

Can zooplanktivorous fish really affect lake thermal dynamics?

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With 7 figures and 1 table in the text

Abstract

Recent work has suggested that by reducing light absorption and light penetration in water, increased algal abundance resulting from the suppression of zooplankton by zooplanktivorous fish can result in reduced mixing depth (epilimnion), water temperatures and heat content. Here I present data collected during two summers from 14 small, morphometrically similar freshwater ponds containing various densities of zooplanktivorous fish that support the above relationship between zooplanktivorous fish and lake thermal dynamics. During both years, mean summer water temperatures declined with increasing algal abundance (decreasing water transparency) and biomass of zooplanktivorous fish. Although this experiment was performed in small ponds, results presented here add to the growing body of information demonstrating that biological properties can have major influences on physical and chemical properties in freshwater ecosystems.

Introduction

MAZUMDER et al. (1990) suggest that by increasing algal abundance via zooplankton suppression, zooplanktivorous fish may affect water temperature and thermal dynamics in lakes. A comparison of two lakes, one containing low and the other high densities of zooplanktivorous fish, revealed a shallower thermocline, lower heat content and cooler metalimnetic waters in the lake with high fish density. MAZUMDER et al. (1990) attributed these thermal differences to reduced light absorption and light penetration in the lake with dense fish populations resulting from increased algal abundance due to suppression of herbivorous zooplankton by the fish. Though a similar pattern in thermal structure was also demonstrated in small (8-m diameter) enclosures, the two study lakes differed in a number of morphometrical aspects, such as surface area and volume, that can affect lake thermal dynamics and thereby poten-

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tially confound their interpretations. Here I present data collected during two summers from 14 small, morphometrically similar freshwater ponds containing various densities of zooplanktivorous fish as an experimental test of MAZUMDER *et al.*'s hypothesis that fish can affect lake thermal dynamics.

Methods

The study was conducted using 14 ponds at the Cornell University Experimental Ponds Facility during the summers of 1989 and 1990. When full, the ponds were ca. 0.12 ha in surface area with mean and maximum depths of ca. 1.6 and 2.5 m, respectively. Atmospheric and ground water exchange represented the only natural inflows and outflows of water to the ponds. Originally, all ponds were filled by pumping from a large reservoir to maximum levels in the spring of 1988. In early summer 1988, five ponds were stocked with zooplanktivorous fathead minnows (*Pimephales promelas*) and pumpkinseed sunfish (*Lepomis gibbosus*); five ponds were stocked with fathead minnows, pumpkinseed sunfish and piscivorous largemouth bass (*Micropterus salmoides*); four ponds contained no fish. Elimination of fathead minnows and a shift in size structure of pumpkinseed populations toward large benthivorous sizes due to bass predation greatly reduced the level of planktivory in the ponds containing bass during 1989 and 1990 (HAMBRIGHT *in press*). Upon termination of the experiment in 1990, the five fish ponds with bass contained intermediate densities of zooplanktivorous fish (12.5 ± 5.0 kg/ha juvenile pumpkinseeds) compared with high densities of zooplanktivorous fish (149.2 ± 50.8 kg/ha fathead minnows and juvenile pumpkinseeds) in the five fish ponds without bass and no zooplanktivorous fish in the four ponds not stocked with fish.

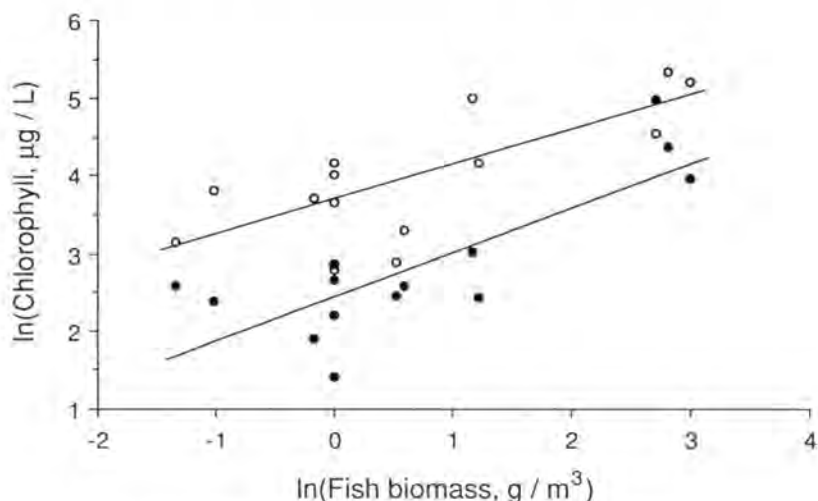


Fig. 1. Relationship between mean summer chlorophyll-a concentrations in ponds during 1989 (open circles) and 1990 (closed circles) and planktivorous fish biomass ($\ln(\text{biomass} + 1)$) at the end of the experiment (September 1990). Regression equations are: 1989, $y = 0.45x + 3.7$, $r^2 = 0.57$, $P_{(\text{slope} \neq 0)} = 0.002$; 1990, $y = 0.57x + 2.4$, $r^2 = 0.64$, $P_{(\text{slope} \neq 0)} = 0.001$.

Algal abundance (measured as chlorophyll-a and Secchi depth transparency), temperature, and dissolved oxygen (DO) were monitored approximately biweekly during summer 1989 and 1990 in the deepest part of each pond. Five to eight depth-integrated samples were collected from the surface to within 10 cm of the bottom, mixed in a bucket, and subsampled for standard chlorophyll analysis (APHA 1985). Temperature and DO were measured (using a YSI model 57 dissolved oxygen meter) at the surface, 0.5, 1, 1.5, and 2 m in each pond 1–2 h before sunset. Mean water column temperatures and mean areal heat contents for each pond were calculated using volume adjusted temperature profile data assuming uniform water temperature in each 0.5-m depth increment below each measured depth. All data were analyzed by ANOVA with each year analyzed separately because weather patterns, which will obviously affect thermal parameters and may obscure the detection of important relationships, were different between the two years.

Results and discussion

During both years (1989 and 1990), mean summer chlorophyll was positively related with biomass of zooplanktivorous fish recovered from the ponds in 1990 (Fig. 1). Though a variety of factors can affect water transparency, algal abundance is typically a dominant factor affecting light attenuation, especially in highly productive eutrophic lakes (KIRK 1983). Algal abundance (estimated as summer mean chlorophyll) and water transparency (as summer mean Secchi depth) were strongly related in ponds, with Secchi depth decreasing as a logarithmic function of mean summer chlorophyll concentration during both years (Fig. 2).

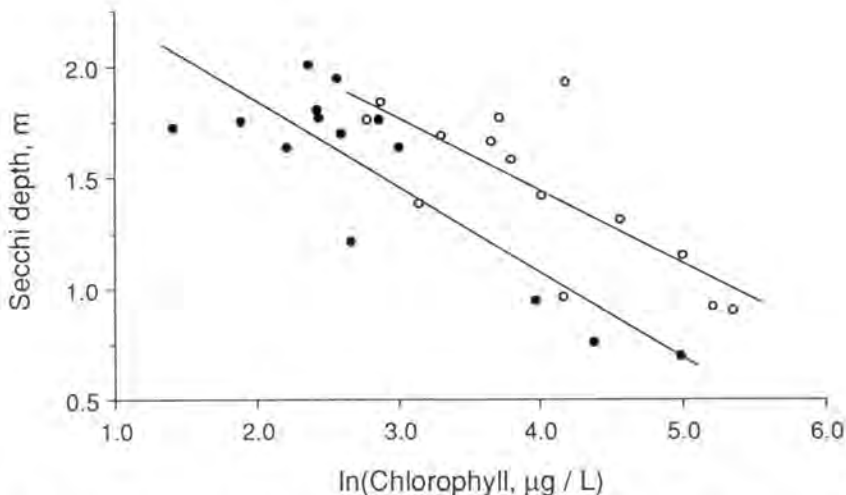


Fig. 2. Mean summer Secchi depth transparencies plotted against natural logarithm of mean summer chlorophyll concentrations in ponds during 1989 (open circles) and 1990 (closed circles). Regression equations are: 1989, $y = -0.33x + 2.7$, $r^2 = 0.57$, $P_{(\text{slope} \neq 0)} = 0.002$; 1990, $y = -0.38x + 2.6$, $r^2 = 0.72$, $P_{(\text{slope} \neq 0)} < 0.001$.

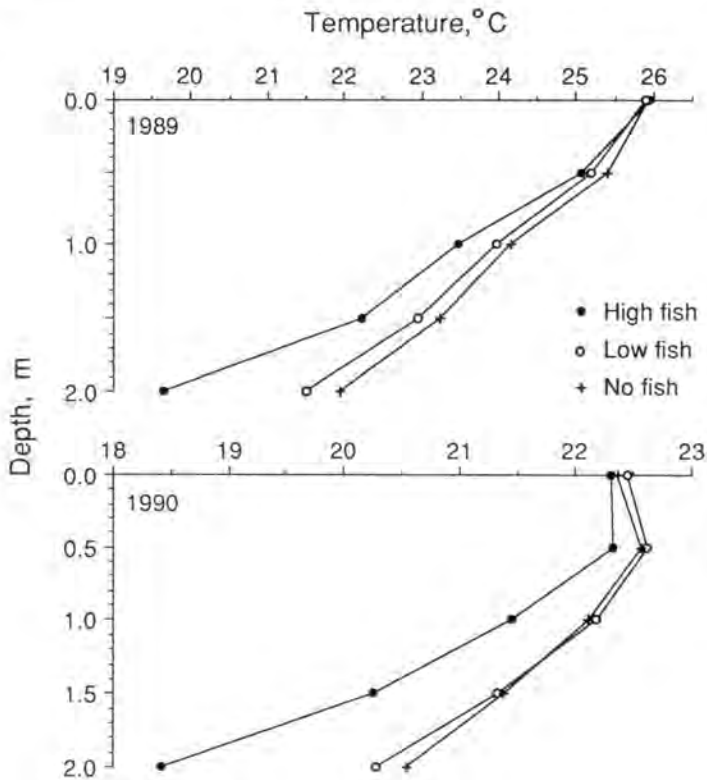


Fig. 3. Mean depth profiles of temperature in ponds with no planktivorous fish, low planktivorous fish biomass, and high planktivorous fish biomass during 1989 and 1990.

Table 1. Results of ANOVA of temperature in ponds as affected by fish treatment (Trt) and depth (Z).

Source	df	MS	F	P
1989				
Trt	2	4.53	21.4	<0.001
Z	4	52.7	248	<0.001
Trt \times Z	8	1.08	5.09	<0.001
Error	55	0.212		
1990				
Trt	2	5.00	9.60	<0.001
Z	4	18.1	34.8	<0.001
Trt \times Z	8	0.824	1.58	0.151
Error	55	0.520		

In general, temperature profiles revealed thermal stratification in all ponds, with bottom waters in high fish density ponds consistently cooler than

in ponds with low fish densities or with no fish (Fig. 3, Table 1). Though basin morphometry is typically considered to be the major determinant of mixing depth in lakes within a given climatic region, the temperature gradient, and hence density gradient, across the metalimnion can be a principal determinant of mixing depth within a single lake or across morphologically similar lakes (HUTCHINSON 1957, LEWIS 1973, ARAI 1981, HAMBRICHT *et al.* in press). The frequency of sampling used (*i.e.*, 0.5-m intervals) relative to the pond depths prevents discrimination of specific mixing depths, although the temperature difference between 0 and 2 m increased with decreasing Secchi depth and increasing fish biomass (Fig. 4), suggesting that the pond mixing depths differed. While mean summer water temperatures in ponds increased with increasing Secchi depth, mean and maximum areal heat content varied independently of Secchi depth and hence, fish biomass (Fig. 5). However this inconsistency between volumetric (mean temperature) and areal estimates of heat content is probably an artifact of treatment-independent variability in pond depths due to differential influences of groundwater fluxes (Fig. 6). Obviously pond volume increases with depth, hence ponds with larger volumes contained more heat per unit area. However, mean temperature decreased with pond depth because deeper ponds contained more cold water (*i.e.*, more water below 2 m). Nevertheless, pond depth and Secchi depth (or fish biomass) varied independently from one another and mean summer temperatures at 1, 1.5, and 2 m did vary with Secchi depth (Fig. 7), indicating that differences in pond temperatures observed are not artifacts of variable pond depths, rather they are consequences of variable fish biomass.

Conclusions

Though there are many sources and sinks of heat in lakes, heat content is determined by a balance primarily between gains from absorbed solar radiation and losses via evaporation (HUTCHINSON 1957, WETZEL 1983). Characteristics of absorption of solar radiation in lakes are generally considered to be influenced mostly by various physical and chemical properties of the water. However, certain biological properties can also be important. For example in highly productive eutrophic lakes, abundant phytoplankton can reduce the total amount of absorption of solar radiation, as well as reduce the depth of penetration into the water (KIRK 1983).

MAZUMDER *et al.* (1990) concluded that lakes with similar size but greater clarity will have deeper mixing depths and greater heat content compared with lakes of lower clarity. Consequently, high densities of zooplanktivorous fish producing high algal abundance and low water clarity can affect lake stratification and heat content. Due to the nature of data presented and the shallowness of ponds used in this study, quantitative conclusions regarding effects of zoo-

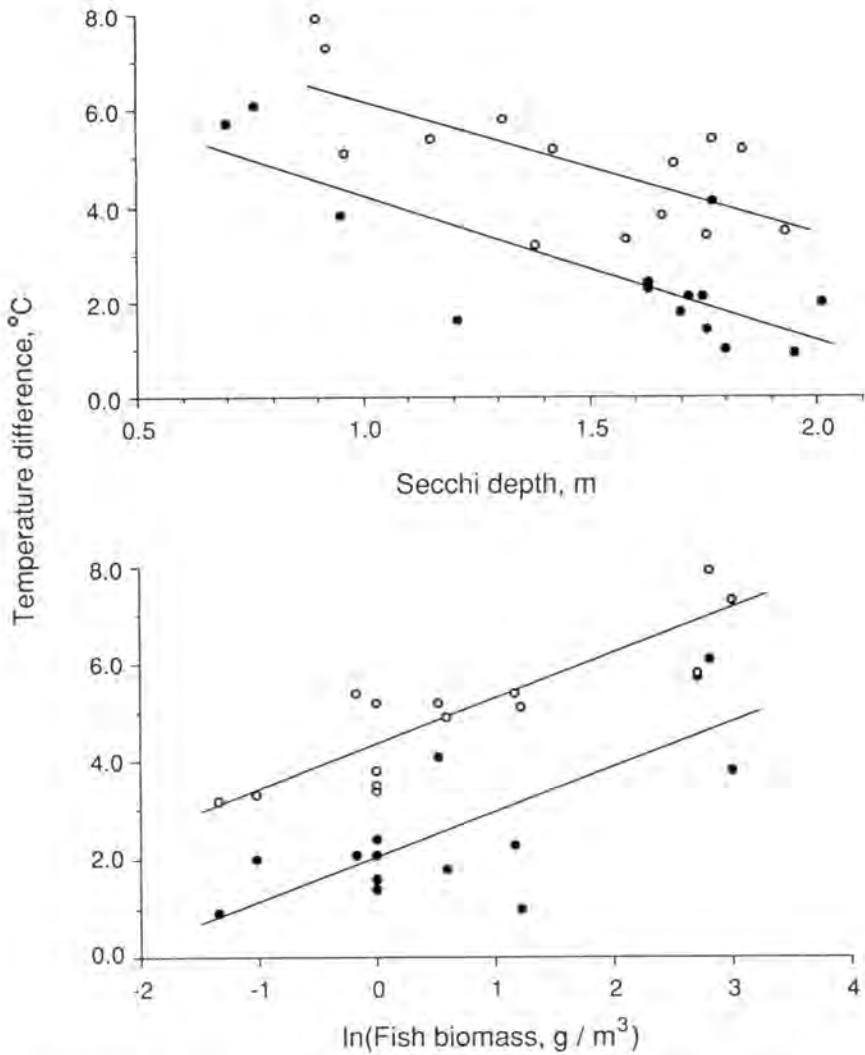


Fig. 4. Relationship between mean summer temperature difference between 0 and 2 m in ponds during 1989 (open circles) and 1990 (closed circles) and mean summer Secchi depth and planktivorous fish biomass ($\ln(\text{biomass} + 1)$) at the end of the experiment (September 1990). Regression equations relating temperature difference to Secchi depth are: 1989, $y = -2.7x + 8.9$, $r^2 = 0.46$, $P_{(\text{slope} \neq 0)} = 0.008$; 1990, $y = -3.0x + 7.3$, $r^2 = 0.64$, $P_{(\text{slope} \neq 0)} = 0.001$. Regression equations relating temperature to $\ln(\text{fish biomass} + 1)$ are: 1989, $y = 0.92x + 4.3$, $r^2 = 0.76$, $P_{(\text{slope} \neq 0)} < 0.001$; 1990, $y = 0.93x + 2.0$, $r^2 = 0.58$, $P_{(\text{slope} \neq 0)} = 0.002$.

planktivorous fish on pond mixing depths are not possible. However, these data clearly support MAZUMDER et al.'s findings that water clarity as affected by

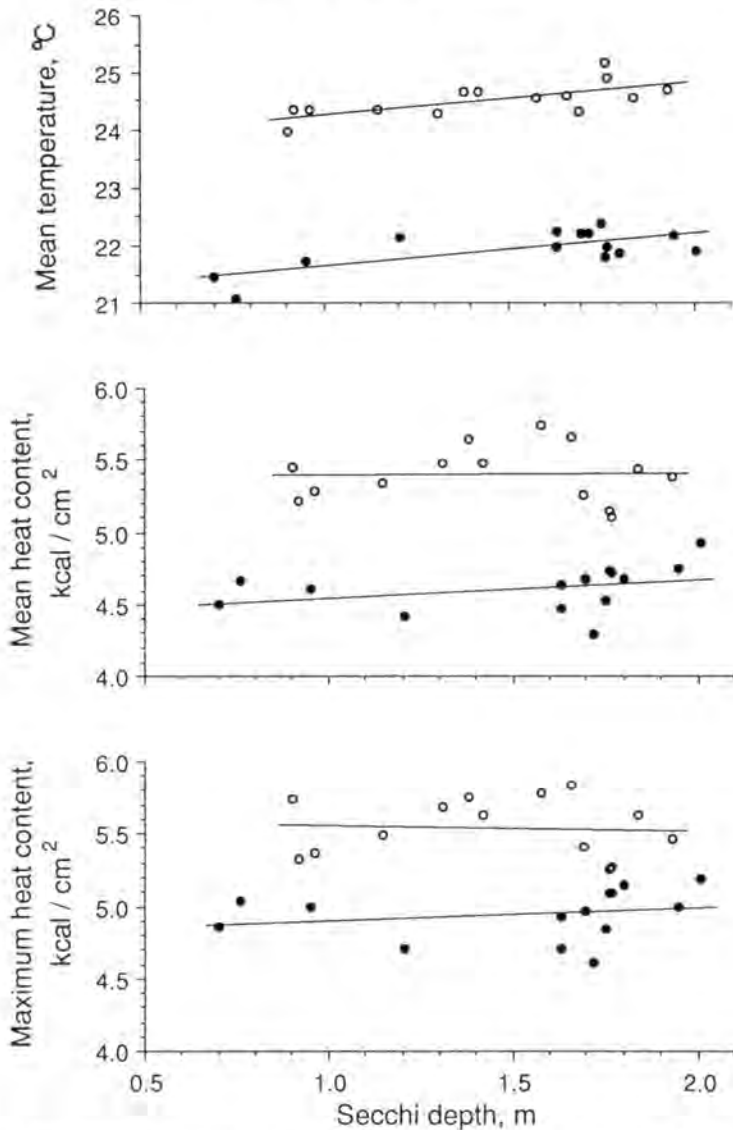


Fig. 5. Relationships between mean summer temperature, mean summer heat content, and maximum heat content with mean summer Secchi depth in ponds during 1989 (open circles) and 1990 (closed circles). Regression equations relating mean temperature and Secchi depth are: 1989, $y = 0.58x + 24$, $r^2 = 0.48$, $P_{(\text{slope} \neq 0)} = 0.006$; 1990, $y = 0.57x + 21$, $r^2 = 0.50$, $P_{(\text{slope} \neq 0)} = 0.005$. Slopes of regression equations relating mean and maximum heat content with Secchi depth are not significantly different from 0.

zooplanktivorous fish can influence lake thermal dynamics. As described by MAZUMDER *et al.* (1990), reduced water transparency (i.e., shallow Secchi

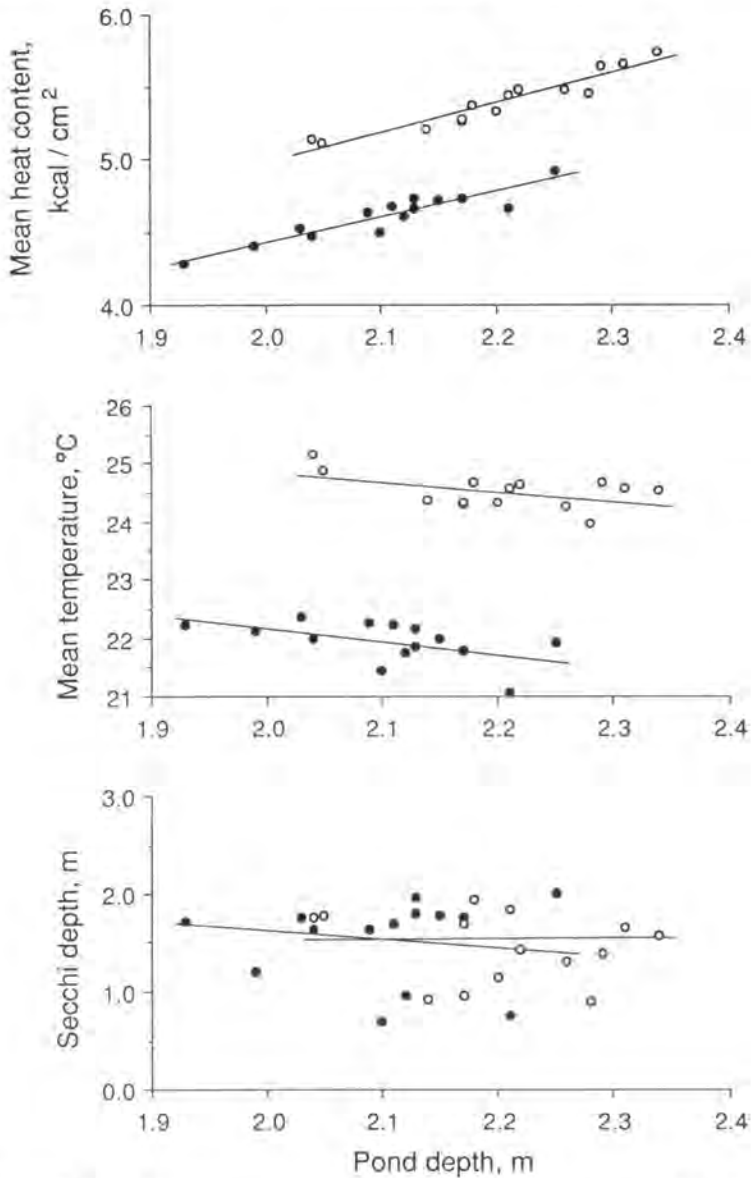


Fig. 6. Relationships between mean heat content, mean temperature, and Secchi depth with pond depth during 1989 (open circles) and 1990 (closed circles). Regression equations relating heat content and pond depth are: 1989, $y = 2.1x + 0.77$, $r^2 = 0.91$, $P_{(\text{slope} \neq 0)} < 0.001$; 1990, $y = 1.7x + 0.97$, $r^2 = 0.83$, $P_{(\text{slope} \neq 0)} < 0.001$. Regression equations relating mean temperature and pond depth are: 1989, $y = -1.7x + 28$, $r^2 = 0.24$, $P_{(\text{slope} \neq 0)} = 0.073$; 1990, $y = -2.3x + 27$, $r^2 = 0.30$, $P_{(\text{slope} \neq 0)} = 0.041$. Slopes of regression equations relating Secchi depth and pond depth are not significantly different from 0.

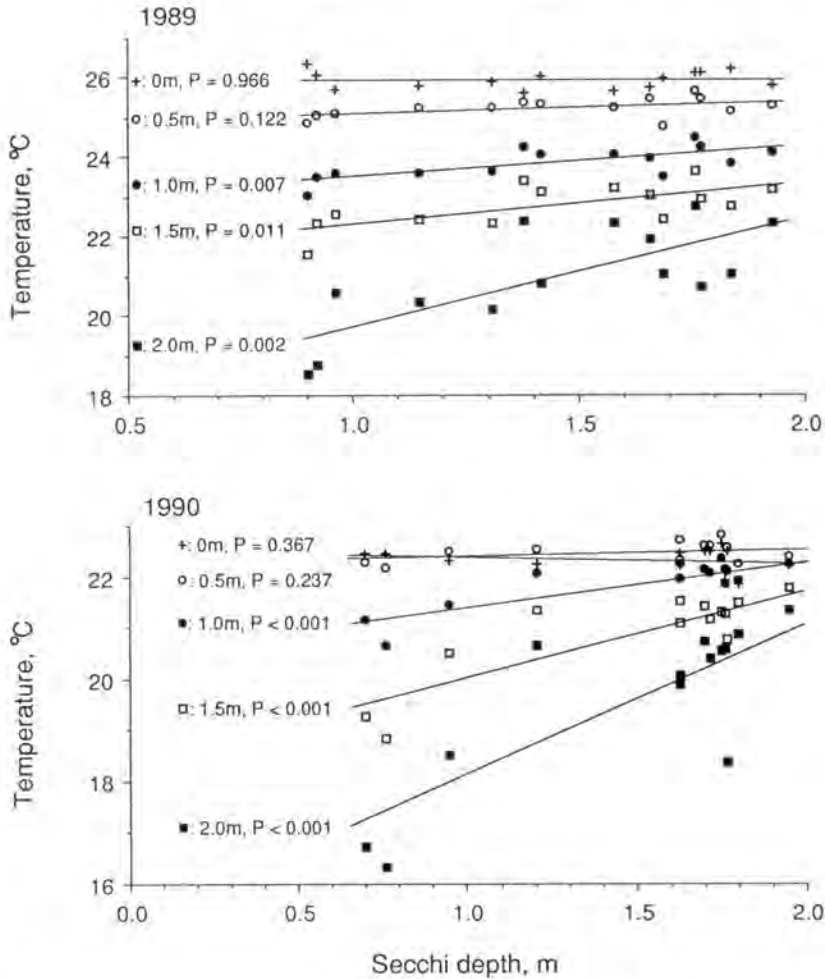


Fig. 7. Relationships between mean water temperatures at 0, 0.5, 1, 1.5, and 2 m with mean summer Secchi depths in ponds during 1989 and 1990.

depth), and hence restricted light penetration, reduced the downward distribution of heat such that bottom waters were consistently cooler in ponds containing high densities of zooplanktivorous fish compared with either ponds with low densities of zooplanktivorous fish or with no zooplanktivorous fish. Considering that since the beginning of limnology as a formal science, physical and chemical properties of lakes have been viewed as the key determinants of many, if not most, biological properties (ELSTER 1974), the growing body of information demonstrating the converse (i.e., that biological properties can have major influences on physical and chemical properties in lakes)

will necessarily alter the way limnologists perceive hierarchical interactions in lakes.

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