Predator driven changes in community structure

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Summary. The zooplankton community of a small pond changed markedly with temporal variation in predation pressure. Long term changes in zooplankton community structure occurred following the replacement of planktivorous fish by phantom midge (Chaoborus americanus) larvae as the predominant predator of zooplankton. The interannual changes following the establishment of Chaoborus included the apparent or near extinction of species ill adapted to the new predation pressure and the successful colonization of well adapted species. Seasonal changes in the species composition and size distribution of the zooplankton community correlate with temporal variation in predation intensity associated with temperature-activity patterns of the predator or changes in the stage structure of the predator population.

Key words: Size-selective predation – Community structure – Predation intensity – Seasonal – Species sorting

The role of predators or grazers in determining the numbers or types of species present in communities is well established for several environments (Paine 1966; Black 1976; Zaret 1980; Sih et al. 1985), and more controversial for others (Sih et al. 1985; Thorp 1986; Hairston 1987). One of the simplest and potentially most dramatic effects of predation is to remove some species from the community while leaving others relatively untouched. The net result is that in the presence of the predator population one group of prey species dominates while in its absence another group is primarily found. The process is probably most widely recognized in a number of communities of the marine intertidal zone (Paine 1966; Menge 1976), but also is found in a broad variety of other aquatic and terrestrial environments (Harper 1969; Inouye et al. 1980; Duggins 1980; Risch and Carroll 1982). One of the most, if not the most, consistent effect of this type has been found in freshwater zooplankton communities. Visually foraging planktivorous fish selectively remove the prey that they can see; in general species with larger body size (O'Brien et al. 1976; O'Brien 1979; Lazzaro 1987). In the presence of these fish, small species dominate zooplankton communities. In their absence larger species are found. Although the effect has been recognized for over 20 years (Hrbacek 1962; Brooks and Dodson 1965; Galbraith 1967) and reported from lakes all over the world (Grygerek et al. 1966; Wells 1970; Hutchinson 1971; Nilsson 1972, 1985; DeBernardi and Guissani 1975; Drenner et al. 1982; Ziebell et al. 1986), virtually without contradictory evidence, it has been surprisingly ignored by the general ecological audience. A survey of 11 widely used introductory ecology texts (Brewer 1979; McNaughton and Wolf 1979; Smith 1980; Odum 1983; Ricklefs 1983; Lederer 1984; Kormondy 1984; Krebs 1985; Begon et al. 1986; Begon and Mortimer 1986; Colinvaux 1986) revealed that only 3 contain any reference to selective predation upon freshwater zooplankton. Of these only 2 discuss the result in the context of predation effects on community structure.

Although the community level effects of planktivorous fish are now well established, the role played by zooplanktivorous invertebrates is less clear. Behavioral and population level studies have documented repeatedly the potential for these predators to have significant impact (Hall 1964; Dodson 1972, 1984; Allan 1973; Kerfoot 1975, 1977a, b; Walton 1988), but community level effects have only rarely been investigated, and with varying results (Lane 1979; Neill 1981, 1984; Walton 1986). Zaret (1980) reviewed this literature and concluded that predatory invertebrates typically select for small and medium sized prey and drive zooplankton populations and communities to larger sizes.

The best demonstrations of the importance of size-selective predation upon zooplankton communities come from studies following the introduction of planktivorous fish to lakes from which such predators had been absent. Brooks and Dodson (1965), Wells (1970), Warshaw (1972) and others invariably concluded that the newly introduced planktivore eliminated large zooplankton species from the community and resulted in zooplankton assemblages that were presumably better adapted to the new predation pressure. Similar studies demonstrating the magnitude of the direct impact of predatory invertebrates upon zooplankton communities are rare. Many researchers (including O'Brien and Schmidt (1979); O'Brien et al. (1980); Hebert and Loaring (1980); von Ende and Dempsey (1981) and Dodson (1984)) have presented correlative evidence that particularly vulnerable prey forms or species are not found in association with certain predatory invertebrates and then have concluded that the prey are eliminated or prevented from becoming established in lakes with these predators. Only studies of the introduction of Mysis to Lake Tahoe (Richards et al. 1975; Morgan et al. 1978; Goldman et al. 1979; Threlkeld et al. 1980) however, have studied directly the intro-
duction of a predatory invertebrate to a zooplankton community and found decimation or extinction of vulnerable species.

We have examined the zooplankton community of Little Bullhead Pond, Rhode Island, over a seven year period, during which the dominant predator of zooplankton changed from exclusively redbreast sunfish (Lepomis auritus) to phantom midge larvae (Chaoborus americanus). Prior to 1980 the pond contained a dense population of the sunfish (Hastin et al. 1983), but in 1980 and 1981 a prolonged drought dried the pond and killed the fish. When the pond refilled in 1982 fish were absent and the predatory midge larvae became established, reaching high midsummer densities. We have documented the size and species composition of the zooplankton community for at least eight dates in each of two years when fish were present (1978 and 1979) and two years when fish were absent (1982 and 1983). Our data demonstrate the existence of clearly distinct, temporally separated "fish structured" and "Chaoborus structured" zooplankton communities in Little Bullhead Pond. The predominant position of predation in controlling community type is seen in the rapid transition from one assemblage to the other, including the near extinction of certain species and the appearance of other species. We have also documented distinct seasonality in the composition and size structure of the zooplankton community that correspond to seasonal changes in the intensity of predation, but differ depending on whether the predation is by fish or Chaoborus.

**Study site**

**Description of little bullhead pond**

Little Bullhead Pond is spring fed and contained in a closed basin 3 km west of Perryville, R.I. The site of the pond varies with seasonal and annual fluctuation in rainfall, but mean surface area is approximately 0.1 ha and mean maximum depth is less than 3 m. The pond dried completely in 1981 and although records for the pond are incomplete prior to the mid 1970s, rainfall and USGS groundwater data for a nearby site indicate that the pond probably dried on two other occasions in the last 35 years (Hastin unpublished work).

The pond contained sunfish at least since the 1960s when it was stocked by the landowners (J.E. O’Brien pers. comm.). It supported a very dense population of redbreast sunfish (Lepomis auritus) until 1981 (Hastin et al 1983). The fish were killed during a prolonged drought in late 1980 and early 1981 when the pond froze to the bottom, then dried completely (Fig. 1). Fish were not restocked following the fish-kill, and have not been reintroduced naturally because the pond lacks inflow and outflow streams.

**Methods**

The zooplankton community of Little Bullhead Pond was sampled at least once every month from 25 April 1978 through 1984. When conditions permitted the pond was sampled with a Clarke-Bumpus sampler fitted with a 75 μm mesh nylon net. Duplicate oblique tows were made, during the day, of the entire water column and preserved in the field with 10% buffered Formalin. Most samples taken in this manner were concentrations of zooplankton from 100 to 1000 L of water. When ice conditions prevented use of the Clarke-Bumpus sampler, the pond was sampled with a "Thirsty Mate" bilge pump. Duplicate 50 L samples were collected and filtered through a 75 μm mesh net, then preserved as before.

In the laboratory, zooplankton collections were subsampled, placed in a petri dish and examined under a stereomicroscope. The total lengths of randomly selected individuals of all common taxa of microcrustacea present were measured using a drawing tube and a GTCO digitizer that was regularly calibrated with a stage micrometer. At least 40 individuals of each taxon were measured when possible. When fewer than 40 individuals of a taxon were present in an entire sample, all the individuals present were measured. Total length of cladocerans was measured from the anterior end of the head capsule to the base of the tail spine. Copepod total length was measured from the anterior end of the cephalothorax to the base of the caudal rami. Rotifers and protozoa were excluded from this analysis.

Selected zooplankton samples were used to determine size distributions of the zooplankton community. Zooplankton collections were subsampled, placed in a petri dish and examined under a stereomicroscope. The total lengths of randomly selected individuals of all common taxa of microcrustacea present were measured using a drawing tube and a GTCO digitizer that was regularly calibrated with a stage micrometer. At least 40 individuals of each taxon were measured when possible. When fewer than 40 individuals of a taxon were present in an entire sample, all the individuals present were measured. Total length of cladocerans was measured from the anterior end of the head capsule to the base of the tail spine. Copepod total length was measured from the anterior end of the cephalothorax to the base of the caudal rami. Rotifers and protozoa were excluded from this analysis.

Selected zooplankton samples were also used for an "instar analysis" of the Chaoborus americanus population. At least 30 individual midge larvae were randomly selected from each of 16 monthly samples and the head size and body size of each individual were measured using the criteria introduced by Swift and Federkon (1975). The information gathered in this way was used to identify the instar of each larva and to determine the stage structure of the larval population in each sample.

Sunfish activity in Little Bullhead Pond was monitored using an unbaitsed fish trap, with 3 m vanes on each side and a 10 cm opening, placed perpendicular to the shore in 1 m deep water for 24 hr, from sunset to sunset. The trap was set 46 times between 15 April 1980 and 21 December 1980 and activity was recorded as the number of captures per 24 h. Since the pond lies in a closed basin there was no immigration or emigration of fish. The assumptions we will make are that when fish were more active, they were more likely to be captured by the trap, and that more active fish fed more on zooplankton. Direct measures of fish predation on copepods in Little Bullhead Pond and a second, nearby pond support these assumptions (Hastin et al. 1983; Hastin and Munns 1984).

The feeding behavior of each instar of Chaoborus americanus larvae preying upon different sized copepods or Cladocera was examined in experiments run in the laboratory at 12°C. C. americanus larvae were collected from Little

![Fig. 1. Maximum depth of Little Bullhead Pond during 1978–1983](image-url)