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Planktonic hydroids on Georges Bank: ingestion and selection by predatory fishes☆

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Abstract

Planktonic colonial hydroids (*Clytia gracilis*) recently have been found to be abundant, but patchily distributed in time and space, on Georges Bank, northwest Atlantic Ocean. However, the processes regulating the occurrence of these hydroid colonies (i.e., seasonality, growth, advection, diffusion, sinking, and predation) are not well understood. The objective of this study was to identify and quantify the potential role of predation by fish upon the unattached hydroids. The two components of this study were (i) analyses of historical fish trawl surveys and stomach contents data collected in the coastal northwest Atlantic Ocean (including Georges Bank), and (ii) laboratory experiments testing for the presence of selective feeding by juvenile cod (*Gadus morhua*) on hydroids relative to two co-occurring planktonic copepods (*Calanus finmarchicus* and *Centropages hamatus*). We found that 32 and 11 species of fish ingested hydroids in the coastal northwest Atlantic Ocean and Georges Bank, respectively, during 1973–1990. However, hydroids were rarely an important part of the diet of these fishes. The most important predator of these cnidarians on Georges Bank was winter flounder, with 28.0% of its population having ingested hydroids, with a mean % (by weight) of hydroids in the diet of 4.1%, during 1973–80. Laboratory experiments indicated juvenile cod ingested planktonic hydroids, but overwhelmingly preferred either of the two copepods as prey. While field and laboratory results indicated that a wide variety of fishes feed on hydroids, we concluded that emergences and disappearances of planktonic hydroids on Georges Bank are not greatly impacted by fish predation. Other factors, in particular physical processes (i.e., advection, diffusion, and sinking), seasonal cycles of activity and inactivity, and predation by invertebrates, should be examined. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

It has recently been noted (Madin et al., 1996, 1997; Sullivan et al., 1997) that *Clytia gracilis*, a planktonic leptothecate hydroid, occurs sporadically, but in very high abundance (10–25 individuals l^{-1}) in the vicinity of Georges Bank, northwest Atlantic Ocean. These organisms can have a significant impact as competitors, and perhaps even predators, on larval Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). For instance, *C. gracilis* was estimated to remove up to 40 % of the daily production of copepod nauplii in the central, well-mixed shoal ($\leqslant$ 60 m) portion of the Bank during late spring (Madin et al., 1996, 1997). However, the life history of these planktonic hydroids, and especially the processes responsible for their seasonal occurrence on Georges Bank, are not well understood.

Although most hydroids are attached to firm substrates, a few species occur as individuals or colonies in the plankton (Fraser, 1944). In the western North Atlantic, planktonic hydroids have frequently been observed on Georges Bank (Bigelow, 1915; Fraser, 1915; Madin et al., 1996, 1997; Sullivan et al., 1997, Concelman et al., 2001). For instance, Bigelow (1915), based on the observations of Fraser (1915), stated: "At the station on the northwest side of Georges Bank, a rather surprising discovery was made, namely that the surface water was full of campanularian hydroids (*Obelia*) broken from their attachments, and many of them entirely regenerated". Earlier, another species had been reported floating in waters of the North Sea (van Breeman, 1905, as *Clytia pelagica*). It is not unusual to find hydroids that have torn from their substrate and lived on their own for a short period, but in the case of *C. gracilis*, the hydroid studied by Fraser (1915, as *Clytia cylindrica*), the hydroid colonies had grown and regenerated without attachment. *C. cylindrica* had rounded rather than broken ends on the colony and was in most cases free of any stolon material, having produced a zooid in its place. In addition, these free-living hydroids had well-developed hydranths, some that had recently fed, and gonangia that were releasing medusae.

More recently, *C. gracilis* has been found to be patchily distributed, both temporally and spatially, in the vicinity of Georges Bank (Madin et al., 1996, 1997; Sullivan et al., 1997), with peak abundances occurring in the late-spring to early-summer in the central region of the bank. Perhaps the only other historical data on planktonic hydroids on Georges Bank are those collected from 1939 to 1941 by Clarke and Bumpus on the R/V *Atlantis*; these data indicate that planktonic hydroids were absent from September 1939 to March 1940, present from April 1940 to June 1940, then absent again from March to June 1941 (Concelman et al., 2001). However, as noted above, the mechanisms responsible for these sporadic occurrences are not known. It has been postulated (Madin et al., 1996) that benthic disturbances, such as storms, heavy wave action, or perhaps even bottom trawling, may break off the hydroid colonies and introduce them into the water column; and that their disappearance may be the result of lateral advection and diffusion (Concelman et al., 2001), sinking (Sullivan et al., 1997), predation or temperature-dependent seasonal cycles of activity and inactivity (Calder, 1990).

This report concentrates on identifying and quantifying the potential role of predation by fish upon the colonial, stalked hydroids. Predation on hydroids has not been well studied. In a recent review of hydroid ecology, Gili and Hughes (1995) state that "Turbellarians, aplacophorans, gastropods, polychaetes, and pycnogonids are some of the preferential consumers of cnidarians … …fishes may also feed on hydroids incidentally". These comments seem to refer primarily (or exclusively) to benthic hydroids. There are two components to the current study. First is an analysis of historical fish trawl survey data and stomach contents data collected between 1973 and 1990 in the coastal northwest Atlantic Ocean (including Georges Bank). This analysis is intended to demonstrate which fishes prey upon planktonic hydroids in nature. The second component is a laboratory study testing for the presence of selective feeding by juvenile cod (*G. morhua*) on hydroids relative to two alternate, co-occurring prey: the planktonic copepods *Calanus finmarchicus* and *Centropages hamatus*.

2. Methods

2.1. Field study

Bottom trawl surveys were conducted from 1973 to 1990 in the continental shelf waters of the northwestern Atlantic from Cape Fear, North Carolina to Browns Bank, Nova Scotia (Fig. 1) by the Northeast Fisheries Science Center (NEFSC), National Marine Fisheries Service (NMFS),

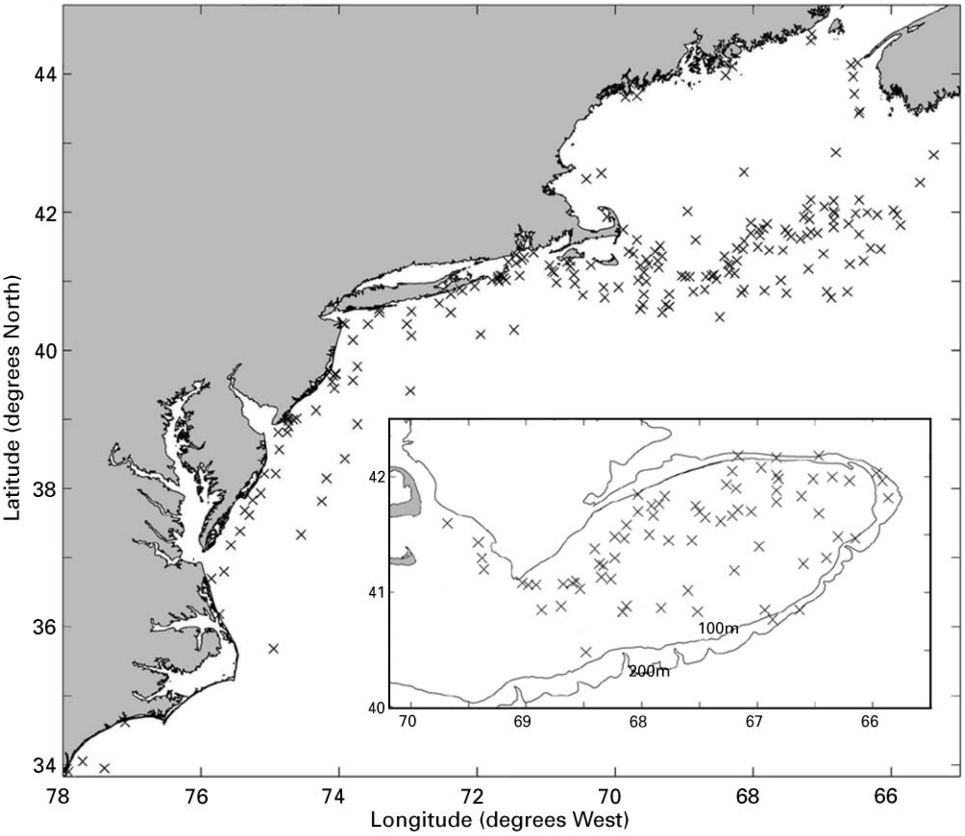

Fig. 1. Occurrences of fish stomachs containing hydroids (X) along the coastal northwest Atlantic Ocean and Georges Bank (inset; 100 and 200 m isobaths as shown) during 1973–90.

National Oceanic and Atmospheric Administration (NOAA). Detailed descriptions of collection and sample processing can be found in Bowman and Michaels (1983) and Azarovitz et al. (1985), but are summarized below. Although there was some variation in the type of otter trawl deployed, all nets were equipped with 13-cm-mesh cod ends and towed for 30 min at 3.5 kt ($7\,\mathrm{m\,s^{-1}}$). Trawls were taken using a stratified-random sampling design with bottom depths ranging from 3 to 400 m (Azarovitz et al., 1985). Fish were then sub-sampled from the trawl with a two-stage (juvenile; adult) cluster sampling design; up to 10 fish of each species in a length (stage) class were selected at random to be analyzed for stomach contents.

During 1973–80, 40,077 fish stomachs were preserved and then processed in an onshore laboratory; stomach contents were wet weighed to the nearest 0.01 g, divided into taxonomic categories, and then re-weighed (Bowman and Michaels, 1983). In these samples, invertebrates were more accurately identified to lower taxonomic levels. During 1981–90, stomachs from 83,693 fish were collected; individual stomach contents were analyzed onboard the vessel and were estimated to the nearest volume of $0.1\,\mathrm{cm}^3$. The 1981–90 samples focused on the piscivorous fishes and stomach contents were more coarsely classified, with contents less likely to be identified to lower taxonomic levels (e.g., hydroids).

Those stomachs containing class Hydrozoa, excluding order Siphonophora, were deemed by us to contain hydroids. However, the data do not distinguish between benthic or planktonic forms. Nevertheless, our analysis should provide a first-order estimate of which fishes serve as important predators on hydroids. Percent of diet consisting of hydroids (by weight and volume) was calculated for each species by averaging all fishes of the same species from a given net.

Because of the slightly different methods of processing samples in the field studies during 1973–80 versus 1981–90, we present data from these two periods separately. Likewise, we have separated the data sets into the larger and more general “coastal northwest Atlantic Ocean” (including Georges Bank), to give the broadest possible coverage, and the smaller, more specific “Georges Bank”, the area over which planktonic hydroids have been noted to be particularly abundant (Madin et al., 1996, 1997; Sullivan et al., 1997; Concelman et al., 2001). We have defined Georges Bank as the area between 40 and 42.5°N and 65.5 and 70°W and less than 200 m bottom depth (NMFS sampling strata 13–23 and 25).

2.2. Laboratory feeding experiments

A series of three replicated experiments was conducted to assess the feeding selection of juvenile Atlantic cod (*G. morhua*) on planktonic hydroids and two planktonic copepods (*C. finmarchicus* and *C. hamatus*) known to be abundant and co-occurring on Georges Bank (Davis, 1987). In addition, several control experiments were run to estimate the loss of hydroids due to handling and cannibalism. In general, these experiments followed the standard protocols for discerning planktivore selection between two prey types (e.g., Bollens and Frost, 1991; Bollens et al., 1993; and references therein). Thirteen juvenile Atlantic cod (*G. morhua*), ranging in size from 47 to 59 mm, were provided by the University of Rhode Island (URI) where they were hatched and reared in a flow-through tank system (12°C) and fed fish pellets, *Artemia* nauplii, and frozen *C. finmarchicus*. Fish were transported from URI to the Woods Hole Oceanographic Institution where they were kept in two 40-l tanks in a 12°C environmental chamber. Approximately half of the water of each tank was replaced daily with 45 μm filtered seawater. A mixture of frozen *C. finmarchicus* and wild plankton collected from Dyers Dock, Woods Hole, MA (predominantly *Acartia* spp., *Temora* spp. and *Centropages* spp.) was fed to the fish three times per day (c. 0.5 g per tank per feeding). The night before an experiment, two fish were removed from each of the two holding tanks, placed in two 40-l experimental tanks, and starved for 12–16 h.

The first experiments consisted of placing 50 *C. gracilis* colonies that had been grown in culture into each of two tanks in each of two separate experiments. The mean number of feeding and "budding" (having not yet fully developed tentacles) hydranths per colony was assessed ($\bar{x} = 5.6$ hydranths). Before the hydroids were added to the tank, a wet weight for the combined 50 hydroid colonies was measured, yielding a mean weight per colony of 505 μg or c. equal to that of an adult *C. finmarchicus* (Davis, 1987).

Upon the addition of prey, fish feeding behaviors were continuously monitored and enumerated for the first hour and the first 10 min of each subsequent hour. Behaviors were classified as (i) ingestion, (ii) rejection (i.e., when the prey was spit out after being attacked) or (iii) approach only (i.e., when an actively searching fish approaches, but does not ingest a prey). The tanks were stirred approximately every 10 min during the first hour, and once per hour thereafter, to resuspend the hydroids. Observations continued until the strikes numbered 75% of the initial prey count (to protect against the ingestion of all prey) or for 7 h, whichever came first. At the conclusion of the experiment, fish were removed and standard length measured to the nearest 0.1 cm. The water from each experimental tank was siphoned through a 250-μm sieve and the prey counted under a dissecting microscope. Missing prey were assumed to have been consumed by the fish.

In the second set of experiments, a mixed-prey assemblage was offered to the cod (*G. morhua*) consisting of: (i) 50 hydroid colonies, as described above, and (ii) either 40 *C. finmarchicus*, stage V copepodites, or 50 *C. hamatus* adult females. *C. finmarchicus* were captured on Georges Bank (41°16′N, 68°36′W) for the first experiment and off Gay Head, Martha's Vineyard (41°19′N, 70°53′W) for the second experiment. *C. hamatus* were caught from Dyers Dock, Woods Hole, MA. In both experiments, strikes on prey were noted as described above. Because the fish consumed nearly all of the *C. finmarchicus* before the first hour had elapsed, this experiment was terminated after 1 h. The strikes upon *C. hamatus* were slightly less frequent and this experiment was run for 2 h. At the end of each experiment, remaining hydroid colonies and copepods were counted as described above.

3. Results and discussion

In the coastal northwest Atlantic Ocean during 1973–80, 31 different species of fishes were observed to have ingested hydroids (Fig. 2). However, only 5 species from this eight-year period included greater than 10 individuals: winter flounder, (*Pseudopleuronectes americanus*, 165 of 1545), spiny dogfish (*Squalus acanthias*, 19 of 2367), winter skate (*Raja ocellata*, 16 of 640), red hake (*Urophysis chuss*, 15 of 1881) and haddock (*M. aeglefinus*, 14 of 1978). Species whose diets consisted of a larger fraction of hydroids (in terms of mean % of stomach content by weight) often had only a few individual specimens with hydroids in the diet; these species included spottail pinfish (*Diplotus holbrooki*, 7.38%, $n = 6$), scup (*Stenotomus caprinus*, 0.89%, $n = 68$), Atlantic croaker (*Micropogon undulatus*, 0.44%, $n = 242$), spiny dogfish (0.24%, $n = 2367$), butterfish (*Peprilus*

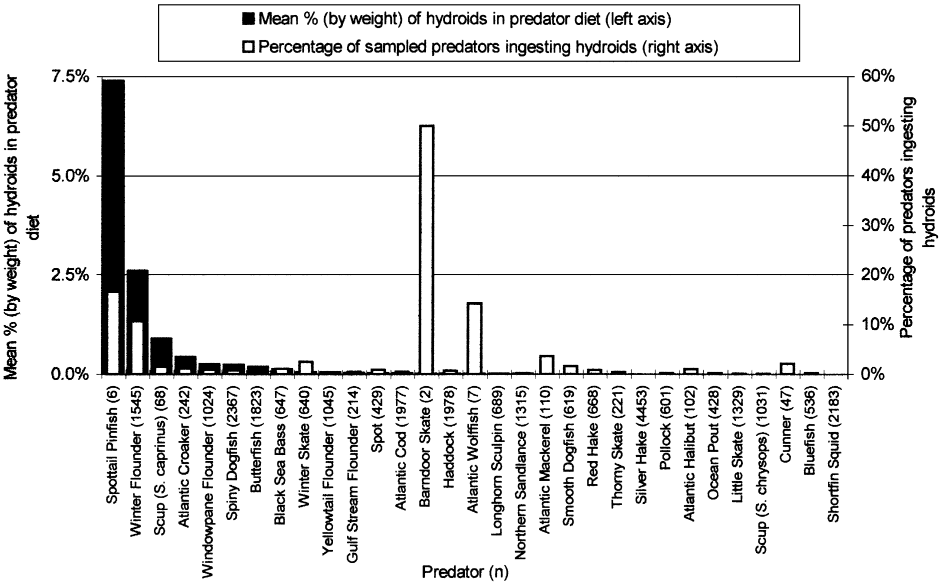

Fig. 2. Percentage of each fish population (n = number of stomachs sampled) ingesting hydroids and mean % (by weight) of hydroids in predator diets along the northwest Atlantic coast, 1973–80.

triacanthus, 0.19%, $n = 1823$), and black sea bass (*Centropristis striata*, 0.13%, $n = 647$); all other fish in the coastal northwest Atlantic Ocean during 1973–80 had less than 0.1% hydroids.

On Georges Bank during 1973–80, 11 species of fishes were found to have ingested hydroids (Fig. 3), although only 5 species included more than a few individuals: winter flounder (94 of 336), winter skate (14 of 564), haddock (11 of 665), red hake (10 of 401), and spiny dogfish (9 of 693). Hydroids as a mean % (by weight) of stomach contents were greatest in winter flounder (4.07%, $n = 336$) and windowpane flounder (1.29%, $n = 85$); all other species on Georges Bank during 1973–80 had diets of less than 0.10% hydroids.

In the coastal northwest Atlantic Ocean during 1981–90, 8 different species of fish, of which 7 were also found in the 1973–80 data set, were observed to have ingested hydroids (Fig. 4). The most numerous were winter flounder (23 of 1040), spiny dogfish (4 of 19620), and scup (*Stenotomus chrysops*, 2 of 380). The species whose diets were highest in hydroids (% of stomach content by volume) were winter flounder (0.58%, $n = 1040$) and scup (*S. chrysops*, 0.43%, $n = 380$). All other species had less than 0.05% hydroids in their diet.

On Georges Bank during 1981–90, there were only 2 species of fish found to have ingested hydroids: pollock (1 of 483) and spiny dogfish (3 of 4832); mean % (by volume) of hydroids in these fishes' diets were 0.10 and 0.05%, respectively (Fig. 5).

Although there was large variation between species, hydroids were rarely a frequently occurring or abundant component of the diets of fish on Georges Bank or the northwest coastal Atlantic Ocean. These results may provide clues as to how the fishes were ingesting the hydroids and whether or not the predation was incidental or targeted. Higher values for hydroids as % of diet

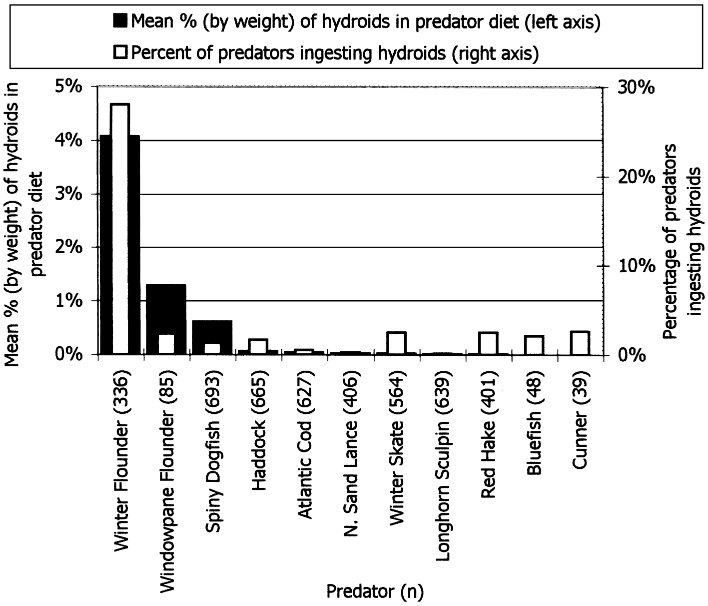

Fig. 3. Percentage of each fish population (n = number of stomachs sampled) ingesting hydroids and mean % (by weight) of hydroids in predator diets on Georges Bank, 1973–80.

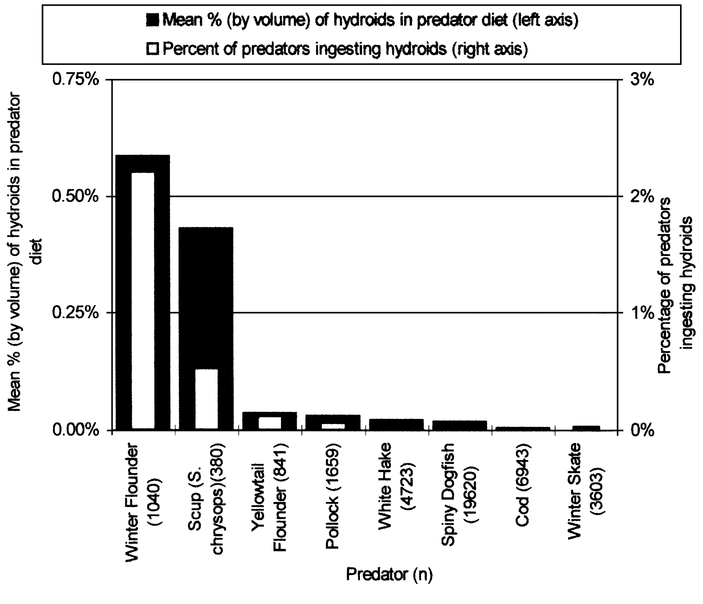

Fig. 4. Percentage of each fish population (n = number of stomachs sampled) ingesting hydroids and mean % (by volume) of hydroids in predator diets along the northwest Atlantic coast, 1981–90.

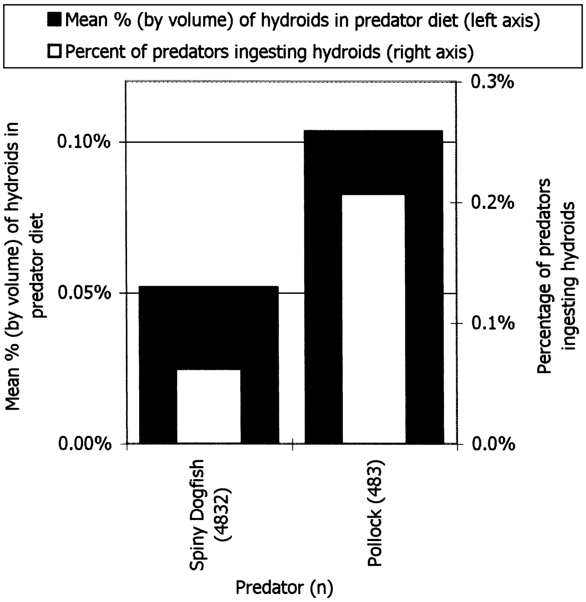

Fig. 5. Percentage of each fish population (n = number of stomachs sampled) ingesting hydroids and mean % (by volume) of hydroids in predator diets on Georges Bank, 1981–90.

may indicate that the hydroids were targeted prey items (e.g., spottail pinfish, Fig. 2). Conversely, lower values may indicate that the hydroids were being only incidentally ingested, perhaps because predators were filter feeding (e.g., Atlantic mackerel, Fig. 2) or targeting other prey, such as amphipods, that reside within the (perhaps benthic) hydroid colonies. Our results suggest that when hydroids were present in the diet, incidental ingestion was the norm.

Small sample size, of course, can confound the issue, e.g., barndoor skate, spottail pinfish, and Atlantic wolffish, in which sample sizes are less than 8 (Fig. 2). Nevertheless, it seems clear that while the occasional fish may ingest a large number (%) of hydroids, rarely does any given species show a significant dependence on hydroids as a major food source. Winter flounder on Georges Bank, 1973–80, may be the extreme case, but even here only 28% of the population contained hydroids, and only 4% of the diet (by weight) consisted of hydroids. Moreover, this may be an overestimate of feeding on planktonic stalked hydroids — recall that the stomach content analyses did not distinguish between the different morphological stages of hydroids, nor for that matter, between different species of hydrozoans.

An obvious question arises as to whether smaller fish are disproportionately choosing hydroids compared to larger fish. In examining the 14 fish species with greater than one individual ingesting hydroids, there was no statistically significant trend in the percentage of the diet consisting of hydroids versus fish size (e.g., winter flounder, Fig. 6).

In the laboratory experiments, predation on hydroids was very low when the fish were presented with only hydroids (Table 1). No more than 15% of the hydroids were consumed at the completion of the experiment. When hydroids were first introduced into the tank, the fish investigated and often ingested them, but in most cases the hydroids were spit out a second or two later, perhaps due to the release of nematocysts by the hydroids. As each experiment progressed, the fish became

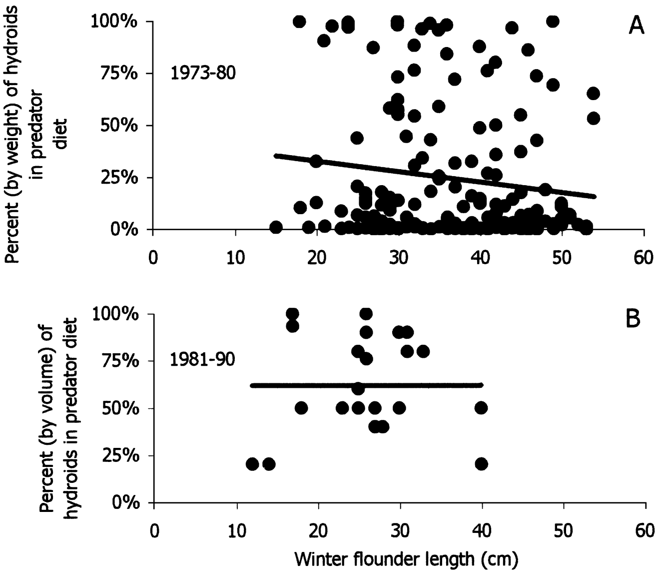

Fig. 6. Linear regressions showing non-significant relationships between winter flounder length and % of hydroids in diet: (A) 1973–80 (contents by weight), $y = -0.005x + 0.429, R^2 = 0.0194$; and (B) 1981–90 (contents by volume), $y = 9E - 05x + 0.619, R^2 = 8\mathrm{E} - 06$.

Table 1
Hydroid colonies consumed by *Gadus morhua* in the single-prey experiment

Replicate	Tank	Hydroids	Hydroids consumed	% hydroids consumed[a]
1	A	50	6	9
	B	50	8	13
	A + B	100	14	11
2	A	50	0	0
	B	50	6	9
	A + B	100	6	3
Total		200	20	7

[a] The percentage of hydroids consumed has been corrected for the estimated 3% loss due to handling.

increasingly disinterested in the hydroids and ignored them altogether as the hydroids settled to the bottom of the tank. This pattern of activity repeated itself with each stirring of the hydroids off the bottom; interest remained low throughout the remainder of each experiment.

In both mixed-prey experiments, in which the fish were presented with hydroids and either *C. finmarchicus* or *C. hamatus*, the copepods were overwhelmingly the preferred prey ($p < 0.01$;

Table 2
Percentages of hydroids and *Calanus finmarchicus* consumed by *Gadus morhua* in mixed-prey predation experiments. Probability (p) values based upon binomial distribution (Sokal and Rohlf, 1981)

Replicate	Tank	Hydroids consumed[a] (%)	Copepods consumed (%)	p
1	A	1	100	< 0.01
	B	11	88	< 0.01
	A + B	6	94	< 0.01
2	A	21	100	< 0.01
	B	7	100	< 0.01
	A + B	14	100	< 0.01
Total		10	97	< 0.01

[a] The percentage of hydroids consumed has been corrected for the estimated 3% loss due to handling.

Tables 2 and 3). In addition, fish feeding activity was high only when copepods were present; once copepod numbers declined, fish searching and striking behaviors decreased dramatically.

The laboratory prey selection experiments indicate that juvenile Atlantic cod, *G. morhua*, does not target the stalked hydroids, either suspended or settled on the bottom, even though the hydroids were of the same approximate wet weight as the much preferred copepods. The field study results corroborate this, since only 1% of the cod population preyed on hydroids, and hydroids comprised no more than 0.02% of cod stomach contents. Indeed, semi-demersal or pelagic fishes (e.g., Atlantic cod, pollock, and hake) generally do not seem to target the hydroids.

The only fish that had a substantial percentage ($> 10\%$) of its population ingesting hydroids was winter flounder. However, this fish is an omnivorous predator, usually preying upon epibenthic amphipods, cumaceans, and polychaetes (Levings, 1974; Klein-MacPhee, 1978; Steimle et al., 1994), suggesting that they might be ingesting the benthic rather than the pelagic forms of hydroids.

In summary, based on the field and laboratory experimental data reported here, we conclude that hydroids are consumed by a wide variety of fishes in the coastal NW Atlantic Ocean and on Georges Bank. However, planktonic hydroids are not a preferred prey and are probably not significantly impacted by fish predators. Thus, we conclude that loss (mortality) terms other than fish predation are the causes for the periodic declines in populations of planktonic hydroids on Georges Bank, as well as their near absence elsewhere in the NW Atlantic. In particular, we point to physical processes — namely advection, diffusion, and sinking as potentially more important. Although sinking rates of 0.03–0.3 $\mathrm{cm\,s^{-1}}$ (26–260 $\mathrm{m\,d^{-1}}$) have been presented by Sullivan et al. (1997), the physical loss terms in the population dynamics of planktonic hydroids on Georges Bank are largely unstudied. Alternatively, temperature-dependent seasonal cycles of hydroid occurrences, such as has been noted by Calder (1990), could explain the seasonal abundance patterns. Predation by invertebrates, as found to be important in similar-sized planktonic organisms such as

Table 3
Percentages of hydroids and *Centropages hamatus* consumed by *Gadus morhua* in mixed-prey predation experiments. Probability (*p*) values based upon binomial distribution (Sokal and Rohlf, 1981)

Replicate	Tank	Hydroids consumed[a] (%)	Copepods consumed (%)	*p*
1	A	5	70	< 0.01
	B	13	76	< 0.01
	A + B	9	73	< 0.01
2	A	3	96	< 0.01
	B	53	98	< 0.05
	A + B	28	97	< 0.01
Total		19	85	< 0.01

[a] The percentage of hydroids consumed has been corrected for the estimated 3% loss due to handling.

larval fishes (e.g., Bailey and Houde, 1989) and copepods (e.g., Davis, 1984), also should be studied. Examination of these processes will require more field observations and the use of coupled biological–physical models such as those currently being developed under the aegis of GLOBEC (e.g., Werner et al., 1993, 1996; Lynch et al., 1998).

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