers of tusks in the core above 9 cm decreased rapidly and none were found at the surface. The beginning of the decline in tusk numbers at 9 cm, based on sediment accumulation rates, is dated to 1960, very close to the 1955 disappearance of *Hexagenia*.

If we accept that the western basin profile provides a valid chronological record, the profiles from the central basin suggest that the deeper, offshore waters have never supported populations of *Hexagenia*, even though the substrate, a silty mud, is ideal for a burrowing species such as *Hexagenia*. This could be due to a number of factors such as water depth, distance from shore, temperature requirements or the oxygen regime. However, *Hexagenia* has been reported at depths greater than 33 m (Rawson 1930), deeper than the central basin of Lake Erie. Distance from shore should not be a factor in Lake Erie. For example, *Hexagenia* is an important component of the Lake Winnipeg benthic community (Flannagan 1979) a lake of similar area (24,530 km² v. 25,820 km² for L. Erie) and

mean depth (13 m v. 21 m for L. Erie) to Lake Erie (Hutchinson 1975) and is distributed throughout the lake at distances of up to 20 miles from shore (Flannagan, personal comm.). The distance from shore in central Lake Erie is no greater than this and is therefore unlikely to be the reason for its absence. The oxygen regime is undoubtedly important. For example, *Hexagenia* was formerly an important component of the benthic community of Oneida Lake, being present both above and below the thermocline (Jacobsen 1966). The disappearance of *Hexagenia* from Oneida Lake has been attributed to eutrophication and consequent hypolimnetic anoxia (Jacobsen 1966).

We argue that the most likely explanation for the historical absence of *Hexagenia* from the offshore waters of the central basin of Lake Erie is that periodic anoxia has always occurred in those deeper waters. Consequently a management target requiring that the central basin always be oxygenated is neither realistic nor achievable. However, these data do not provide any indication of the frequency or duration of anoxia, as brief (1 -2 day) events are sufficient to preclude the presence of *Hexagenia* populations.

It is highly likely that the extent and frequency of anoxia in the central basin are greater as a result of enrichment. That this is the case is suggested by the change in the distribution patterns of tusks in the central basin profiles. There were large historic populations in the nearshore areas of the central basin where the

substrate was suitable (Fig. 4). These populations have been eliminated from large areas and this corroborates the reports from Cleveland of the disappearance of adults from the south shore. This suggests that hypolimnetic anoxia was historically of much shorter duration and affected a smaller area than in recent times.

Delorme (1982) using evidence from fossil remnants of ostracodes from sediment cores has also suggested that periodic anoxia has occurred in the central basin for hundreds of years. His conclusions were based on the presence of *Candona caudata*, a species tolerant of low levels of oxygen, and the absence of *C. subtriangulata* and *Cytherissa lacustris*, both species with high oxygen requirements, from sediment cores taken from the central basin.

Two lines of biological data, this study and the evidence from ostracode fossils, support the view that the deeper waters of the central basin exhibited periodic anoxia prior to European colonization. However, these data suggest that there were significant populations of *Hexagenia* in the central basin probably limited to an area above the thermocline (< 20 m) and in suitable substrate. It is likely these nearshore areas that, as a result of enrichment, supported the nuisance emergences recorded by shoreline communities in the early part of the 20th century. It is from these same areas that mayflies were subsequently eliminated either by the extension of the anoxic area and its duration or possibly in

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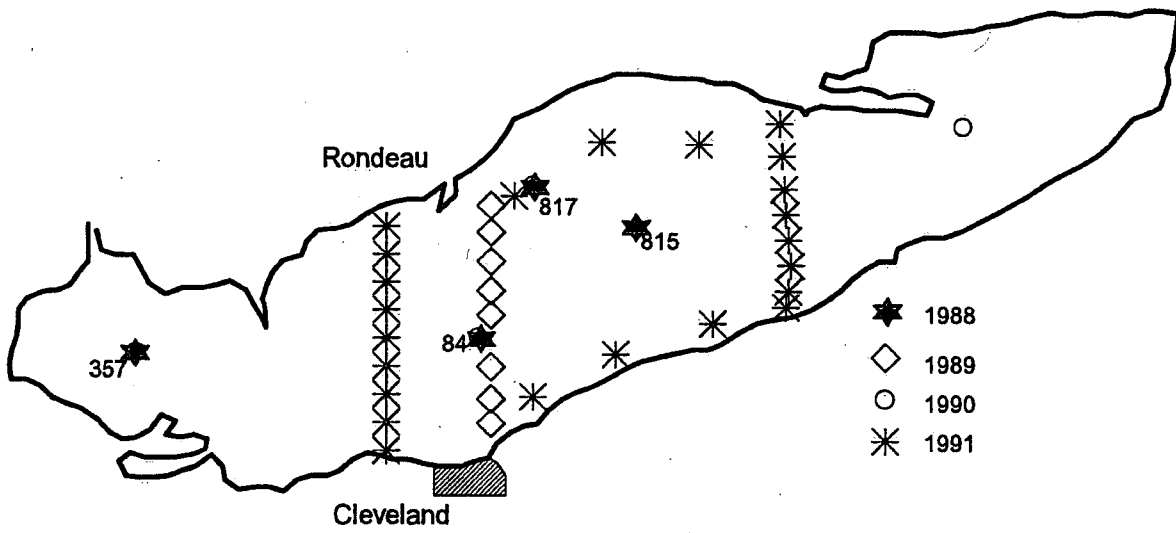
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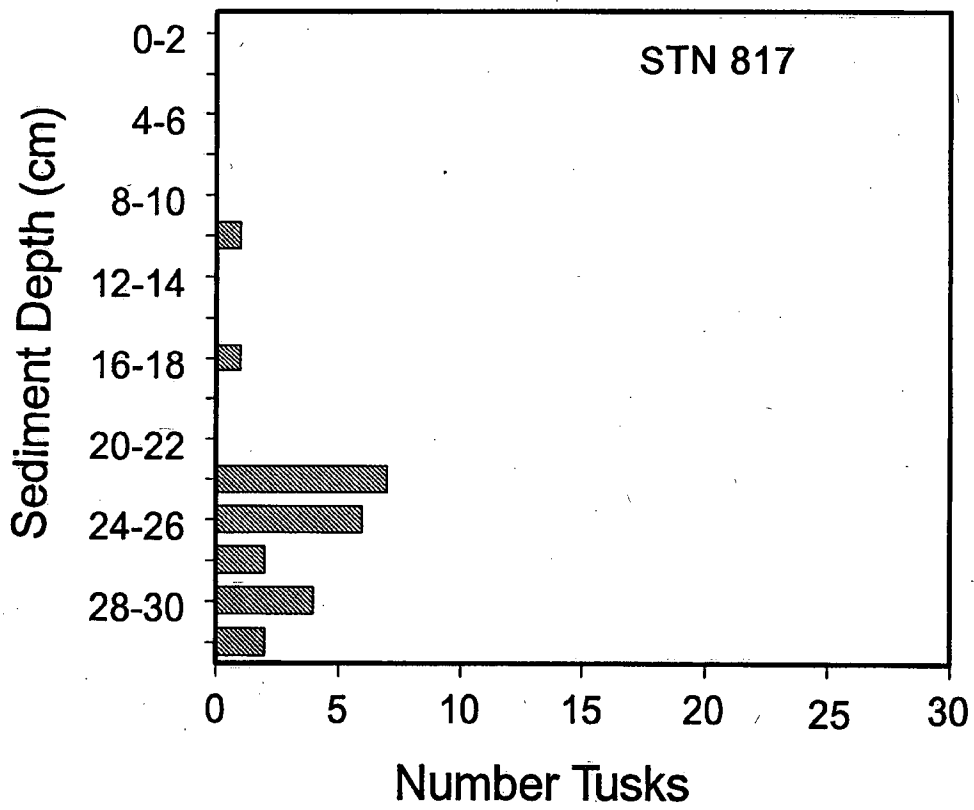
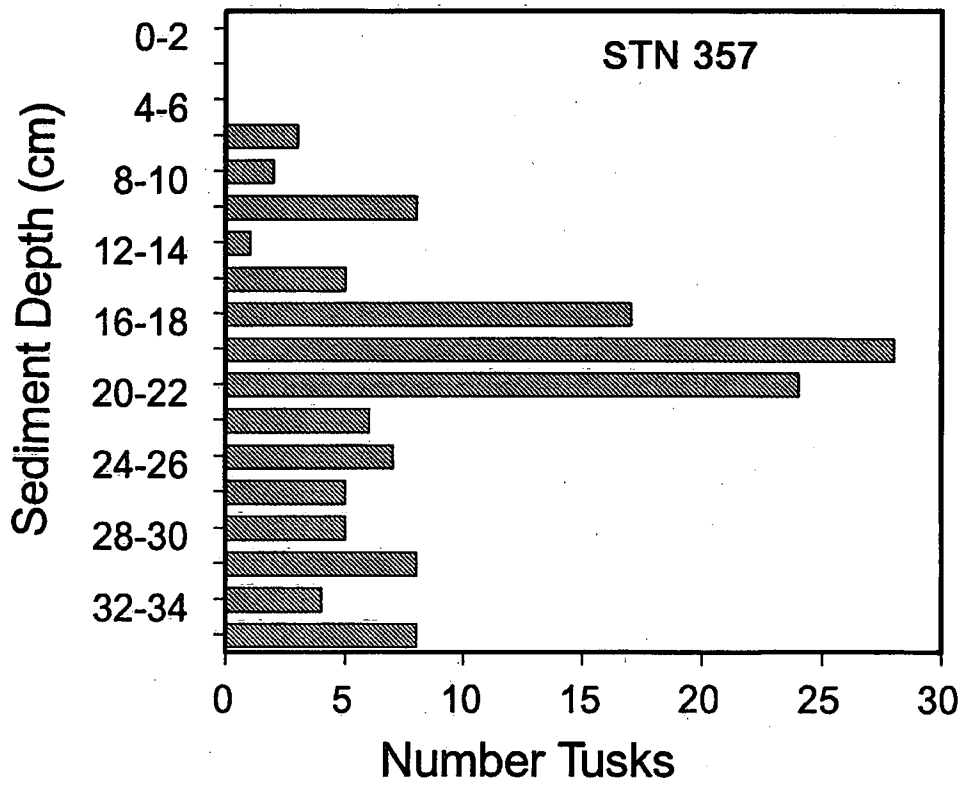
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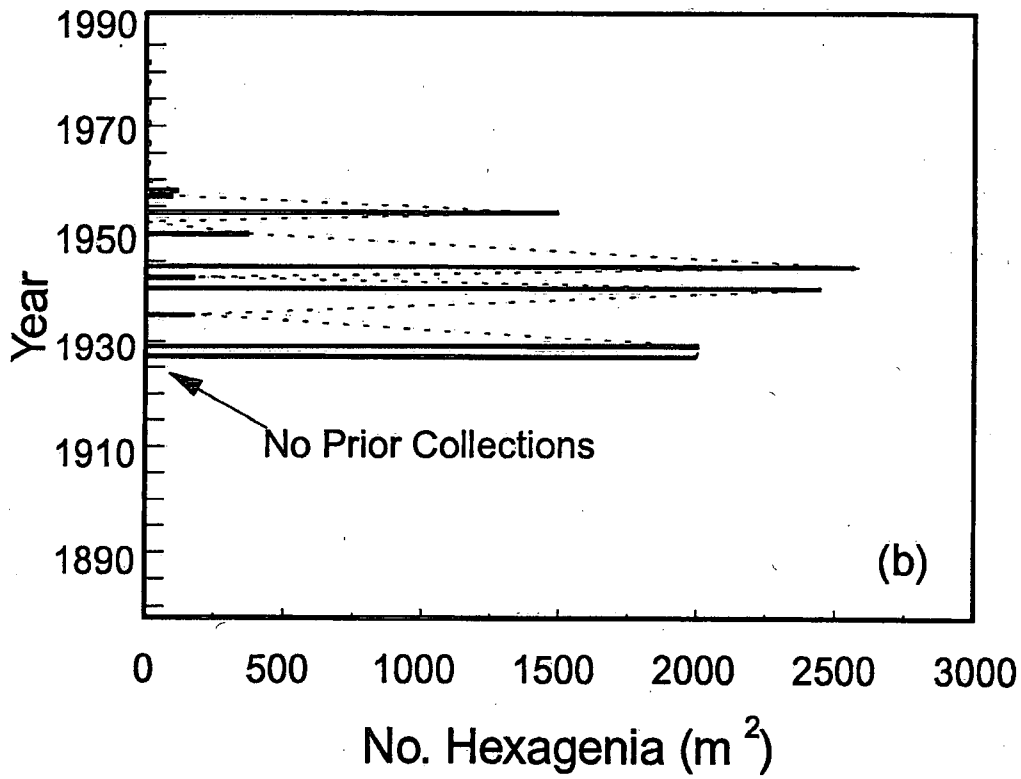
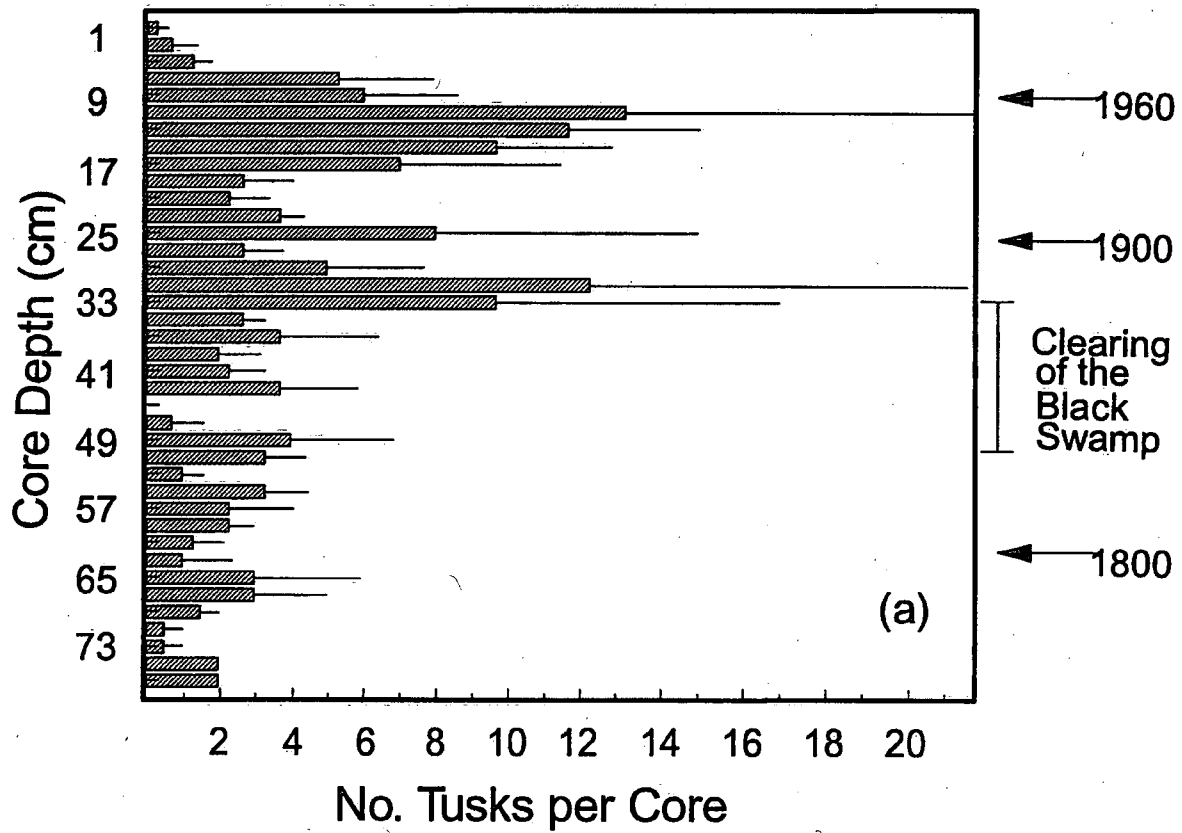
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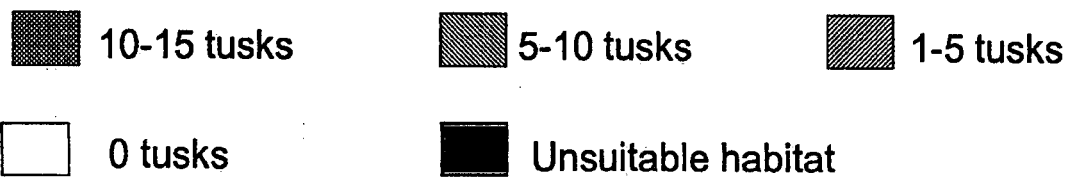
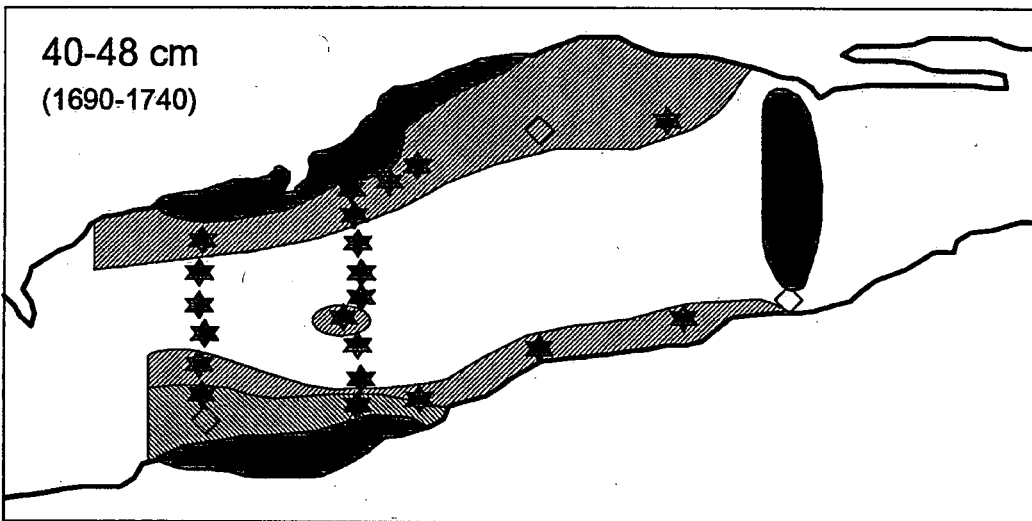
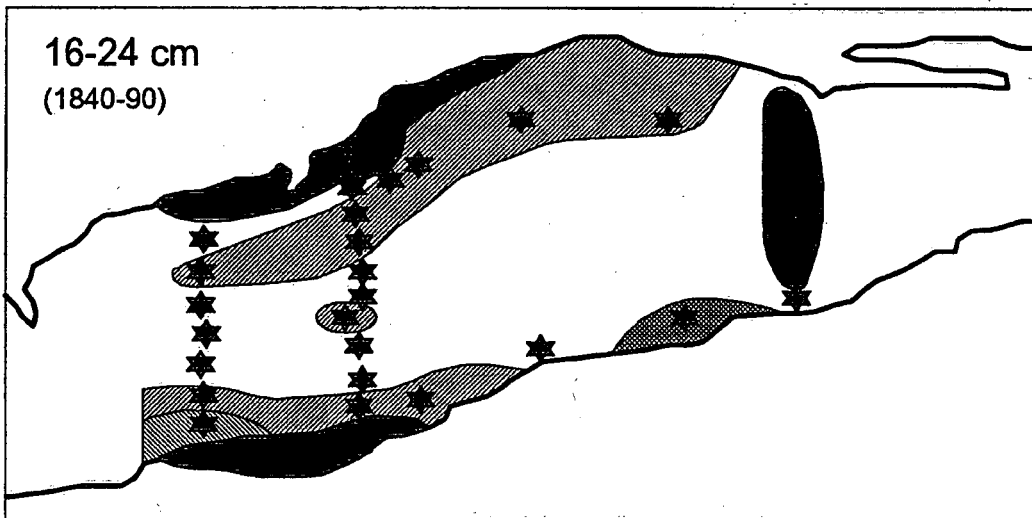
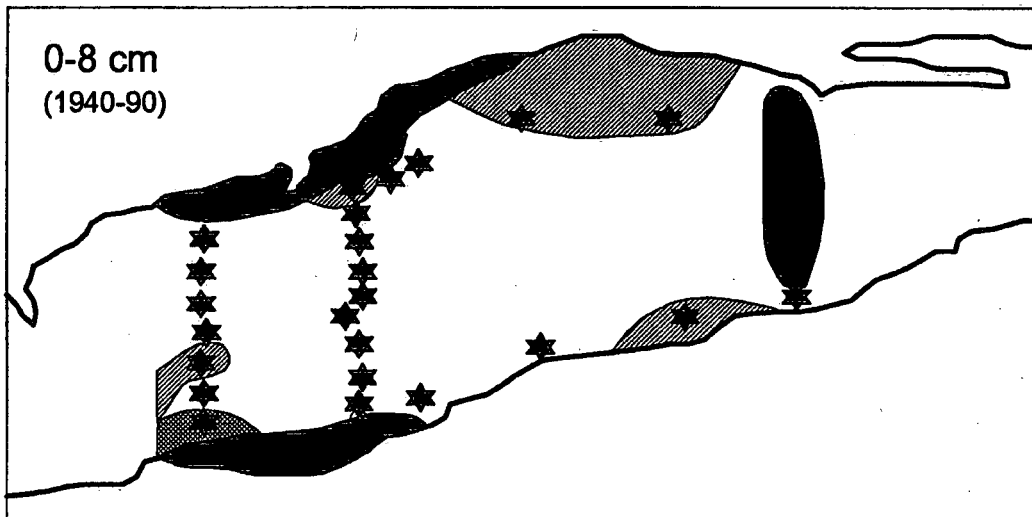


Table 1. Sampling locations for tusk profiles in Lake Erie.

Site	Year	Method	Lat.	Lon.	Water Depth (m)	Core Depth (cm)
357	1988	Box	41°49'46"	82°58'20"	11	36
357	1990	Benthos (3)	41°49'51"	82°58'16"	10.8	64-78
84	1988	Box	41°55'49"	81°39'15"	23	40
84	1989	Benthos	41°55'52"	81°39'33"	25.2	138
84	1990	Benthos	41°56'02"	81°39'38"	25	94
815	1988	Box	42°13'59"	81°07'30"	23	29
817	1988	Box	42°22'02"	81°32'29"	23	33
817	1990	Benthos	42°22'15"	81°32'36"	22	88
206	1989	No core	42°26'54"	81°39'03"	11.7	stones
207	1989	No core	42°24'54"	81°39'08"	15.8	sand/gravel
208	1989	No core	42°22'54"	81°39'04"	19.5	sand/shale
210	1989	Benthos	42°21'12"	81°39'06"	22	122
217	1989	Benthos	42°16'11"	81°39'06"	23	135
219	1989	Benthos	42°11'15"	81°39'09"	23	120
229	1989	Benthos	42°06'18"	81°39'09"	24	100
230	1989	Benthos	42°01'13"	81°39'09"	24	60
231	1989	Benthos	41°51'08"	81°39'15"	24	130
232	1989	Benthos	41°46'21"	81°39'09"	22.5	150
233	1989	Benthos	41°41'20"	81°39'02"	20	83
234	1989	No core	41°39'20"	81°38'56"	18.5	gravel
235	1989	No core	41°37'22"	81°39'08"	16	sand/stones
236	1989	No core	41°35'14"	81°39'08"	15	sand/gravel
237	1989	No core	41°33'15"	81°39'06"	12	sand/gravel
400	1991	Benthos	41°59'07"	80°33'19"	11	16
401	1991	No core	42°04'02"	80°33'20"	12	sand
402	1991	No core	42°08'42"	80°33'30"	20	sand
404	1991	No core	42°18'40"	80°33'47"	20	sand
406	1991	No core	42°28'20"	80°34'21"	14	clay
407	1991	No core	42°23'28"	80°34'09"	20	clay
408	1991	Benthos	42°25'25"	81°01'23"	20	52
409	1991	Benthos	42°27'00"	81°28'15"	20	24
410	1991	Benthos	42°12'58"	81°47'30"	23	104
411	1991	No core	42°10'52"	82°11'18"	20	sand
412	1991	Benthos	42°05'59"	82°11'23"	21	64
413	1991	Benthos	42°00'33"	82°11'19"	20	100
414	1991	Benthos	41°54'13"	82°11'20"	20	104
415	1991	Benthos	41°49'15"	82°11'20"	20	96
416	1991	Benthos	41°44'29"	82°11'18"	19	68
417	1991	Benthos	41°39'29"	82°11'19"	18	84
418	1991	Benthos	41°34'23"	82°11'16"	15	28
420	1991	Benthos	41°39'30"	81°49'28"	20	108
421	1991	Benthos	41°49'01"	81°26'20"	21	104
422	1991	Benthos	41°57'28"	81°55'29"	20	96
23	1990	Benthos	43°30'17"	79°53'57"	62.5	98

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