Hypolimnetic Aeration and Zooplankton Distribution: A Possible Limitation to the Restoration of Cold-Water Fish Production

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Hypolimnetic aeration of a 1.23-ha eutrophic kettle lake during two consecutive summers increased $[O_2]$ to more than 4mg/L in the hypolimnion for extended periods. This improvement did not lead to the expected development of crustacean populations in the previously anoxic, zooplankton-deficient hypolimnion. The rotifer *Filinia longiseta* was the only zooplankter present, as isolated populations, in both the epilimnion and hypolimnion during summer. Eighty percent of the summer zooplankton community occurred exclusively in the epilimnion, and this was related to the development of an anoxic and toxic metalimnion that restricted migration from the epilimnion to the hypolimnion. Confinement of the zooplankton to the epilimnion coupled with predation by fathead minnows (*Pimephales promelas*) appeared to be responsible for the change in the zooplankton community from large cladocerans and copepods to smaller species. This study suggests that hypolimnetic aeration as a means of restoring or enhancing the production of cold-water fish may be thwarted by the development of a stable anoxic and toxic metalimnion that precludes the development of the zooplankton food resource.

L'aération hypolimnétique d'une marmite eutrophe d'une superficie de 1,23ha durant deux étés consécutifs eut pour effet d'augmenter $[O_2]$ à plus de 4mg/L dans l'hypolimnion pendant de longues périodes. Cette amélioration n'a pas causé le développement anticipé des populations de crustacés dans un hypolimnion pauvre en zooplankton, précédemment anoxique. Le rotifère *Filinia longiseta* était le seul zooplancton présent, en populations isolées, à la fois dans l'épilimnion et l'hypolimnion en été. Quatre-vingt pour cent des communautés zooplanctoniques estivales ont été trouvées exclusivement dans l'épilimnion, et ceci a été attribué à la formation d'un métalimnion anoxique et toxique, imposant des restrictions à la migration de l'épilimnion vers l'hypolimnion. L'emprisonnement du zooplancton dans l'épilimnion, joint à la prédation par le tête-de-boule (*Pimephales promelas*), semble avoir été responsable du changement qui s'est produit dans la communauté zooplanctonique, depuis de gros cladocères et copépodes à des espèces plus petites. Cette étude donne à penser que l'aération hypolimnétique comme moyen de rétablir ou d'améliorer la production de poissons d'eau froide peut être limitée par la formation d'un métalimnion anoxique et toxique stable empêchant le développement de la ressource alimentaire zooplanctonique.

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Artificial techniques of lake restoration, including aeration, have met with varied success (Dunst et al. 1974; U.S. EPA 1980; Pastorok et al. 1981). The most common aeration method, destratification aeration, destroys the integrity of a stratified water column and produces warm (during summer) isothermal conditions unsuitable for cold-water fish. Hypolimnetic aeration, developed by Bernhardt (1967), permits the oxygenation of the hypolimnion without altering the natural thermal structure of the water column. A major goal of hypolimnetic aeration is to increase $[O_2]$ in the hypolimnion of eutrophic lakes to the point at which cold-water fish can exist (Fast 1973, 1975, 1979; Overholtz et al. 1977; Keup 1979; Pastorok et al. 1981). Changes induced in water chemistry by hypolimnetic aeration are well documented (reviewed in Taggart and McQueen 1981), and to a lesser extent so are the effects on phytoplankton communities (Fast et al. 1973; Smith et al. 1975; Hickel 1978; Taggart 1980). Zooplankton are an important food for cold-water fish, yet there are no published studies on the effect of hypolimnetic aeration on zooplankton. This study was initiated to examine that effect on the vertical and temporal distribution of the zooplankton community in a small eutrophic lake.

Materials and Methods

Study Site

The study was carried out in Tory Lake, a 1.23 ha-eutrophic kettle lake situated 25 km north of Toronto, Ontario. The lake has a maximum depth of 10 m and an average depth of 4.5 m and has historically developed a strong thermocline between 2 and 4 m below the surface during summer. Additional details on morphometry are given in Taggart and McQueen (1981).

In May 1973, Tory Lake was anoxic below 0.3 m (Pope 1974), and during the summer of 1974, 90% of the zooplankton community was confined to the upper 2 m of the water column where $[O_2]$ was 2 mg/L, decreasing to 0 mg/L at 5 m and below (Ellis and Tait 1981). Destratification aeration experiments by

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Ellis and Tait (1981) during the summers of 1975 and 1976 created isothermal conditions, a uniform O_2 profile that did not exceed 3 mg/L, and a uniform depth distribution of zooplankton down to 8 m.

In my study, the lake was subjected to hypolimnetic aeration from May to October 1978 and from May to November 1979. Full details of the aeration technique and the physical and chemical changes induced by aeration are given in Taggart and McQueen (1981, 1982); a relevant summary is provided below.

During periods of hypolimnetic aeration, the thermocline occurred between 2 and 6 m in 1978 and between 1 and 4 m in 1979. Accidental aerator leakage (pumping cold hypolimnetic water into the epilimnion) in early June 1978 caused partial destratification and subsequently a deeper thermocline when it restabilized by the end of June. The volume of water contained in the hypolimnion during summer stagnation was 7200 m^3 in 1978 and 17 700 m^3 in 1979. The epilimnion volume was 22 100 m^3 in 1978 and 11 600 m^3 in 1979. The metalimnion volume of 26 000 m^3 was equivalent in both years, but the zone was deeper and thicker in 1978. Aeration increased hypolimnetic $[O_2]$ to >2 mg/L between 15 May and 14 August and to >4 mg/L between 26 June and 15 July 1978 (Fig. 1a). In 1979, hypolimnetic $[O_2]$ exceeded 2 mg/L from 21 May to 14 July and exceeded 4 mg/L from 23 June to 6 July. Aeration was unable to satisfy hypolimnetic O_2 demand after mid-August 1978 and after mid-July 1979. From mid-June to late-September of both years the metalimnion was anoxic and potentially toxic due to concentrations of hydrogen sulfide, which periodically exceeded 5 mg/L (Fig. 1b).

Sampling Methods

Weekly (May–October) and biweekly (November–April) zooplankton collections were made between 10 May 1978 and 10 October 1979 at a station located 30 m northeast of the aerator, which was positioned over the deepest part of the lake (10 m). All samples were taken between 11:00 and 14:00 at discrete 1-m depth intervals ranging from surface to 7 m. A diaphragm pump (Parr, model 34600-00) connected to a weighted 2.5-cm (inside diameter) transparent vinylon tube was used for sampling. Sample volume was constant (50 ± 2.1 L) and pumping rate was 35 ± 0.1 L/min. Potential sample bias due to zooplankton avoidance and overdispersion was reduced by towing the intake tube through an arc of at least 15 m around the sampling station. Sampling studies with a similar system have shown that stationary sampling severely underestimates zooplankton abundance (D. J. McQueen, York University, Toronto, Ont., unpublished data). In winter, the sampling tube was lowered to the desired depth through a hole in the ice and was raised and lowered through a distance of 0.5 m at each sampling depth. The pump and hose were flushed between samples by pumping at least 20 L of water from the next depth to be sampled. Each sample was filtered through an 80-μm net and the concentrate preserved immediately in 5% formalin. Sample volume was later adjusted to 60–100 mL depending on the density of organisms in the concentrated sample.

To determine plankton density, four 1-mL vertical subsamples were withdrawn from each sample with a Hensen-Stempel pipette. All organisms in each subsample were counted using a Sedgewick-Rafter counting chamber and a Leitz SM-Lux compound microscope at 100 or 200× magnification. Representatives of three taxa (Cladocera, Copepoda, Rotatoria) were enumerated according to species, sex, and developmental stage (where possible). All counts were averaged and expressed as number per litre. Except when animals were scarce, the standard error was less than 10% of the density estimate. Although 29 species were identified from the limnetic zone, only 11 species and their subgroupings (total = 19) are considered here. Seventeen of the 18 species not considered were rotifers, which either did not form summer populations or occurred infrequently in the samples and at densities usually less than 5/L. Most were small soft-bodied rotifers, which are not sampled effectively by an 80-μm net (Likens and Gilbert 1970). The remaining species, *Bosmina coregoni*, occurred in only 5 of the 464 samples.

Analysis

To assess summer population densities, the data were divided according to three limnetic zones defined by the position of the thermocline during summer stagnation (i.e. 22 June–21 September 1978 and 4 May–27 September 1979). By these criteria, the epilimnion included sample data from 0, 1, 2, and 3 m in 1978 and 0, 1, and 2 m in 1979; the metalimnion included data from 4 and 5 m in 1978 and from 3 and 4 m in 1979; the hypolimnion included data from 6 and 7 m in 1978 and from 5, 6, and 7 m in 1979.

To determine whether significant differences in depth distribution of species groups among zones occurred during summer stagnation, the densities of each group at each depth were summed and the percent depth distribution was calculated. Individuals of a group had to be present at at least one depth for that date to be included in the group data set. Prior to analysis, these data were arc sine square root transformed to normalize their distributions. Data were grouped according to their respective limnetic zones. The mean of the transformed densities for each zone and group by sampling date was calculated. Analysis of variance was performed on the means of each group. The significance of differences among zonal means was tested using Duncan's multiple range test ($\alpha = 0.05$).

Results

Species Distribution

Cladocera

Daphnia pulex numbers increased rapidly in June 1978 (Fig. 2). At this time, hypolimnetic water was being inadvertently pumped into the epilimnion, which resulted in mixing of the water column to a near isothermal condition, and $[O_2]$ reached >2 mg/L to a depth of 7 m. Subsequently, *D. pulex* was present in all depth strata, but the majority of the population remained above 3 m. Reestablishment of the thermocline and the development of the anoxic metalimnion coincided with the collapse of the population. A small residual population remained in the hypolimnion until mid-August, when $[O_2]$ fell below 2 mg/L. In 1979, *D. pulex* was replaced by concurrent populations of *Daphnia parvula* (not shown) and *Diaphanasoma brachyurum* (Fig. 2). The latter species was also present in the second half of 1978 but at a relatively low density (Fig. 2). Virtually all *D. brachyurum* were restricted to the epilimnion in 1979. The depth distribution of *D. parvula* was similar to that of *D. brachyurum*.

Copepoda

Most copepods were restricted to the epilimnion during summer stagnation, especially the copepodids of the large predatory cyclopoid *Mesocyclops edax*, which was more numerous in 1978 than in 1979 (Fig. 3). The herbivorous calanoid *Diaptomus oregonensis* did not appear in the lake until late July

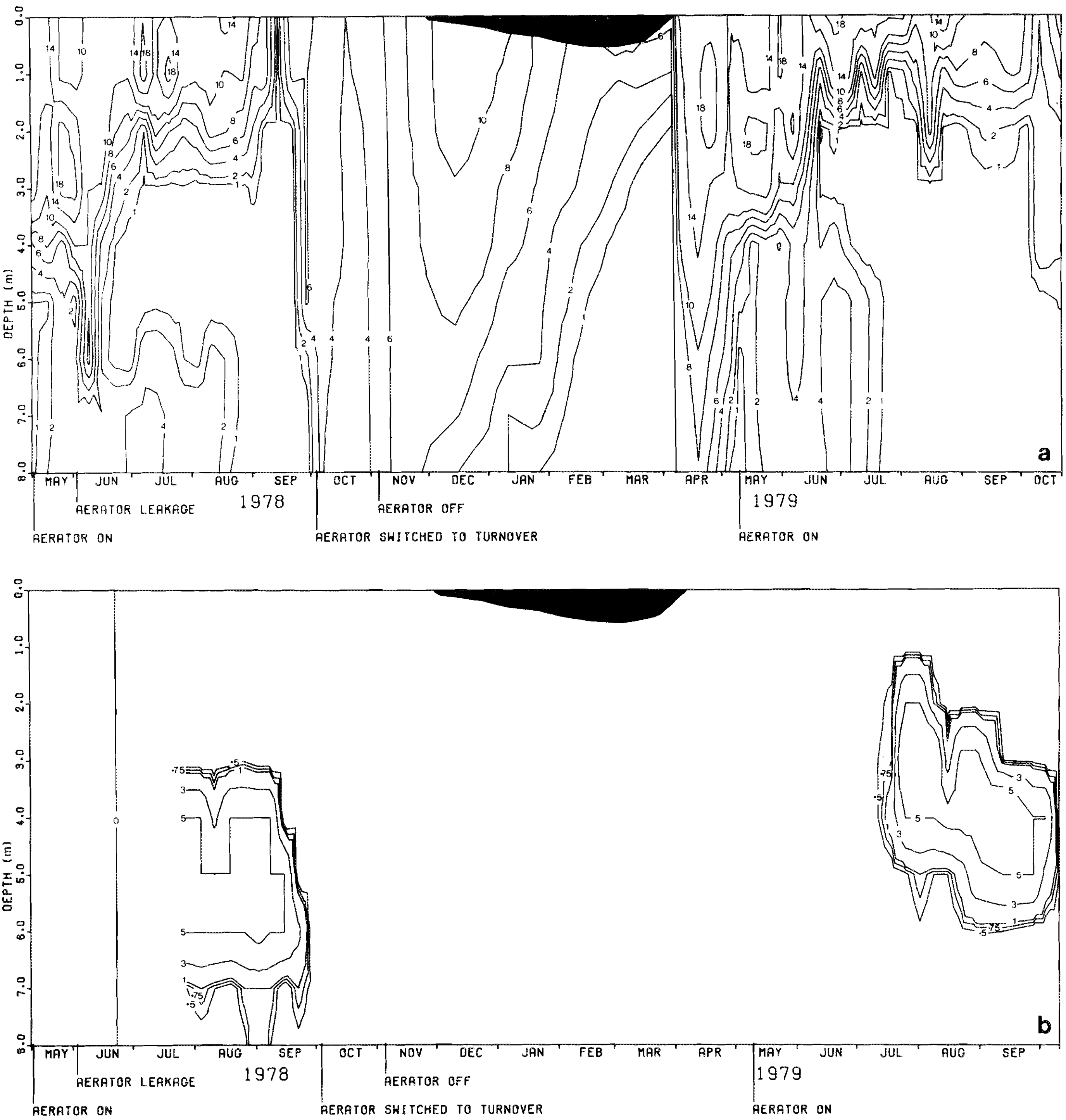

FIG. 1. (a) Dissolved O_2 isopleths (mg O_2/L) and (b) H_2S isopleths (mg H_2S/L) from Tory Lake in 1978 and 1979 at the zooplankton sampling station. H_2S data between 29 June and 20 July 1978 are unavailable. Ice cover is drawn to scale here and in subsequent figures.

1978, following the collapse of the adult population of *M. edax* (not shown). Adult *D. oregonensis* were present in the lake until the end of the study and were also restricted to the epilimnion during summer (Fig. 4). The small cyclopoid *Tropocyclops prasinus-mexicanus* became well established in June 1979 and was similarly restricted to the epilimnion. All copepod nauplii were confined to the epilimnion except during accidental destratification in June 1978 and at fall turnover (Fig. 5).

All copepod populations displayed progressive vertical restriction that coincided with the upward expansion of the anoxic metalimnion. This was particularly evident in June and July 1978 (Fig. 3 and 5) and in June and July 1979 (Fig. 3–5). A similar restriction was observed during winter for *D. oregonensis* (Fig. 4) when [O_2] progressively decreased with time and depth. Depth distribution of all crustacean species expanded at spring and fall turnover.

Rotatoria

All but one rotifer species were virtually absent from the hypolimnion during summer stagnation. This was true even

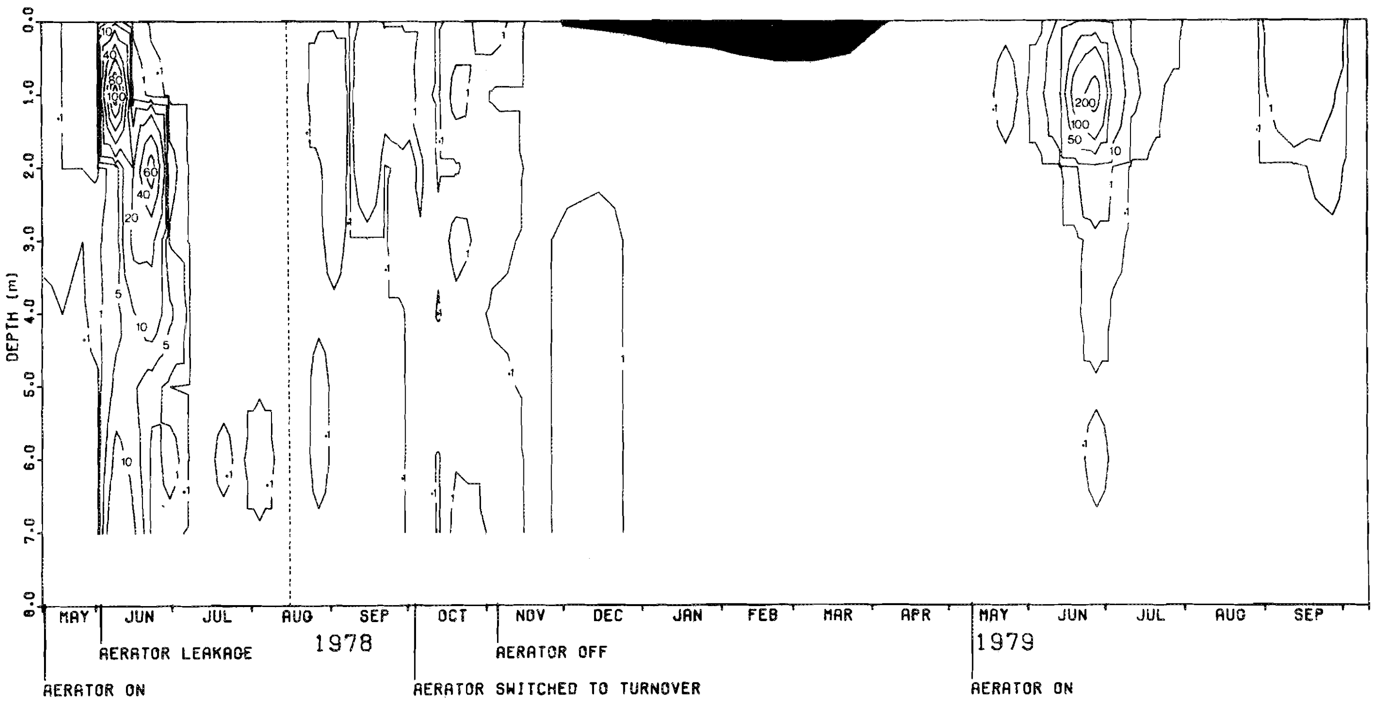

FIG. 2. Density isopleths (No./L) of *D. pulex* mature females (left of broken line) and *D. brachyurum* (right of broken line) in the limnetic zone of Tory Lake during 1978 and 1979.

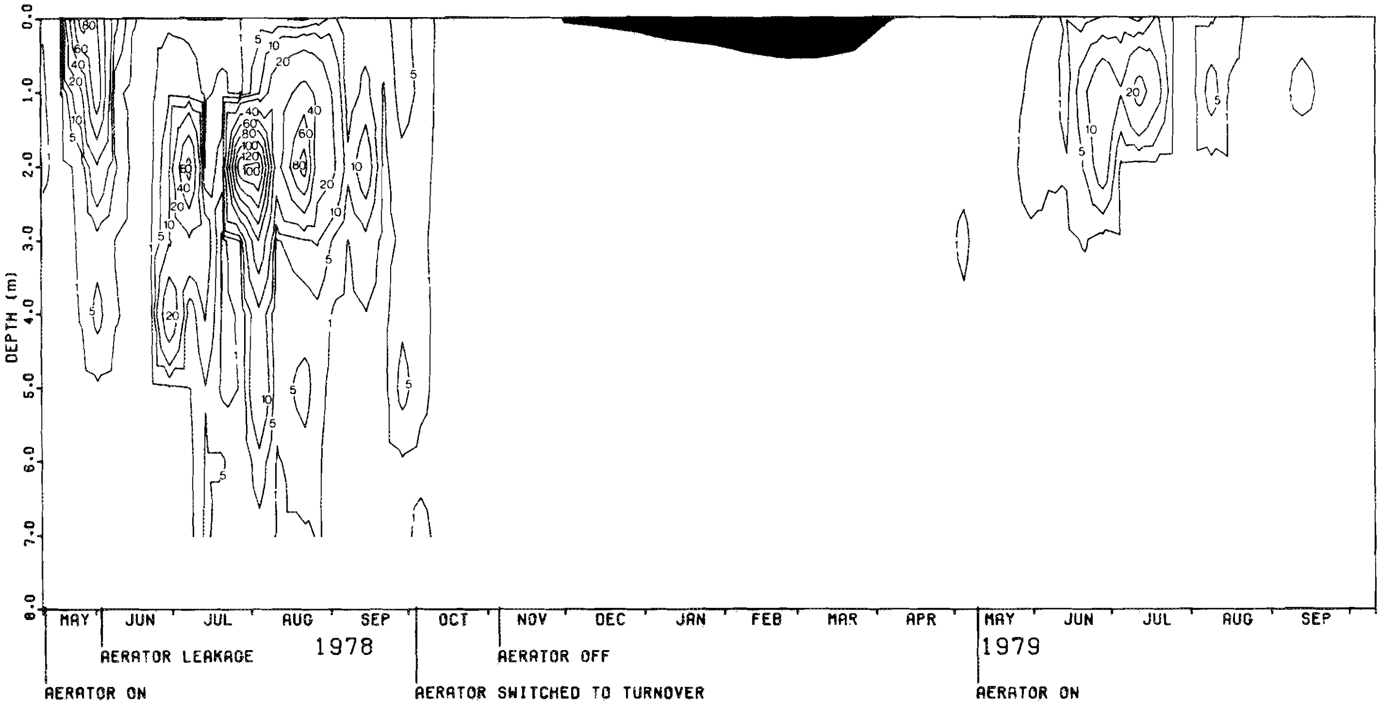

FIG. 3. Density isopleths (No./L) of *M. edax* copepodids in the limnetic zone of Tory Lake during 1978 and 1979.

when $[O_2]$ in the hypolimnion exceeded 4 mg/L. The sole exception was the rotifer *Filinia longiseta*, which was well established early in 1979 and became progressively more restricted to the epilimnion as metalimnetic $[O_2]$ decreased with time (Fig. 6). Immediately following spring turnover and the onset of aeration in 1979, the density of *F. longiseta* in the hypolimnion increased to a maximum of 2095/L by mid-July. This was followed by the development of a second but smaller population in the epilimnion. These two populations were separated by the metalimnion, where densities fell well below 25/L. The epilimnetic population persisted through to fall turnover, but the hypolimnetic population collapsed at the end of July when $[O_2]$ fell below 1 mg/L.

General Distribution Pattern

Eleven of 16 zooplankton groups displayed large differences ($P < 0.0001$) in their distribution among zones (Table 1). Of the

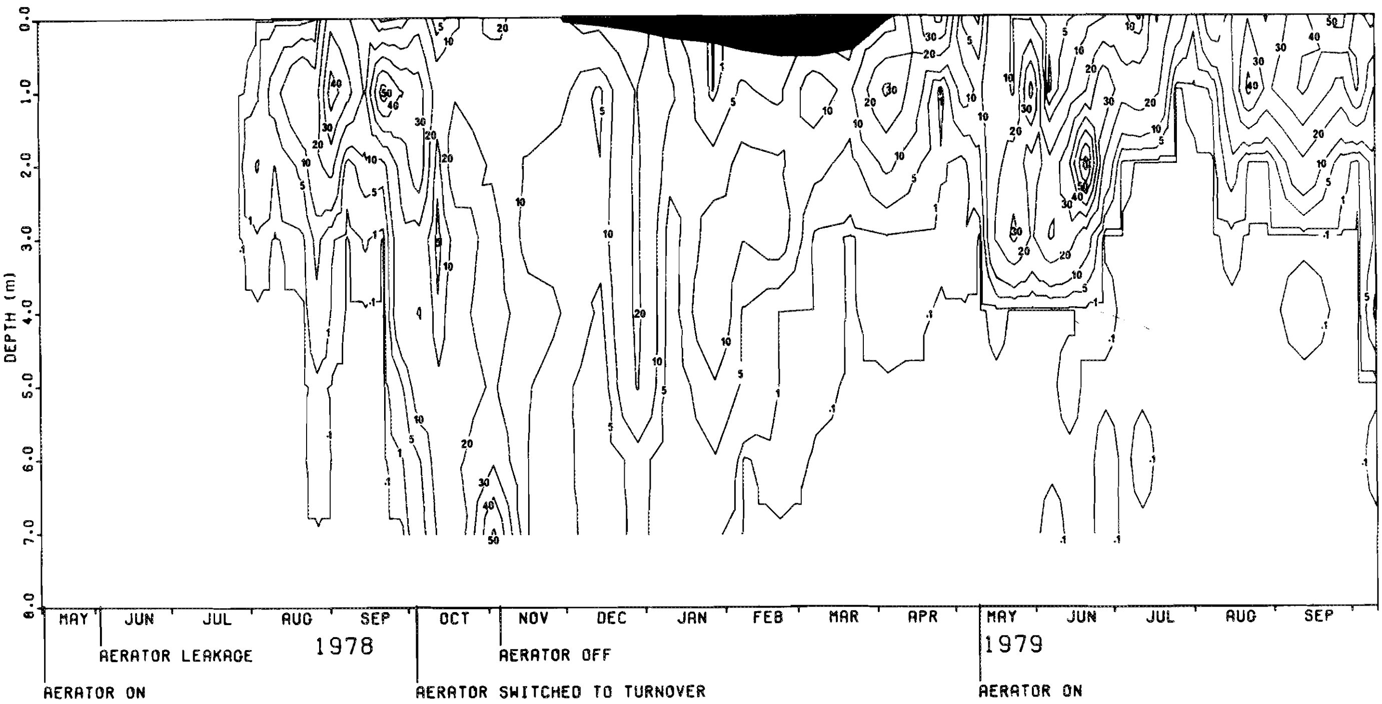

FIG. 4. Density isopleths (No./L) of *D. oregonensis* mature females in the limnetic zone of Tory Lake during 1978 and 1979.

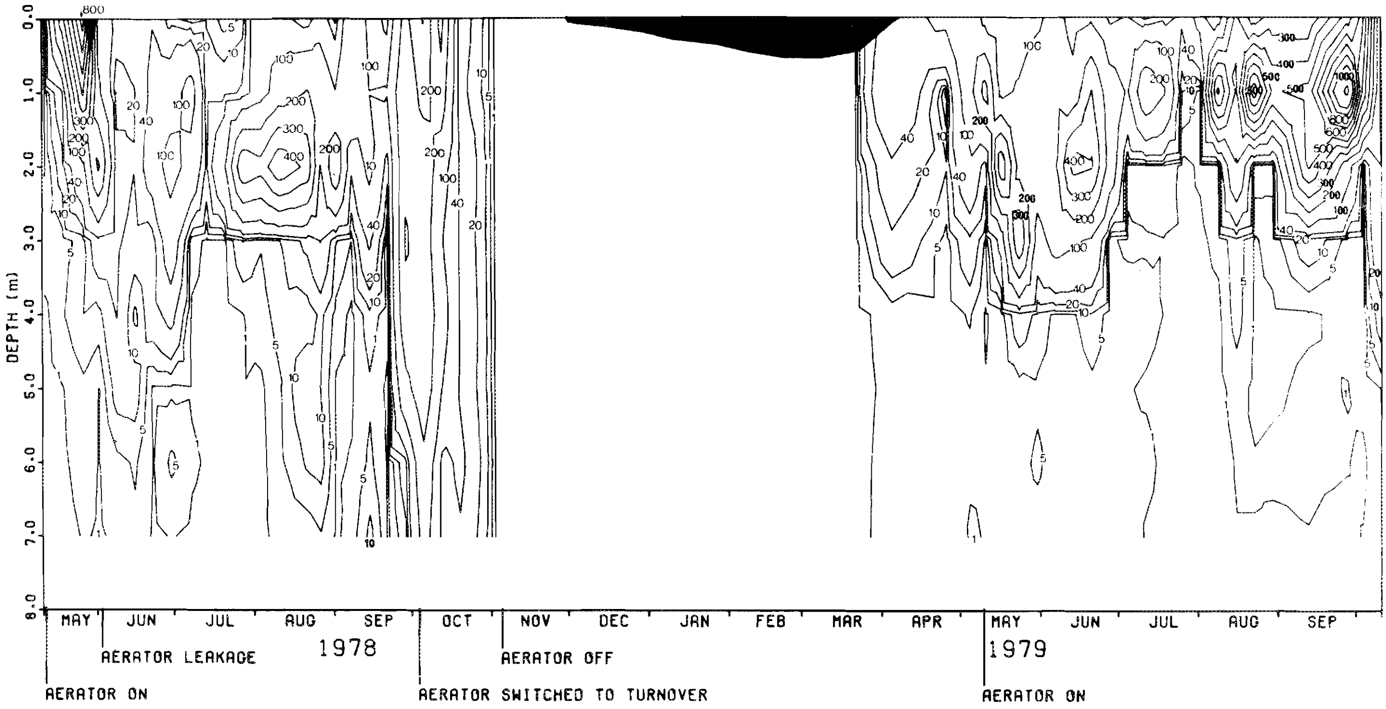

FIG. 5. Density isopleths (No./L) of copepod nauplii in the limnetic zone of Tory Lake during 1978 and 1979.

11, each of the 3 *D. oregonensis* groups and all copepod nauplii had an average of 93.4% of their total density concentrated in the epilimnion. The metalimnion contained an average 5.9% of the populations, and this was in each case significantly greater than the average of 0.7% found in the hypolimnion. Greater than 90% of the remaining seven groups (containing representatives of cladocerans, copepods, and rotifers) were also concentrated in the epilimnion. An average of 62% of *D. pulex* females and neonates and female *M. edax* were found in the epilimnion. However, these three groups showed no significant stratifications with depth.

Anomalous distributions of *Polyarthra* sp. and *F. longiseta* were apparent. *Polyarthra* was significantly more concentrated in the metalimnion, but it should be noted that this species was not observed after the end of June 1979 when the metalimnion became anoxic. *Filinia longiseta* was concentrated in the epilimnion and the hypolimnion, with only 13% of the population found in the metalimnion. Between 13 June and 25

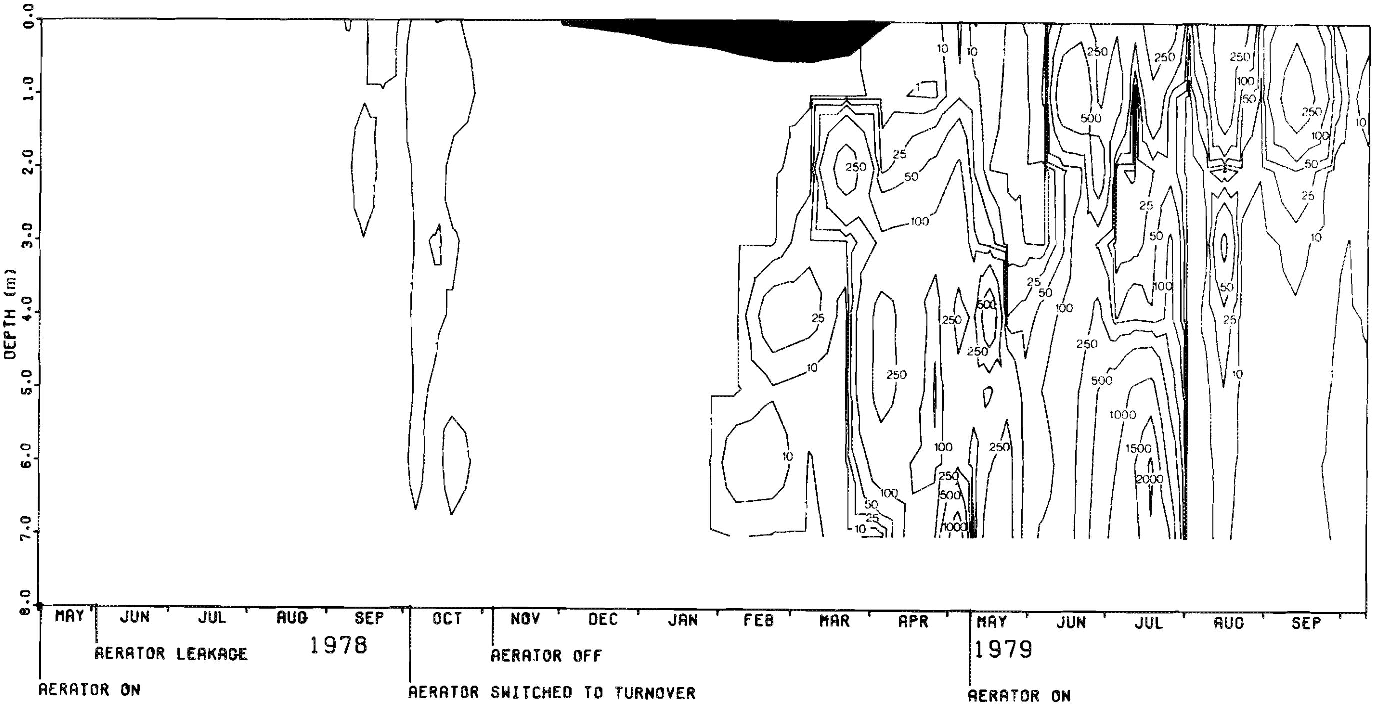

FIG. 6. Density isopleths (No./L) of *F. longiseta* in the limnetic zone of Tory Lake during 1978 and 1979.

July 1979, when the hypolimnetic population of *F. longiseta* was well developed (see Fig. 6), a significantly greater proportion (65.1%) was concentrated in the hypolimnion.

Overall, an average of 78.8% of the zooplankton community was found in the epilimnion during summer stagnation and less than 9.4% was found in the hypolimnion while it was being aerated.

Diel sampling conducted during 4–5 July 1979 indicated that none of the groups penetrated below 1 m and there was no upward movement to the metalimnion by the hypolimnetic *F. longiseta* population.

Discussion

The main results of this study are as follows: (1) in spite of aerator-induced hypolimnetic $[O_2]$ to >4 mg/L for extended periods, virtually all crustacean plankton populations were restricted to the epilimnion during summer stagnation; (2) only the rotifer *F. longiseta* established a significant hypolimnetic population during aeration that collapsed when $[O_2]$ fell below 1 mg/L; (3) large cladoceran and copepod species (e.g. *D. pulex* and *M. edax*) present early in 1978 were replaced by smaller species (e.g. *D. parvula*, *D. brachyurum*, and *T. prasinus-mexicanus*). The implication here is that researchers and managers involved with lake restoration and hypolimnetic aeration who have the declared intention of enhancing or restoring cold-water fish production should consider carefully the trophic, thermal, and chemical structure of their lake during summer stagnation prior to making a research or managerial commitment.

The restriction of zooplankton populations to the epilimnion and the change in the species composition appear to be linked and to result from a migration barrier imposed on the community by the presence of an anoxic and toxic metalimnion. Restriction of the zooplankton to the epilimnion increases their vulnerability to fish predation.

Tory Lake contained a large population of fathead minnows (*Pimephales promelas*) in 1978 and 1979 at a density of 1.69 ± 0.11 and 1.46 ± 0.08 fish/m^3, respectively, in the epilimnion, where the fish were also naturally confined (Taggart 1980). These fish feed almost exclusively on large cladocerans and large copepods (Held and Peterka 1974). Lynch (1979) established that the species can eliminate their large prey by mid-summer, at which time smaller cladocerans and rotifers (*D. parvula*, *D. ambigua*, *Brachionus*, *Filinia*, and *Keratella*) become established. These observations are supported by the results of destratification aeration studies.

During the destratification of Tory Lake during 1975 and 1976 (Ellis and Tait 1981), *D. pulex* was the most abundant cladoceran in the limnetic zone, was uniformly distributed with depth, and persisted at $[O_2]$ between 2 and 3 mg/L. *Daphnia pulex* was absent, while *D. parvula* and *D. brachyurum* were present in Heart Lake (a small eutrophic kettle similar to Tory Lake) during the "control" years of 1968 and 1969 (Haney 1970). In 1976, when Heart Lake was subjected to destratification aeration (Strus 1976), *D. pulex* became well established, while *D. parvula* became rare and *D. brachyurum* disappeared. Similar results were observed among the copepod populations when *Cyclops bicuspidatus thomasi* was replaced by *M. edax* and to a lesser extent by *T. prasinus-mexicanus* following destratification aeration. Destratification aeration in Lake Calhoun also resulted in *D. pulex* establishing a limnetic population (Shapiro et al. 1975). The above authors suggested that the success of populations of large zooplankton in destratified lakes results from the increased ability of larger individuals to avoid fish predators through prey dilution and their inhabiting deeper waters. Both factors result from the expanded limnetic habitats created by destratification aeration.

The metalimnion may not be a barrier to vertical migration if

TABLE 1. Average percent population density of each zooplankton group in the epilimnion (EPI, E), metalimnion (META, M), and hypolimnion (HYPO, H) of Tory Lake during summer stagnation and hypolimnic aeration in 1978 and 1979. For each group the sample size (*N*), significance level (*P*) resulting from analysis of variance on the arc sine square root, average density, and the density difference between zones determined by Duncan's multiple range test ($\alpha = 0.05$) are given.

Species group	EPI	META	HYPO	*N*	*P*	Duncan's
D. oregonensis males	93.7	5.6	0.7	69	<0.0001	E ≠ M ≠ H
D. oregonensis females	92.3	7.6	0.2	84		
D. oregonensis copepodids	94.0	5.2	0.7	84		
Nauplii	93.6	5.3	1.2	102		
T. prasinus mexicanus females	100.0	0.0	0.0	39	<0.0001	E ≠ M = H
D. brachyurum	95.2	1.7	3.1	36		
D. parvula	94.2	5.2	0.6	15		
Brachionus sp.	88.3	7.8	3.9	51		
M. edax copepodids	88.2	6.5	5.3	90		
Keratella cochlearis	84.7	8.4	6.9	84		
Asplanchna sp.	84.7	4.5	10.8	30		
D. pulex neonates	68.4	13.7	17.9	9	<0.25	E = M = H
D. pulex females	53.3	36.6	10.1	6	<0.53	
M. edax females	64.9	10.2	24.9	90	<0.22	
Polyarthra sp.	24.3	58.0	17.7	24	<0.004	E = H ≠ M
F. longiseta	40.3	12.9	46.8	60	<0.026	E = M ≠ M = H
F. longiseta (peak population)	28.6	6.4	65.1	21	<0.0002	E = M ≠ H

the resident zooplankton are nonmigratory. All species found in Tory Lake, and their close relatives, are migratory in systems where chemical conditions are less extreme. Where chemical conditions become suboptimal, the animals move upward in the water column where preferred conditions exist (Langford 1938; Hutchinson 1967; George and Fernando 1969, 1970; Haney 1973; Hoffman 1975, 1977, 1982; Fairchild et al. 1977; Threlkeld 1979; Burns and Mitchell 1980).

The fact that *F. longiseta* became established in the hypolimnion indicates that hypolimnetic aeration can be effective in creating suitable conditions for the establishment of hypolimnetic zooplankton populations. However, as the treatment has no effect on the metalimnion, the populations tend to remain isolated. A similar but naturally occurring situation has been documented in Lake Johnson, New Zealand, where concentrated zooplankton populations were isolated in the oxygenated hypolimnion, which was overlain by an anoxic metalimnion (Burns and Mitchell 1980). The authors suggested that some of the populations may have resulted from either lateral migration of individuals from the shore region or vertical migration through the metalimnion. The information presented in the Tory Lake study does not support this second hypothesis. Burns and Mitchell (1980) also assumed that some species became trapped in the hypolimnion by the developing anoxic metalimnion. This is consistent with my view of the establishment of *F. longiseta* in the hypolimnion of Tory Lake. It is possible that the epilimnetic population that developed later resulted from pumping individuals from the hypolimnion when sampling and releasing them into the epilimnion. The same technique used in reverse may be suitable for stocking epilimnetic zooplankton into the hypolimnion, but the persistence of stocked populations will be poor if vertical migration to the productive epilimnion is impeded by the anoxic and toxic metalimnion.

The natural development of metalimnetic O_2 minima in thermally stratified lakes is believed to result from zooplankton and algal biomass settling from the epilimnion and decaying in the metalimnion (Mitchell and Burns 1979). Ironically, the use of hypolimnetic aeration in lakes that are prone to the development of metalimnetic minima and that are frequently regarded as prime candidates for aeration (Ohle 1974; Fast et al. 1975; Wirth et al. 1975) may be misdirected, particularly if the intention is to create improved chemical conditions for cold-water fish. Suitable chemical conditions can be created in the hypolimnion by hypolimnetic aeration, but the results presented here indicate that the development of suitable biological conditions may be limited by the presence of an anoxic, H_2S-rich metlimnion. A metalimnetic minimum cannot be corrected by aeration without destroying thermal stratification (Wirth et al. 1975), which in turn creates conditions that exclude cold-water fish.

Acknowledgments

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POSTSCRIPT ADDED IN PROOF: Subsequent to this paper being accepted for publication I became aware of work by K. I. Ashley (1983. Hypolimnetic aeration and functional components of the lake ecosystem: phytoplankton and zooplankton effects, p. 31–40. *In* J. Taggart and L. Moore [ed.] Lake restoration, protection, and management. Proc. Second Annu. Conf. North Am. Lake Manage. Soc., 26–29 Oct. 1982, Vancouver, B.C. U.S.

EPA 440/5-83-001: 327 p.). The zooplankton in Ashley's partitioned lake (hypolimnetic aeration experiment and control sides) did not respond as expected to the aeration treatment. The vertical distribution of zooplankton was not significantly different between the control and experimental sides. This was attributed to the fact that the control side was partially aerobic during the experiment, thereby negating any experimental difference in hypolimnion oxygen concentration against which zooplankton response could be assessed. Ashley's findings are in support of those presented here, although he suggests that long-term aeration may result in an expanded vertical range of zooplankton.

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