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Altered predator/prey behavior in polluted environments: implications for fish conservation

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Synopsis

Predator/prey behavior has important consequences for individual survival and recruitment into fish populations, both of which can be affected by stressors such as environmental contaminants. The degree to which prey capture or predator avoidance abilities of a predator or prey species are affected will determine the direction in which the balance will be shifted. In a contaminated estuary we have studied, prey capure and predator avoidance of resident mummichogs, *Fundulus heteroclitus*, are impaired, which may account for individuals in that estuary having reduced growth and longevity compared with those from uncontaminated sites. Exposure to sediments, water, and grass shrimp from the contaminated site can impair the predatory abilities of mummichogs from a clean site. An important prey species, the grass shrimp, *Palaemonetes pugio*, has a greater population density and a greater proportion of large individuals at the polluted site, apparently because of reduced predation pressure. Mummichog larvae at the polluted site are initially more active and better at prey capture and predator avoidance than larvae from clean sites, but later they become poorer at both. Differences in predator vulnerability among larvae appear to be due to population differences in behavior, which may be due in part to both genetic and environmentally-caused factors. Conservation of fish populations should consider fish behavior and its interaction with contaminants.

Introduction

Concerns about declining fish populations have generally focused on effects of habitat loss and overfishing. While concern exists about the possible contribution of environmental contamination in reductions in fish populations, published findings generally focus on grossly contaminated areas with low dissolved oxygen and fish kills. Sublethal mechanisms are also important. Toxic pollutants can affect fish populations by impairing reproduction, development, and growth, and by altering behavior. In this paper, we introduce the field of environmental toxicology, examine predator/prey interactions in polluted and clean environments, and review studies of behavioral toxicology, stressing prey capture and predator avoidance and highlighting effects of contaminants on sensitive early life intervals. We then summarize our recent work on behavioral abnormalities in a population of mummichogs from a chronically polluted estuary, and discuss implications of these findings for conservation biology.

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Environmental toxicology

Aquatic pollutants of concern include excess nutrients, which may lead to eutrophication, algal blooms, and reduced levels of dissolved oxygen, which can stress animals. Other contaminants are toxicants which at low concentrations, can damage the structure or function of a biological system. The field of environmental toxicology, while still a young science, has developed considerably from the days when the focus was mainly on establishing lethal levels of various chemicals. Considerable research is now being devoted to studying sublethal effects, such as changes in growth, development, reproduction, pathology, biochemistry, physiology, and behavior. The field is also concerned with the transport, distribution, transformation, and fate of different types of chemicals in the aquatic environment, since it is the amount of exposure which determines an organism's response to a toxicant. Chemicals of greatest concern include ones which are persistent and do not readily break down in the environment, and which readily bioaccumulate in organisms. These include chlorinated hydrocarbon pesticides, polychlorinated biphenyls (PCBs), and dioxin. Other toxicants of concern are metals, such as mercury, cadmium, and lead. Organometallic compounds, such as methylmercury and organotins, are particularly toxic.

A general view in environmental toxicology is that effects at one level of biological organization, such as the cell/biochemical level, can lead to effects at a higher level of organization, such as the organism. Effects at the level of the organism may, in turn, lead to effects at the population and community levels. While these concepts are easily understood, the precise links between them are not often made because most investigators focus their efforts at one level of organization. Behavior is a response which may demonstrate links between effects at different levels of organization, since it is frequently associated with alterations at the biochemical level (neurotransmitters), and may also readily translate into population level effects.

Effects of pollutants on fish behavior

Behavior is very sensitive to contaminants. Atchison et al. (1987) thoroughly reviewed behavioral toxicology of metals in fishes, and stressed two points: (1) that studies should have ecological relevance, and (2) that investigators should try to validate their observations in the field. Subsequently, Henry & Atchison (1990) also emphasized the importance of ecologically meaningful behavioral measures (endpoints) and validation in the field, and noted the possibility of verifying field observations by controlled studies in the laboratory, i.e., by reversing the order of events.

Little et al. (1990) analyzed effects of agricultural chemicals (pesticides) on feeding behavior among other activities, and detected behavioral changes at concentrations below the aquatic life criteria levels set by the Environmental Protection Agency (USEPA). They reported that reduced feeding behavior, which can retard growth and decrease survival in fish larvae, was a consistent and highly sensitive endpoint (see also Cairns & Loos 1967, Morgan & Kiceniuk 1990). Pollutants may impair feeding behavior by affecting the motivation to feed and/or by impairing coordination and reducing the ability to capture prey. Little et al. (1990) noted that the frequency of strikes was less sensitive to certain toxicants than the actual prey capture, indicating that coordination was impaired. However, Brown et al. (1987) found that pentachlorophenol-treated fish performed fewer feeding acts, reflecting decreased motivation to feed.

Vulnerability to predation is also influenced by toxicants, and has potentially major ecological implications. Impaired predator avoidance by organisms exposed to contaminants has been noted in several studies (Little et al. 1990, Farr 1977, Sullivan et al. 1978, Kraus & Kraus 1986). Toxicants can affect swimming performance and compromise the ability to escape predators. Prey can be more vulnerable to predation due to failure to detect predators, poor fast-start performance, inability to shoal effectively, and increased conspicuousness due to erratic behavior or hyperactivity (Mesa et al. 1994).

By altering feeding and predator avoidance behaviors, pollutants can therefore cause changes in

predator-prey interactions, resulting in population changes of the predator, prey, or both, ultimately affecting community structure (Auclair et al. 1993). Reduced predation rates can lead to population changes (reduced growth, survival and reproduction) in predator species. The ecological outcome of a contaminant stress depends on the relative effects of the contaminant on the predator and the prey (e.g., Breitburg et al. 1994). If feeding behavior of a predator is more strongly influenced by a contaminant than is the predator avoidance of the prey, prey may benefit from reduced predation pressure. Different species are likely to have differential susceptibilities; thus population and community outcomes can be altered in different ways depending on differential susceptibility to a particular suite of stressors.

Fish embryos and larvae

Larvae are particularly sensitive to environmental contaminants; the egg envelopes, which can partially protect fish embryos from many toxicants, are no longer present after hatching. Embryos and larvae may also be affected by toxicants put into the yolk during vitellogenesis and by toxicants in the water during embryogenesis. A critical event occurs when fish switch from yolk dependency to reliance on exogenous food sources. Since fish larvae starve easily, normal development of feeding behavior is critical. Mortality of larvae is very high in the first weeks of life because of starvation and predation (Helfman et al. 1997). Any factor interfering with prey capture or predator avoidance at this time could adversely affect survival, and contaminants have these effects. For example, the early feeding behavior of largemouth bass larvae exposed to pentachlorophenol is impaired substantially (Brown et al. 1987).

In some studies, behavioral changes have been observed in larvae following embryonic exposures to chemicals (Ostrander et al. 1990). Mummichog larvae were exposed as embryos to methylmercury (meHg) concentrations below those which cause structural malformations. The larvae were then raised in clean seawater. They were less effective in capturing brine shrimp than controls, but the effects disappeared over time (Weis & Weis 1995a). Mummichog larvae are able to depurate mercury which accumulates during embryonic exposure (Zhou et al. 1998). Mummichog larvae that had been exposed to meHg as embryos were both hyperactive and more susceptible to predation (Weis & Weis 1995b). The increased predation may have resulted from greater visibility due to hyperactivity. These effects of embryo exposure were also transient.

When larvae were exposed to meHg, decreased predator avoidance was seen in one-month old larvae after one week of exposure. However, these larvae had reduced activity levels compared to controls (Weis & Weis 1995b).

Population differences in mummichog behavior in contaminated and uncontaminated habitats

The mummichog is a very abundant fish that plays an intermediate role in the trophic structure of east Coast marshes. Adults consume primarily crustaceans and annelids, which they capture on the marsh surface at high tide. Adults are significant predators of the grass shrimp, *Palaemonetes pugio* (Knieb 1986). Mummichogs also consume detritus, although it is of little nutritional value to them (Prinslow et al. 1974). Mummichogs are in turn consumed by migratory fishes such as white perch and striped bass, but such predators are rare in the tidal creeks which are the principal habitat of mummichogs. The mummichog's major predator is probably the blue crab, *Callinectes sapidus* (Knieb 1987).

Previous studies (reviewed in Weis & Weis 1989) demonstrated a number of differences between populations from clean reference areas and mummichogs inhabiting Piles Creek (PC), a polluted tributary of the Arthur Kill in Linden, NJ. Surrounded by industrial sites, a sewage treatment plant, a power plant and a major highway, the sediments and biota of Piles Creek have elevated levels of many contaminants including organic chemicals, mercury, and lead (Khan & Weis 1987). PC embryos have increased tolerance to effects of methylmercury, but adults do not show this tolerance. Adults have reduced growth and condition and a shorter lifespan compared with fish from clean reference

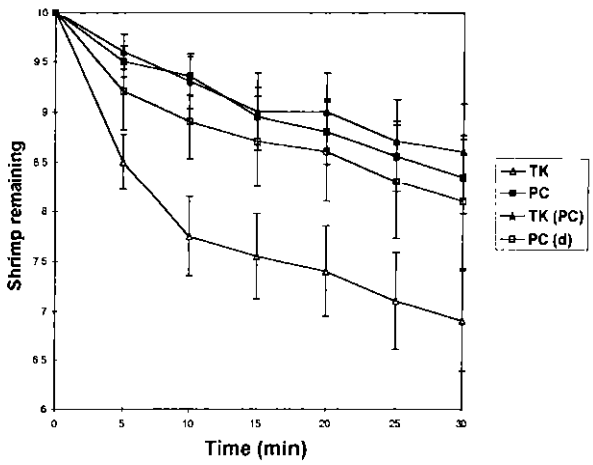

Figure 1. Capture of *P. pugio* by adult *F. heteroclitus* from Piles Creek (PC), Tuckerton (TK), PC fish kept in clean water (PC (d)), and TK fish kept in PC water and sediments (TK(PC)) Reprinted with permission from Elsevier (from Smith & Weis 1997).

sites in East Hampton, NY (EH) and Tuckerton, NJ (TK). Nevertheless, the PC population persists due to compensation via increased reproductive effort (Toppin et al. 1987): PC fish become mature at a smaller size and younger age. However, the PC population, in addition to having fewer large individuals, is also considerably less dense (measured by catch-per-unit-effort) than the TK population (Santiago 1996). The population size difference may partially result from bait fishing at PC, in addition to pollution effects.

Behavioral modifications, particularly impaired prey capture ability, can lead to decreased condition and growth of PC fish. Laboratory studies comparing the rate at which PC and EH adults captured food (baby guppies) demonstrated that PC fish caught fewer prey in a given time interval (Weis & Khan 1991). PC fish that had been exposed to mercury in the laboratory for a week were even slower in capturing prey (Weis & Khan 1990). When a more appropriate prey species, the grass shrimp, was used, a similar result was obtained: PC fish were poor predators compared to fish from TK (Smith et al. 1995). Impaired predation was correlated with elevated mercury and lowered levels of the neurotransmitter serotonin in the brains of PC fish. Other workers (Block & Nilsson 1990, Spieler et al. 1995, Weber et al. 1991) have also noted altered levels of neurotransmitters associated with behavioral changes in toxicant-exposed fish.

When TK fish were maintained in an aquarium with PC sediments and water and fed PC grass shrimp, their prey capture ability declined to that of PC fish after one month (Figure 1). Analysis of their brains revealed that their mercury levels had increased to levels of the PC fish. When PC fish were maintained in clean water for two months, prey capture ability increased only slightly, and brain mercury did not decrease (Smith & Weis 1997). This correlation of behavioral changes with brain mercury does not mean that this contaminant is mainly responsible for the altered behavior; other contaminants may contribute as well. Analysis of videotapes showed that poor prey capture resulted from fewer capture attempts, rather than from poor coordination (Smith & Weis 1997).

Fish from the polluted estuary also exhibited impaired predator avoidance behavior. PC fish, being generally 'slow', showed lower spontaneous activity and were more vulnerable than TK fish to predation by blue crabs (Smith & Weis 1997). This increased vulnerability may facilitate transfer of contaminants to higher trophic levels.

Analysis of gut contents of mummichogs revealed that PC fish ate more detritus and sediment, and far less live food (including grass shrimp), than TK fish (Smith & Weis 1997). Since detritus has low nutritional value (Prinslow et al. 1974) this poor diet may be largely responsible for the poorer growth and condition previously noted.

In contrast, the predator-avoidance ability of the grass shrimp at PC was not different from that of conspecifics from TK (Smith & Weis 1997). This is in agreement with the mummichog gut contents data, and has community level implications. It is known that predation can exert 'top down' effects on populations of prey species (Sih et al. 1985), and that mummichog predation can affect grass shrimp populations (Posey & Hines 1991). The decreased predation pressure on PC grass shrimp (due to a smaller mummichog population and reduced predator efficiency) is associated with increased numbers and a larger size-frequency distribution of grass shrimp at PC compared with TK (Santiago 1996).

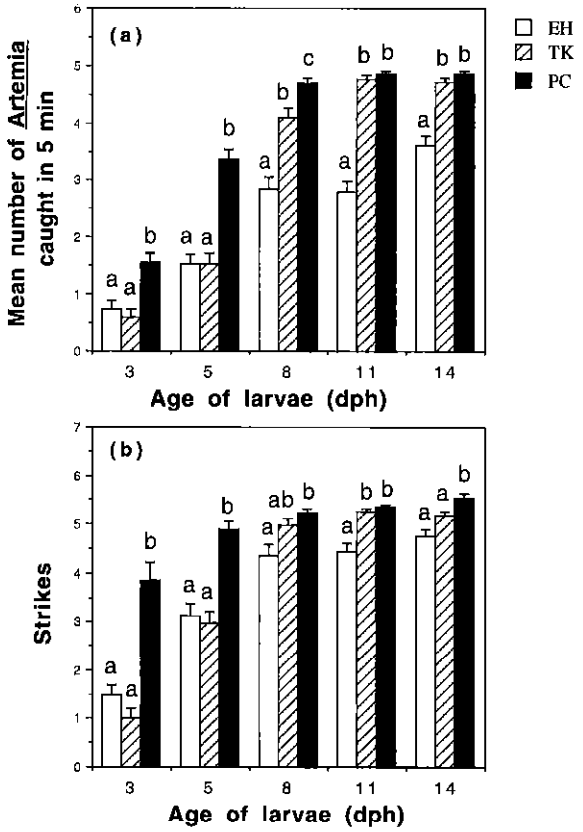

Figure 2. a – Number *Artemia* caught in 5 min and b – number of feeding strikes by mummichog larvae of different ages (dph = days after hatching) from East Hampton (EH), TK, and PC. Bars with different letters are significantly different, $p < 0.05$; Tukey multiple comparison tests

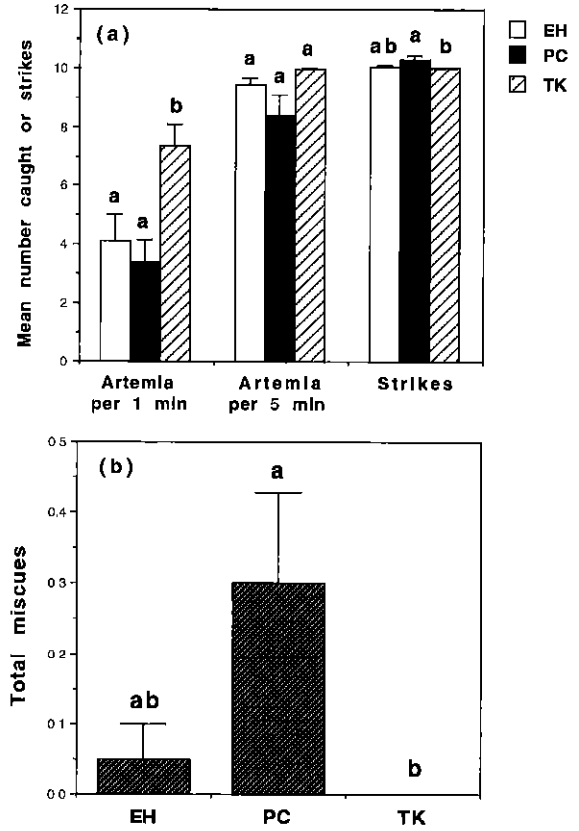

Figure 3. Prey capture ability of 1-month old mummichogs from EH, PC, and TK, measured as: a – mean (± SE) number prey caught in 1 min or 5 min and feeding strikes, and b – total number of miscues during the time taken to capture 10 *Artemia*. Bars with different letters are significantly different, $p < 0.05$; Tukey test.

Population differences in behavior of mummichog larvae and juveniles

To investigate the development of the behavioral differences in PC fish, feeding behavior in larvae from PC and two reference sites (TK and EH) was studied (Zhou 1997). Larvae raised in the laboratory in clean water, field-collected juveniles (3–4 months old, 30–40 mm), and yearlings (40–50 mm) were tested for prey capture rates, feeding strikes, miscues, and capture efficiency. Early PC larvae were not initially poor predators, but rather were more active than the reference larvae, which increased their encounter rate with prey. PC larvae had more feeding strikes and captured prey (*Artemia* nauplii) faster than EH or TK larvae, although PC larvae had more miscues and therefore a lower efficiency than TK or EH larvae. In all populations, prey capture rates increased with age. However, by one month after hatching, TK fish exhibited superior prey capture ability (Zhou et al. 1996) (Figures 2, 3). They were more active and searched more for food. PC fish continued to have more miscues and thus had lower prey capture efficiency. Since all fish were raised in clean water, inherited factors probably contribute to the differences in behavior. Prey capture abilities of PC and EH larvae and juveniles (3–4 months of age) were comparable, despite EH being a clean site. It is not clear why EH fish were relatively poor in prey capture in comparison to TK fish. Juveniles and yearlings sampled from the field at PC or EH were slower and less efficient feeders than those from TK (Figure 4). Genetic differences among the populations may play a role in this be-

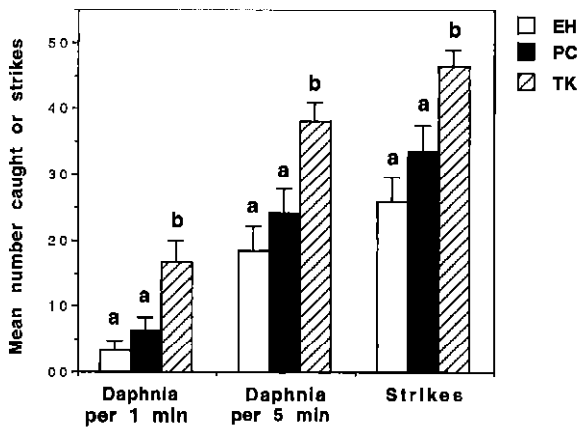

Figure 4. Prey capture ability of 3–4 month old mummichogs from EH, TK and PC measured by mean ± SE of *Daphnia* caught in 1 min and 5 min, and mean number of feeding strikes. Bars with different letters are significantly different $p < 0.05$; Tukey

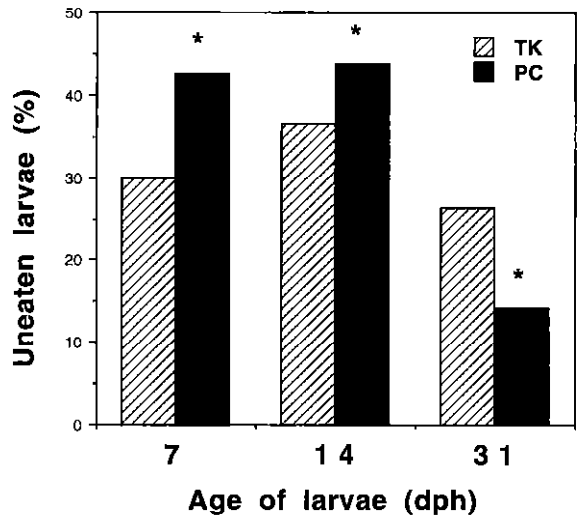

Figure 5. Predation by yearling mummichogs on PC and TK larvae of different ages (dph = days after hatching) (* = significantly different, $p < 0.05$, Chi-square test).

havior. The three populations have genetic differences in allozymes and mitochondrial DNA (Mugue 1996). Differences in tolerance to environmental factors (Weis & Weis 1989) appear also to have a genetic basis.

Reciprocal exposure experiments were performed with PC and TK larvae, in which fish were raised in mud and water from both sites. The polluted environment of PC reduced prey capture ability and efficiency (reduced capture rates and feeding strikes), survival, and growth of larvae in both populations, but the PC larvae were less affected, reflecting increased tolerance. Overall, the data indicated that both innate factors and the polluted environment contributed to the behavioral differences between the populations. The reduced feeding performance of PC fish does not appear to be solely a result of contaminants, since it was seen in larvae raised in clean water in the laboratory. However, differences in prey capture behavior might also be in part a delayed effect of maternally-transferred contaminants. Contaminants stored in the liver of female fish can be transferred to the eggs during vitellogenesis and can subsequently affect larvae as they metabolize the yolk (Savino et al. 1993). While we have found that the mercury level in newly hatched PC embryos (raised in clean water) is not different from that of TK embryos (Zhou 1997), we do not know about levels of other contaminants which might persist from maternal transfer into PC eggs.

We also studied the development of predator avoidance behavior in mummichog larvae from the different sites (Zhou 1997). Larvae were raised in the laboratory and tested for spontaneous activity, swimming performance, and predation by adult mummichogs (from TK). Larvae became more active as they grew and their swimming performance generally improved. PC larvae were initially more active, but after two weeks became more sluggish compared with TK larvae. We found that 1 week and 2 week old PC larvae were less vulnerable than TK larvae to predation by adult mummichogs, whereas by one month, TK larvae were more active, showed greater endurance, and were more successful at avoiding predation (Figure 5).

Differences in activity, swimming ability, and predator avoidance behavior of TK and PC larvae accounted for their differences in vulnerability. In the presence of the predator, PC larvae tended to hide beneath the rock or remain motionless on the surface of the water or at the edge of the tank. The 'immobile' state was advantageous for the younger, smaller larvae since it reduced the likelihood of being detected. However, the older, larger larvae were more conspicuous, and the same state was less effective for them. In contrast, older TK larvae, which

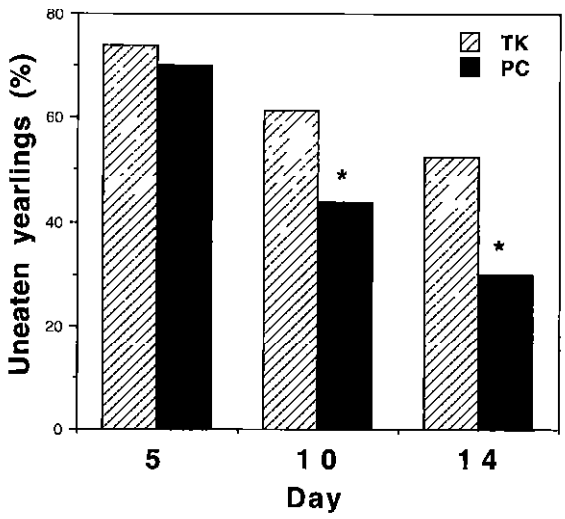

Figure 6. Predation by blue crabs on yearling PC and TK mummichogs over a 14 day test period (= significantly different, $p < 0.05$, Chi-square test).

were more active and showed higher endurance than PC larvae, were less vulnerable to the predator. Since reduced predator avoidance was seen in PC fish raised in clean water in the laboratory, it again appears that genetic factors play a role in the behavior. It is possible that selection pressures in the polluted PC environment, which presumably has fewer predators, may favor different antipredator behaviors than at cleaner sites. It is also possible that the differences in predator avoidance behavior shown at one month of age might also be a delayed effect of maternally-transferred contaminants.

We also examined predation by blue crabs on early and year old juvenile mummichogs collected from the different sites. TK juveniles remained less vulnerable than PC fish to predation by blue crabs (Figure 6).

Discussion and conclusions

Understanding normal behavior patterns is important to the conservation of fishes, as is made clear in the other papers of this issue. Although the mummichog is a resilient and abundant species and not one of concern to conservation biologists, study of its responses to contaminants may be applicable to other species which are of greater concern. It is possible that populations of other fishes may also exhibit abnormal behavior patterns when affected by neurotoxic contaminants. As we have shown, such contaminant exposure may impair prey capture and predator avoidance ability in both young and adult fish. These altered behaviors may, in turn, result in reduced growth and longevity, particularly when they occur in sensitive early life history intervals. Reduced survival and growth of larvae, due to reduced feeding and/or increased predation, may result in reduced recruitment, and thus reduced population size. Altered predator/prey behavior may affect community structure. Reduced predation on a prey species may result in altered size-structure and/or population density, if the prey species is less sensitive to the contaminants than its predators. Increased vulnerability to predation by pollution-exposed organisms may also result in greater amounts of contaminants being transferred to higher trophic levels. Differential sensitivities of different species to the same stressors can alter predator/prey relationships and energy flow in ecosystems.

However, population differences in predator/prey behaviors and abilities are not necessarily always due to direct exposure to contamination; genetic factors, habitat differences, and maternal transfer may also contribute to such population differences. It is important for conservation biologists to be aware of potential genetic population differences in behavior, as well as those which may result from environmental pollution.

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