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LANE REPLIES—Wurtsbaugh *et al.* state that I concluded fish to be unimportant with regard to zooplankton community structure[1]. I did not draw this conclusion. They confuse two questions: (1) Which predators, vertebrate or invertebrate, exert the most predation pressure on lake zooplankton?, and (2) what is the significance (importance) of these predation pressures? My paper was concerned with providing a quantitative answer for question (1). With regard to question (2) I was careful not to make value judgements. I stated that vertebrate predators often have "dramatic effects" on lake zooplankton. I shall reply to the three methodological criticisms of Wurtsbaugh *et al.*, then clarify the problem of significance (silver bullet obsession).

(1) Fish density: my report gave only a small part of a 4-yr collection effort of the Gull Lake fish community. In addition to gill nets, mark and recapture, a high-speed sampler, a purse seine, sonar, dip nets and hand lines were used for field sampling, and experimental cages were used for predation studies on immature fish. We did not have access to a midwater trawl which has been successfully used in the Great Lakes[2]. Our laboratory studies showed that clipped smelt were highly susceptible to fungus infections and exhibited high mortalities. Others have found summer marking to be impractical[3]. Consequently, we abandoned this method of estimating fish populations. As Wurtsbaugh *et al.* point out, most types of fishing gear are selective[4]; however, sonar traces gave reasonable agreement with gill-net results.

They are correct in stating that juvenile fish "may affect significantly total piscine predation rates" for some environments and there is undoubtedly some error there. Their argument for designating juvenile fish as important predators was based on the reasoning that they are more numerous and have greater relative consumption rates than adults. When I used a similar argument in comparing vertebrate with invertebrate predators, Wurtsbaugh *et al.* failed to acknowledge it. The reasoning is correct for both arguments, if smaller predators are more numerous. The combined sampling methods failed to reveal large numbers of immature fish occupying the central station. References to littoral *Menidia audens*, the Mississippi silverside, which inhabits shallow, warm Clear Lake, California, are irrelevant to the Gull Lake situation for almost all comparable criteria[5–15]. My study[1] was restricted to the pelagic zone.

Fish consumption rates: all diurnal sampling was done with four periods as Table 1 of my paper clearly shows. Use of sonar to check the absence of fish during the day and their diurnal movements were mentioned in Fig. 1 legend. In a subsequent study, smelt were collected on transects from the central station to shore. Data on their stomach contents provided no evidence of inshore feeding during the day or of a dawn feeding peak. Wurtsbaugh *et al.* make two useful points about linear compared with exponential models of gut evacuation and the assumption of independence of feeding and gut evacuation. Usually gut evacuation time and feeding periodicity are determined experimentally. The smelt did not cooperate in our laboratory studies thus I kept the model as simple as possible.

Invertebrate predation rates: these do differ by an order of magnitude over the large range of conditions in my experiments. Feeding rates for filter-feeding zooplankton are also as variable; density relationships are even more variable. Environmental heterogeneity and feeding periodicity also contribute to rate variations. I stated in Fig. 1 legend[1] that many other invertebrate predators consume the prey species; this would underestimate the degree of invertebrate predation extant in Gull Lake[16,17].

(2) Significance: I concluded that smelt account for ~5% of the total predation on Gull Lake zooplankton[1]. This does not mean that invertebrate predators are 20 times more important than vertebrate predators. Important to whom?—A particular population? The daphnids? The community? Important in what way?—For calculating nutrient and energy budgets? For determining community structure and trophic networks? For quantifying stability?

In aquatic ecology there is an obsession with the silver bullet—the belief that a single factor can be found to explain ecosystem dynamics. For example, the limiting factor in eutrophication studies[18], the arguments on density-dependent versus independent population regulation, the controversy regarding whether competition or predation regulates the intertidal zone and now the pelagic zone, and the suggestions that aquatic ecosystems should be organized around the axis of body size. Some of these are parameter inputs. They do not control the ecosystem but rather set particular variables in motion. Variables included within a network possess similar rates whereas parameters are faster or slower. Wurtsbaugh *et al.* believe that fish are a variable—this may be true for littoral species in particular. In testing the Gull Lake data set with loop analysis, it seems that smelt act as a parameter input to *Chaoborus* spp. and large *Daphnia pulex*. Inclusion of smelt as a variable reduced the agreement of model predictions with the data. In fact, smelt are not even the predominant input—those enter at nutrient and algal levels. This is why I stated that "smelt probably have little effect on the myriad of interactions among most zooplankton species".

It is not possible to take one predation link out of a whole ecological network and declare that this controls the system or is the most important part of the dynamics[18]. The effect of any given parameter or variable on another variable is a consequence of the configuration of the whole network. In addition, indirect pathways often swamp direct ones. Smelt have reduced *Chaoborus* spp. populations, which in turn have eased the predation pressure on many small prey species. Thus, ignoring indirect pathways could cause substantial overestimates of smelt predation. Similar results have been noted elsewhere[19]. This positive effect on small species demonstrates that ecologists should not hasten to load their ecological pistols with silver bullets for they will undoubtedly be caught in the cross-fire.

PATRICIA A. LANE

Department of Population Sciences,
Harvard School of Public Health,
Harvard University,
Boston, Massachusetts 02115, USA
and
Department of Biology,
Dalhousie University,
Halifax, Nova Scotia,
Canada

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