The distribution of *Heterotrissocladius oliveri* Saether (Diptera: Chironomidae) in Lake Michigan

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Abstract

Fifty one chironomid species were identified from 504 samples collected at depths ranging 8 to 267 m in Lake Michigan, U.S.A. *Heterotrissocladius oliveri* Saether occurred in 32% of these samples and had an average abundance of 22 m^{-2} which was similar to other estimates from the Great Lakes. Maximum average lake-wide density was at 30 to 60 m (41 m^{-2}). At depths ≥ 60 m, *H. oliveri* was the dominant chironomid species comprising 75% of total Chironomidae. The substrate preference of *H. oliveri* differed within each depth regime considered: at 30–60 m, 2–3 ϕ; at 60–120 m, 3–5 ϕ, 7–9 ϕ; and at 120–180 m, 6–8 ϕ. Abundance was notably reduced at all depths in substrates characterized as medium silt (5–6 ϕ). On a lake-wide basis, the distribution pattern suggested *H. oliveri* was most numerous from 30 to 60 m along the southwestern, eastern, and northern shorelines and at 60–120 m depths along the southern and eastern shorelines. Increased abundance in the South Basin was concurrent with evidence of increased sedimentation at 60 to 100 m. However, in several other areas of the lake, high densities were associated with medium to very fine sands relatively free of silts and clays. This observation suggested occurrence of *H. oliveri* was minimally affected by sediment type.

Widely variable, but generally elevated water temperatures likely prevent *H. oliveri* from establishing a substantial population density at depths <30 m. With increased depth, temperature fluctuation is negligible and food is more stable, though the source is variable. Factors limiting abundance of *H. oliveri* at depths ≥ 30 m were related to decreased food supply due to distance from shore, food sources of lower value (clays), and, most importantly, to reproductive replenishment.

Although still oligotrophic in nature, high density occurrences in both high and low sedimentation areas of the lake suggest the trophic indicator status of *H. oliveri* might be broader than previously thought.

Introduction

First identified in the Great Lakes as *Brillia* sp. (Merna, 1960, in Mozley & Howmiller, 1977), *Heterotrissocladius oliveri* Saether has been listed as *Spaniotoma* sp., *Hydrobaenus* sp., *Metriocnemus* sp., *Orthocladius* sp., and *Heterotrissocladius subpilosus* (Henson, 1966; Brinkhurst *et al.*, 1968; Mozley & Howmiller, 1977). With the revision of the *Heterotrissocladius* by Saether (1975a), the nearctic form is now properly referred to as *H. oliveri,* while its palaearctic sister species is *H. subpilosus* Kieffer. *H. oliveri* is an indicator of cold stenothermic, ultraoligotrophic to strongly oligotrophic conditions (Saether, 1975b, 1979), which occur over a broad area of the Laurentian Great Lakes, and it is part of a community composed of *Pontoporeia hoyi* (Amphipoda), *Stylodrilus heringianus* (Oligochaeta), and *Pisidium conventus* (Pisidiidae) inhabiting deep, well-oxygenated waters. These animals represent an oligotrophic group that covers a greater area of the

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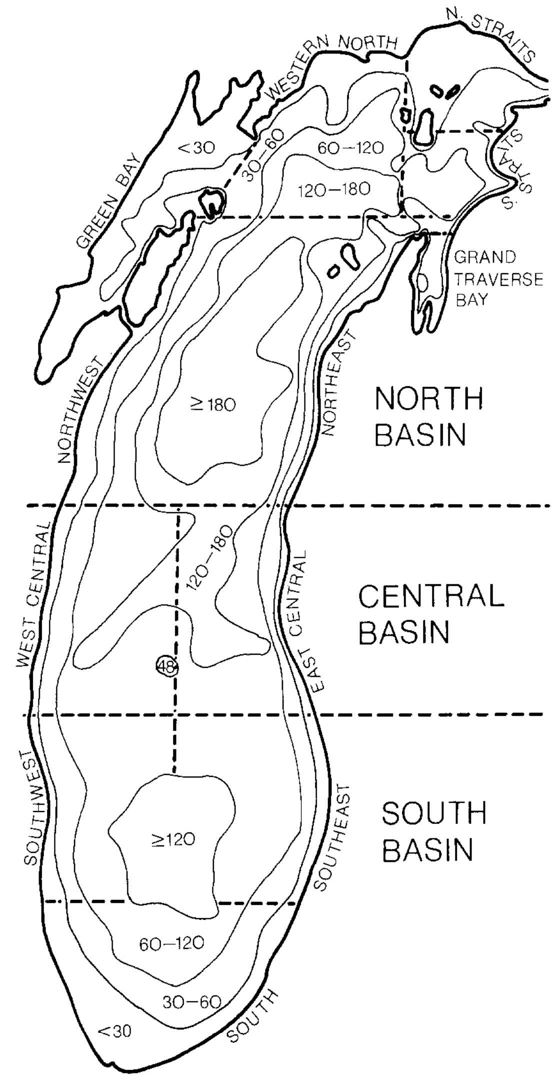

Fig. 1. Areal partitioning of Lake Michigan into major bays and basins with corresponding meter depth regimes. As defined here, shorelines extend from 0–120 m and were uniquely titled to indicate the location of each within respective basins and the lake in general.

Table 1. Chironomidae collected in 1975 and 1977 from Lake Michigan. Species identified from samples collected at depths ≥60 m indicated by *.

Taxon
Chironominae
Chironomini
Chironomus anthracinus-gr.
Chironomus fluviatilis-gr.
Chironomus halophilus-gr.
Chrionomus semireductus-gr.
Cryptochironomus cf. *rolli*
Cryptochironomus sp. 1
Cryptochironomus sp. 2
Dicrotendipes sp.
Harnischia sp.
Microtendipes sp.
Parachironomus cf. *abortivus*
Parachironomus cf. *pectinatellae*
Parachironomus sp. 3
Paracladopelma cf. *nereis*
Paracladopelma cf. *undine*
**Paracladopelma* cf. *winnelli*
Paralauterborniella sp.
Paratendipes sp.
Phaenopsectra sp.
Polypedilum cf. *scalaenum*
Polypedilum cf. *tuberculum*
Pseudochironomus sp.
Robackia demeijerei
Saetheria tylus
Stictochironomus sp.
Tanytarsini
Cladotanytarsus sp.
**Micropsectra* sp.
Stempellina sp.
Stempellinella sp.
Tanytarsus cf. *curticornis*
**Tanytarsus* sp.
Zavrelia sp.
Orthocladiinae
Acricotopus sp.
Corynoneura sp.
Cricotopus sp.
Diplocladius sp.
Heterotrissocladius changi
**Heterotrissocladius oliveri*
Hydrobaenus sp.
Nanocladius sp.
Parakiefferiella sp.
**Psectrocladius* sp.
Pseudosmittia sp.
Synorthocladius sp.
Thienimanniella sp.
Tanypodinae
**Procladius* sp.
Diamesinae
Diamesini
Diamesa sp.
Potthastia longimanus
Protanypodini
Protanypus sp.
Prodiamesinae
Monodiamesa depectinata
Monodiamesa tuberculata

Great Lakes than any other species assemblage (Brinkhurst *et al.,* 1968).

Although *H. oliveri* is widely distributed in the Great Lakes, only a few surveys (Hiltunen, 1969; Kinney 1972; Nalepa & Thomas, 1976; Mozley, 1974, 1975; Cook, 1975; Loveridge & Cook, 1975) have sampled sufficiently in waters deep enough to estimate its overall abundance, and no studies have attempted to examine lake-wide distribution patterns of *H. oliveri* with respect to either depth or localized areal differences.

In 1975, the Canada Centre for Inland Water conducted a benthic survey of all of Lake Michigan focusing primarily on the deeper areas. These data were supplemented in 1977 by a large series of nearshore transects around the lake under the sponsorship of the U.S. Environmental Protection Agency. Both sets of data were then available to examine lake-wide depth and areal density differences, to ascertain general and specific spatial distribution trends, and to establish lake-wide distribution patterns of *H. oliveri* in Lake Michigan.

Methods

In August 1975, 273 benthic samples were collected from Lake Michigan by the Canada Centre for Inland Waters (CCIW) aboard the *C.S.S. Limnos.* One double Shipek grab was taken at each intersection of a 14×14 km Universal Transverse Mercator (UTM) grid over most of the lake. A 7×7 km grid was used in Green Bay and the northeast-most corner of the lake. One portion of the double grab was analyzed for benthic organisms and the other used for sediment particle size determinations. Benthos samples were field sorted through a 250 μm sieve and preserved with 4% buffered formalin. These samples and the unsorted samples were obtained by the Great Lakes Research Division in 1977.

As the 14×14 km UTM grid produced very few shallow or nearshore stations, a second Lake Michigan cruise was undertaken aboard the *R/V Simons* in July and August 1977 sponsored by the U.S. Environmental Protection Agency. Samples on this cruise were taken along 21 transects evenly spaced around the lake approximately 60 km apart. Each transect was aligned along the steepest gradient perpendicular to the shoreline. Station depths at each transect were 9 m, 18 m, 36 m, and 54 m. Two double Shipek grabs were taken at each site. From the first grab, both samples were retained for benthic organisms. From the second grab, one sample was saved for benthos and one for sediment particle size analysis. Benthos samples were elutriated aboard ship using a 100 μm sieve and preserved in 4% buffered formalin for later sorting. Transect 16 from the North Straits area of the northeast corner of the lake did not contain a 54 m station as most of this area is fairly shallow. A total of 251 benthic samples were collected in the nearshore survey. Of the 524 samples available to us, the chironomids were missing from 20 samples, thereby yielding 504 samples for the lake-wide analyses.

H. oliveri occurring in samples collected were analyzed with respect to depth, substrate particle size, and location (area) in the lake. Depth of occurrence was partitioned such that the littoral and sublittoral zones were estimated by the <30 m depth regime, and the profundal zone was estimated by the 30–60-, 60–120-, 120–180-, and $\geq$180-m depth regimes. Substrates were characterized by particle size determinations based on units of phi (ϕ). Occurrence of *H. oliveri* with respect to location within the lake was based on geographic partitioning of the lake and superimposing the previously noted depth regimes (Fig. 1). The 48 m station circled in the West Central portion of the Central Basin denotes its deviation from otherwise considerably deeper water.

In several instances, densities at given location/depth strata were strongly dependent upon a single observation. To illustrate this dependence, all strata densities were recalculated as follows:

(Mean density × n) – (Maximum observed density)/n-1, where n = number of samples in a given stratum.

Results

Relationship to depth

Fifty one species of chironomids were identified from the 504 samples comprising the Lake Michigan data sets. Depths ranged from 8 to 267 m ($\bar{X}=61$ m) (Table 1). *Heterotrissocladius oliveri* occurred in 32% of all samples collected with an average density of 22 m^{-2}. Mean density of *H. oliveri* ranged from a maximum of 41 m^{-2} in 30 to 60 m deep samples to a minimum of 1 m^{-2} at sample depths ≥180 m (Table 2). The greatest percentage of total Chironomidae for *H. oliveri* and percent occurrence among samples collected was in the 60 to 120 m depth range (81 and 57%, respectively). In general, *H. oliveri* occurred abundantly and consistently between 30 and 180 m deep in Lake Michigan.

While all 51 species occurred at depths <60 m, only 6 species were identified from samples ≥60 m ($\bar{X}$=126 m). At depths ≥60 m, *H. oliveri* averaged 19 m^{-2}, comprised 75% of total Chironomidae, and occurred in 42% of all samples collected. Of the other 5 chironomid species at depths ≥60 m, only the density of a *Micropsectra* sp. (4 m^{-2}) exceeded 1 m^{-2}. This species made up 17% of total Chironomidae and occurred in 7% of all samples. *Paracladopelma winnelli, Procladius* sp., *Psectrocladius* sp., and *Tanytarsus* sp. were represented by no more than 1 to 6 individuals total for all samples collected at ≥60 m and together comprised the remaining 8% of the chironomid population in the deepest portion of the lake.

Relationship to substrate type

The substrate preference of *H. oliveri* was different within each depth regime considered. At 30 to 60 m, greatest numbers of *H. oliveri* occurred in fine sand (2–3 ϕ); at 60 to 120 m in very fine sand to coarse silt (3–5 ϕ) and very fine silt to coarse clay (7–9 ϕ); and at 120 to 180 m in fine silt and very fine silt (6–8 ϕ) (Fig. 2). The shallowest and deepest depth regimes were excluded in this analysis, because occurrence of *H. oliveri* was minimal. Between 30 to 180 m deep, the only substrate type in which *H. oliveri* densities were consistently reduced was medium silt (5–6 ϕ).

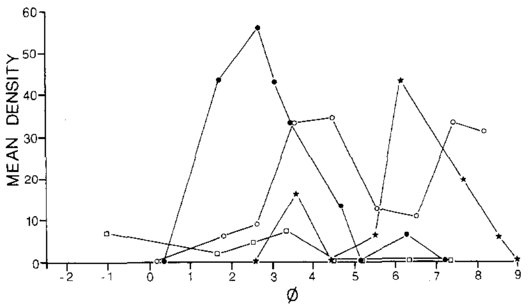

Fig. 2. Mean density (no. m^{-2}) for *Heterotrissocladius oliveri* within the range of sediment types (units of ϕ) at <30 m (squares), 30–60 m (solid circles), 60–120 m (open circles), and ≥120 m (stars).

Distribution in Lake Michigan

Plots generated from the CCIW (Fig. 3) and EPA (Fig. 4) surveys show lake-wide distribution and abundance patterns for *H. oliveri*. Based on the defined areas within the lake (Fig. 1), *H. oliveri* density did not exceed 8% (15 m^{-2}) of total

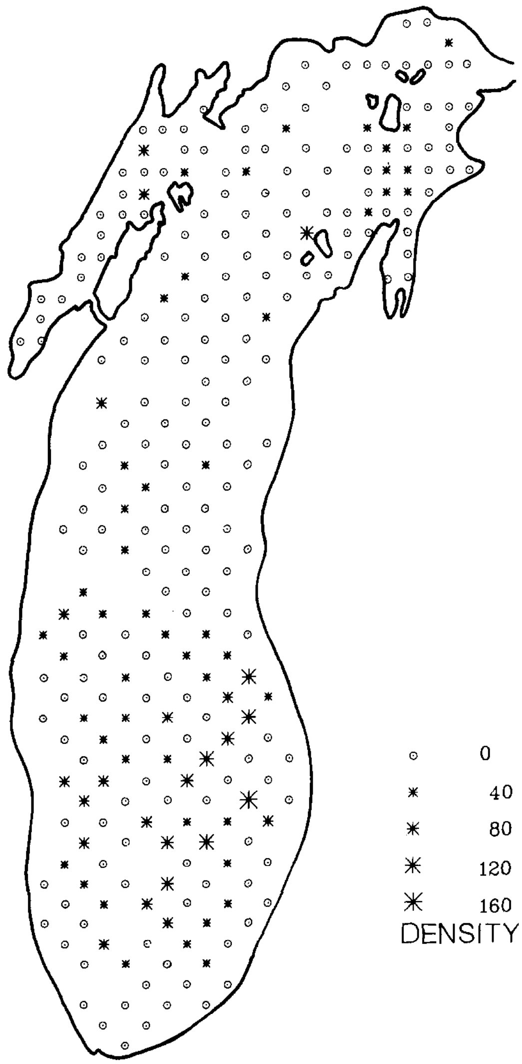

Fig. 3. Distribution and density of *Heterotrissocladius oliveri* in Lake Michigan based on the CCIW sample grid (see Methods), n=1 for each point.

Table 2. Occurrence of *H. oliveri* among selected areas within Lake Michigan (see Fig. 1 for location of lake areas). Density expressed in numbers per m^{-2}. Relative density is percentage of total Chironomidae. Frequency of occurrence is percent occurrence among samples collected. Number of samples collected is n. Actual number of samples examined for *H. oliveri* is in parentheses.

Lake area	Mean density	Relative density (%)	Frequency of occurrence (%)	Mean depth (m)	Mean ϕ	n
<30 m	4.2	<1	7	15	2.00	168
Shoreline						
South	0	0	0	16	2.56	30
Southwestern	0	0	0	15	0.05	13
Southeastern	0	0	0	15	2.69	14
West central	4.2	1	8	14	3.27	12
East central	2.1	<1	8	14	2.20	12
Northwestern	1.3	<1	5	14	1.46	19
Northeastern	13.2	<1	11	13	1.50	19
Western North	12.5	1	14	14	0.31	14
North Straits	1.9	<1	8	17	2.62	14 (13)
South Straits	4.2	<1	17	14	1.26	6
Green Bay	7.8	7	19	18	3.17	17 (16)
Grand Traverse Bay	–	–	–	–	–	–
30–60 m	41.4	41	47	45	3.07	176 (172)
Shoreline						
South	10.6	28	35	46	3.40	27 (26)
Southwestern	55.8	78	77	45	2.58	13
Southeastern	20.0	50	40	46	4.56	14
West central	14.3	53	50	45	3.07	14
East central	59.6	74	69	44	2.85	14
Northwestern	12.5	14	27	45	2.60	22
Northeastern	84.4	50	71	46	2.11	22 (21)
Western North	59.5	56	33	46	2.51	21
North Straits	66.7	21	33	35	4.06	7 (6)
South Straits	87.5	27	70	47	2.41	11 (10)
Green Bay	3.1	14	13	36	6.36	8
Grand Traverse Bay	0	0	0	42	2.42	3
60–120 m	25.9	81	57	90	5.19	97 (88)
Shoreline						
South	35.7	77	86	83	5.35	8 (7)
Southwestern	26.8	100	64	87	5.17	15 (14)
Southeastern	51.6	77	69	88	6.51	18 (16)
West central	12.5	100	44	89	4.77	17 (16)
East central	22.9	100	42	95	5.90	12
Northwestern	8.3	100	33	94	3.68	6
Northeastern	25.0	100	50	94	5.09	5 (4)
Western North	12.5	75	50	98	5.53	6
North Straits	–	–	–	–	–	–
South Straits	17.9	42	71	87	3.14	9 (7)
Green Bay	–	–	–	–	–	–
Grand Traverse Bay	–	–	–	107	–	1 (0)
120–180 m	15.6	62	32	144	7.04	55 (53)
Basin						
South	25.0	50	36	139	7.93	14
Central	20.0	68	47	142	6.82	15
North (lower)	9.7	100	28	148	6.61	19 (18)
North (upper)	0	0	0	149	7.52	7 (6)
≥180 m						
Basin						
North (lower)	1.1	50	4	219	8.48	23
All depths	21.7	4	32	61	3.78	521 (504)

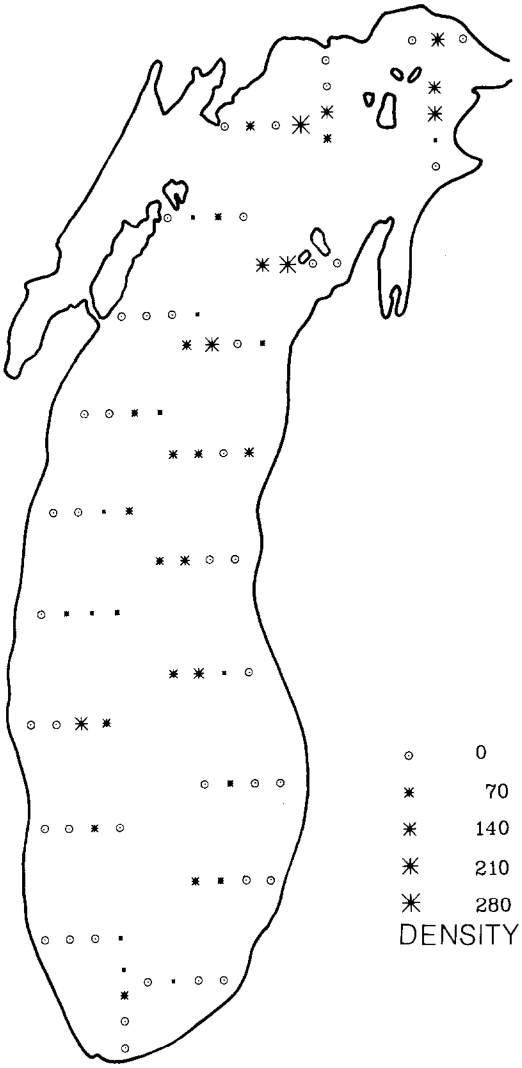

Fig. 4. Distribution and mean densities of *Heterotrissocladius oliveri* in Lake Michigan based on the EPA sample grid (see Methods), n=3 for each point. Location of points along each transect on map do not indicate distance from shore nor exact positioning of station depths (9, 18, 36, and 54 m) but rather are intended to display relative density differences among transects and stations within transects.

Chironomidae, and frequency of occurrence did not exceed 20% at depths <30 m in any area. Lake-wide abundances were maximal at 30–60 m in areas along the East Central shoreline northward and westward to near Green Bay. In remaining areas of the lake, high abundance occurred along the Southwestern shoreline at 30–60 m. Lowest densities at 30–60 m were noted along the South shoreline, along the West Central and Northwestern shorelines, and in Green Bay itself. In general, at depths 30–60 m, the eastern and northern shorelines of Lake Michigan supported greater densities of *H. oliveri* than did the southern and western shorelines.

At 60–120 m, a density distribution pattern similar to that for 30–60 m was evident except it was more restricted tó the southern and mid-northern areas of the lake. Densities ranged 23–52 m^{-2} from the Southwestern shoreline, eastward and northward along the eastern shoreline. All remaining areas of the lake at 60–120 m averaged 8–18 m^{-2}. In general, the southern and eastern shorelines supported greater densities of *H. oliveri* at 60–120 m than did the northern and western shorelines.

At depths ≥120 m, similar densities of *H. oliveri* were noted in the South (25 m^{-2}) and Central (20 m^{-2}) Basins (Table 2). In the North Basin, densities averaged <10 m^{-2}, but with none found in the northern-most region. In general, there was a steady decrease in *H. oliveri* density in a northerly direction at depths ≥120 m.

When examining depth, substrate type, and lake-wide occurrence, several distributional patterns were evident (Fig. 5). At depths <30 m, observed densities either were zero or were largely dependent upon a single sample estimate regardless of area of occurrence in the lake. At 30–60 m, the variability of areal abundances was low in all areas of the lake except along the northern-most shoreline. In addition, nearly all areas 30–60 m deep occurred in nondepositional zones of the lake (<4 ϕ, see Cahill 1981). At 60–120 m, the location of nearly all areas in this depth regime were in transitional zones of the lake (4–7 ϕ, see Cahill 1981). In this latter depth regime, densities in the northern-most areas were the most variable of the areas. In the deepest areas of the lake (≥120 m), densities were similarly variable and occurred in depositional or near depositional zones of the lake (≥7 ϕ, see Cahill 1981).

Discussion

Reported abundances and distributions of *H. oliveri* in the Great Lakes are quite variable. Hiltunen (1969) gave an average of 239 m^{-2} at c. 90 m and 119 m^{-2} at 180 to 225 m depths in

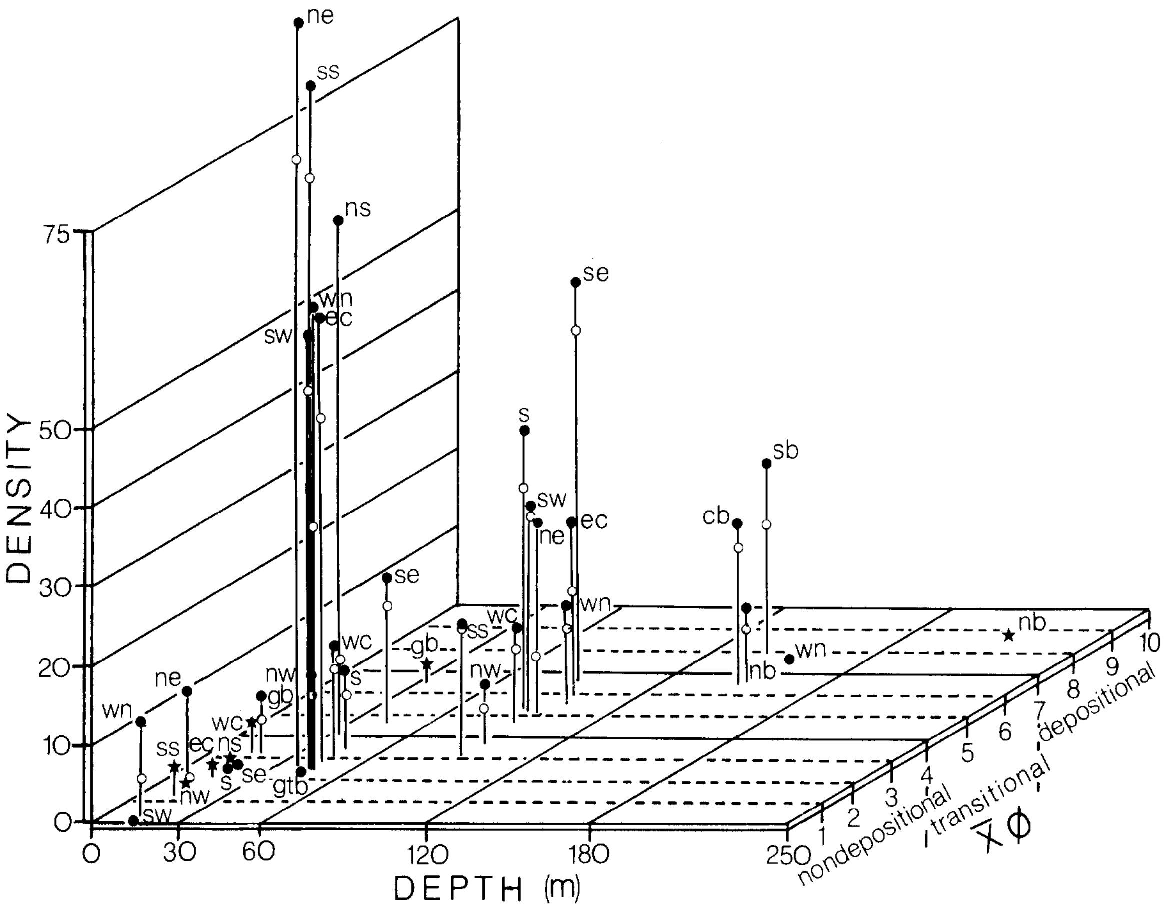

Fig. 5. Three dimensional relationship of average density (no. m(−2)), average depth (<30, 30–60, 60–120, 120–180, and ≥180 m), and mean phi (ϕ) for each area (see Fig. 4) of Lake Michigan. Areas within the lake have been abbreviated as follows: s=south, se=southeast, sw=southwest, sb=south basin, ec=east central, wc=west central, cb=central basin, ne=northeast, nw=northwest, nb=north basin, wn=western north, ns=north straits, ss=south straits, gb=Green Bay, and gtb=Grand Traverse Bay. Mean densities based on all samples in each area, depth, and phi stratum and are denoted by solid circles. Open circles denote recalculated mean densities with the largest single observation removed. Strata with stars denote all except one sample were devoid of *H. oliveri.*

Lake Ontario. However, for the same lake, densities listed by Kinney (1972) averaged only 14–16 m^{-2} at depths >47 m, and densities from Nalepa and Thomas (1976) only 3–4 m^{-2} at depth >50 m. *H. oliveri* is apparently absent from the western and central basins of Lake Erie (Brinkhurst, 1969). For Lake Huron, *Heterotrissocladius* sp. (=*Spaniotoma*) average density was 7 m^{-2} (Teter, 1960), assuming all specimens from 'deep water' stations (25–119 m) were *H. oliveri.* Averaging density values reported by Loveridge & Cook (1975) from Georgian Bay and from the North Channel, Lake Huron, *H. oliveri* density was 41 m^{-2} at stations 11 to 151 m deep. Similarly, in Lake Superior, *Heterotrissocladius* sp. averaged 14 m^{-2} from 11 to 379 m deep based on values we recalculated from Cook (1975). Within Lake Michigan, the lake-wide average density of *H. oliveri* (22 m^{-2}) reported here was not strongly dissimilar to that of other Laurentian Great Lakes. With the exception of the unusually high densities reported by Hiltunen (1969), mean Great Lakes abundances of *H. oliveri* tend to be less than 40–50 m^{-2}.

Occurrence of *H. oliveri* is affected by many factors, but central to these are the three interrelated factors of sediment type, depth, and temperature. Being a cold stenotherm occurring primarily in ultraoligotrophic to strongly oligotrophic water

(Saether, 1975b, 1979) and feeding primarily by ingestion of silty-detrital material (Davies, 1975), very limited occurrence at depths <30 m was expected. However, temperature as opposed to sediment type is likely the primary factor controlling occurrence at depths <30 m as average mean phi (2.00 ϕ) at depths <30 m differed only slightly from that at 30–60 m (3.07 ϕ), but *H. oliveri* densities differed by an order of magnitude (4 m^{-2} and 41 m^{-2}, respectively). Because temperature varies considerably in the shallower waters of the lake both seasonally and within a period of a few hours (Mozley & Winnell, 1975) and is more continuously depressed at depths ≥30 m, we conclude that temperature more than substrate controls the near-shore occurrence of *H. oliveri.*

At depths ≥30 m where temperature is stable, factors that control occurrence of *H. oliveri* are more difficult to distinguish. Edgington & Robbins (1975) demonstrated that maximum sedimentation occurs along the eastern shoreline of the South Basin of Lake Michigan between 60 and 100 m. Maximum abundance of *H. oliveri* in the South Basin generally occurred at 60–120 m, which was most strongly evident along the Southeastern Shoreline (Table 2) implying elevated *H. oliveri* abundances are related to increased sedimentation. In this area of higher deposition, average grain size was regularly near 6–7 ϕ (fine silt).

However, even higher densities occurred along the northern portion of the eastern shoreline largely in high wave-energy environments at 30–60 m. At these locations, predominant medium to very fine sands are mostly free of silts and clays, implying minimal deposition. When comparing the percentage of samples characterized by each phi size against mean density of *H. oliveri* within the depth ranges 30–60, 60–120, and 120–180 m, there was a positive correlation (r^2=0.84, 0.51, and 0.40, respectively) (Fig. 6). The relationship suggests that, regardless of depth regime, maximum numbers of *H. oliveri* occur in the substrate type most common to a particular depth regime. We conclude from this that occurrence of *H. oliveri* is minimally dependent upon substrate type at depths <180 m.

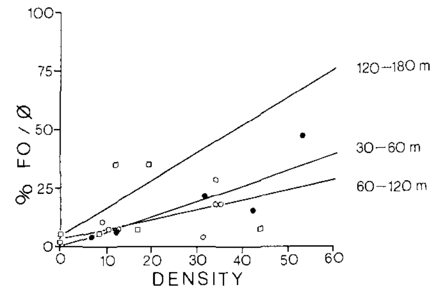

Fig. 6. Linear regression of mean abundance (no. m^{-2}) and percent frequency of occurrence (number of samples with *Heterotrissocladius oliveri* present divided by total number of samples) within each unit of phi (%FO/ϕ) at 30–60 m (solid circles), 60–120 m (open circles), and 120–180 m (squares) in Lake Michigan.

Factors which we feel affect the occurrence of *H. oliveri* are distance from shore as it affects the amount and quality of food arriving at a site and reproductive success. The general distribution pattern observed at depths ≥30 m is one of decreasing density with increasing depth (Table 2). Low densities of *H. oliveri* at these depths, but most particularly at depths ≥180 m, may be more strongly related to reproductive success than to food supply as food supply should be maximal at 35–100 m. The likelihood of an egg or early instar larva migrating through the water column to reach the bottom at 200 m and successfully establishing itself should be considerably lower than that at 100 m. Potential difficulties for the early pelagic stages include currents or storms, which might increase the amount of time needed to reach the bottom. Under these conditions, increased time in the water column increases chances of predation or mishap and ultimately reduces the number of eggs or larvae reaching the bottom. Reproductive success in combination with food supply function strongly to reduce the abundance of *H. oliveri* at depths >30 m.

Based on the above interpretations, we conclude that established, regularly occurring populations of *H. oliveri* are limited to depths where water temperatures are consistently low, where the probability of reproductive success is moderate, and where distance from shore provides a moderate amount of food input. In areas of the lake where these three conditions are met, *H. oliveri* occurs abundantly in a variety of substrates having widely disparate quantities of silty-detrital food sources. *H. oliveri* appears to be able to survive in a variety of deepwater habitats and might best be described as a generalist. This mode is most sensible, given the stable, but harsh environment which an egg or first instar larva first encounters.

High density occurrence in areas experiencing quite variable sedimentation rates suggests to a greater degree that occurrence of *H. oliveri* may not be as narrowly confined to α- and β-oligotrophic conditions (Saether, 1979) as previously thought. High densities reported by at least one study of Lake Ontario (Hiltunen, 1969) and moderate abundances in the Southern Basin of Lake Michigan in conjunction with high sedimentation rates suggest that, although *H. oliveri* is the dominant chironomid in ultraoligotrophic to strongly oligotrophic conditions, its occurrence does not necessarily imply that these conditions prevail wherever *H. oliveri* is found. It is not possible to determine whether *H. oliveri* distributions and abundances have increased or decreased due to eutrophication, particularly in the Southern Basin of Lake Michigan (Schelske *et al.,* 1983), because no historical species abundances records for Chironomidae are available. It is thought that excessive increases in sedimentation accompanying increased eutrophication in portions of Lake Erie decreased or eliminated the occurrence of *H. oliveri* (Brinkhurst, 1969). Within the limits of these processes in Lake Michigan, the density response of *H. oliveri* was variable and leads us to conclude that its trophic status may be broader, although still oligotrophic in nature.

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