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Prey responses to fish predation in freshwater communities

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Predation by planktivorous and piscivorous fish has a major impact on zooplankton communities, juvenile fish survival, and the composition of the benthic fauna. In addition, the level of invertebrate predation is closely associated with the presence of predatory fish and influences both the invertebrate and vertebrate prey. Prey species, in turn, show active avoidance of predation by fish.

Our aim is to review the recent literature on the responses of different types of prey (fish, benthic animals and zooplankton) to fish predation in freshwater communities. The responses include behavioural responses, predator-induced morphological or chemical defences, and alterations in life history traits. The anti-predator tactics adopted depend on the possibilities of predicting future environmental changes.

The consequences of the anti-predator tactics may be evident at the individual or population level. The possible costs of the responses reflect a trade-off between survival and reproduction and/or growth, and may be evident as a lowered intrinsic growth rate of the population. In studying prey responses, account should be taken of the effects of predation on the competitive interactions among the prey.

1. Introduction

Predation by planktivorous fish has been shown to have a major impact on zooplankton species composition and diversity (Hrbáček et al. 1961, Brooks & Dodson 1965, Hutchinson 1971, Warshaw 1972, Lynch 1979, Mires et al. 1981, Langeland 1982, Vanni 1987a, 1987b), and on the age structure, size-frequency distributions and life history traits of the zooplankton prey (Green 1967, Hrbáček 1969, Kerfoot 1974, Northcote & Clarotto 1975, Langeland 1978, Northcote et al. 1978, Lynch 1980, Vanni 1986, Arts & Sprules 1988). Predation by fish may also greatly affect juvenile fish survival (Miller et al. 1988), and the composition of the benthic fauna in aquatic systems (Post & Cucin 1984, Gilliam et al. 1989). In addition, the level of invertebrate predation is closely associated with the presence of predatory fish (e.g. Zaret 1980, Vanni 1987a). Invertebrate predation may, in turn, affect both the zooplankton and vertebrate prey (e.g. Hartig et al. 1982, Foster et al. 1988).

In order to survive and reproduce under intense size-selective predation, the prey species must either reduce its spatial and temporal overlap with the predator or develop means to decrease vulnerability to predation (e.g. Williamson et al. 1989). Prey responses to fish predation vary from escape behaviours to predator-induced morphological or chemical responses that serve a defensive function. The responses of individual prey species may be reflected at the population level and in alterations in the species composition of the entire freshwater community. There are few experiments showing the impact of prey response on predator populations.

The purpose of this paper is to review the recent literature (1987 onward) on the types of response shown by different freshwater prey organisms to fish predation and to survey the consequences of the predator-induced responses evident at individual or population level in the prey. We will focus on active, environment-cued responses by the prey. Discussion on community-level changes will be limited to cases in which these changes can be regarded as consequences of predator-induced prey responses.

2. Fish as predators and prey

Piscivorous fish form the main predator group of juvenile fish. Prey species try to escape selection pressure by predatory fish mainly by behavioural means. Intense predation also selects for fast growth, which enables the juvenile stages to proceed rapidly to less vulnerable life stages. Predation may also have more indirect effects by altering the competitive relationships among the prey.

2.1. Growth rate vs. predation

All juvenile and other small fish are vulnerable to predation by piscivorous fish. Small fish can escape from predation by accelerating growth: large size is one of the best defences against piscivorous predators, since most predators are limited by gape (Zaret 1980). The favoured size of prey fish usually increases with predator size (Werner & Gilliam 1984, Tonn & Paszkowski 1986, Werner & Hall 1988). Since the smallest size classes of predators are almost always the most numerous, predation usually focuses on the smallest juvenile fish. In consequence, predation pressure strongly favours rapid growth (Reimchen 1988). Even subtle differences in size between individuals may have profound effects on survival (Miller et al. 1988).

The rate of growth through the vulnerable size classes determines the total predation risk. Rapidly growing juveniles survive better than those that grow slowly, because they remain vulnerable to predation for a shorter period (Werner & Gilliam 1984, Lyons & Magnuson 1987). The first-year mortality of young yellow perch is negatively correlated with growth (Tarby 1974, Nielsen 1980). Post and Prankevicius (1987) showed that in a slowly growing population the young-of-the-year yellow perch that survived their first growing season were the larger and faster growing members of their cohort; in a faster growing population there was minimal size-selective mortality. Similar size-selective mortality was observed in juvenile sockeye salmon, *Oncorhynchus nerka* (West & Larkin 1987).

2.2. Behavioural responses

At the behavioural level small fish can try to avoid predation in several ways (e.g. Mittelbach 1986): they may form schools, increase their vigilance, seek refuge from the predators (Mittelbach 1981, Cerri & Fraser 1983, Werner et al. 1983a, Schlosser 1987), or simply decrease their activity, reducing foraging distances, and/or limiting feeding time and intake (Dill & Fraser 1984, Sih 1986, 1987, Prejs 1987).

Shoaling is a common response to predation (Seghers 1974, Pitcher 1986, Morgan & Colgan 1987, Magurran 1990), and even relatively large fish may gather in dense shoals, especially outside the growing season (e.g. roach). Shoals provide antipredator benefits through dilution, confusion and vigilance effects (discussed in Morgan & Colgan 1987). However, shoaling does not always reduce the number of prey attacked by a piscivorous fish. In the experiments of Savino & Stein (1989b), largemouth bass and northern pike captured both shoaled and dispersed bluegills without preference. On the other hand, shoaled minnows were attacked less often than dispersed ones (Savino & Stein 1989b).

Hiding in a structurally complex environment, such as littoral vegetation, enhances the survival probability of the prey. Plant cover may decrease encounter rate (Hershey 1985) or predation rate (Savino & Stein 1982, Coull & Wells 1983). However, some predators, such as northern pike (*Esox lucius*), are adapted to catching their prey among vegetation, and other predators may change their predatory tactics with the environment; for instance, the largemouth bass (*Micropterus salmoides*) switches from searching to ambushing as plant density increases (Savino & Stein 1989a). Predators may seek vegetated areas if the appropriate prey is present. Thus, structural complexity alone does not guarantee refuge from predators; the prey must utilize the structural complexity to avoid predators (e.g. Main 1987, Savino & Stein 1989a).

The brook stickleback, *Culaea inconstans*, shows size- and morphology-dependent variation in its response to predation by northern pike (Reist 1983). The brook stickleback is polymorphic, having two main phenotypes, one with a pelvic skeleton and associated spines, the other without any pelvic structures. Stickleback spines, both pelvic and dorsal, are known to deter small predators (Hoogland et al. 1957, Reist 1980). The phenotypes without spines sought cover earlier and retreated from the predator more often than the spined phenotypes, which immediately "froze" if far from cover. The "timid" behaviour of the former is advantageous in a predator-rich environment, although it slows down the feeding rate compared to that of the "bolder" phenotypes with spines. Thus, morphological and behavioural adaptations to predation interact to maintain the high frequency of both phenotypes. The possible costs of growing and maintaining pelvic spines are unknown.

Although Post & McQueen (1988) claim that predator avoidance is not a probable reason for the ontogenetic changes in the habitat distribution of young yellow perch, a thorough analysis by Werner & Hall (1988) convincingly shows how the habitat selection of bluegills is modified by predation by the largemouth bass. The observed habitat shifts of bluegills could be predicted from a dynamic optimization model of habitat choice, which took into account the trade-off between growth rate (food availability) and risk of predation (Werner & Hall 1988). In pond experiments, in which predators were removed, bluegills of all sizes shifted to open water if this habitat provided the highest foraging gains (Werner et al. 1983b). The initial migration of bluegills to the pelagic region may also be related to the abundance of potential predators of newly hatched larvae in the littoral (Werner & Hall 1988). Experiments show that the bluegills are able to assess differences in food levels and switch their habitat accordingly (see Werner & Hall 1988).

Assessment of differences in food level and predation risk have also been reported in several other fish species. Creek chubs, *Semotilus atromaculatus*, are capable of assessing both feeding rate and predation risk when choosing the habitat in which to feed (Gilliam & Fraser 1987). Small fry (<15 mm) of three-spined stickleback use littoral vegetation as a refuge from cannibalism; larger fry forage outside vegetation. In the absence of adults, small fry also spend more time outside vegetation (Foster et al. 1988). The presence of predatory adult smallmouth bass causes juvenile fishes to select riffle and raceway refugia in streams, rather than the deeper pools that they choose when bass are absent (Schlosser 1987). Food availability and the risk of predation were likewise identified as the determinants of the microhabitat selection of fish in a tidal freshwater marsh (McIvor & Odum 1988). This observation is supported by several other studies (Metcalfe et al. 1987, Morgan & Colgan 1987, Huntingford et al. 1988, Magnhagen 1988a, Abrahams & Dill 1989). In some studies, however, the response of fish to predation risk has been found to be independent of the food reward (Cerri & Fraser 1983, Holbrook & Schmitt 1988).

Microhabitat use by individual fish is thus dynamic and flexible. Competitive and mutualistic interspecific interactions combined with predation risk further affect the use of habitats. This is well documented in several stream minnow species (Gorman 1988). Behavioural responses of fish to the presence of predators can be very rapid and may cause distinct shifts in habitat use within a few hours (Power et al. 1985).

Hungry fish have been found to be less responsive to predators (Milinski & Heller 1978, Dill & Fraser 1984, Magnhagen 1988b), as predicted by the foraging models of Mangel & Clark (1986) and McNamara & Houston (1986). Starved gobies had a higher consumption rate than fed fish in both the presence and absence of predators (Magnhagen 1988a). Starved fish were thus taking higher risks of being eaten than fed fish. An animal can be expected always to choose the behaviour that maximizes the probability of survival. By evaluating the metabolic state of the animal, it is possible to predict, for instance, what risks it will take, its habitat choice and activity level (Magnhagen 1988a).

2.3. Competition and predation

In stream or lake littorals, the behavioural avoidance of predation severely reduces the acceptable space for small fishes. Intra- and interspecific competition for food and spatial resources are both accentuated when competing fishes must share a common refuge, as in the case of small bluegills and pumpkinseeds in Michigan lakes (Mittelbach 1986, Mittelbach & Chesson 1987). In streams, minnows used only 20–40% of the available habitat; areas avoided by minnows were occupied by numerous piscivorous fishes (Gorman 1988). Such aggregation may lead to population declines, as in a lacustrine population of three-spined sticklebacks, *Gasterosteus aculeatus* (Jakobsen et al. 1988). These examples contrast with the situation in marine intertidal communities or in freshwater limnetic communities, where predation usually acts to alleviate competition (e.g. Paine 1969, Menge & Sutherland 1976, Garrity & Levings 1981, Dungan 1987; see Gorman 1988). Predation may be indirectly advantageous, reducing both intra- and interspecific competition (Mittelbach 1986, Wilbur 1987).

In many fish populations, the size structure seems to be a sensitive indicator of the balance between predation and competition for food resources (e.g. Mills & Schiavone 1982, Tonn & Paszkowski 1986, Piironen & Holopainen 1988, Paszkowski et al. 1990). In an environment with few predators, fish populations comprise enormous numbers of small and slowly growing fish. If piscivores are abundant, the prey size distribution is more even and extends to much larger sizes. Predation releases the young fish from excessive food competition and thus improves their growth.

Predation may have other positive effects on the prey populations. Parasitized sticklebacks were more susceptible to fish predation than healthy ones, and the long-term effect of fish predation was almost to eradicate the parasite from the population (Jakobsen et al. 1988).

3. Benthic fauna and fish predation

Studies on predation as a force structuring benthic communities (e.g. Paine 1969, Menge 1976, Menge & Lubchenko 1981; experimental studies on meiofauna were summarized by Coull & Palmer 1984) or the population biology of individual species (Peterson 1982) have mostly been done in a marine environment. In freshwaters, there is no consensus about the importance of predation for the zoobenthos. Invertebrate predators seem to have little effect at the community level in either lentic or lotic habitats (Thorp 1986, Williams 1987; but see Peckarsky 1983, Johnson et al. 1987). Experimental manipulations of fish densities in lakes have given ambiguous results (reviewed by Thorp 1986), although introductions of non-native fish have usually produced dramatic changes in the zoobenthos (e.g. Post & Cucin 1984). In particular, large and mobile invertebrates may be drastically reduced by increased fish predation (Macan 1977, Cooper 1988). Notonectids, corixids and dytiscid larvae appear in the pelagic area of fishless lakes and disappear if the fish populations recover (Henrikson & Oscarson 1978, Evans 1989). Many species in these insect groups are known to possess glands producing distasteful or toxic substances, acting as chemical defences against fish (Scrimshaw & Kerfoot 1987).

Conflicting interpretations of experimental results are largely explained by the qualitative changes produced by the predators: a decrease in total prey biomass is usually accompanied by a considerable decrease in the mean size of the prey, and thus often by an increase in numbers (Hall et al. 1970, Crowder & Cooper 1982, Post & Cucin 1984, Mittelbach 1988). Such changes are likely to increase the production to biomass ratio at least, and sometimes also the absolute production of the zoobenthos (Chesney 1985).

In streams, the effect of fish predation on the zoobenthos may vary both spatially and temporally and depend on the fish species present (Gilliam et al. 1989, Schlosser & Ebel 1989). Both field data and experiments indicate that in southern English streams, the abundance of the caddis *Plectrocnemia conspersa* is determined by brown trout (*Salmo trutta*) predation (Schofield et al. 1988). Uneven distribution of the benthivorous fish may explain why reports on the influence of vertebrate predators on the abundance of stream invertebrates range from no effect in shallow, rocky habitats (Reice 1983, Flecker & Allan 1984) to a dramatic effect in pools or slow-flowing stream sections (Cooper 1984, Angermeier 1985, Gilliam et al. 1989, Schlosser & Ebel 1989).

Monitoring the foraging activity of fish in the littoral of two oligotrophic lakes revealed high and relatively constant median levels of exposure of each benthic site to fish predation (Butler 1989, Collins 1989), suggesting that benthic organisms spend a high proportion of their time in risk-reducing positions or behaviour (Collins 1989).

Habitat structure is important for prey survival. Without the refuges afforded by mats, leaves and stalks of vegetation, benthic invertebrates are much more susceptible to predators (Brusven & Rose 1981, Crowder & Cooper 1982, Gilinsky 1984, Hershey 1985, Thorp 1988). The presence of vegetation as a potential refuge reduced the risk of six *Notonecta* species being eaten by *Lepomis* sunfishes (Cook & Streams 1984), facilitating escape from attacks by fish. The six *Notonecta* species escaped sunfish attacks by different means. The smaller species tended to remain motionless in the presence of fish, and remained undetected for long periods. Some species could even climb up from the water. Sih (1982) has described an ontogenetic shift in the use of space in response to risk of cannibalism in *Notonecta hoffmanni*.

In a Florida lake, predation by fish (bluegill sunfish) was patchy and temporally variable in mid-depth and deep lake habitats (Butler 1989). Under such a variable predation regime even the preferred prey may escape predation in temporary spatial refugia. The effects of variable predation may cascade through the system via second-order predators or other indirect mechanisms, precipitating complex changes in community composition (Butler 1989).

On bare bottoms, benthic invertebrates may adjust their vertical distribution in the sediment in response to predation. Animals moving on the surface are most vulnerable to predation by zoobenthivorous fish that locate their prey visually (e.g. trout). Fish species using chemical cues or other non-visual sensory systems in their feeding (e.g. ruffe) are probably also restricted to taking their food close to the surface. The feeding efficiency of bream, white bream and roach on chironomid larvae decreases steeply with increasing depth of the larvae in the substrate (Lammens et al. 1987). Thus benthic animals can largely avoid fish predation by remaining as much as possible within the sediment. Accordingly, in Marion Lake, USA, only small percentages of the populations of the amphipods *Crangonyx occidentalis* and *Hyalella azteca* were located on the surface of the bottom (Ware 1973).

Predation may also affect the habitat preferences (Wellborn & Robinson 1987, Cooper 1988) and activity patterns of the benthic animals. Stream-living larvae of a mayfly, *Baetis tricaudatus*, which were vulnerable to predators when grazing periphyton growing on stones, strongly modified their foraging behaviour in the presence of a benthos-feeding fish (the mottled sculpin, *Cottus bairdi*) even when the fish were not allowed to attack prey (Kohler & McPeek 1989). The larvae reduced the time spent on the top surface of stones and their movement rate. *Baetis* larvae accepted greater risk of predation when they were starved or when food availability was high, which suggests that they were making adaptive compromises between feeding and avoiding sculpin. In contrast, larvae of a caddisfly, *Glossosoma nigrior*, which were much less vulnerable to predators, did not respond to the presence of the sculpin (Kohler & McPeek 1989).

In the presence of smallmouth bass, *Micropterus dolomieui*, the crayfish *Orconectes propinquus* selected substrates affording most protection (Stein & Magnuson 1976). Active behaviour patterns such as walking and feeding were suppressed, while defensive patterns, such as burrowing and chelae display, increased. Small, vulnerable crayfish were most affected, and large males with large chelae were least affected. In the field, crayfish exposed on the substrate were larger than those buried, and fewer females than males were exposed (Stein & Magnuson 1976). The abundance of exposed crayfish on sandy substrates was also negatively correlated with the relative abundance of fish in two lakes (Stein 1977). In the laboratory, ovigerous females and adult males were least susceptible to predation by fish (Stein 1977). Morphologically more susceptible life stages adopted behavioural modifications to reduce predation mortality.

Large *Orconectes* thus have a partial size refuge from predation by bass. However, most benthic invertebrates do not grow large enough to avoid fish predation, and, in contrast to *Orconectes*, the largest size classes are subject to the most intense predation (e.g. Gilliam et al. 1989). In chironomid communities, however, chironomid availability to predatory fish may be inversely related to size (Hershey 1985).

4. Zooplankton as the prey of planktivorous fish

The body size of the cladoceran prey has been shown to be of major importance in the food selection of visually feeding planktivorous fish (e.g. Eggers 1982, Lazzaro 1987). Other factors also enhance the vulnerability of zooplankton to predation by fish. For instance, zooplankton females carrying eggs are more visible and thus more vulnerable to the predator than nongravid individuals (Vuorinen et al. 1983, Tucker & Woolpy 1984). Prey vulnerability is also affected by body shape, coloration and transparency (Kerfoot et al. 1980).

As a result of size-selective predation, prey body size is reduced (e.g. Hrbáček 1962, Brooks & Dodson 1965, Wells 1970, Warshaw 1972, Vanni 1987a). The reduced mean prey body size may be caused by at least two different types of mechanisms: by elimination of the largest prey individuals, or by a demographic shift in the prey towards reproduction at an earlier age and/or smaller size. Smaller-sized individuals may, in turn, be more vulnerable to invertebrate predation (Nero & Sprules 1986, Moore & Gilbert 1987, Stenson 1987, Moore 1988, Vanni 1988). However, young fish also often prefer the smallest size groups of prey (e.g. young yellow perch, Hansen & Wahl 1981; small vendace fry, Huusko et al. 1988, Sarvala et al. 1990, and unpubl.). The prey species counteract the selection pressure exerted by predators by different strategies, which may involve alterations in behaviour, morphology, and life history characteristics.

4.1. Behavioural responses

Diel vertical migration

In zooplankters, behavioural means of escaping planktivore predation include migration and formation of swarms. Diel vertical migration has been the most intensively studied aspect of zooplankton behaviour in recent decades. Many hypotheses, not always strictly formulated or nonexclusive, have been put forward to explain the phenomenon. As several reviewers have speculated on the possible adaptive value of migration from the point of view of the various hypotheses (e.g. McLaren 1963, Vuorinen 1986, Lampert 1989), we will not examine them in detail.

The hypothesis that has received most support in explaining diel vertical migration is predator avoidance (Zaret & Suffern 1976, Wright et al. 1980, Stich & Lampert 1981, Iwasa 1982, Vuorinen et al. 1983, Fancett & Kimmerer 1985, Gliwicz 1986, Bollens & Frost 1989), though direct confirmation of the hypothesis appears difficult to obtain.

In many fish species foraging and prey selection are light-dependent. The efficiency of prey selection usually decreases strikingly as light intensity decreases, though there are fish species that can forage visually in low illumination, for instance in moonlight. The light-dependency of visual prey selection enables prey species to avoid fish predation by utilizing darkness. There are some energetic disadvantages, however, of staying permanently in deep water: food is sparse and the lower temperatures decrease growth and reproduction. For grazers, the richest food layer is usually situated in the warm epilimnion. In addition, the quality of food is usually poorer in greater depths, where bacteria and detritus are more abundant than algae. Many zooplankton species have coped with these constraints by migrating vertically to the surface layer at night and to the deep water layers during the day (Hutchinson 1967). This enables the zooplankton to utilize food reserves close to the surface without being exposed to intense illumination and to avoid staying too long in cold water layers.

If light-dependent predation by planktivorous fish is the ultimate cause of zooplankton diel vertical migration, the predation pressure ought to be reflected in the migratory pattern of zooplankters. There are some difficulties, however, in connecting the pattern solely with visual fish predation. For instance, it is possible to predict the daytime distribution of zooplankton but not the night-time distribution. The distribution at night has to be predicted on the basis of other factors, such as the food and temperature regimes.

Size-selective visual predation of planktivorous fish on large-bodied zooplankton species and individuals is likely to be responsible for the vertical distribution pattern, when large-sized zooplankters stay in deeper water layers than small zooplankters during the daylight hours (Hutchinson 1967, Zaret & Suffern 1976, Wright et al. 1980, George 1983, Dini et al. 1987, Pijanowska & Dawidowicz 1987). Further, the smaller zooplankton species and juvenile stages of larger species may not migrate vertically at all. Fish usually select egg-carrying female zooplankters, which may lead to avoidance of surface water by these zooplankters (Vuorinen et al. 1983).

Changes in predation pressure by fish have been reported to coincide with alterations in zooplankton vertical migration behaviour in both freshwater and marine habitats (e.g. Cunningham 1972, Dini & Carpenter 1988, Bollens & Frost 1989). Gliwicz (1986) provided evidence for a predator-related pattern of diel vertical migration in alpine mountain lakes with different fish-stocking histories. The diel vertical migration of *Cyclops* was more pronounced in lakes stocked with fish a long time ago, and in a lake with a long-standing natural fish stock, than in lakes without planktivorous fish. From one lake there was evidence of a switch from non-migratory behaviour to clear diel vertical migration, which was probably related to the exposure of copepods to fish predation. The results suggest that diel vertical migration may evolve over a long period if predators change the gene frequency distribution of the prey population. Thus, it is possible that the overall migration pattern is dependent on the genetic composition of the population. Genetically distinct behaviour types, upon which selection could operate, have been found in *Daphnia* (Weider 1984, Dumont et al. 1985, De Meester & Dumont 1988).

In vertically migrating freshwater zooplankton, evidence of direct responses to the presence of fish is sparse. In laboratory vials, several species of *Daphnia* show specific chemically mediated responses to invertebrate predators and bluegill sunfish, *Lepomis macrochirus* (Dodson 1988). In herbivorous zooplankters, direct responses to changes in the food regime are more plausible than direct responses to predators, because grazing involves immediate physical contact with algae, which probably helps the animals to assess the food availability. Contact with a fish predator, on the other hand, may leave little opportunity for the zooplankter to show any further responses.

Light-related predation by fish is not the only explanation suggested for diel vertical migration of zooplankton. The results of recent studies indicate that concurrently with fish predation, other critical factors affecting the zooplankton growth and reproduction must be included to provide a more realistic insight into migration. Migration can improve survival, but at the same time it involves growth and reproduction costs because of low temperatures and diminished food availability.

Diel vertical migration of zooplankton may affect the productivity of primary producers. Pronounced vertical migration causes rhythmical fluctuations of grazer biomass in the epilimnion (e.g. Redfield & Goldman 1978). In a eutrophic lake, Lampert & Taylor (1985) showed that grazing of phytoplankton in the productive epilimnion was negligible during the day, but strong at night. Sometimes ascending is coupled with more active feeding by grazers (e.g. Haney & Hall 1975, Enright 1977). Migrators can also have an indirect impact on primary producers by translocation of nutrients (Kitchell et al. 1979). There is some evidence that large vertically migrating daphnids can cause a net downward flux of phosphorus from the epilimnion to the hypolimnion (Wright & Shapiro 1984, Dini et al. 1987, Angeli & Balvay 1989).

Vertical migration of zooplankton may have consequences for the feeding behaviour of planktivorous fish. Some freshwater planktivores, such as the freshwater sardine, *Limnothrissa miodon* (Begg 1976), and alewife, *Alosa pseudoharengus* (Janssen & Brandt 1980), are able to follow their migratory zooplankton prey. Alewives can switch from selective visual feeding to nonselective feeding if the light intensity decreases (Janssen 1980). Planktivorous fish also have their own predators that hunt by sight. These fish thus face a complex optimization problem: they should maximize energy intake by feeding on zooplankters (which may avoid them by migrating vertically) and at the same time minimize mortality caused by piscivores. Clark and Levy's (1988) recent model predicts that the optimal behaviour for juvenile sockeye salmon (*Oncorhynchus nerka*) in British Columbian lakes is to migrate to the surface layer to feed only at dawn and dusk. During these hours of intermediate light intensity, the ratio of the risk of light-related mortality to the feeding rate should reach its minimum.

Diel horizontal migration

The zooplankton prey may also decrease the risk of predation by migrating horizontally. Horizontal migration occurs mainly in the shallow littoral, where there is no effective depth gradient that can be utilized for extensive vertical migration. Diel changes in the abundance of zooplankters in the littoral areas concurrent with inverse changes at more pelagic sampling stations indicate active onshore-offshore migration (Davies 1985, Boikova 1986). Diel horizontal migration of zooplankton may contribute to predation avoidance, but at least to our knowledge direct evidence for this is lacking. Diel horizontal migration between the littoral and pelagic areas has been reported in many fish species (e.g. Hall et al. 1979, Bohl 1980, Vøllestad 1983, Wurtsbaugh & Li 1985, Naud & Magnan 1988, Post & McQueen 1988). Such fish movements most probably contribute to diurnally varying feeding pressure on the littoral zooplankton. Indeed, a relation between fluctuating abundance of littoral cladocerans and changing fish predation has been documented in a few studies (Fairchild 1982, Boikova 1986, Jakobsen & Johnsen 1987, Cryer & Townsend 1988, Winfield & Townsend 1988).

Some zooplankters appear to avoid the shore (Hutchinson 1967). As in vertical migration, light seems to be the key factor responsible for this phenomenon (Siebeck 1980, Ringelberg 1987). The species avoiding the shore are usually larger than the species abundant in littoral areas (Boikova 1986). Shore avoidance may be advantageous for large zooplankters because their main predators, the juveniles of many fish species, tend to concentrate in the vegetation of natural lakes, probably to lower the risk of predation (Hall & Werner 1977, Laughlin & Werner 1980, Werner et al. 1983a, 1983b, Lehtovaara & Sarvala 1984, Mittelbach 1984, Werner & Hall 1988).

Swarming

Swarming has been reported in a few cladoceran species (e.g. Dumont 1967, Klemetsen 1970, George 1981, Jakobsen & Johnsen 1988a, 1988b). High density of prey organisms may reduce the feeding efficiency of a planktivorous fish foraging by visual cues. This "confusion effect" (Milinski 1977) may be caused either by aggregation of the zooplankton prey in certain habitats or by formation of swarms. In swarms, the high density of individuals, usually of a uniform size, will decrease the risk of predation for each individual.

Fish shoals can be maintained by visual, chemical, lateral line-repelling or tactile stimuli (Blaxter 1988), but in freshwater zooplankton the mechanisms keeping the animals in dense aggregations are unknown. Large patches of zooplankton (tens of metres – kilometres) can be caused by advective effects related to wind-induced water movements or by reproductive differences between populations experiencing different food or temperature regimes (George 1981).

Escape reactions

Zooplankters may also escape predators by sudden, strong movements. Mainly copepods utilize escape reactions when in danger of being eaten; in the other two large zooplankton groups — rotifers and cladocerans — similar escape responses are not as common (Kerfoot et al. 1980). Cladocerans and rotifers tend to rely more on morphological defences, which is manifested by the great phenotypic variability in these groups.

4.2. Morphological responses

Recently, much research has focused on the indirect effects of predators upon their prey (e.g. Sih 1987). Effects that appear as changes in the prey morphology may be chemically mediated via cues emitted by the predator. The prey may escape predation by these predator-induced changes.

In freshwater zooplankton, different kinds of morphological responses have been documented. Mostly in pelagic cladocerans, and in a few littoral species (*Daphnia* spp., *Bosmina* spp., *Holopedium gibberum*), helmeted, crested, or spined morphotypes have been reported (e.g. Krueger & Dodson 1981, Havel 1985, Hebert & Grewe 1985, Jacobs 1987, Stenson 1987). Morphological responses may be classified as cyclomorphic (e.g. Hutchinson 1967, Black & Slobodkin 1987, Jacobs 1987) or predator-induced (reviewed in Havel 1987).

Direct evidence of a causal relation between planktivore predation and morphological responses in zooplankton is, as far as we know, lacking. There is, however, some evidence of the importance of these responses as a protection against invertebrate predators (e.g. Havel 1987). It is possible that some of the responses are also induced by fish.

Cyclomorphosis may be controlled by environmental seasonal factors, such as temperature, turbulence and food, and by a changing predation regime (Hutchinson 1967, Hebert 1978, Jacobs 1987). It has been shown that newborn *Daphnia pulex* exposed to compounds excreted by an invertebrate predator, *Chaoborus*, carry neck spines during various prereproductive instars (Havel 1985, Vuorinen et al. 1989, Walls & Ketola 1989). Similar responses are induced by *Notonecta* sp. and bluegill sunfish (Dodson 1989).

Little is known about the adaptive significance of these responses. The possible costs of defence, evident in survival, reproduction and/or growth, have only recently aroused interest and led to experimental research.

4.3. Life history traits and population level changes in zooplankton

Predator-induced morphological changes in individual prey animals may be further reflected in the life history characteristics of the prey. In freshwater cladocerans, shifts in life history characteristics have been observed as a consequence of intense planktivore predation.

In a study on *Holopedium gibberum*, the maternal lipid investment in eggs was shown to be affected by fish predation (Arts & Sprules 1988). In lakes with high planktivore predation, *H. gibberum* females were smaller and tended to carry smaller eggs than in lakes with low levels of predation. Interestingly, the smaller eggs contained relatively less fat than larger eggs. At its greatest the difference in maternal lipid investment was four-fold, which indicates that the starvation resistance of neonates was severely affected by fish predation. Arts and Sprules (1988) suggested that the difference in the maternal lipid investment of *H. gibberum* was caused by clonal replacement mediated by size-selective predation by fish.

In the presence of planktivorous fish in Dynamite Lake, USA, the cladocerans *Bosmina longirostris*, *Ceriodaphnia lacustris*, and *Diaphanosoma birgei* started to reproduce earlier and, consequently, had smaller offspring (Vanni 1987a). All three cladoceran species showed great flexibility in life history traits such as the timing of and size at first reproduction and offspring size. This flexibility allows the cladocerans to withstand size-selective predation by planktivorous fish (Vanni 1987a). DeMott & Kerfoot (1982) have also reported a change in the minimum size at reproduction and in the size of the first instar after introductions of planktivorous fish.

In cyclopoid copepods, diapause during juvenile stages is regarded as an escape from predation during a vulnerable period (Nilssen 1977, 1978). In Little Bullhead Pond, USA, the diapause of the calanoid *Diaptomus sanguineus* was adapted to environments with high fish predation. After a fish-kill and a resultant change in the predation pressure, *D. sanguineus* was unable to coexist with the dominant invertebrate predator. The timing of the diapause in *D. spatulocrenatus*, however, enabled coexistence with *Chaoborus americanus* (Black & Hairston 1988).

Changes in life history traits, such as the age at first reproduction, clutch size and longevity have effects evident at the population level. Demographic indices, for instance the intrinsic rate of population growth, are commonly used to summarize and integrate the effects of environmental factors, e.g. predation, on age- or stage-specific rates of mortality, fertility, and growth (e.g. Caswell 1989).

The costs of inducible defences in *Daphnia pulex* are measurable at both the individual and population levels. The effects of predator-induction in the vital rates at the individual level (stage-specific rates of mortality, fertility, and growth) can be translated into effects on the population growth rate. In the laboratory at high food density, the spined morph of *D. pulex* had an intrinsic rate of population growth about 5% lower than the typical morph (Havel 1987). This indicates that a measurable cost may be associated with predator-induced defences. The cost may be evident in the population growth and is likely to depend on the resources available.

In addition to the evidence of the negative effects of planktivore predation, a few studies have reported indirect positive effects on zooplankton prey populations. In *Bosmina* and *Ceriodaphnia*, size-specific clutch sizes were greater when the animals coexisted with fish (Lynch 1979). Similar observations have been reported for *Bosmina* and *Daphnia rosea* in the presence of fish (DeMott & Kerfoot 1982) and for *Daphnia* spp. in fish hatchery ponds (Culver et al. 1984). Such changes may simply be due to the larger amounts of food per capita available for the surviving individuals in the exploited population.

There are also data that show high levels of planktivorous fish associated with elevated levels of phytoplankton biomass (Kerfoot 1987). Hence, planktivorous fish may indirectly alter zooplankton population dynamics through their effects on phytoplankton abundance (Vanni 1986). Earlier, Neill (1975) demonstrated that the juvenile survivorship of some zooplankton species was improved in the presence of intense fish predation. This was due to the positive effects of fish predation on phytoplankton abundance.

Alterations in the structure of the food web may affect community composition at all food web levels. In an experiment on Tuesday Lake, USA, addition of piscivorous largemouth bass and removal of planktivorous minnows caused an increase in the number of large cladoceran herbivores and a consequent change in the phytoplankton community (Elser & Carpenter 1988). Due to decreased planktivore predation, an increase was observed in the biomass of *Daphnia pulex* and in the abundance of *Holopedium gibberum*. After the introductions of piscivores into Tuesday Lake, the phytoplankton community began to resemble that of the nearby Paul Lake, where piscivores had prevailed earlier (Elser & Carpenter 1988).

In Little Bullhead Pond, USA, the zooplankton community changed in response to temporal variation in the predation pressure (Black & Hairston 1988). Long-term changes in the zooplankton community structure were observed as a consequence of a natural fish-kill in the lake during 1980–81. The main planktivorous fish, the redbreast sunfish, was replaced by *Chaoborus americanus* and the spined form of *Daphnia pulex* subsequently replaced the unspined form in the lake. Changes were also observed in the presence and frequency of two copepod species, *Diaptomus sanguineus* and *D. spatulocrenatus* (Black & Hairston 1988).

5. Concluding remarks

The prey of fish predators may display active predator-induced responses — both behavioural responses and morphological or chemical defences — that reduce prey vulnerability. Such defensive responses imply that the prey is able to detect the predator and predict the risk of predation.

A flexible means of responding to predation is behaviour. Prey behaviour is often more important in predator avoidance than mere physical habitat barriers or cryptic coloration (Main 1987). Even invertebrates are much more plastic in their behaviour than was previously believed (Kohler & McPeek 1989). Plasticity of behaviour can be regarded as adaptive, because it allows individuals to modify their behaviour to accord with changing environments (Dill 1983, 1987). The development of avoidance behaviour is one of the recent subjects of anti-predator studies (Caro 1989). Behavioural responses were evident in all the prey groups surveyed — fish, benthic animals and zooplankton.

Active predator-induced morphological responses have been intensively researched in recent years. Induction of morphological changes in the prey by invertebrate predators is well documented, but evidence of planktivore-induced morphological changes is still scarce. Morphological responses are evident in zooplankters (mostly cladocerans) that cannot escape predators by rapid movement. Recently, progress has been made in determining the supposed energetic, ecological and evolutionary costs associated with induced defences (Havel & Dodson 1987, Havel 1987, Walls & Ketola 1989). The costs may be measurable in terms of e.g. reduced fecundity and slower growth as compared with unaffected individuals.

The interaction between predation and competition should be taken into account in studying responses to predation. Through anti-predator behaviour of the prey, the predators indirectly affect the diet and habitat use of a species, and thus inter- and intraspecific competition. These indirect effects mediated through changes in behaviour take place much more rapidly than those due to numerical changes (Abrams 1984, Power et al. 1985, Mittelbach 1986) and may turn out to be more important than the relatively small percentage of prey that the predators actually consume (Mittelbach 1988). The behavioural and distributional responses may have important effects on the fitness of prey taxa, merely because the prey may not be able to forage efficiently in refuge areas (Stein 1979).

Feedback effects of predation may be evident in the predator population. Intense predation on zooplankton by planktivorous fish may in certain circumstances lead to cyclic variation in the year-class strength of the fish population, when reduced zooplankton populations combined with decreased mean body size impair the availability of food for adult fish and reduce their fecundity (Cryer et al. 1986). However, examples of feedback effects on the predator are few and require further study.

The examples from fish, zoobenthos and zooplankton all show that the responses to predation cannot be examined separately from other important aspects of the life history. The expression of predator avoidance tactics, be they behavioural or morphological, usually depends on a trade-off between survival and growth and/or reproduction.

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