Abstract.— A 39-month study of the effects of cessation of sewage sludge disposal in the New York Bight apex on the diets of certain fishes and on the benthic macrofaunal community provided an opportunity to examine predator-prey relationships of winter flounder, Pleuronectes americanus, one of the common predators in the area. Benthic macrofauna and winter flounder were collected monthly and bimonthly, respectively, from July 1986 through September 1989 at three sites in the Bight apex that are variably influenced by sewage sludge. There were limited changes in winter flounder diets and abundance of dominant benthic macrofaunal species following cessation of sewage sludge disposal. The comparison of volumetric contribution of common prev in flounder stomachs to potential-prev abundance in benthic samples suggested several relationships. These included evidence of preferential predation on the polychaete Pherusa affinis: this selective preference may be associated with its high caloric content as well as with its average high biomass density. Other common prey, primarily polychaetes but including an anthozoan, were also preyed upon in proportions greater than their abundance in the environment. Some moderately abundant potential prey, such as the small near-surface-dwelling mollusc Nucula proxima and the ribbon worm Cerebratulus lacteus were not commonly preved upon suggesting they were unavailable as prey or were avoided by winter flounder. Corresponding fluctuations in abundances and predation of the pollution-tolerant polychaete Capitella sp. and the pollution-sensitive amphipod Unciola irrorata suggested a proportional consumption relationship in association with sludge disposal and its cessation.

Manuscript accepted 30 December 1993. Fishery Bulletin 92:608–619 (1994).

Predator-prey relationships of winter flounder, *Pleuronectes americanus*, in the New York Bight apex

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Predator diets provide information on sources of prey, predominant prey types, levels of particular prey use and availability, and prey preference or avoidance, when compared with the availability of potential prey in the environment (Levings, 1974; Diehl, 1992). For predatory fish such as winter flounder. Pleuronectes americanus, this information increases our understanding of prey selection, based on evidence of prey preference or avoidance, and how selective predation can affect or be affected by prey population dynamics.

In studies of aquatic environmental health, benthic macrofaunal diversity and certain indicator species are often used as response variables. Monitoring predator diets during such studies can aid in determining how predation can function as a confounding factor in interpreting macrofaunal change as solely the product of altered abiotic factors. Monitoring diets can also indicate how benthic species abundance and the overall community structure can be affected by predation. Predation studies can also aid in estimating the effect of benthic macrofaunal changes (natural or anthropogenic) on predator-prey

relationships (i.e. loss of a seasonally or energetically important prey) or be used to define potential contaminant uptake pathways (Clements and Livingston, 1982; Gendron, 1987; Schindler, 1987).

Studies of the linkage between prev abundance and predation by marine fish are scarce, especially studies based on samples taken over an extended period of time or during an environmental change. An opportunity to examine predatorprey relationships was provided by the availability of the results of a comprehensive 39-month study of the effects of sewage sludge disposal abatement in the New York Bight apex (the coastal area at the mouth of New York Harbor). This study included monitoring the diets of several common fishes and large decapod crustaceans, the abundance of benthic macrofauna, as well as other biological and environmental variables (Environmental Processes Div., 1988).

The winter flounder, *Pleuronectes americanus* Walbaum (Robins et al., 1991) is an abundant demersal fish in the New York Bight apex. It was the third most important contributor (10%) to the total fish biomass collected during the study (Wilk et al., 1992). Winter flounder also rely almost entirely on small benthic macrofauna for food; thus, variability in predation and macrofaunal community structure can have important consequences for both the predator and its benthic prey (Kurtz, 1975; Clements and Livingston, 1982; Pihl et al., 1992).

This paper compares the diets of winter flounder with the abundance of benthic macrofauna at three stations in the New York Bight apex variably affected by sewage sludge, for evidence of 1) selective predation (preference or avoidance), 2) variation in the proportional consumption of benthic prey over time, and 3) the manner in which predator-prey relationships influenced the macrofauna with the cessation of sewage sludge disposal.

Materials and methods

Winter flounder and benthic macrofauna collection methods, sample processing, and primary data analyses for this study have been described in detail elsewhere (Reid et al. in press;

Steimle, in press). In brief, three stations, R2, NY6, and NY11 (Fig. 1), were sampled systematically from July 1986 to September 1989 (Environmental Processes Div. 1988). These stations represent a gradient of conditions related to sewage sludge disposal, e.g. variable levels of total organic carbon (TOC) and chemical sediment contamination, such as chromium (Cr), that changed to some degree after cessation of disposal in December 1987 (Table 1). Station NY6 was the most sludge-affected area, with a markedly altered benthic community characterized by a relatively low species richness, low biomass, and high levels of TOC sediment contaminant such as Cr (Table 1). Station R2 was moderately affected by sludge and was biologically enhanced; it showed relatively high species richness and macrofaunal biomass and moderate levels of sediment contamination compared with NY6 (Table 1). Station NY11 was the least affected by sludge disposal, having relatively high species richness but low macrofaunal biomass and low levels of sediment contamination (Table 1). All stations were about 30 m in depth and had similar sediment types (silty-fine sands) and hydrographic characteristics (Table 1).

Triplicate benthic macrofaunal samples were collected monthly with a 0.1-m² Smith-McIntyre grab



sampler and sieved through a 0.5-mm mesh screen. Materials retained were preserved in buffered formalin and later transferred to 70% ethanol. The samples were sorted and organisms were identified to the lowest possible taxon (usually species), counted, and moist-weighed (Reid et al., in press). Data from a total of 350 benthic macrofaunal samples were available for analysis.

Adult winter flounder were collected bimonthly (additional collections were made in August) with a small otter trawl at the same stations and during the same week as the benthic grab sampling. Each periodic trawl collection consisted of six daytime tows of 0.5 km, deployed in an array across the center of the station. Generally, at least 30 fish were collected from each station per collection period. Stomach contents were analyzed in the field or laboratory by using semi-quantitative, visual estimates of stomach volume from comparison of stomach boluses with variable-diameter, volume-calibrated cylinders. All identifiable items in the stomachs were identified to the lowest possible taxon and separated to visually estimate their individual percent contribution to total stomach volume (Langton et al., 1980; Steimle, in press). This method provides reasonable results compared with more labor intensive methods (Hyslop, 1980).

Table 1

Habitat characteristics (means) of three sampling sites in the New York Bight apex for the 18 months before (A) and 21 months after (B) sewage sludge disposal cessation; benthic biomass (wet wt) does not include the biomass of two large bivalves, *Pitar morrhuanus* and *Arctica islandica*.

			Sta	tions			
	R2		N	¥6	NY11		
	Α	В	A	В	Α	В	
Depth (m)	29			31	29		
Sediment							
grain size (phi) ¹	3.1	3.2	3.6	3.5	3.1	3.1	
TOC (% dry wt) ¹	0.9	0.9	4.6	2.3	0.3	0.3	
Cr (ppm dry wt) ²	37.2	36.7	163.0	96.5	15.8	12.9	
Bottom water ³							
min. dissolved oxygen (mg/L)	4.2	5.7 ⁴	4.3	5.84	5.3	5.54	
temp. range (°C)	~3-17 for all sites ⁵						
Benthos							
biomass (g/m ²)	218.2	202.8	63.4	28.2	66.6	73.2	
species (n)/grab	30	33	19	33	41	45	

⁷ Packer et al., in press.

² Zdanowicz et al., in press

³ Arlen, L., A. Draxler, and R. Bruno. Hydrographic observations in the bottom water of the New York Bight at the "12 mile" dumpsite: 1983–1990. Unpubl. manuscr.

⁴ Dissolved oxygen content of <3 mg/L was recorded in September, 1989.

⁵ Summer levels in 1988 were 2-3°C lower than the long-term mean.

The mean proportional volume (percent of the total volume) of a given prey item in the stomach was compared with the mean proportional biomass of that prey in the benthic macrofauna, and the relationship between these proportions was used to determine whether selective predation was evident. Although this approach to examining predator-prey associations differs from the traditional use of prey numerical abundance in stomachs and the environment, it is nonetheless realistic and useful because 1) prey volume can be a more precise dietary variable compared with uncertain enumeration of prey that are easily fragmented and for which only parts are present and 2) volume and biomass are approximately equivalent for most common prey taxa (see below). However, amphipods were also considered numerically because they are usually eaten whole and their exoskeletons are resistant to digestion and thus allow a reasonably accurate assessment of the number of individuals eaten.

The stomachs of 3,556 adult winter flounder, 18– 30 cm total length, examined from the three study sites had identifiable food in them. To examine overall predator-prey relationships, stomach content and benthic data from the entire study period were pooled for each station because there were only minor changes in dominant prey and benthic species associated with sludge disposal cessation (Reid et al., in press; Steimle, in press). The use of pooled stomach content data to estimate prey preference by a predator population is recommended by some authors, e.g. Rachlin et al. (1987). Changes in predator-prey relationships related to cessation of sludge disposal are considered separately. Any seasonal or annual variability was assumed to be distributed equally within the pooled data as there were no gaps in collections. Log transformation of Shorigin's forage ratio index (K=rt/pt), adapted from a numerical approach for prey volume and biomass, was used to estimate prey selectivity (Berg, 1979): $K = \text{Log}_{10}(rt/pt)$, where rt = proportion of prey in the diet estimated by contribution to stomach volume and pt = proportion of prey in the benthic biomass. Positive K values suggest a degree of selective predation. Near-zero K values suggested that predation is directly proportional to abundance. Negative K values suggest underutilization or avoidance of a potential prey relative to its availability.

The use of volume and biomass to calculate K is reasonable because 1 mL or cm³ of prey volume is considered approximately equivalent to 1 g of macrofauna wet weight (Bowman, 1986). We partially verified this assumption by determining the mean volume to wet weight ratios for a number of individuals for a range of common prey taxa. The ratios for an anthozoan, Ceriantheopsis americanus, a polychaete, Pherusa affinis, and the sand shrimp Crangon septemspinosa varied between 0.96 and 1.00 ($n=\geq 26$). However, the ratios for calcareous-shelled prey were lower, 0.70 for the bivalve mollusc Nucula proxima (n=50), and 0.77 for the sand dollar Echinarachnius parma (n=30).

All fish were collected near mid-day; therefore, the effects of digestion on stomach volume estimates were not considered a major factor. Winter flounder are primarily daytime feeders and all but the most softbodied prey should remain identifiable in their stomachs for several hours (MacDonald et al., 1982).

Results

Diet spectrum and dominance

Forty-nine prey taxa were identified in winter flounder stomachs, although only about 30 taxa were identified in the stomach contents at any individual station (Table 2). These are conservative estimates because of some uncertainties in identification caused by digestion. This prey spectrum represents about a quarter of the total available benthic macrofaunal taxa identified at station NY6 (119 species) and R2 (133 species), and about a fifth of the 154 species identified at station NY11.

Dominant prey, defined as species that composed at least 2% of the total stomach volume of fish from any station, were the polychaetes *Pherusa affinis*, *Asabellides oculata*, and *Nephtys incisa* and the tubedwelling anthozoan *Ceriantheopsis americanus*. The rhynchocoel *Cerebratulus lacteus*, juvenile rock crabs *Cancer irroratus*, and other polychaetes, including *Capitella* sp. and *Scoletoma (Lumbrineris)* spp., were dominant in the diet at one or two stations (Table 3). Collectively these eight taxa constituted between 76% and 96% of the winter flounder diet by volume at the three stations (Table 3).

Predation patterns

The log forage ratio (K) indices were positive for several dominant species. The K index was consistently high $(\geq +0.25)$ for the polychaetes, P. affinis and A. oculata. High positive K values were also calculated for other prey, but at only one or two stations (Table 3). The K indices were near zero (± 0.20) for some dominant species at some stations, such as C. americanus. For other prey or at other stations the K indices were low (<-0.25). This was especially evident for C. americanus, Spio setosa, Glycera sp., and the molluscs (Table 3).

Comparison of the contributions of these dominant prey species to flounder diets and to macrofaunal

Table 2

List of winter flounder, *Pleuronectes americanus*, prey identified in stomachs collected from three stations in the New York Bight apex.

		Statio	n
Prey	R2	NY6	NY11
Algae	Х	x	
Coelenterates		-	
Ceriantheopsis americanus	Х	Х	Х
Hydrozoans	х		х
Rhynchocoels	Х	Х	Х
Nematodes		Х	
Chaetognaths			х
Bryozoans		Х	
Molluscs			
Nucula proxima	Х	Х	Х
Yoldia sp.			Х
Nudibranchia			х
Ilyanassa trivittata		х	
Polychaetes			
Nephtys sp.	X	X	X
Nephtys incisa	x	х	х
Ninoe nigripes	X		
Scoletoma (Lumbrineris) sp.	х	х	X
Scoletoma acicularum			X
Pherusa affinis	X	X	X
Asabellides oculata	х	X	х
Ampharete acutifrons		X	
Spionidae		х	X
Spio setosa	X		X
Spiophanes bombyx	х	x	х
Cirratulus cirratus		х	
Tharyx sp.	X		
Tharyx acutus	X	х	X
Capitella sp.	X	х	Х
Mediomastus ambiseta	Х		
Phyllodoce arenae	х		х
Drilonereis sp.	х	Х	х
Glycera sp.	X	Х	Х
Ophioglycera gigantea	х		
Chone infundibuliformis			Х
Aglaophamus circinata	х		
Nereis succinea		х	
Isopods			
Edotea triloba	Х	Х	Х
Cirolana sp.		Х	
Cumaceans			
Diastylis sp.	х	х	х
Amphipods			
Leptocheirus pinguis	Х	х	х
Unciola irrorata	Х	х	х
Monoculodes edwardsi		Х	Х
Photis pollex			х
Dyopedos sp.		х	
Mysids	Х		
Decapods			
Cancer sp.	х	х	х
Cancer irroratus	х	х	х
Crangon septemspinosus	x	x	X
Echinoderms			
Echinarachnius parma			х
Tunicates			
Molgula sp.	х		

Table 3

Comparison of the average contribution of dominant prey in the diet of winter flounder, *Pleuronectes americanus* (mean % total stomach volume), to that of prey and dominant benthic infauna (infn) species (mean % total wet weight biomass) at stations in the New York Bight apex, 1986–1989. Seventy two benthic grab samples (triplicate samples at 24 collection periods) are included. K' is the log forage ratio.

Species	Stations								
	NY6			R2			NY11		
	prey	infn	(K')	prey	infn	(K')	prey	infn	(K ')
Ceriantheopsis americanus	28.0	18.5	0.18	7.0	6.6	0.03	27.3	6.4	0.63
Pherusa affinis	25.1	2.7	0.97	76.3	42.8	0.25	48.3	9.7	0.70
Asabellides oculata	9.2	3.8	0.38	3.4	<0.1	>1.83	2.0	<0.1	>1.60
Nephtys incisa	3.5	3.5	0	4.9	4.9	0	2.0	0.7	0.46
Capitella sp.	6.0	11.7	-0.29	0.3	<0.1	>0.78	<0.1	<0.1	0
Cerebratulus acteus	3.0	45.3	-1.15	2.4	2.0	0.08	0.8	2.0	-0.40
Scoletoma sp.	1.5	<0.1	>1.48	2.1	<0.1	>1.62	4.1	3.3	0.09
Cancer irroratus	11.3	2.4	0.67	1.5	4.4	-0.47	1.2	0.3	0.60
Spio setosa	<0.1	0.6	<-1.10	<0.1	0.1	<-0.30	0.8	7.5	-0.96
Nucula proxima	0.1	1.9	-1.30	<0.1	0.5	<-1.00	0.1	6.6	-1.70
Glycera sp.	0.6	0.8	-0.12	<0.1	0.2	<-0.60	0.1	6.5	-1.70
Pitar morrhuanus	0.0	0.1		0.0	30.7		0.0	14.7	
Arctica islandica	0.0	0.1		0.0	<0.1	 ∞	0.0	28.1	00
Ensis directus	0.0	<0.1		0.0	3.1		0.0	<0.1	
Totals	78.2 ¹	91.8		97.9	95.3		86.6	85.8	
Nonempty stomachs (n)		1405			1628			523	

biomass over time illustrates trends in the predatorprey association not evident in the pooled data (Table 3). For example, there was an apparent proportional consumption association (level of prey consumption was closely associated with level of abundance) for the anemone *C. americanus* at all stations, although the strength of the association varied at times (Fig. 2).

However, the proportional contribution of the polychaete P. affinis to winter flounder diets was greater than the prey's proportional contribution to total benthic macrofaunal biomass (Table 3, Fig. 3). The contribution of this prey to the winter flounder diet generally paralleled its contribution to macrofaunal biomass at all stations during the study period. Peaks in consumption are often consistent with peaks in proportional contribution to total community biomass, especially at stations NY6 and NY11 (Fig. 3). For the entire study period, the difference in proportional consumption and biomass for P. affinis ranged from 9.3 fold at station NY6 (25.1% stomach volume vs. 2.7% benthic biomass; K=0.97) to 1.8 fold at station R2 (76.3% volume vs. 42.8% biomass; K=0.25); station NY11 had an intermediate difference of 3.7 fold and K=0.70 (Table 3).

Some benthic species that were dominant in the overall benthic biomass were seldom identified in the flounder stomachs. For example, the rhynchocoel C. lacteus, which was particularly abundant at station NY6, was not often found in flounder stomachs, despite its relative importance in the benthic biomass (Table 3). This underutilization of potential prey was also evident at station NY11, where the polychaetes, Glycera spp. (mostly G. dibranchiata) and Spio setosa, as well as several mollusc species, composed >5% of the mean macrofauna biomass but were never important items in the flounder diet (Table 3). However, a substantial portion of the small, unidentified polychaete fragments found in some winter flounder stomachs may have been S. setosa. The predationabundance trends over the study period for these and other less common prey are not presented but were similar to the trends presented for C. americanus (Fig 2).

In general, there was little evidence of predation on molluscs by winter flounder, despite their sometimes high contribution to overall macrofaunal biomass. For example, the minute (<5 mm shell width) Atlantic nut clam, *Nucula proxima*, a consistent, although only moderate component of the infaunal biomass, was not commonly found in winter flounder stomachs (Table 3).

Cessation of sewage sludge disposal

The change in abundance of two benthic species, the polychaete Capitella sp. and the amphipod U.



irrorata, was associated with the cessation of sludge disposal (Reid et al., in press). These changes were also reflected in the occurrence of these two prey in winter flounder stomachs. When sludge disposal

> ended in 1987, the abundance of the stresstolerant *Capitella* sp. declined and so did its occurrence in stomachs at station NY6 (Fig 4). For the more stress-sensitive *U. irrorata*, predation was also generally associated with abundance at two stations (Fig. 5). At station NY6, where the effect of sludge disposal was greatest, the abatement of sludge disposal was accompanied by a seasonally varying increase in the abundance of this amphipod and a corresponding increase in the frequency of occurrence in winter flounder stomachs (Fig. 5).

Discussion

Diet spectrum and dominance

The spectrum of prey and dominant prey taxa consumed by winter flounder in the New York Bight apex (Table 2) is similar to that reported in other winter flounder diet studies (Wells et al., 1973; Hacunda, 1981; Langton and Bowman, 1981; Bharadwaj, 1988; Steimle and Terranova, 1991). Winter flounder diet studies in estuaries and to the north also report the dominance of similar prey taxa (Tyler, 1972; Wells et al., 1973; Worobec, 1982). With the possible exception of *Capitella* sp., dominant prey are usually macroscopic, supporting Keats' (1990) hypothesis that winter flounder show a preference for the largest available prey that can be consumed.

Predation patterns

The results of this study provide evidence that some prey species are consumed preferentially, but this was not temporally or spa-

Figure 2

Trends in the percent contribution of the burrowing anemone *Ceriantheopsis americanus* to total stomach volume of winter flounder, *Pleuronectes americanus*, compared to the anemone's percentage of the total benthic macrofaunal biomass at three sites in the New York Bight apex variably affected by sewage sludge disposal. Disposal gradually abated during 1987 and ceased by December 1987. tially consistent. The parallel temporal relationship of the contribution of the anemone C. americanus to overall benthic biomass and to winter flounder diets



at stations R2 and NY6 (Fig. 2) suggests a proportional consumption association. The forage ratio indices (K) for this prey are near zero (0.03 to 0.18,

Table 3); these suggest that winter flounder neither preferred nor avoided this prey, consuming it at a level closely related to its availability at these two stations. Although, this relation was more variable at station NY11 (Fig. 2), a moderately high, positive K value (0.63) suggests some preference for this prey (Table 3).

The proportional consumption differences (Fig. 3) and strong positive K values at each station for P. affinis (Table 3) strongly suggest that winter flounder have a preference for this prey. Heavy predation on P. affinis may be energetically advantageous to winter flounder because this species has a high caloric equivalence ($\bar{x} = 1.9$ Kcal/g wet weight; Steimle and Terranova, 1985). This is about double that of other major prey, which range from 0.9 to 1.1 Kcal/g wet weight, although some amphipod species, such as U. irrorata (consumed to a minor extent), are equally energy rich (Steimle and Terranova, 1985). The energy content of prey has been discussed as an important consideration in optimum foraging theories (Mangel and Clark, 1986) and the winter flounder preference for this high energy prey provides support for these theories. It is also possible that preference for this prey is related to the long-term dominance of P. affinis in the macrofauna of siltier areas of the New York Bight apex, as this relatively productive species has been common in the area and has been preyed upon since at least the mid-1960's (Steimle and Stone, 1973; Steimle, 1985, 1990; Steimle et al., 1990). This extended period of dominance may have contributed to winter flounder becoming experienced predators on this species (and other abundant prey species) and thus maintaining the preference (Gendron, 1987).

Figure 3

Trends in the percent contribution of the polychaete *Pherusa affinis* to total stomach volume of winter flounder, *Pleuronectes americanus*, compared to the polychaete's percentage contribution of the total benthic macrofaunal biomass at three sites in the New York Bight apex variably affected by sewage sludge disposal. 6 87

7

collection periods

8

9

10 11 12 1 2 3

------ stomach volume

4

56

5

70

60

50

40

30

20 10 0

8

86

9 10 11 12 1





Figure 5

benthic biomass

2 3 4

Trends in the frequency of occurrence of the amphipod Unciola irrorata in the diet of winter flounder, Pleuronectes americanus, compared to its numerical abundance in the benthic macrofaunal community at two stations in the New York Bight apex variably affected by sewage sludge disposal and its cessation in December 1987.

With the exception of *P. affinis* and perhaps C. irroratus, there is limited evidence of prey preference by winter flounder. This is consistent with the results of many qualitative winter flounder feeding studies that report a diverse diet, but also with limited evidence of a prey species' preferences (Tyler, 1972; Klein-MacPhee, 1978; Keats, 1990).

However, several dominant members of the benthic macrofaunal community at the three study stations were not commonly consumed by winter flounder. This underutilization may be related to prey size, burrowing depth, defense or escape mechanisms, or a variety of other factors (Main, 1985). For example, there was limited predation on C. lacteus, a major contributor to benthic biomass at station NY6. This nonproportional consumption or possible "avoidance" of this species is evident in the difference between the proportional consumption and abundance levels at this station (3.0% stomach volume vs. 45.3%

benthic biomass) and the strong negative K (-1.15; Table 3); this difference at NY6 was fairly consistent over the study period (Fig. 6). Proportional preda-



tion or slight underutilization of this prey was evident at the other stations where it was less abundant and K ranged from +0.08 to -0.40 (Table 3).

der, *Pleuronectes americanus*, compared to the rhynchocoel's percentage contribution to total benthic macrofaunal biomass at NY6, the station most affected by sewage sludge disposal and its cessation, in the New York Bight apex. The limited predation on *C. lacteus* could be re-

lated to its possession of defensive toxins in its tissues or to secretion of mucus that is strongly acidic, both of which can be offensive to potential predators (Kem, 1985; McDermott and Roe, 1985). Paradoxically, rhynchocoels are collected for fish bait in some areas and eaten by other fishes. It is possible, however, that this rhynchocoel's large size (>100 cm in length and >2 cm in width; Gosner, 1971), not its reported toxicity, is responsible for its limited use as prey for the small-mouthed winter flounder.

The underutilization of the small bivalve mollusc N. proxima (Table 3) is probably the result of its lack of availability as this species burrows into the sediment. The other molluscs common in the area, such as P. morrhuanus, A. islandica, Ilyanassa trivittata, and Ensis directus, are probably either too large or deeply buried to be suitable prey for winter flounder. However, N. proxima, as well as these other molluscs, except P. morrhuanus, were noted as prey in the diets of winter flounder elsewhere (Kurtz, 1975; Gilbert and Suchow, 1977; Klein-MacPhee, 1978; MacDonald et al., 1982; Worobec, 1982). The molluscan contribution to winter flounder diets in Narragansett Bay, Rhode Island, was also considered negligible (Bharadwaj, 1988).

Cessation of sewage sludge disposal

The cessation of sewage sludge disposal was expected to result in a substantial change in abundance of dis-

posal-sensitive species in the benthic macrofaunal community. Any macrofaunal changes because of cessation were expected to be reflected in some predation variables (Spies, 1984; Cross et al., 1985; Environmental Processes Division, 1988). However, the only significant changes in the benthic community detected after cessation from 1987 to 1990 were in the overall abundance of a few pollution-tolerant or pollution-sensitive taxa, such as the polychaete Capitella sp. or amphipods at station NY6, nearest to the former disposal area. The abundance of other dominant benthic species at NY6, such as P. affinis, N. incisa, and C. americanus, did not change to any significant degree (Reid et al., in press).

The pollution-tolerant Capitella sp. has been a consistent, but variably abundant (hundreds to tens of thousands of individuals/m²), member of the degraded benthic community at station NY6 since at least the early 1970's (Caracciola and Steimle, 1983). Its density in the macrofauna declined drastically (<100 individuals/m²) after the cessa-

tion of sewage sludge disposal (Reid et al., 1991). Predation by winter flounder on this prey is probably related to the response of *Capitella* sp. to cessation of disposal.

There were increases in abundance of contaminant-sensitive amphipods, especially Photis pollex and U. irrorata, at station NY6 after disposal abatement began in 1987. Although contributions of amphipods to winter flounder diets were generally less than 1% of total stomach volumes (and thus not included in Table 3), numerical increases in amphipod abundance in the macrofaunal community coincided with increases in their frequency of occurrence in winter flounder stomachs. The general increase in the numerical abundance of one amphipod, U. irrorata, in benthic samples at NY6, especially after cessation, was accompanied by a corresponding increase in their occurrence in winter flounder stomachs (Fig. 5). However, a similar predation relationship for this prey was somewhat evident at station NY11, which was minimally affected by sludge disposal and cessation (Fig. 5). At both stations, the frequency of occurrence of U. irrorata in the diets closely paralleled seasonal (winter-spring) peaks in abundance, including reduced predation during an apparently poor recruitment year at NY11 in 1988 (Fig. 5). If the effects of the sludge were more general and included some effect at NY11, the pattern of predation on this species, which increased in abundance after cessation, could be associated with this cessation.



Predation influence on benthic populations and energetics

Strong selective predation by winter flounder on certain benthic macrofaunal taxa can influence the population dynamics of these prey and be a factor in interpreting benthic community change relative to disposal abatement. This affect may be evident in the predation-abundance patterns for *Capitella* sp., although the decline in the abundance of this species could be a result of its short life span as well as predation.

A short life span is not a factor for *P. affinis* as it lives for up to two years (Steimle et al. 1990). However, since winter flounder are visual predators (Klein-MacPhee, 1978; Bharadwaj, 1988), P. affinis may be at greater risk to predation because it is relatively large (up to 7.5 cm in length and 0.5 cm in width) and lives in vertical burrows with its fanned, setaceous cephalic cage (head and bristles) usually exposed. It also actively probes the sediment surface with feeding palps that may attract predator attention (J. Vitaliano, personal observ.; P. Ferri¹). The persistent abundance and strong predation on P. affinis by winter flounder (Fig. 3) and other predators at station R2 (Steimle and Terranova, 1991; Steimle, in press) is interesting in that it suggests that this prey must be very productive in this area to sustain heavy predation pressure. This suggestion is supported by results of a previous study of the secondary production of this species that found it to be almost twice as productive near R2 as at NY6 and NY11 (Steimle et al., 1990).

The results of this study are subject to potential biases inherent in most stomach content analyses, such as differential digestion of different prey types (MacDonald et al., 1982). Partial digestion of prey can underestimate a prey's contribution to diets based on stomach volume. Thus, the estimated proportional contribution to diets of some soft-bodied prey will be conservative. This study also assumes that the stomach contents of fish represented feeding at or very near where the benthic infauna samples were collected (Steimle, in press) and that if a large proportion of the prey was consumed in nearby areas, the benthic community structure did not differ substantially from that at the actual benthic collection site. Some preliminary data from peripheral benthic stations sampled during the study suggest that this assumption was valid, although there were substantial changes in community structure in some parts of the trawling zones (Fromm, personal observ.).

In summary, diets of winter flounder in the New York Bight apex 1) were dominated by a few prey species, typically polychaetes, an anthozoan, and small crustaceans; 2) showed a preference for the energy-rich polychaete *Pherusa affinis*; 3) suggested there was underutilization or "avoidance" of molluscs and rhynchocoels; and 4) showed that apparent responses of some benthic macrofaunal species (*Capitella* sp. and *U. irrorata*) to cessation of sludge disposal and natural fluctuations in abundance were reflected in corresponding changes in their use as prey.

Acknowledgments

We thank S. Fromm, C. Zetlin, and R. Koch for their contribution to data processing and graphics, and D. Packer, S. Chang, D. Mountain, and others for helpful comments and suggestions.

Literature cited

Berg, J.

1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). Mar. Biol. 50:263-273.

Bharadwaj, A.

1988. The feeding ecology of the winter flounder, *Pseudopleuronectes americanus* (Walbaum), in Narragansett Bay, Rhode Island. M.S. thesis, Univ. Rhode Island, Kingston, RI, 129 p.

Bowman, R. E.

- 1986. Effects of regurgitation on stomach content data of marine fishes. Environ. Biol. Fish. 16:171–181.
- Caracciola, J. V., and F. W. Steimle.

1983. An atlas of the distribution and abundance of dominant benthic invertebrates in the New York Bight apex with reviews of their life histories. NOAA Tech. Rep. NMFS SSRF-766, 58 p.

- Clements, W. H., and R. J. Livingston.
 - **1982.** Overlap and pollution-induced variability in the feeding habits of filefish (Pisces: Mona-canthidae) from Apalachee Bay, Florida. Copeia 2:331-338.
- Cross, J. N., J. Roney, and G. S. Kleppel.

1985. Fish food habits along a pollution gradient. Calif. Fish Game 71:28–39.

- Diehl, S.
 - **1992.** Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology 73:1646-1661.

Environmental Processes Division.

1988. Plan for study-response of habitat and biota of the inner New York Bight to abatement of sewage sludge dumping. NOAA Tech. Memo. NMFS F/NEC-55, 34 p.

¹ Ferri, P., U.S. Environmental Protection Agency, Narragansett, RI 02882. Personal Commun., 1992.

Gendron, R. P.

- 1987. Models and mechanisms of frequency-dependent predation. Am. Nat. 130:603-623.
- Gilbert, W. H., and E. F. Suchow.
 - 1977. Predation by winter flounder (*Pseudopleur-onectes americanus*) on the siphons of the clam, *Tellina agilis*. Nautilus 91:16-17.

Gosner, K. L.

1971. Guide to identification of marine and estuarine invertebrates, Cape Hatteras to the Bay of Fundy. Wiley-Interscience, NY, 693 p.

Hacunda, J. S.

1981. Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine. Fish. Bull. 79:775-788.

Hyslop, E. J.

1980. Stomach contents analysis—a review of methods and their application. J. Fish. Biol. 17:411–423.

Keats, D. W.

1990. Food of winter flounder *Pseudopleuronectes americanus* in a sea urchin dominated community in eastern Newfoundland. Mar. Ecol. Prog. Ser. 60:13-22.

Kem, W. R.

1985. Structure and action of nemertean toxins. Am. Zool. 25:99-111.

Klein-MacPhee, G.

1978. Synopsis of biological data for the winter flounder, *Pseudopleuronectes americanus* (Walbaum). NOAA Tech. Rep. NMFS Circ. 414, 43 p.

Kurtz, R. J.

1975. Stomach content analysis in relation to differences in growth rate of winter flounder (*Pseudopleuronectes americanus*) from two Long Island Bays. M.S. thesis, Long Island Univ., Greenvale, NY, 60 p.

Langton, R. W., and R. E. Bowman.

1981. Food of eight northwest Atlantic pleuronectiform fishes. NOAA Tech. Rep. SSRF-749, 16 p.

Langton, R. W., B. M. North, B. P. Hayden,

and R. E. Bowman.

1980. Fish food habits studies—sampling procedures and data processing methods utilized by the Northeast Fisheries Center, Woods Hole Laboratory, USA. Int. Counc. Explor. Sea, C. M. 1980/ L:61, 16 p.

Levings, C. D.

1974. Seasonal changes in feeding and particle selection by winter flounder (*Pseudopleuronectes americanus*). Trans. Am. Fish. Soc. 103:828-832.

MacDonald, J. S., K. G. Waiwood, and R. H. Green.

1982. Rates of digestion of different prey in Atlantic cod (Gadus morhua), ocean pout (Macrozoarces americanus), winter flounder (Pseudopleuronectes americanus) and American plaice (Hippoglossoides platessoides). Can. J. Fish. Aquat. Sci. 39:651-659.

Main, K. L.

1985. The influence of prey identity and size on se-

lection of prey by two marine fishes. J. Exp. Mar. Biol. Ecol. 88:145–152.

- Mangel, M., and C. W. Clark.
 - **1986.** Towards a unified foraging theory. Ecology 67:1127–1138.

McDermott, J. J., and P. Roe.

1985. Food, feeding behavior and feeding ecology of nemerteans. Am. Zool. 25:113–125.

Packer, D., T. Finneran, L. Arlen, R. Koch, S.

Fromm, J. Finn, S. A. Fromm, and A. Draxler.
In. Press. Fundamental and mass properties of surficial sediments in the inner New York Bight and responses to the abatement of sewage sludge dumping. In A. Studholme, J. E. O'Reilly, and M. C. Ingham (eds.), Effects of the cessation of sewage sludge dumping at the 12-mile site. NOAA Technical Rep. NMFS.

Pihl, L., S. P. Baden, R. J. Diaz,

and L. C. Schaffner.

1992. Hypoxia-induced structural changes in the diets of bottom-feeding fish and Crustacea. Mar. Biol. 112:349-361.

Rachlin, J. W., A. Pappantoniou,

and B. E. Warkentine.

1987. A bias estimator of the environmental resource base in diet preference studies with fish. J. Freshwater Ecol. 4:23-31.

Reid, R., D. Radosh, A. Frame, and S. Fromm.

1991. Benthic macrofauna of the New York Bight, 1979–89. NOAA Tech. Rep. NMFS 103, 50 p.

Reid, R., S. Fromm, A. Frame, D. Jeffress,

J. Vitaliano, D. Radosh, and J. Finn.

In press. Limited responses of benthic macrofauna and selected sewage sludge components to phaseout of sludge dumping in the inner New York Bight. In A. Studholme, J.E. O'Reilly, and M.C. Ingham (eds.), Effects of the cessation of sewage sludge dumping at the 12-mile site. NOAA Technical Rep. NMFS.

Robins, C. R., R. M. Bailey, C. E. Bond,

J. R. Brooker, E. A. Lachner, R. N. Lea,

and W. B. Scott.

1991. Common and scientific names of fishes from the United States and Canada (5th ed.). Am. Fish. Soc. Spec. Publ. 20.

Schindler, D. W.

1987. Detecting ecosystem responses to anthropogenic stress. Can. J. Fish. Aquat. Sci. 44 (Suppl.1): 6-25.

Spies, R.

1984. Benthic-pelagic coupling in sewage-affected marine ecosystems. Mar. Environ. Res. 13:195– 230.

Steimle, F.

- **1985.** Biomass and estimated productivity of the benthic macrofauna in the New York Bight: a stressed coastal area. Estuarine Coastal Shelf Sci. 21:539-554.
- 1990. Benthic macrofauna and habitat monitoring on the continental shelf of the northeastern United

States. I: Biomass. NOAA Tech. Rep. NMFS 86, 28 p.

Steimle, F. W.

In press. Effects of sewage sludge disposal abatement on winter flounder, red hake, and lobster feeding and diets in the New York Bight Apex. In A. Studholme, J. E. O'Reilly, and M. C. Ingham (eds.), Effects of the cessation of sewage sludge dumping at the 12-mile site. NOAA Technical Rep. NMFS.

Steimle, F. W., and R. B. Stone.

1973. Abundance and distribution of inshore benthic fauna off southwestern Long Island, N.Y. NOAA Tech. Rep. NMFS SSRF-673, 50 p.

Steimle, F. W., and R. Terranova.

- 1985. Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. J. Northwest Atl. Fish. Sci. 6:117-124.
- 1991. Trophodynamics of select demersal fishes in the New York Bight. NOAA Tech. Memo. F/NEC-84, 11 p.

Steimle, F. W., P. Kinner, S. Howe, and W. Leathem.

1990. Polychaete population dynamics and production in the New York Bight associated with variable levels of sediment contamination. Ophelia 31:105-123.

Tyler, A. V.

- 1972. Food resource division among northern, marine, demersal fishes. J. Fish. Res. Board Can. 29:997–1003.
- Wells, B. D., D. H. Steele, and A. V. Tyler.

1973. Intertidal feeding of winter flounder (*Pseudopleuronectes americanus*) in the Bay of Fundy. J. Fish. Res. Board Can. 30:1374–1378.

- Wilk, S., R. Pikanowski, A. Pacheco, D. MacMillan, and L. Stehlik.
 - 1992. Response of fish and megainvertebrates of the New York Bight apex to the abatement of sewage sludge dumping. NOAA Tech. Memo. NMFS F/ NEC-90, 78 p.

Worobec, M. N.

- **1982.** Field analysis of winter flounder *Pseudopleuronectes americanus* in a coastal pond: abundance, daily ration, and annual consumption. Ph.D. thesis, Univ. Rhode Island, Kingston, RI, 115 p.
- Zdanowicz, V. S., S. L. Cunneff, and T. W. Finneran.
 In press. Reductions in sediment metal contamination in the New York Bight apex with the cessation of sewage sludge dumping. In A. Studholme, J. E. O'Reilly, and M. C. Ingham (eds.), Effects of the cessation of sewage sludge dumping at the 12-mile site. NOAA Technical Rep. NMFS.