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Glacial Particles On The
Macrozooplankton Community
Structure Within Glacial Lakes

by
John M. Edmundson and
J. P. Koenings, Ph.D.
Number 67



Alaska Department of Fish & Game
Division of Fisheries Rehabilitation,
Enhancement and Development

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ABSTRACT

Alaska lakes exhibiting turbidity levels as low as 5 NTU because of suspended particles ($\geq 1\mu\text{m}$ $< 20\mu$) derived from glacier meltwater support relatively sparse populations of zooplankters and show a highly restrictive community composition.

Suspended glacial particles effectively reduce the depth of the euphotic zone (defined by the light compensation point), thereby decreasing areal net primary production. Such lowered primary production results in reduced densities of herbivorous macrozooplankters that forage on the algal community. Regardless of the presence or absence of planktivorous fish, filter feeding cladocerans (e.g., *Bosmina* and *Daphnia*) are uniquely absent from the zooplankton community of glacial lakes. In addition, while primary production and summer temperatures are low, they are not beyond the lower limit for clear-water systems that contain robust populations of cladocerans. We provide evidence suggesting that the overlapping size-ranges of algal material and glacial silt allow ingestion of the glacial particles by non-discriminating filter feeders. Such an inefficient foraging strategy, especially when particle concentrations are high and algal numbers low, results in the eventual elimination of *Bosmina* and *Daphnia*. Thus the macrozooplankton community of glacial lakes consists entirely of the selective herbivore *Diaptomus* and the raptorial feeding *Cyclops*.

KEY WORDS: turbidity, suspended glacial silt particles, euphotic volume, chlorophyll a, Cladocera, Copepoda, indiscriminate filter feeder, selective filter feeder.

INTRODUCTION

Limnological sampling of Alaskan lakes containing suspended glacial-silt particles and having turbidity levels ranging from 5 to 45 NTU reveals the total absence of the indiscriminate filter-feeding cladocerans *Bosmina* sp and *Daphnia* sp from the zooplankton community (Koenings et al. 1985). This was puzzling, since these species are well represented in several higher altitude clear-water lakes that drain into these glacially turbid systems. Summer water temperatures, primary production, and fish-predation pressure cannot explain the absence, since nearby clear-water lakes, which overlap these same features, support healthy populations of cladocerans.

Our observations led us to question if suspended glacial-silt particles act directly to eliminate these species. Indeed, McCabe and O'Brien (1983) have shown that *Daphnia pulex* exposed to suspended silt and clay particles have suffered decreased filtration, ingestion, and reproductive rates. However, Robinson (1953) found that suspended silt actually stimulated the birth rate of *Daphnia magna*, but only at low concentrations. Regardless of seemingly contradictory results, such studies, including that of Gerritsen and Porter (1982), suggest that fine particles are actively filtered from the water by feeding cladocerans. Thus ingested glacial-silt particles may act either to produce sufficient mortality or interfere with the reproductive process, resulting in the total elimination of cladoceran zooplankters.

After *Daphnia* had been transferred from a clear-water lake (0 NTU) to the high-turbidity environment of a glacial lake (45 NTU), controlled lake experiments were performed to show the effects of silt particles on their survival and reproduction and determine whether such exposure could cause sufficient immediate or long-term mortality to cause extinction. Finally, controlled laboratory tests that manipulated food (chl a) and turbidity

levels (NTU) were conducted to determine if suspended silt particles act as independent agents or interact with other agents or limiting factors.

METHODS AND MATERIALS

The study area for these experiments is located on the central Kenai Peninsula, southcentral Alaska. Three lakes were utilized for our field experiments. Johnson Lake, a small clear-water lake, was the source for *Daphnia galeata mendotae*; whereas, Hidden Lake, a large clear-water system, and Tustumena Lake, a glacially turbid lake, were used as field-experiment sites. Interlake differences in water-quality features (specifically, temperature, pH, conductivity, and alkalinity) and chl a were monitored to provide additional information that might clarify our explanation of field and laboratory results.

Daphnia galeata mendotae, identified after Pennak (1978), were collected from Johnson Lake using a 0.2-meter-diameter plankton net with 153- μ m mesh. Non-egg-bearing, female *Daphnia* were separated under a microscope, and 10 individuals were placed into each of twenty-four 500-ml polyethylene bottles containing Johnson Lake water strained through 153- μ m mesh. Twelve bottles were transported to Hidden Lake, a large clear-water lake (NTU of 0.5) containing healthy populations of *Daphnia* and *Bosmina*, to act as a control group; and 12 bottles were transported to Tustumena Lake, a large glacial lake (NTU of 45) containing only calanoid and cyclopoid copepods. To create six sets of duplicate tests per lake, the contents of each polyethylene bottle were emptied into 1-liter plexiglass biochambers (O'Brien and Kettle 1981). To eliminate handling and transport as test variables, we transferred the zooplankters to two lakes, instead of just to the glacial system. The biochambers were then submerged 1 m below

the surface; two biochambers from each lake were removed every 48 hours. Individual *Daphnia* were examined under a microscope to compare the reproduction and survivorship rates between the clear and turbid treatments. Total numbers of survivors and total amount of new production, including eggs, developing embryos, and newly hatched young were monitored every 48 hours for 240 hours.

In the laboratory experiments, Johnson Lake water was strained through a 153- μm mesh net and placed into eighteen 1-liter glass jars. Duplicate chambers were used at each of three treatments of turbidity (0, 30, and 60 NTU) and food level (0.5, 1.0, and 2.0 $\mu\text{g L}^{-1}$ of chl a). Chl a levels for Johnson Lake were determined using the fluorometric method after Koenings et al. (1985). The water treatments were changed every 48 hours to control bacterial growth and to maintain chl a at desired levels throughout the experiment. Turbidity levels were checked daily, and adjustments were made by the additions of concentrated silt. To arrive at the chl a treatment levels, each 1-liter jar of Johnson Lake water was filtered through a 4.25-cm GF/F, 0.7- μm filter to the necessary dilution and the filtrate added back to the required unfiltered Johnson Lake water.

To create the various turbidity levels, glacial silt was obtained directly from glacier ice by centrifuging the boiled meltwater and removing the concentrated silt with a pipette. The silt was stored frozen in sterile centrifuge tubes; individual tubes were thawed for each experiment. The silt extract was added to the jars to attain the proper NTU levels; turbidity was monitored with a DRT-100 (H. F. Instruments) laboratory turbidimeter. Six non-egg-bearing female *Daphnia galeata mendotae* were placed into each of the 1-liter glass jars, and the jars were placed into a water bath (to a level just below the lids) maintained at the same temperature as Johnson Lake (14°C). Total numbers of *Daphnia* survivors and new production (including eggs, developing embryos, and newly hatched young) were recorded every 48 hours for 288 hours.

RESULTS

In-Lake Reproduction and Survivorship Rates

Comparisons between the clear-water control turbid group (Hidden Lake) and the turbid group (Tustumena Lake) revealed a reduced survivorship and greatly lowered reproduction of *Daphnia* in the turbid group (Figure 1). Specifically, after 220 hours only 15% of the turbid group remained alive, while 55% of the control group were still living. Thus the mortality rate for the turbid group equalled 1.9 adults/d, compared to 1.0 adult/d for the clear-water group. In addition, seven times the number of young were found in the clear-water chambers, compared to those found in chambers exposed to the turbid environment.

The second lake experiment produced an even greater divergence between the clear and turbid treatments (Figure 2). In this test, all animals within the turbid group had died after 240 hours, compared with only 40% mortality for the clear-water control group. In this experiment, the mortality of the turbid group equalled 2.0 adults/d compared to 0.7 adults/d for the clear-water group. However, a major wind storm on Tustumena Lake may have affected our results, as wave action may have exacerbated mortality. Nonetheless, the control group also exhibited a 12-fold increase in new production over that of the turbid group.

The results from these experiments show that mortality rates from exposure to the suspended glacial-silt particles are increased but not necessarily immediately and that the most severe impact appears to occur on the reproductive potential of *Daphnia*. Additionally, examination of individual animals under a microscope (equipped with a video camera and monitor) revealed the ability of *Daphnia* to rapidly filter, ingest, and pass silt particles through the gut. Filtering rates were 0.31 ml/animal-hour or 8.3×10^6 particles/animal-hour. This suggests that ingestion of silt particles along with algal material of

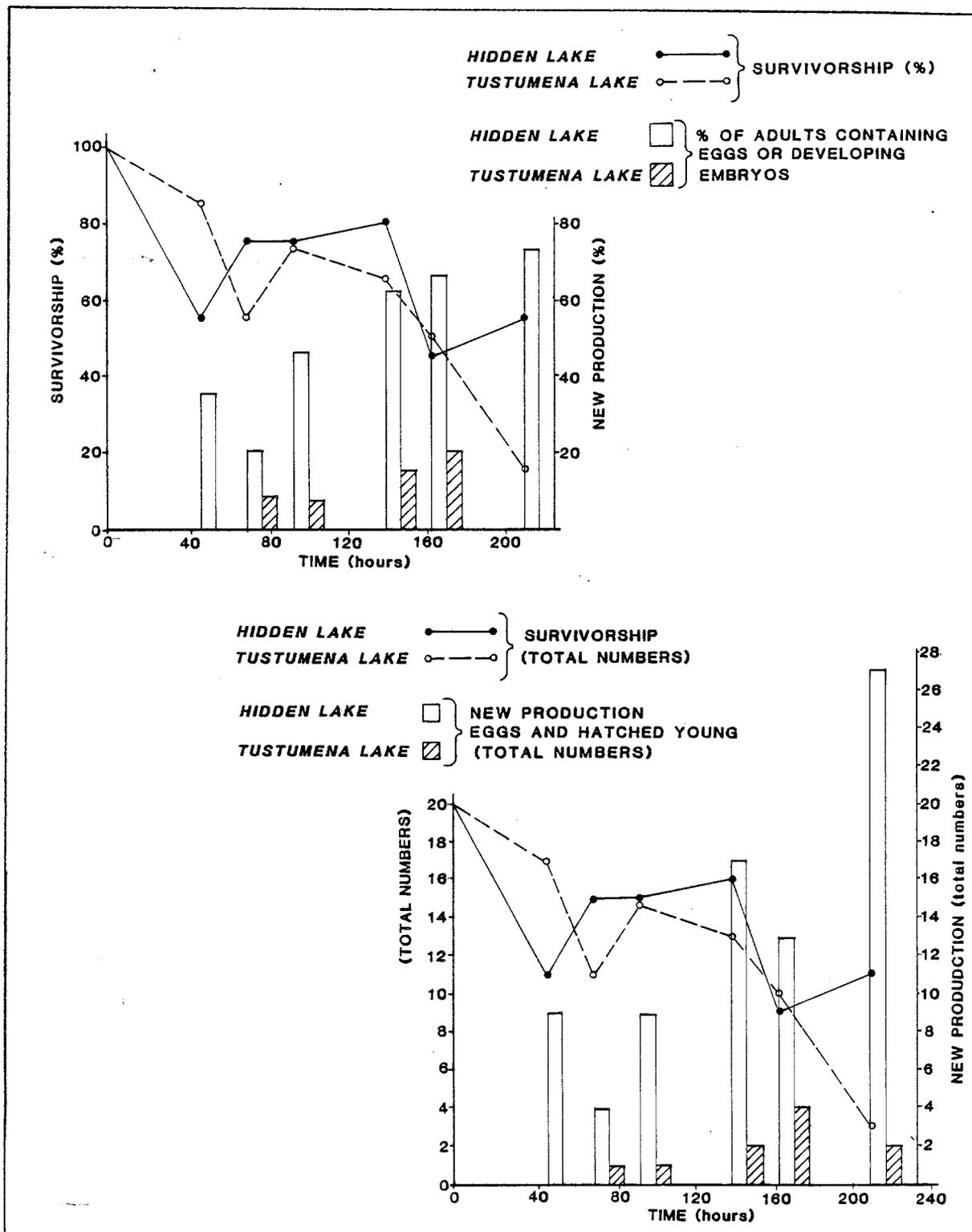


Figure 1. The effect of turbidity on survivorship and new production of *Daphnia* after exposure in Hidden Lake (<1 NTU) and in Tustumena Lake (45 NTU).

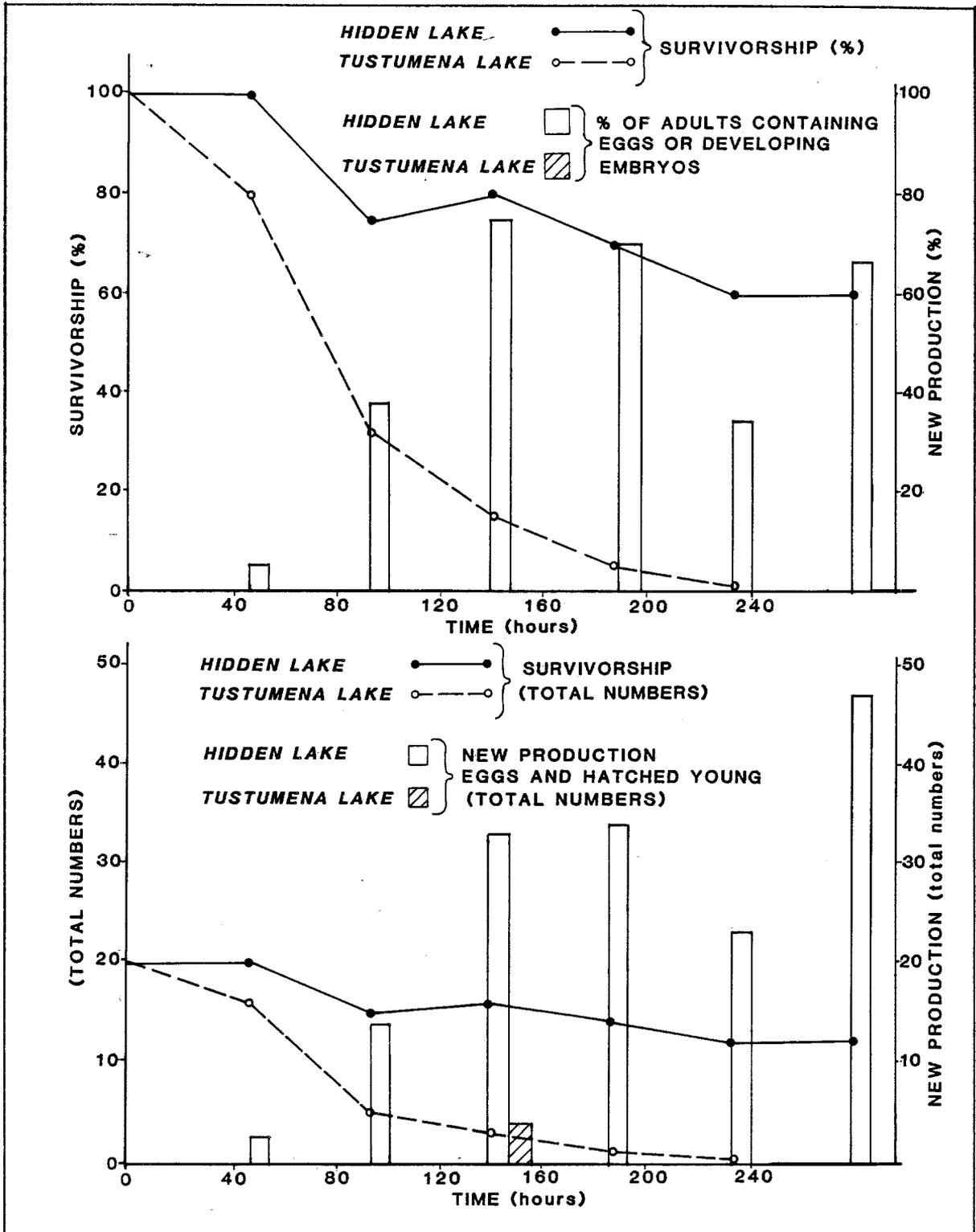


Figure 2. The effect of turbidity on survivorship and new production of *Daphnia* after exposure in Hidden Lake (<1 NTU) and in Tustumena Lake (45 NTU).

overlapping size ranges may interfere with the energy requirements of individual *Daphnia*, increasing mortality and disrupting reproduction.

Reproduction and Survivorship Under Manipulated Food and NTU Regimes (I)

In these experiments, we prepared three different food levels (0.5, 1.0, and 2.0 $\mu\text{g L}^{-1}$ of chl a) using varying ratios of filtered/unfiltered Johnson Lake water. In addition, we simulated three separate turbidity levels (0, 30, and 60 NTU) by adding varying values of concentrated glacial silt to each of the three food levels. Finally, all treatments were replicated, resulting in 18 chambers (3 food levels x 3 turbidities x 2 replicates).

Unexpectedly, we observed that for all food regimes *Daphnia* reproduction and survivorship fared best under turbid conditions, usually at the highest turbidity level (60 NTU); while clear-water conditions (0 NTU) proved the least successful (Figures 3 and 4). Specifically, at 60 NTU a total of 235 young were produced across all food levels, compared to 140 young at 30 NTU and 85 young at 0 NTU (Figure 3). In addition, at the end of the 60 NTU experiment, 26 adults (out of the original 36) were still alive, resulting in a mortality rate of 0.8 adults/d, compared to 1.4 adults/d at 30 NTU and 1.5 adults/d at 0 NTU. When we compared turbidity treatments within equivalent food levels, we found that recruitment for the 0.5 $\mu\text{g L}^{-1}$ chl a level equalled 130 young, compared to 175 young at 1.0 $\mu\text{g L}^{-1}$ and 155 young at 2.0 $\mu\text{g L}^{-1}$ (Figure 4). Overall, mortality rates at the lower food level equalled 1.5 adults/d, compared to 1.3 adults/d at the intermediate food level and 0.9 adults/d at the higher food level. In general, reduced food levels seemed to reduce survivorship and, to a more limited extent, recruitment; whereas, increased turbidity appeared to drastically increase reproductive success and, at the same time, reduce mortality.

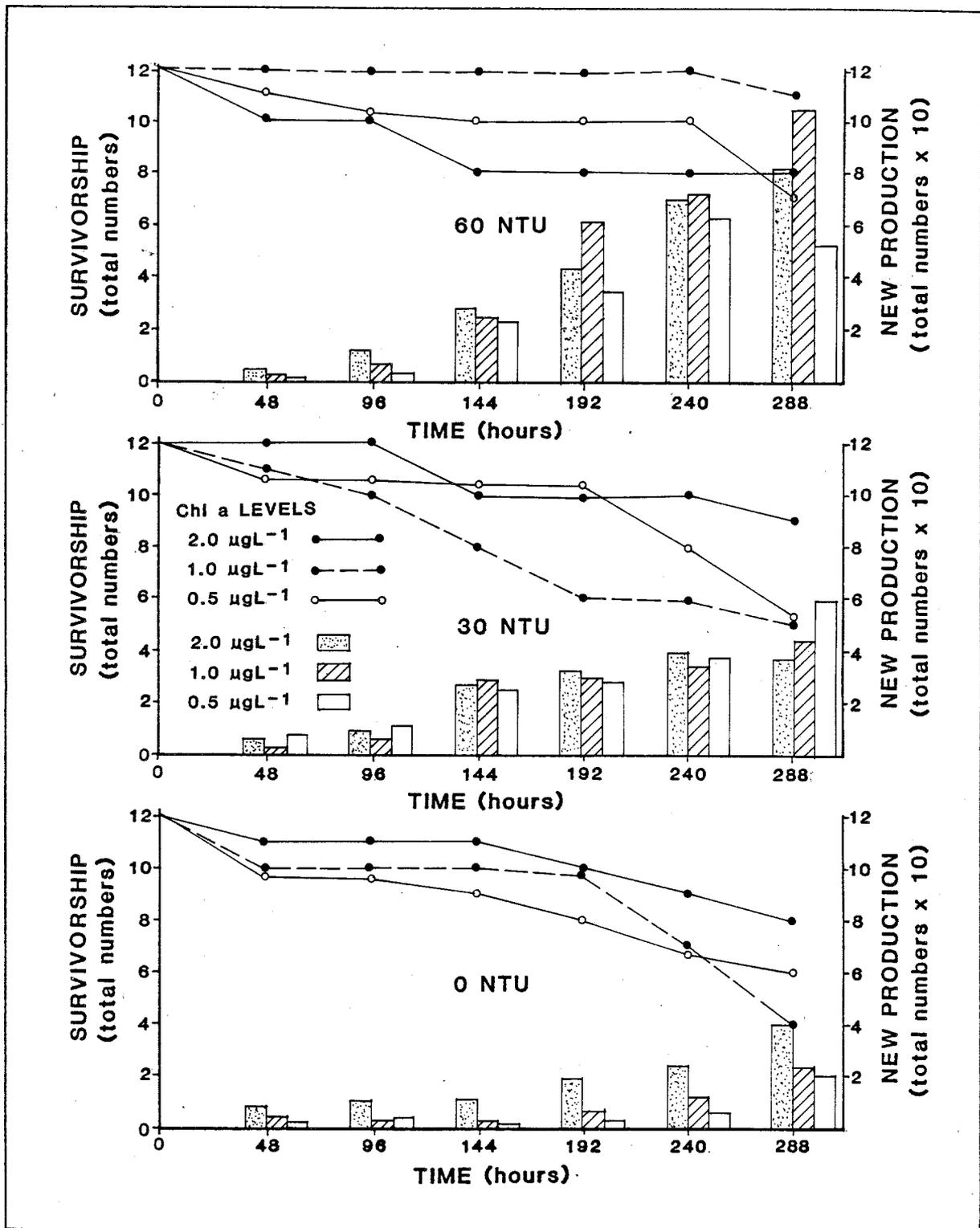


Figure 3. The effects of turbidity levels (0, 30, and 60 NTU) on *Daphnia* survivorship and reproduction when exposed to three food (chl a) levels (0.5, 1.0, and 2.0 µg L⁻¹) without water renewal.

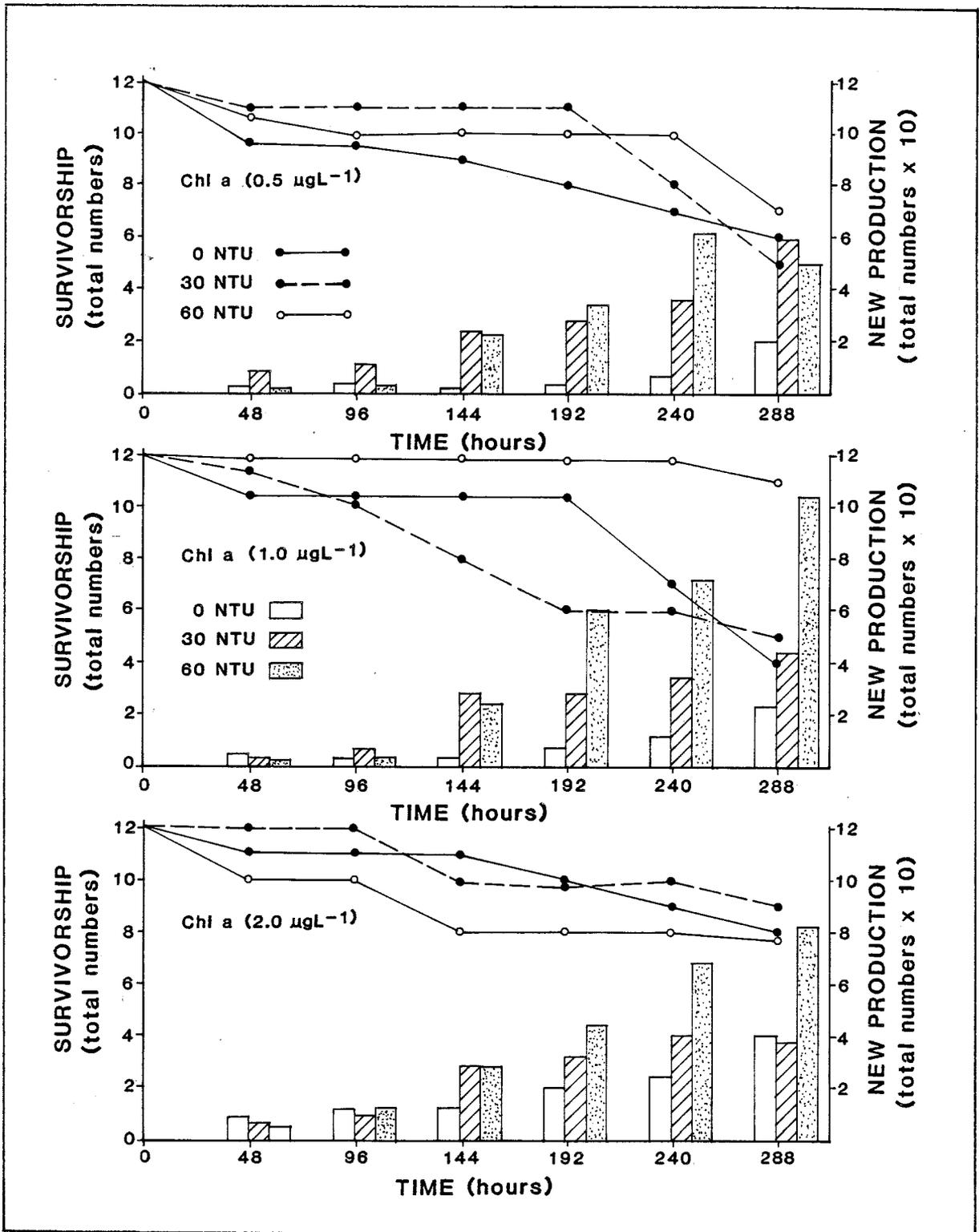


Figure 4. The effect of food (chl a) level (0.5, 1.0, and 2.0 $\mu\text{g L}^{-1}$) on *Daphnia* survivorship and reproduction when exposed to three turbidity levels (0, 30, and 60 NTU) without water renewal.

These results, although conflicting with field-test results, show that *Daphnia* can survive, reproduce, and thrive in a high-turbidity environment. Thus silt, by itself, cannot be held responsible for the absence of cladocerans from the zooplankton community. However, we grew curious about the lack of a constant reproductive response to different food levels within an NTU treatment (Figure 3) and the fairly consistent positive benefit on recruitment of increased turbidity within and across food levels (Figure 4). We theorized that the deposition and accumulation of fecal pellets, containing significant amounts of silt particles, at the bottom of the glass jars was furnishing an inoculum for bacterial growth. This provided an unlimited food source for the *Daphnia* exposed to turbid water. As bacterial population growth is roughly proportional to the amount of exposed surface (Robinson 1957), this would explain why recruitment failed to respond proportionally to the originally established chl a levels. That is, the different algal food levels were masked by an overwhelming bacterial food supply as the higher turbidity levels provided a greater medium for bacterial growth (Arruda et al. 1983). Indirectly, increasing turbidity levels up to 60 NTU provided the best environment (bottles) for *Daphnia* survival and reproduction.

Reproduction and Survivorship Under Manipulated Food and NTU Regimes (II)

To eliminate the problem of suspected bacterial contamination, the experiment was repeated; as an added precaution, however, the water was changed, and food and turbidity levels were reset every 48 hours. This process also simulated the continuous water-exchange conditions that existed in the submerged biochambers during the lake experiments (where the water-exchange rate equalled 12 liter/hr).

Across the turbidity levels, survivorship and recruitment for the combined food (chl a) levels were relatively unaffected as

turbidity increased (Figure 5). At 60 NTU, the overall mortality equalled 0.8 adults/d, compared to 0.8 adult/d at 30 NTU and 0.6 adult/d at 0 NTU. Moreover, at 60 NTU, production of young *Daphnia* equalled five animals; whereas, production at 30 NTU equalled 13 young, and at 0 NTU, it increased slightly to 14 animals. However, as both food levels decreased within each turbidity level, we found a major drop in survivorship and recruitment (Figure 5). For example, at 60 NTU the mortality at $2.0 \mu\text{g L}^{-1}$ chl a equalled 0.3 animals/d, compared to 0.8 animals/d at $1.0 \mu\text{g L}^{-1}$ chl a and 1.5 animals/d at $0.5 \mu\text{g L}^{-1}$ chl a.

Across food levels (chl a), the greatest survivorship and production for combined turbidity levels occurred at the highest food level of $2.0 \mu\text{g L}^{-1}$ chl a (Figure 6). An overall mortality rate at $0.5 \mu\text{g L}^{-1}$ chl a equalled 1.8 animals/d, compared to 0.7 animals/d at $1.0 \mu\text{g L}^{-1}$ chl a and only 0.4 animals/d at $2.0 \mu\text{g L}^{-1}$ chl a. Greater food levels also promoted recruitment, as numbers of young increased from zero at low chl a concentrations to three at intermediate food levels and to 29 at the highest food level. Within a given food level, survival was not greatly affected by increased turbidities, except at the lowest chl a level. For example, at $1.0 \mu\text{g L}^{-1}$ chl a the mortality rates for 30 NTU and 60 NTU treatments were equal; they were also equal for 60 NTU and 0 NTU at $2.0 \mu\text{g L}^{-1}$ chl a. The major exception occurred within the lowest food level; mortalities seemed to be exacerbated by increased levels of glacial silt. Finally, recruitment of young was not observed at $0.5 \mu\text{g L}^{-1}$ chl a, regardless of turbidity level; whereas, at $1.0 \mu\text{g L}^{-1}$ chl a new production occurred only in the 0 NTU and 30 NTU treatments, and at $2.0 \mu\text{g L}^{-1}$ chl a recruitment occurred at all turbidities. At this higher food level, increasing turbidity levels slowed recruitment, as five young were produced at 60 NTU, 11 young at 30 NTU, and 13 young at 0 NTU.

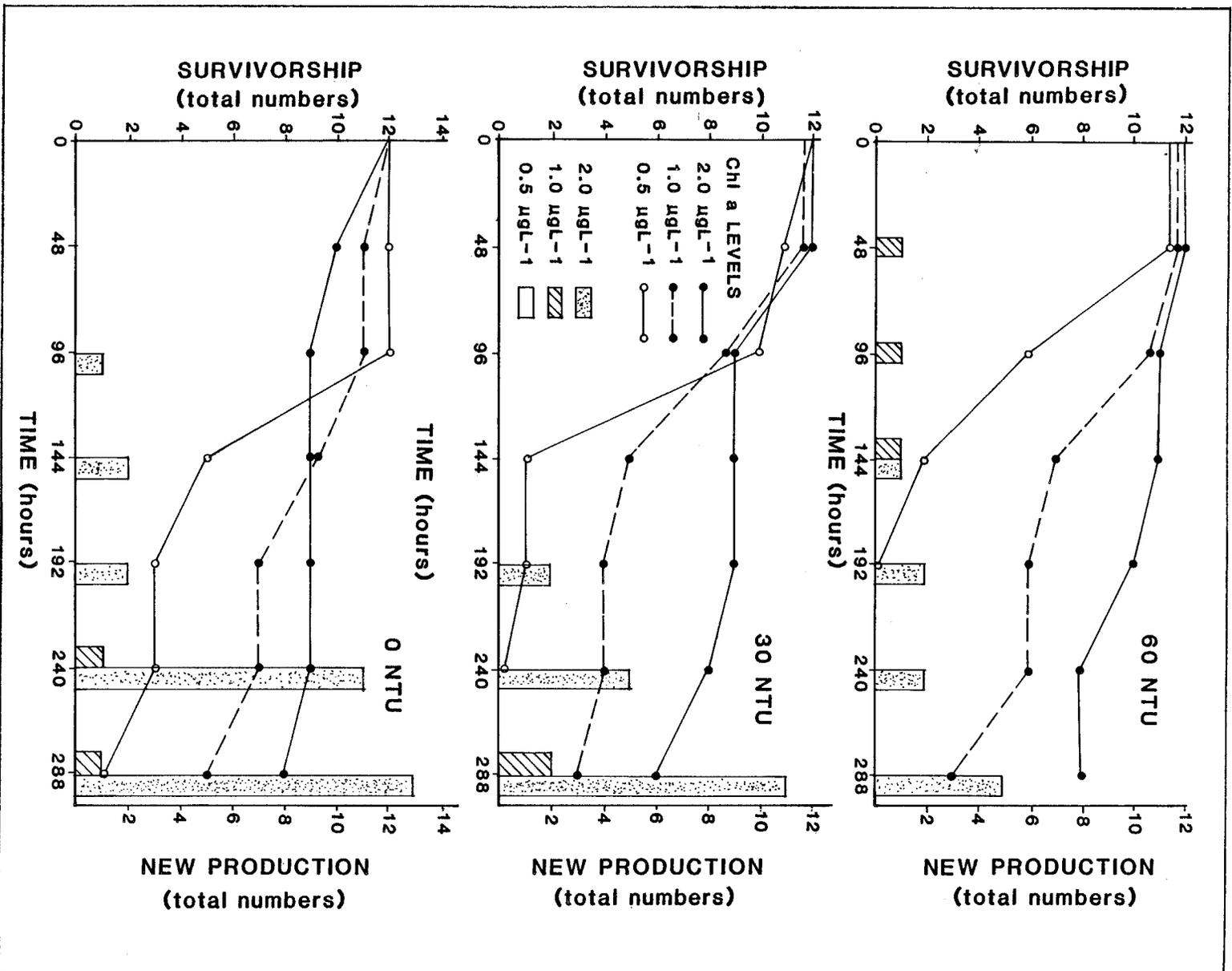


Figure 5. The effects of three turbidity levels (0, 30, 60 NTU) on *Daphnia* survivorship and reproduction when exposed to three food (chl a) levels (0.5, 1.0, and 2.0 µg L⁻¹) with water renewal.

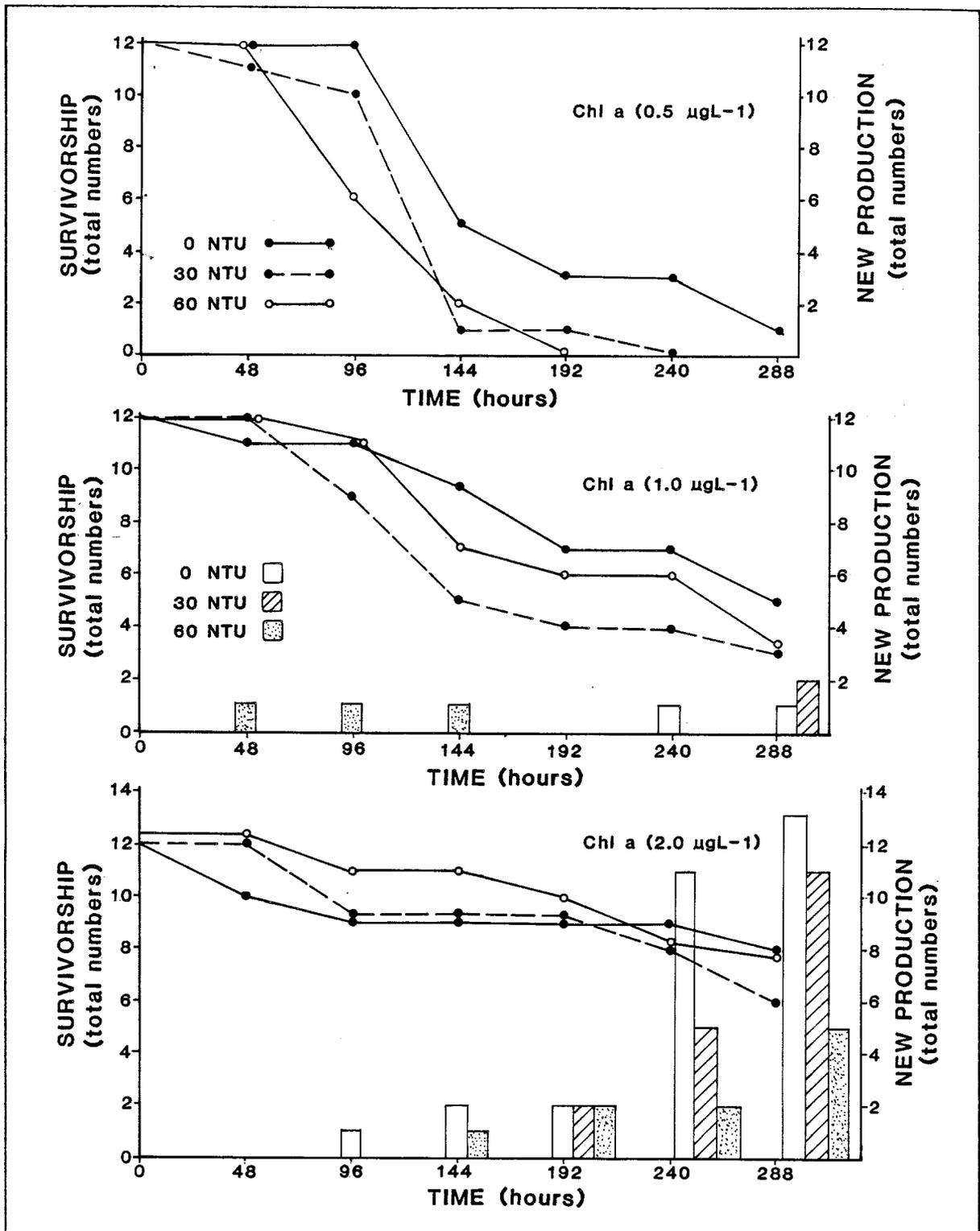


Figure 6. The effects of food (chl a) level (0.5, 1.0, and 2.0 µg L⁻¹) on *Daphnia* survivorship and reproduction when exposed to three turbidity levels (0, 30, and 60 NTU) with water renewal.

DISCUSSION

Results from our initial laboratory experiments, which presumably allowed the buildup of bacteria, suggest that cladocerans can inhabit lake environments of high turbidity, provided there is a high level of available food. These findings are consistent with observations from reservoirs located in agricultural watersheds in the southwestern and southeastern United States. Arruda et al. (1983) have suggested that a combination of high turbidity, warmer water temperatures, and high primary production benefits foraging cladocerans by providing conditions for bacterial growth and, thus, an additional food source. Particles derived from melting glaciers, however, have little opportunity to form such associations, especially in colder, unproductive Alaskan lakes; ingestion of these particles in nature therefore provides little benefit (Stockner, pers com, 1983).

Clogging of filtering appendages was also considered as a cause for the absence of cladoceran zooplankters, but it was rejected because microscopic examination showed the ability of *Daphnia* to filter, ingest, and pass silt particles through the gut. Individual *Daphnia* were also observed using the abdominal claw to remove unwanted particles from the food groove, which never became clogged. Predation by planktivorous fish was also eliminated as a process of sufficient intensity to cause the total elimination of cladocerans from turbid glacial systems. McCabe and O'Brien (1983) have surmised that suspended silt particles provide the cladocerans with protection from fish predation by reducing visibility. Such protection apparently overrides the deleterious effects of reduced filtration, ingestion, and reproduction rates. If this were true for Alaskan glacial lakes, we would expect to find thriving cladoceran populations; however, we have observed cladocerans to be absent from glacial lakes, regardless of the presence or absence of foraging planktivorous fish. Also, clear-water lakes of the same

region that have dense populations of planktivorous fish (i.e., sockeye salmon fry) support large numbers of cladocerans. We suggest that, in nature, the harmful effects of suspended glacial particles outweigh the beneficial effects of reduced predation and are a factor in limiting cladoceran populations.

Our field experiments demonstrate that *Daphnia* suffers lowered recruitment and survival in glacial water (NTU of 45), compared to that observed in a clear-water (NTU of <1) environment. Since chl a levels ranged from 0.4 $\mu\text{g L}^{-1}$ to 1.0 $\mu\text{g L}^{-1}$ in the clear lake and from 0.5 $\mu\text{g L}^{-1}$ to 2.5 $\mu\text{g L}^{-1}$ in the glacial lake during the experiment, algal biomass levels were not responsible for the increased mortality within the glacial lake. However, we realized that algal quality as well as quantity are important factors in zooplankton nutrition (Porter 1975, 1977). Thus decreased algal availability may have caused the increased mortality and failed recruitment in the biochambers incubated in glacial water. This, in turn, would mean that all glacial lakes are populated by species of inedible phytoplankton, as none are capable of supporting cladoceran zooplankters (Table 1). As unlikely as this seemed, we tested the effect of increased turbidity (using the same silt stock for each turbidity treatment) by employing different ratios of filtered and unfiltered Johnson Lake water. Thus the cladocerans were exposed to equivalent conditions, except for varying levels of the same glacial silt and/or chl a. Given these conditions, our results again showed that glacial silt was not solely responsible for increased mortality (Figure 3). Glacial silt exacerbated *Daphnia* mortality and lessened recruitment only as chl a levels dropped to around 0.5 $\mu\text{g L}^{-1}$ (see Figures 4 and 5). At this decreased level of algal biomass, mortality followed turbidity increases, a trend that lessened as the chl a levels increased. As seasonal mean chl a levels in glacial lakes (n=15) equal 0.4 $\mu\text{g L}^{-1}$ (Edmundson and Koenings 1985), glacial silt may act to exclude populations of cladocerans through reducing autochthonous primary production.

Table 1. Comparison of zooplankton community composition (May-November) between glacial (> 5 NTU) and non-turbid (< 5 NTU) lakes. Represented lakes are examples taken from a more complete data set (glacial [n=18], non-turbid [n=78]) that includes lakes throughout southcentral and southeast Alaska. Relative densities are represented as follows: absent (-), < 33% (+), >34% < 66% (++) , and >67% (+++).

Taxa/Lake	Glacial (>5 NTU) lakes								Non-turbid (<5 NTU) lakes						
	Tustumena	Kenai	Crescent	Grant	Ptarmigan	Crescent	Miners	Kushtaka	Upper		Hidden	Packers	Lesiore	Karluk	Badger
<u>Cladocera:</u>															
<i>Bosmina</i> sp.	-	-	-	-	-	-	-	-	++	+	+	+	+++	+	+
<i>Daphnia</i> sp.	-	-	-	-	-	-	-	-	++	+	+	+	+	+	+
<i>Holopedium gibberum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Alona</i> sp.	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Polyphemus pediculus</i>	-	-	-	-	-	-	-	-	++	-	-	-	-	-	+
<u>Copepoda:</u>															
<i>Cyclops</i> sp.	+	++	+	++	++	+++	++	++	-	+++	+	+	+	+++	+++
<i>Diaptomus</i> sp.	+	+	-	-	++	-	-	-	-	-	+	++	+	+	+
<i>Epiachura</i> sp.	-	-	-	-	-	-	-	-	+	-	+	+	-	-	-
<u>Rotifera:</u>															
<i>Kellicottia longispina</i>	+	+	+	+	+	+	+	+	+	+	++	-	-	-	+
<i>Asplanchna</i> sp.	-	-	+++	+	-	-	-	+	-	-	-	-	-	-	-
<i>Keratella</i> sp.	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
<i>Conochiloides</i> sp.	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-

The primary effect of suspended glacial particles on *Daphnia* is to cause an inadequate food supply, thus indirectly affecting reproduction. In Alaskan lakes, suspended glacial-silt particles become a limiting factor for the survival and reproduction of cladocerans by decreasing light penetration, reducing euphotic volume, and thus decreasing net primary production. When food levels are low and silt concentrations high, the nonselective foraging strategy of cladocerans results in the ingesting of glacial particles together with algal material of overlapping size ranges; therefore, cladocerans may be able to acquire sufficient energy for short-term survival, but successful reproduction is curtailed (McCabe and O'Brien 1983).

Indeed, our results from tiered food-level experiments suggest that the first major effect of reducing algal biomass from $2.0 \mu\text{g L}^{-1}$ chl a to $1.0 \mu\text{g L}^{-1}$ chl a is a drastic reduction in recruitment (*see* Figure 6). A further drop in chl a to $0.5 \mu\text{g L}^{-1}$ results in drastically increased mortality, especially at the higher turbidity levels. These data support the contention of Richman and Dodson (1983): under extremely low food abundances, calanoid, not cladocerans, dominate the zooplankton community; because calanoids ingest a lower number of select food particles per unit time, requiring less energy. The inefficient filtering process of cladocerans, however, requires a great deal of energy because a large amount of water must be filtered to collect a small amount of food. In addition, during the summer months cladocerans rely on a parthenogenic reproductive strategy that rapidly produces many broods of young to take advantage of abundant food supplies and combat huge predation losses. Under abundant food conditions, this strategy works well, especially for inefficient filter feeders that are extremely vulnerable to predation. We suggest that the effects of suspended silt on cladoceran populations (from interference with this type of reproductive strategy) are more deleterious than on calanoid copepods, which expend less energy to support a slower-paced sexual reproduction strategy. The net result (*see* Table 1) is

that cladocerans are unable to obtain the required energy for successful survival and reproduction; therefore, glacial lakes in Alaska are populated by the selective herbivore *Diaptomus* and the raptorial feeding *Cyclops*.

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