LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

Hypolimnetic Aeration and Zooplankton Depth Distribution

In a recent *Journal* paper, Taggart (1984) discussed the effect of hypolimnetic aeration on zooplankton depth distribution and concluded that the development of a stable anoxic metalimnion may preclude the development of the zooplankton food resource and therefore thwart the effectiveness of hypolimnetic aeration for restoring or enhancing cold-water fish production. I believe there are several inconsistencies in Taggart's (1984) experimental design and conclusions that require further explanation.

The main result of Taggart's (1984) experiment was that "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." However, the seasonal oxygen isopleths in Tory Lake (Taggart 1984, fig. 1) were similar to that seen in unaerated dimictic eutrophic lakes, i.e. temporary hypo- and meta-limnetic anoxia during summer and winter stratification (Wetzel 1983). This suggests that the aeration system had little effect on hypolimnetic oxygen concentrations. As a result, the observed zooplankton behaviour (i.e. avoidance of the hypolimnion, confinement to the epilimnion, and subsequent size-selective predation by fathead minnows) may have been unrelated to the experimental treatment.

Hypolimnetic aeration, when correctly designed, significantly increases hypolimnetic oxygen concentrations (Fast 1971; Ashley 1983a) and provides suitable habitat for cold-water fish and zooplankton (Overholtz et al. 1977; Ashley 1983b). The development of an anoxic metalimnion, which is a natural occurrence in certain lakes (Wetzel 1983), should not reduce the effectiveness of hypolimnetic aeration for enhancing cold-water fish production. Under these conditions, trout which would normally be excluded from the hypolimnion, may feed on the benthic community recolonizing the aerated hypolimnion (Fast 1971) or make occasional forays through the anoxic metalimnion into the productive epilimnion (Serns 1976; Garrell et al. 1978).

Undersized equipment is a problem in hypolimnetic aeration and reflects the difficulties associated with correctly designing aerators and predicting hypolimnetic oxygen consumption during aeration (Lorenzen and Fast 1977). Taggart and McQueen (1982) recommend equivalent cross-sectional areas in riser and return manifold tubes; however, Taggart's (1984) return tube area was only 1/8 to 1/2 the riser tube area. Ashley (1984) recently proposed an empirical sizing formula for hypolimnetic aerators which should reduce this problem.

The design of Taggart's (1984) experiment was not well suited to studying zooplankton depth distribution. Hypolimnetic aeration is a whole-lake perturbation, and assessment of its effects requires appropriate comparison between control and treatment conditions, e.g. before and after, split-lake, side by side lakes, or in-lake controls. Taggart's (1984) experiment involved two treatment years (1978 and 1979) and no control data. The recent history of Tory Lake was confounded by 2 yr of destratification (1975 and 1976; Ellis and Tait 1981) which could effect zooplankton species composition and distribution (Fast 1971; Lackey 1973). In addition, in the first treatment year (1978) aerator leakage partially destratified the lake and during the second treatment year (1979) external nutrient loading increased 4.6-fold from 1978 (Taggart and McQueen 1981).

A frequent statement throughout Taggart's (1984) paper was that an "anoxic and toxic metalimnion" imposed a migration barrier on the zooplankton community. However, no data are given to specify lethal concentrations of oxygen or hydrogen sulfide, and only one 24-hr sampling period (July 4–5, 1979) was used to detect vertical migration in the Tory Lake zooplankton community. Burns and Mitchell (1980) suggested that zooplankton may migrate vertically through an anoxic metalimnion to reach an oxygenated hypolimnion.

In summary, I suggest that experimental design and equipment problems invalidated the main conclusions presented by Taggart (1984), and that an anoxic metalimnion may not preclude the development of epi- and hypo-limnetic zooplankton populations or reduce the effectiveness of hypolimnetic aeration for restoring cold-water fish production — Ken Ashley, *Ministry of Environment, Fish and Wildlife Branch, Fisheries Research Section, 2204 Main Mall, University of British Columbia, Vancouver, B.C. V6T 1W5.* *(J7877a)*

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Reply with Explanations and Additional Evidence

Ashley (1984) has levelled several criticisms against the experimental design and conclusions presented in Taggart (1984) which I believe derive in part from a superficial reading of the paper, some misconceptions, and an uncritical interpretation of other works on hypolimnetic aeration. Before responding in detail to each of Ashley's specific criticisms I wish to make clear that nowhere did I imply that an anoxic, H_2S-rich metalimnion would preclude the development of epilimnetic zooplankton populations, nor did I imply that hypolimnetic aeration *in general* is not effective in establishing suitable conditions for cold-water fish. I contended only that suitable biological conditions for cold-water fish production may be *limited* by the presence of an anoxic and H_2S-rich metalimnion. This conclusion was clearly indicated as tentative by the title of the paper. The paper was also meant to serve as a warning to researchers and lake managers that trophic, chemical, and thermal structure of their lakes should be considered carefully before managerial and research commitments to hypolimnetic aeration programmes are made — commitments that may prove to be costly and unrewarding.

It should also be emphasized that when the Tory Lake hypolimnetic aeration programme was implemented in 1978, this treatment was gaining acceptance as an ideal technique for restoring cold-water fish production in normally dimictic but oxygen-deficient lakes. Several fish stocking experiments were qualitatively successful, but no reports on zooplankton responses to hypolimnetic aeration had been published. A need for such information was later articulated by Fast (1979).

I turn now to Ashley's specific criticisms and deal first with his suggestion that aeration had little effect on hypolimnetic oxygen concentration. The facts are as follows: (1) During 1973–74, and early 1975 (prior to any type of aeration), Tory Lake had an anoxic meta- and hypo-limnion when stratified (see references in Taggart 1984). (2) Hypolimnetic aeration stripped H_2S from the hypolimnion and prevented hypolimnetic anoxia for two consecutive summers, but the anoxic, H_2S-rich metalimnion was unaffected. (3) Aeration of Tory Lake ceased in mid-July 1980, and monitoring since then shows that the lake has reverted to meta- and hypo-limnetic anoxia, and H_2S-rich conditions when stratified (D. J. McQueen, York University, Toronto, Ont., pers. comm. and unpubl. data). These facts are inconsistent with Ashley's assertion that aeration had little effect on hypolimnetic $[O_2]$ in 1978–79.

Ashley (1984) cites Overholtz (1977) and Ashley (1983b) to support his claim that a suitable cold-water habitat for zooplankton and fish can be created by hypolimnetic aeration. I do not question this, but it should be made clear that no anoxic, H_2S-rich metalimnion formed in either of the lakes referred to in those papers. Ashley further cites Serns (1976) and Garrell et al. (1978) as evidence that trout "make occasional forays through the *an*oxic metalimnion" (my italics). In neither of the studies cited was the metalimnion anoxic (0.5–0.7 mg O_2/L in Larson Lake, Serns 1976; 0.2 mg O_2/L in Lake Waccabuc, Fast et al. 1975), and more important, there was no report of H_2S in the metalimnion of either lake during aeration. The evidence for fish movement through the hypoxic metalimnion provided by Serns (1976) is convincing, though based on a sample of only 10 marked fish. That provided by Garrell et al. (1978), however, was based not on distributional observations, but rather on the analysis of the stomach contents of nine fish collected 2 yr after aeration and stocking began, and no data on the condition of the metalimnion at the time of capture were reported.

Trapping of fathead minnows (*Pimephales promelas*) on 29 October 1978, in Tory Lake (at 1-m intervals from surface to 5 m), when the lake was destratified and $[O_2]$ was slightly less than 4 mg/L, resulted in a total catch of 1532 vigorous individuals which were uniformly distributed through the water column (Taggart 1980). Fish trapping was conducted a second time to a depth of 8.5 m on 4 July 1979 when the lake was well stratified and $[O_2]$ was 4.3 mg/L in the hypolimnion. A total of 655 individuals were captured. None were captured in the hypolimnion, and although 191 were captured at 2 m, and 2 individuals at 3.5 m, the combined mortality was 98.4% at the time of trap retrieval (7 h after set). Mortality at 0.5 and 1.0 m was 0.0%. These observations indicate that the dead fish were asphyxiated, and that although capable of penetrating the metalimnion, there is no evidence that they passed through it. Magnuson and Karlen (1970) have observed that several freshwater fish species occasionally sound into an anoxic layer containing H_2S, but note that the behavior is most pronounced shortly before death occurs, and caution that the behavior may have been an artifact of the experiment.

Ashley's (1984) concern for aerator design is justified, as aerator design can have critical effects on water flow and oxygen transfer efficiency, but he has misinterpreted the design model of Taggart and McQueen (1982). It is true that the return manifold in the Tory Lake aerator was undersized during 1978. In 1979 the manifold area was increased fourfold (Taggart and McQueen 1981) and was easily capable of handling maximum water flow from the riser, indicating not that the return manifold was undersized, but rather that the riser was oversized. In fact, the design model indicated that the radius of the riser was at least 1.5 times greater than required (Taggart and McQueen 1982, table 1).

Ashley's (1984) requirement for "control" and treatment comparisons in a whole lake manipulation broaches the subject of pseudoreplication (Hurlbert 1984). The Tory Lake aeration programme can be classified as simple or temporal pseudoreplication, which is "neither surprising nor bad" when one is manipulating a whole lake, when a rough estimate of the treatment effect is anticipated, and when the cost of replication is financially crippling (Hurlbert 1984). Furthermore, the conclusion and accompanying warning in Taggart (1984) were not given "the unmerited veneer of rigor by the erroneous application of inferential statistics" (Hurlbert 1984).

Destratification aeration of Tory Lake during 1975–76 (Ellis and Tait 1981) may well have affected zooplankton species composition as Ashley suggests, and it certainly did affect depth distribution (see Taggart 1984). What should be recognized however, is that during periods of hypolimnetic aeration (when $[O_2]$ in the hypolimnion exceeded 3 and 4 mg/L) only rotifers were found there. Ellis and Tait (1981), on the other hand, showed that at equivalent and lower $[O_2]$, but in the absence of an anoxic H_2S-rich zone, zooplankton significantly increased their depth distribution to 8 m.

Ashley has also pointed out the fact that Tory Lake partially destratified early in 1978 and increased external nutrient loading was experienced in 1979. These were unfortunate and unforseeable events. However, the short period of destratification served only to increase the depth distribution of zooplankton to the hypolimnion (Taggart 1984, fig. 2, 3, 5). Moreover, while oxygen conditions in the hypolimnion were improved by aeration following restratification, none of the "stocked" species persisted. The aerator was capable of handling the increased nutrient loading when compared with 1978 (Taggart and McQueen 1981), and therefore, I see no reason why increased loading per se should affect the depth distribution of zooplankton. (In retrospect it is interesting to note that the establishment of the only hypolimnetic zooplankton population occurred in the year of increased loading.)

Ashley's criticism of my failure to specify lethal concentrations of O_2 or H_2S is well founded. However, aquatic invertebrates are known to be variable in their ability to tolerate low oxygen conditions (Davis 1975), and there is no general consensus on critical levels. This fact is illustrated by the disagreement between referees of the original manuscript, one of whom argued that most zooplankters are tolerant of low $[O_2]$, while the other argued that most would avoid a concentration of 4 mg/L. When preparing this reply a search was made of four data bases, one extending back to 1967. Several studies from field sampling programmes were identified that confirmed that most, but not all, zooplankton species will respond to and avoid anoxic, H_2S-rich strata (Heberger and Reynolds 1977; Boyd and Smith 1980; Judkins 1980; Chapman et al. 1981; Thain et al. 1981; Hamner et al. 1982; Caumette et al. 1983; see also references in Taggart 1984). Surprisingly, there were no experimental studies on toxicity or tolerance levels of zooplankton to H_2S.

Tolerance and toxicity levels are well documented for fishes, and many species are sensitive to low $[O_2]$, and can tolerate reduced levels for a short period (Davis 1975). H_2S is toxic at levels well below 1 mg/L, and becomes increasingly so as $[O_2]$ decreases and pH and/or temperature increase (Bonn and Follis 1967; Adelman and Smith 1970, 1972; Smith et al. 1976; Broderius et al. 1977). Acclimation to low $[O_2]$ does not appear to decrease H_2S toxicity (Adelman and Smith 1972). Smith et al. (1976) suggested that regular monitoring in the field may not be able to detect the low levels of H_2S known to have toxic effects and therefore "any detectable concentration in the field should be considered detrimental to fish production." This advice is well founded, as inversions or wind-generated mixing of H_2S zones may result in high mortality of fish and zooplankton (Fedorenko et al. 1979; Infante et al. 1979).

Ashley's (1984) criticism of only one 24-h sampling period for detecting vertical migration would be valid had I set out to investigate diel migration per se, where cues, feeding strategies, energetics, predator avoidance, etc., are of prime importance. However, in Tory Lake I was interested only in determining how deep the zooplankton would go and if they penetrated the metalimnion. As virtually all the species recorded in Tory Lake are known to display typical downward migration during the early morning, it was not unreasonable (see for example Thain et al. 1981) to assume that they would be at, or very near, their deepest between 11:00 and 14:00 when the regular sampling was performed. The diel sampling was conducted solely to determine if there was *any* evidence of reverse migration (downward during the evening or night). As there was not the slightest evidence of this rare behavior, even when $[O_2]$ in the hypolimnion was very near the highest observed during the summer, no further diel sampling was thought necessary.

The working hypothesis during the Tory Lake study was that zooplankton populations would establish themselves in the hypolimnion if chemical conditions there were improved by aeration. Conditions were improved (Taggart 1980; Taggart and McQueen 1981), but the expected zooplankton response was not apparent during the 2 yr of treatment. All evidence indicates that the lack of response was due to the anoxic, H_2S-rich metalimnion. The conditional conclusion presented in Taggart (1984) was negative with respect to what is expected to result from hypolimnetic aeration, but only when an anoxic H_2S-rich metalimnion is present. To this I add the following: "if a testable hypothesis produces negative results, with some degree of uncertainty, then that hypothesis is preferable to an untestable one that fits more closely a current or popular paradigm" (Price et al. 1984), particularly if it is one that has never been tested but is becoming accepted and ingrained in the literature.

Indeed, the lack of appreciable response by zooplankton to hypolimnetic aeration may be an even more general phenomenon than I have previously suggested (Taggart 1984). Ashley's own work indicates that in the absence of an anoxic, H_2S-rich metalimnion, and in the presence of a hypolimnion where "Oxygen concentrations were significantly higher" (Ashley 1983a, p. 1348), "zooplankton did not respond as expected to the experimental treatment" (Ashley 1983b, p. 38). — Christopher T. Taggart, *Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Que. H3A 1B1.*

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