Population interactions among free-living bluefish and prey fish in an ocean environment

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Summary. We used sonar to measure relative abundance, location, and depth of prey fish schools (primarily *Anchoa* and *Ammodytes*) in the ocean near Fire Island Inlet, New York from May to August for 4 years to examine predator-prey interactions. Prey fish numbers built through May, peaked in June, and thereafter declined coincident with the arrival of predatory bluefish. Bluefish abundance and feeding behavior correlated inversely with prey fish abundance and depth. Bluefish may drive seasonal patterns of prey abundance and distribution in this area through direct predation and by causing prey to flee.

Key words: *Pomatomus saltatrix* – *Ammodytes* – *Anchoa* – Predator avoidance – Prey regulation

The question of whether predators regulate prey populations has long been of interest. Debate continues over the relative importance of predation, competition, and environmental stress in structuring communities (Connell 1975; Schoener 1983). While competition for limiting resources has long been the dominant emphasis with which ecologists have approached their investigations of community structure, there is growing evidence that predation is a major community determinant (see Holt 1984). Understanding the role of predation in community dynamics is one of the major challenges of community ecology (Schoener 1974), and understanding the behavioral responses of prey to predator pressure is a central problem of behavioral ecology (Sih 1984).

In aquatic systems involving fish, most studies have employed exclosures to compare invertebrate prey communities where fish had access with those where fish were excluded. In some studies fish did not regulate invertebrate prey (reviews by Choat 1982; Quammen 1984; but see Gilinsky 1984; Daag et al. 1984). In others, fish removed substantial proportions of their preferred prey and caused community restructuring, especially when prey did not have adequate structural refuges (e.g., Kneib 1982; Dawidowciz and Pijanowska 1984; Gilinski 1984; Flecker 1984; Morin 1984; Moller 1984). Although there are very few studies of fish predation's effect on population dynamics when fish

are the prey, prey fish numbers have been found to be significantly affected by predatory fish (e.g., Zaret and Paine 1973; Mann 1982; Power et al. 1985).

In addition to population effects, behavioral effects of predatory fish on prey have been shown. Differential use of habitat in direct response to predatory fish presence has been documented in several studies, both where invertebrates were the prey (e.g., Cook and Streams 1984; Cooper 1984), and where fish were the prey (e.g., Major 1977, 1978; Mittelbach 1984; Fraser and Mottolese 1984). Bennet and Streams (1986) showed that the distribution of invertebrate prey relative to vegetative cover differed in ponds with vs. without fish predators. Differentially susceptible crayfish and bluegill sunfish (different sizes and sexes) differed in their response to predatory bass (Stein and Magnuson 1976; Werner et al. 1983). Hobson (1972) and Major (1977) thought that predation was a major factor influencing prey fish behavior. Some fish may avoid shallow or open areas to avoid exposure to piscivorous birds and bats (Power 1984; Romero 1985).

In our present study we sought an understanding of the dynamics of population and behavioral interactions of free-living, schooling predatory and prey fish in a near-shore ocean community. We hypothesized that predator and prey populations varied during late spring and summer, and that predator presence was related to intra-annual patterns in prey abundance and behavior. We further hypothesized that prey respond behaviorally by adjusting their swimming depth in response to predators. This study was part of an investigation of this near-shore continental shelf system with respect to population dynamics among prey fish, predatory fish, and seabirds (Safina and Burger 1985, 1989).

Methods

We conducted our field studies from May through August during 1982–1985 in the northwest Atlantic Ocean near Fire Island Inlet, New York (40° N, 73° W). Data were collected aboard a 5.5 m boat equipped with a Raytheon DC 200 paper-recording echo sounder. The sounder was calibrated over clear water where fish could be seen, and adjusted to the lowest sensitivity at which small fish would be printed. Prey fish, predatory fish, and seabirds usually ignored the boat during transects and may have been habitu-

ated to boats in this area, which is frequented by fishermen in small boats.

Transects were run through foraging flocks of common terns (*Sterna hirundo*). This allowed us to track fish concentrations and feeding schools of predatory fish, which are both tracked by terns (Safina and Burger 1985). Transects were run anywhere in the ocean where birds fed within approximately 10 km of the inlet, at depths ranging up to approximately 18 m. Up to 7 transects were run per morning.

For each transect, any predatory fish seen at the surface within 20 m of the boat were noted manually on the sounder's paper. For predatory fish, size and an index of feeding intensity were determined by trolling multiple-tube lures on wire during each transect. Feeding intensity was classified, depending on the frequency with which fish struck lures, as either no feeding, little feeding (one strike), moderate feeding (2 or 3 strikes), or intense feeding (numerous strikes). Activities of predatory fish were classified as either: (0) not feeding, (1) deep feeding, i.e. with no surface activity, (2) feeding with sporadic surface activity, (3) prolonged surface feeding during which many fish chased prey at the surface. 285 sonar transects were run over the 4 years of field work.

For each transect, fish densities were quantified by overlaying the echo sounder paper with a transparent 7-mm square grid and estimating the percent coverage of prey and/or predatory fishes in each grid square. Predatory and prey fishes were differentiated by their echo marks. Echoes of predatory fish tend to form discrete spikes while prey fish schools appeared as dark, irregularly shaped masses (see illustration in Safina and Burger 1985). This method yieded a variety of useful indices of fish density, abundance, and fish depth. Density was defined as the mean percent coverage of echo marks, and was calculated as the sum of percent coverages in all grid squares with echo marks, divided by the total number of grid squares with and without echo marks. Thus, density could be equal in very short and very long transects. Abundance, defined as a relative index of biomass, was calculated as density multiplied by vertical area of the transect. Fish depth was defined as the mean depth of fish in the echo profile. Sonar records were divided vertically into discrete 1.5 m vertical depth segments. To calculate fish depth, fish density was multiplied by depth for each depth segment, these values were summed, and this sum was divided by the sum of percent coverage of echo marks in each grid square. This yielded a depth-weighted mean.

Data were analyzed using SAS computer programs. Due to their schooling nature, fish were usually either absent or present in substantial numbers, resulting in a bimodal distribution of data that was resistant to normalizing transformations. For this reason, non-parametric analyses were usually performed.

Results

Patterns of prey abundance

Sandeels (*Ammodytes americanus*) and bay anchovy (*Anchoa mitchilli*) were the most abundant prey fishes in the study area and the species most often preyed upon by predatory fish and terns, as evidenced by stomach contents and direct observation of predators chasing prey at the surface.
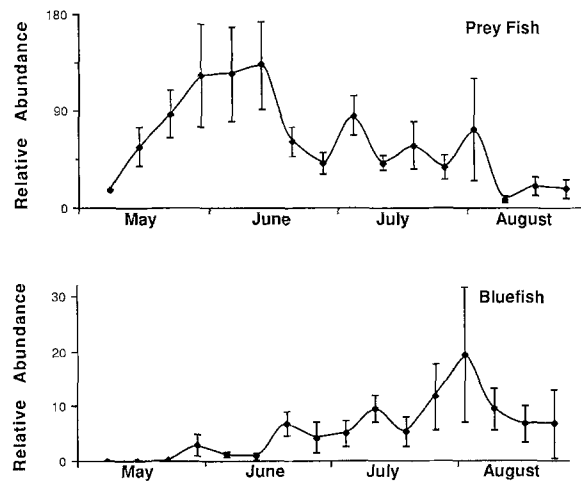

Fig. 1. Temporal patterns of prey fish and bluefish abundance (means ± SE). An echo sounder was used to obtain the relative abundance index, which is calculated from the coverage of marks produced on the sounder from fish echoes

Table 1. Paired comparisons of prey fish density and abundance among months (Kruskall-Wallis Test)

	Prey Fish Density (df = 1)		Prey Fish Abundance (df = 1)	
	X^2	$P<$	X^2	$P<$
May vs. June	0.79	0.4	1.06	0.3
vs. July	3.43	0.06	4.36	0.03
vs. August	12.97	0.0003	15.17	0.0001
June vs. July	14.65	0.0001	18.76	0.001
vs. August	7.89	0.005	8.52	0.004
July vs. August	5.40	0.02	6.16	0.01

Other important prey species for larger fish and seabirds were butterfish (*Peprilus triacanthus*), round herring (*Etrumeus teres*), and the young of four common predators: bluefish (*Pomatomus saltatrix*), long-finned squid (*Lologi pealei*), Atlantic mackerel (*Scomber scombrus*), and pollock (*Pollachius virens*).

Population flux within the prey community was marked. The general pattern was one of relatively low abundance early in May, then a rapid buildup to a peak in the first through third weeks of June, followed by a sudden drop to low levels during the last week in June (Fig. 1). Intermonth variation was highly significant for both prey fish abundance (Kruskall-Wallis test, $X^2 = 14.92$, df = 3, $P < 0.01$) and density (Kruskall-Wallis test, $X^2 = 12.55$, df = 3, $P < 0.01$, Table 1). Prey fish abundance was generally much greater early in the season (up to July 15) than later (Kruskall-Wallis test, $X^2 = 9.37$, df = 1, $P < 0.002$). Prey remained farther from the water's surface early in the season than later ($X^2 = 15.90$, df = 1, $P < 0.0001$). Prey abundance differed significantly among years (Kruskall-Wallis test, $X^2 = 9.75$, df = 2, $P < 0.008$), as did prey density (Kruskall-Wallis test, $X^2 = 7.31$, df = 2, $P < 0.03$).

Patterns of predatory fish abundance

Bluefish constituted 94 percent of our hook and line samples and were frequently seen pursuing prey. Other predato-
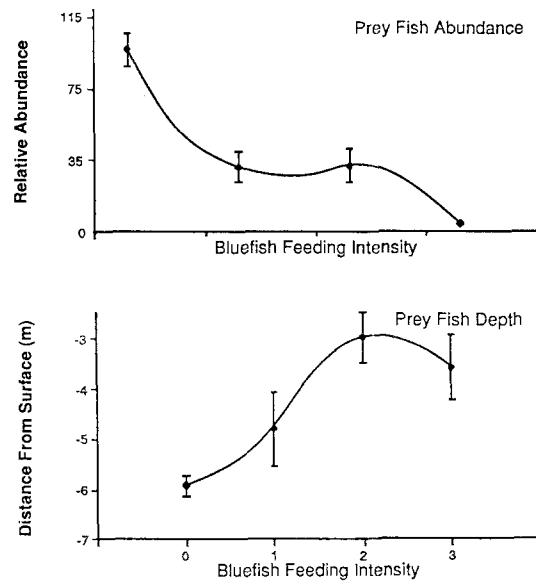
Table 2. Paired comparisons of predatory fish density and abundance among months (Kruskall-Wallis Test)

	Predatory Fish Density (df = 1)		Predatory Fish Abundance (df = 1)	
	X^2	$P<$	X^2	$P<$
May vs. June	8.69	0.003	8.93	0.003
vs. July	22.53	0.0001	22.26	0.0001
vs. August	26.15	0.0001	24.86	0.0001
June vs. July	4.24	0.04	5.25	0.02
vs. August	10.09	0.002	8.97	0.003
July vs. August	4.09	0.04	1.98	0.2
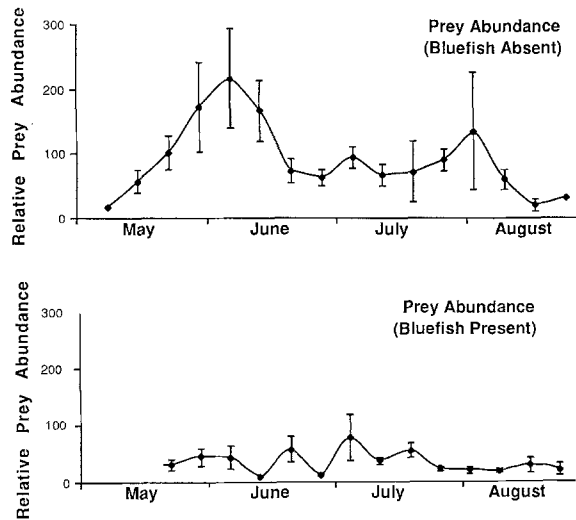
Fig. 2. Prey fish abundance in transects where bluefish were present and in transects where bluefish were absent (means ± SE)

Fig. 3. Prey fish responses to bluefish feeding intensity. Feeding intensity was classified, depending on the rate at which bluefish struck trolled lures, as either: (0) no feeding, (1) little feeding, (2) moderate feeding, or (3) intense feeding

ry fish were rarely encountered. For this reason our discussion of predatory fish will refer to bluefish.

The pattern for bluefish abundance during our study began with arrival and increase in late May and early June (Fig. 1). Inter-month variation was highly significant for both bluefish abundance (Kruskall-Wallis test, $X^2 = 31.70$, df = 3, $P<0.0001$) and density (Kruskall-Wallis test, $X^2 = 32.97$, df = 3, $P<0.0001$; Table 2). Abundance was higher after mid-July ($X^2 = 5.49$, df = 1, $P<0.02$), as was density ($X^2 = 8.35$, df = 1, $P<0.004$). Mean bluefish depth did not change from early to late season (Kruskall-Wallis test, $X^2 = 0.77$, df = 1, $P<0.4$). As with prey species, bluefish abundance varied significantly among years (Kruskall-Wallis

test, $X^2 = 20.17$, df = 3, $P<0.001$), as did density (Kruskall-Wallis test, $X^2 = 25.08$, df = 3, $P<0.0001$). Larger bluefish were found in deeper water (Kendall's coefficient of rank correlation, $tau = 0.5$, $n = 125$, $P<0.0001$).

Population interactions among bluefish and prey fish

Bluefish arrival coincided with changes in prey numbers and prey behavior. Increasing prey abundance early in the season, when bluefish were absent, was followed by a decline in prey that commenced with the arrival of bluefish (Fig. 1). The absence of bluefish was associated with greater prey abundance (Fig. 2, Kruskall-Wallis test, $X^2 = 55.11$, df = 1, $P<0.0001$), prey density ($X^2 = 50.66$, df = 1, $P<0.0001$), and mean prey depth ($X^2 = 52.63$, df = 1, $P<0.0001$). Strong inverse correlations were found between almost all prey and predator variables (Table 3, Fig. 3), except for a positive correlation with bluefish depth (Table 3).

The activities of bluefish may influence the general shoaling of prey that occurs over the course of the season (Fig. 4). Prey were closer to the surface after mid July, when predators were more abundant than they had been earlier (Kruskall-Wallis test, $X^2 = 5.49$, df = 1, $P<0.02$). In addi-

Table 3. Correlations between prey fish and predatory fish variables. Kendall's *tau*

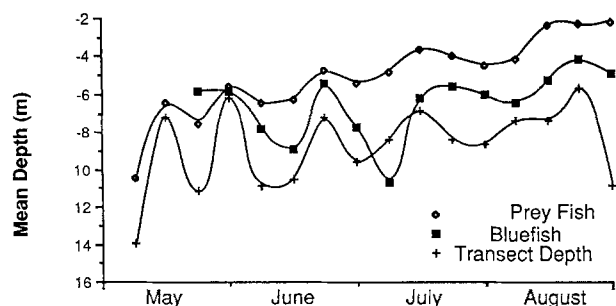|	prey abundance			prey density			prey depth		
	tau	*n*	$P<$	*tau*	*n*	$P<$	*tau*	*n*	$P<$
bluefish:									
density	−0.31	277	0.0001	−0.28	277	0.0001	−0.38	247	0.0001
abundance	−0.30	277	0.0001	−0.30	277	0.0001	−0.35	247	0.0001
feeding intensity	−0.33	271	0.0001	−0.30	271	0.0001	−0.36	242	0.0001
surface activity	−0.40	272	0.0001	−0.35	272	0.0001	−0.38	243	0.0001
depth	−0.07	117	0.2	−0.22	117	0.0001	+0.24	94	0.001

Fig. 4. Temporal changes in the mean depth of prey fish, bluefish, and the water column in transects during summer. The change in water depth indicates a general movement towards shore

tion to moving closer to the surface, prey moved into shallower water over the course of the season (Kendall's $tau = 0.18$, $n = 112$, $P < 0.01$). Prey fish often attempt to escape bluefish and other predators by leaping into the air, and bluefish were observed (directly and by sonar) to travel near the bottom while not attacking prey. These factors may contribute to prey remaining near the surface when predators are present.

Discussion

The general seasonal pattern of prey population variability consisted of early build-up followed by decline during the course of the summer. The primary pattern throughout our data is inverse correlation in prey fish/bluefish interactions. Our observational data suggest that bluefish caused prey population size to change during our study.

Fewer prey were detected in the study area after the arrival of bluefish, and bluefish arrival coincided with changes in prey behavior. That behavioral changes in prey were caused by their relationship with bluefish is suggested by the contrast in mean prey depth with respect to predator abundance. Bluefish abundance was greater after mid July, and prey became significantly shallower after that date.

Prey density was significantly greater in May and June than later, and bluefish density was significantly greater in July and August. The observed reduction in prey fish numbers, and their behavioral responses, occurred rapidly enough to suggest that the lowered prey density and abundance indices are both related to large-scale avoidance by prey (*sensu* Charnov et al. 1976). Our impressions correspond with those of commercial fisherman who often report observations such as "the bluefish have already chased out the mackerel", or "bluefish are early this year, and all the squid are scattered".

Consumption of prey may also have been an important factor in the prey declines we observed. Levings (1974) found that winter flounder (*Pseudopleuronectes americanus*) predation was responsible for a seasonal decline in the population of its preferred amphipod prey, a species that seems incapable of leaving the area in response to predator presence. Also, Moller (1984) reported that the decline of larval herring coincided with the substantial increase of its jellyfish predator in late spring.

Sih (1984) has postulated that when predators and prey are mobile and a spatial refuge exists, the prey's response should dominate predator-prey interactions. Our data seem to support this postulation. Two of our primary prey species, sandeels and anchovies, appear to use the inner estuary

and inlet environs differentially as refugia, and the change in depth of prey fish in the presence of predators can be viewed as a move to a refuge, albeit a tenuous one.

Prey appear not to be tracked relentlessly by bluefish but, rather, are tracked for relatively short periods when the bluefish are feeding. We have often seen actively feeding bluefish terminate a prolonged attack, apparently after satiation, on prey that were completely trapped by a physical barrier and had little chance of escape. Bluefish usually left the immediate area at these times, which seemed to afford the prey what might be thought of as a temporal refuge, a time when lateral movement (i.e., fleeing the area) can disengage predators from prey, and later necessitate the bluefish's travel in search of more prey. A prudent prey fish ought to keep always moving if it has recently been engaged with predators and the probability of encountering predators is not random with respect to direction. This latter condition is often met when fish enter refuges or travel on seasonal migrations. Thus the response of mobile prey, even without a spatial refuge, still seems to dominate. In Sih's (1984) study, mobile invertebrate prey showed stronger movement responses than invertebrate predators, independent of the presence of refuges.

The presence of bluefish coincided with a shift towards the surface by prey. Prey fish often attempt to escape predators by leaping (e.g., Charnov et al. 1976; Major 1977; Colblentz 1985) and bluefish were observed to travel near the bottom. These two factors probably contribute to prey moving closer to the surface when predators are in the vicinity. That they should do so whether or not they are under attack is a simple extension of Dawkins and Krebs' (1979) 'life-dinner principle'; prey cannot afford to be wrong about a predator's feeding motivation or be in the wrong place when its motivation changes. Prey fish also tend to stay away from the surface, where they are vulnerable to predation by birds, when not being attacked from below (Safina and Burger 1988). On numerous occasions we observed that sandeel schools remained 2 m or more below the surface, while individuals made feeding sorties into the dense surface plankton, thereby incurring a greater risk of bird predation. They appeared at these times to dart quickly into the plankton and then back into the school, seemingly balancing risk against hunger (Milinski 1985). At other times, we observed anchovy schools that surfaced *en masse*, apparently feeding while they were at the surface but not remaining more than approximately one minute. Were never saw schools of prey travelling at the surface; our impression is that they only went to the surface either to feed in the plankton or to escape predatory fish. We conclude that predation affects local population sizes and behavior of prey species in the system we studied.

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