

The Feeding Ecology of Flatfish in the Northwest Atlantic

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Abstract

Flatfish are an economically and ecologically important component of continental shelf ecosystems worldwide. These species are impacted from fishing activities, both as direct targets and through indirect effects on habitat and food supply. We examined 25 years of diet data for juveniles and adults of nine species of flatfish in the Northwest Atlantic on the continental shelf off of the USA and parts of Canada in order to understand how flatfish feeding ecology may have changed after decades of fishing and related impacts on the ocean bottom. Atlantic halibut (*Hippoglossus hippoglossus*), summer flounder (*Paralichthys dentatus*) and fourspot flounder (*P. oblongus*) were generally piscivorous. American plaice (*Hippoglossoides platessoides*) ate primarily ophiuroids. Yellowtail flounder (*Limanda ferruginea*), winter flounder (*Pseudopleuronectes americanus*), windowpane (*Scophthalmus aquosus*), witch flounder (*Glyptocephalus cynoglossus*) and gulfstream flounder (*Citharichthys arctifrons*) ate primarily polychaetes, gammarids and other benthic invertebrates. American plaice, summer flounder and fourspot flounder exhibited significant ontogenetic shifts in diet, consuming fewer polychaetes with increasing size. Summer and fourspot flounder also exhibited significant shifts in diet across the time series. None of the benthivorous flatfish exhibited significant changes in diet composition across the time series. The mean weight of stomach contents declined in all species over the past 20 years. The role of flatfish trophic dynamics is discussed in the context of major changes that have occurred in this continental shelf ecosystem.

Keywords: trophic ecology, predator-prey interactions, Northeast continental shelf, benthic habitat, flounder, diet.

Introduction

Flatfish are an economically and ecologically important component of continental shelf ecosystems worldwide. Flatfish comprise a large portion of global fishery landings, accounting for over one million metric tons per year for the past several decades (Garcia and Newton, 1997; FAO, 1998). United States landings of flatfish during 1999 were valued at nearly \$90 million (NMFS, 2000). Flatfish are also important predators in benthic communities. Studies from the Bering Sea/Gulf of Alaska (Livingston, 1993; Yang, 1995) have shown that flatfish primarily consume benthic invertebrates, with some larger, wider-gaped species being almost entirely piscivorous. Other examples from the Kamchatkan Peninsula (Russia; Orlov, 1997), New Zealand waters (Livingston, 1987), the Baltic Sea (Aarnio *et al.*, 1996), the Mediterranean Sea (de Morais and Bodiou, 1984), the North Sea (Kaiser and Ramsay, 1997) and Canadian/American

Atlantic waters (Methven, 1999) are consistent with this global pattern. Flatfish serve as a major energy pathway for conversion of benthic production into a form suitable for human consumption.

The flattened body, robust body shape, pale underside, and binocular topside (Fig. 1) make these fish well adapted to living in benthic environments. Because of the benthic affinity of flatfish, in addition to effects from directed fisheries, these species are highly susceptible to perturbations to the ocean bottom (reviewed in Jennings and Kaiser, 1998; Auster and Langton, 1999; Kaiser and de Groot, 2000). Several researchers have shown that fishing (e.g. trawling, dredging) on the ocean bottom can alter critical habitat, trophic dynamics and ultimately survivability (particularly of juveniles) in various ecosystems. However, some researchers have demonstrated that the effects of fishing may in fact be positive over short time scales, by providing energy subsidies in the form

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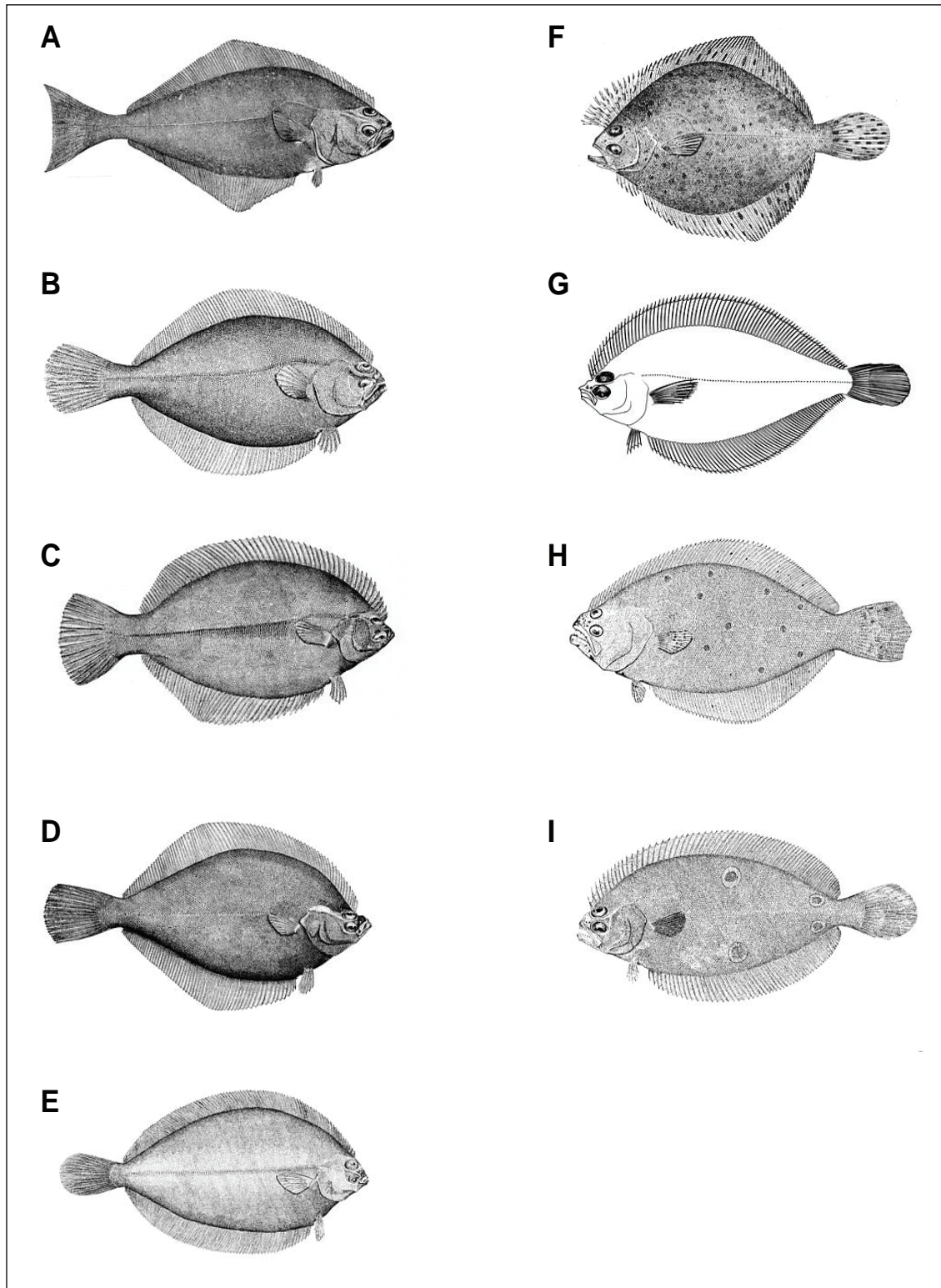


Fig. 1. Line drawings of flatfish species in the current study. Drawings from Flescher (1980). (A) Atlantic halibut (*Hippoglossus hippoglossus*), (B) American plaice (*Hippoglossoides platessoides*), (C) Winter flounder (*Pseudopleuronectes americanus*), (D) Yellowtail flounder (*Limanda ferruginea*), (E) Witch flounder (*Glyptocephalus cynoglossus*), (F) Windowpane (*Scophthalmus aquosus*), (G) Gulfstream flounder (*Citharichthys arctifrons*), (H) Summer flounder (*Paralichthys dentatus*); (I) Fourspot flounder (*P. oblongus*).

of discards or re-suspended sediment and associated benthos (e.g. Kaiser and Ramsay, 1997). A full understanding of the impacts of fishing on benthic habitats and benthic communities requires a detailed knowledge of flatfish ecology.

The Northwest Atlantic fish community has undergone severe exploitation for over 40 years (Fogarty and Murawski, 1998). Because of this intensive fishing, dramatic shifts in the fish community have been observed. This fish community has changed from a demersal one dominated by gadids and flatfish to a pelagic community dominated by elasmobranchs and small pelagic fish (Murawski *et al.*, 1997; Fogarty and Murawski, 1998). Additionally, disturbance of benthic habitat and megafauna caused by intense fishing effort has occurred in this ecosystem (Auster *et al.*, 1996; Collie *et al.*, 1997; Auster and Langton, 1999). The effects of declining habitat complexity and changes in the benthic invertebrate community on flatfish in this ecosystem remain unclear.

The feeding ecology of flatfish from the Northwest Atlantic has been reasonably well documented (e.g. Bowman, 1981; Langton, 1982; Collie, 1987a, b; Steimle and Terranova, 1991; Packer

et al., 1994; Gonzalez *et al.*, MS 1998; Methven, 1999). However, none of these studies have examined flatfish diets across broad spatial or temporal scales, particularly after major perturbations to the ocean bottom from decades of fishing. Additionally, fisheries management and stock assessment science have historically taken a single stock approach to evaluating the population dynamics of exploited species. As stock sizes reach and continue at historically low levels, it will be increasingly important to incorporate species interactions and impacts on benthic habitat into models to effectively predict and manage stock recovery (Jennings and Kaiser, 1998). This requires a detailed understanding of the trophic relationships between taxa, the factors that determine the strength of predator-prey interactions, the functional value of benthic habitat, and the role of habitat in mediating population growth via trophic interactions. Toward this goal, we present an analysis of the trophic patterns of nine flatfish species (Fig. 1), that are important in the Northwest Atlantic continental shelf ecosystem off of the USA and parts of Canada (Fig. 2) using a 25-year time series of food habits data collected in seasonal resource bottom-trawl surveys. We assess the temporal, spatial, and ontogenetic trends in flatfish diets.

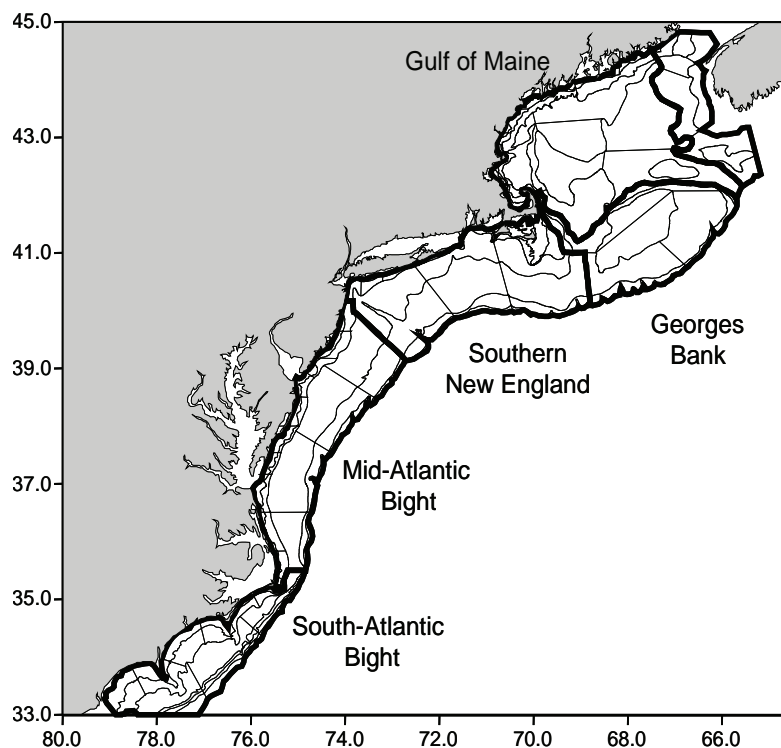


Fig. 2. Sampling area and major geographic regions of the Northwest Atlantic continental shelf ecosystem off the USA and Canada.

Methods

Data collection

The data for this study were collected from seasonal bottom-trawl surveys conducted by the Northeast Fisheries Science Center (NEFSC). The current study encompassed data collected from Cape Hatteras, North Carolina, USA, to southwestern Nova Scotia, Canada between 1973 and 1998 during all seasons. Over 35 000 stomachs from the nine flatfish species were included (Table 1). The surveys employ a stratified random sampling design with strata defined by depth and latitude. Sample depths ranged between 8 and 400 m. Sample stations were defined by 2.5' latitude by 2' longitude rectangular units that were randomly selected within strata. Between 350 and 400 stations on the continental shelf from Cape Hatteras, North Carolina to southwestern Nova Scotia (Fig. 2) were sampled during each seasonal survey of approximately 4–6 weeks in duration (NEFC, 1988). At each station, a 36 Yankee (or similar) bottom trawl was deployed for 30 minutes and towed at a speed of 6.5 km hr⁻¹. Sub-standard tows or those with non-representative sampling due to gear damage were excluded from the analyses. For each tow, catch (in both mass and numbers) at length (1 cm length-

classes) was recorded for all species. Details of the survey sampling design, execution, and efficiency are available in Azarovitz (1981) and NEFC (1988).

In addition to catch data, a subset of species during each seasonal cruise was examined for age and food habits data. The NEFSC has conducted quantitative food habits sampling in seasonal surveys since 1973. Fish stomachs were sampled based on fish size and strata-station quotas irrespective of species abundance. Prior to 1981, stomach contents were preserved and returned to the laboratory for identification of prey. Total stomach content mass and the mass of each prey were measured to the nearest 0.1 g. Since 1981, stomach contents have been examined at sea. The total volume of stomach contents was measured by comparing the stomach bolus to a calibrated volumetric gauge (to the nearest 0.1 g). The proportion of stomach contents comprised by each prey item was then estimated after separating each prey item from the entire stomach contents and measuring these with the volumetric gauge (relative to the total stomach volume).

We converted all stomach content and prey units into weights. In some cases, prey amounts within the

TABLE 1. Sample size and major metrics of flatfish used in this study.

	No. of tows with stomachs sampled	No. of stomachs sampled	Mean weight of stomach contents (g)	Mean length (cm)	Maximum length (cm)	Empty stomachs (%)	Mean body weight (kg)
Atlantic Halibut <i>Hippoglossus hippoglossus</i>	155	229	21.2	58.3	134	29.7	2.661
American Plaice <i>Hippoglossoides platessoides</i>	308	1786	1.0	29.9	70	47.8	0.450
Summer Flounder <i>Paralichthys dentatus</i>	2 077	8 938	2.2	36.1	82	44.4	0.583
Fourspot Flounder <i>P. oblongus</i>	2 002	10 066	1.1	27.1	49	41.4	0.162
Yellowtail Flounder <i>Limanda ferruginea</i>	367	2 015	1.1	30.6	58	32.9	0.327
Winter Flounder <i>Pseudopleuronectes americanus</i>	568	2 733	2.8	31.2	65	29.3	0.431
Witch Flounder <i>Glyptocephalus cynoglossus</i>	279	1 014	0.6	41.7	65	12.8	0.196
Windowpane <i>Scophthalmus aquosus</i>	2 158	8 990	1.5	25.7	41	38.8	0.211
Gulfstream Flounder <i>Citharichthys arctifrons</i>	31	219	<0.1	10.3	18	28.3	ND

same stomachs were measured as both weights and volumes. Using these samples, a linear regression was performed to convert volumes to weights and resolve the differences in prey quantification during the two periods. The regression was highly significant ($r^2 = 0.906$, $p < 0.0001$), and prey volumes from the 1981–98 time period were multiplied by 1.1 to convert volumes to weights based on this analysis (Link and Almeida, 2000). Further details of the food habits sampling methodology are available in Link and Almeida (2000).

Prey and predator categories

The taxonomic resolution of invertebrate prey is generally higher in samples collected prior to 1981, since those stomach contents were identified in the laboratory. For our analysis, fish and invertebrate prey were grouped to family or order to account for differences in taxonomic resolution between the sampling periods. A few (mainly fish) prey were retained at the species level. Unidentifiable fish were an important component of the diets of some flatfish in this study. This component included both well-digested fish remains and small fish that were difficult to identify in both preserved and fresh samples. We also included a category of well-digested, unidentifiable prey. While it was assumed that unidentifiable remains reflect the composition of identifiable prey in the diet, we have chosen to be conservative by including it as a separate prey type in our analyses. There were 35 different prey categories in our analyses.

The flatfish were divided into length categories to account for suspected ontogenetic shifts in diet (Garrison and Link, 2000a). These previous studies revealed similar length categories at which the diet shifted among the different flatfish. These length categories remained consistent across the time series: <20 cm (small), 20–50 cm (medium), and >50 cm (large). Due to small sample sizes, detailed analyses were not conducted for Atlantic halibut, witch flounder or gulfstream flounder and we only present an overall mean for these species. Summary statistics for all species are shown in Table 1.

Diet analyses

Means and variances of prey amount (weight) per stomach were calculated using a weighted, two-stage cluster design to account for survey sampling design and included fish with empty stomachs (Link and Almeida, 2000). Mean stomach contents within a tow were weighted by the number of fish of that species in a size category captured in that tow. We assessed

general trends in means and 95% confidence intervals of relative prey amounts (% of diet by weight) by size category (small, medium, and large), geographic region (Fig. 2), season (winter, spring, summer, and autumn), and time blocks (1973–75, 1976–80, 1981–85, 1986–90, 1991–95, 1996–98) for each flatfish species. The five-year time block provided sufficient resolution of temporal trends while maintaining adequate sample size.

For each species, a canonical correspondence analysis (CCA; ter Braak, 1986) was used to assess the multivariate diet response to the four explanatory factors above. The explanatory factors were coded to ordinal variables reflecting size (small to large), geographic (southern to northern), seasonal (winter to autumn) and temporal (i.e. time blocks from 1973–98) groups. The response matrix consisted of the mean amount of each prey category within each cell of the crossed factors and was log transformed ($\ln[x + 1]$) to account for the lognormal distribution of prey weights. Tows containing <5 fish and cells containing <5 tows were removed from the analysis to avoid inflation of variance due to low sample sizes.

CCA is a multivariate equivalent to a multiple, non-linear regression (ter Braak 1986, 1987). It is a direct gradient method whereby canonical axes that are linear combinations of explanatory variables are correlated to weighted averages of multivariate response variables (prey amounts) within cells. The statistical significance of explanatory factors in the ordination was assessed using permutation tests (ter Braak, 1986). The results of the CCA are best understood by examining prey-environment biplots, the correlation between the canonical axes and explanatory variables, and the amount of variance in the prey matrix explained by the canonical axes (ter Braak, 1986, 1987). CCA is an effective method to statistically assess the quantitative relationship between multivariate response and explanatory variables and is robust to violations of assumptions (e.g. non-normality, ter Braak, 1986; Palmer, 1993). The CCA ordination was accomplished using CANOCO version 4.0. For those species with insufficient data or insignificant results we do not present the CCA nor diet analyses across any of the major factors.

Results

American plaice

This species was unique among the flatfish in this study in that it was an echinoderm specialist.

Echinoderms comprised >70% of the diet, with ophiuroids representing approximately 45% of the diet (Fig. 3A). There was no significant change in diet over the time series, with ophiuroids and other echinoderms the most dominant prey item, at times >90% (Fig. 4A).

Size and season were the significant factors determining the diet, and generally corresponded to the first ($r = -0.694$, $p < 0.001$) and second ($r = 0.481$,

$p < 0.001$) CCA axes respectively (Fig. 5). The first and second CCA axes explained 56.0% and 29.2%, respectively, of the total explainable dietary variation, which was 11.7% ($p < 0.001$). The most important shift in diet across size was from mysids, other crustaceans, small shrimps, other worms and polychaetes eaten by small American plaice to ophiuroids, other echinoderms and sea mice eaten by larger A. plaice (Fig. 5, 6A). The most important dietary shift across season was from echinoderms and other invertebrates in the

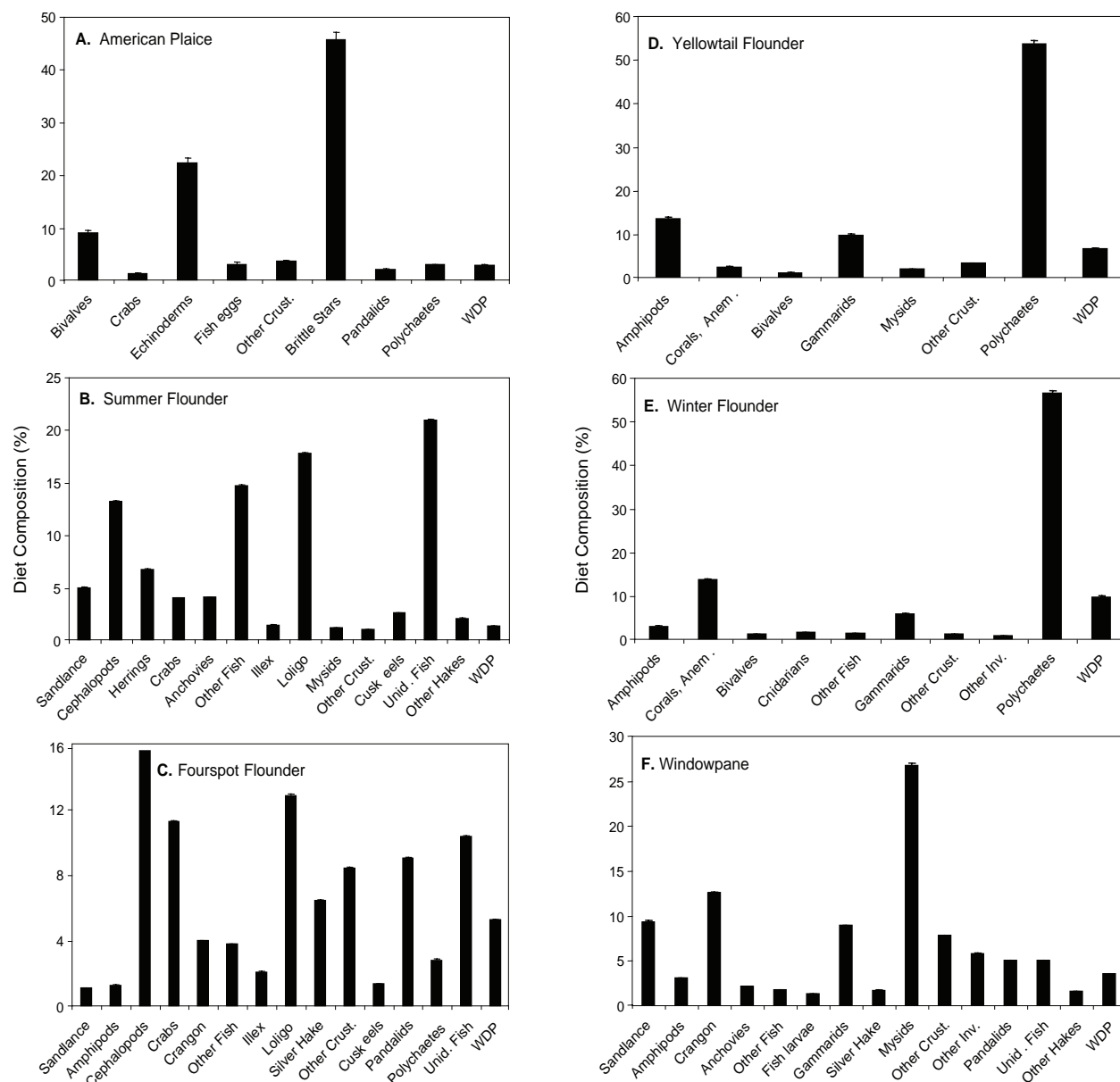


Fig. 3. Diet composition (% weight (g)) of flatfish species in this study. WDP = well digested prey. (A) American plaice, (B) Summer flounder, (C) Fourspot flounder; (D) Yellowtail flounder, (E) Winter flounder, (F) Windowpane, (G) Atlantic halibut, (H) Witch flounder, (I) Gulfstream flounder.

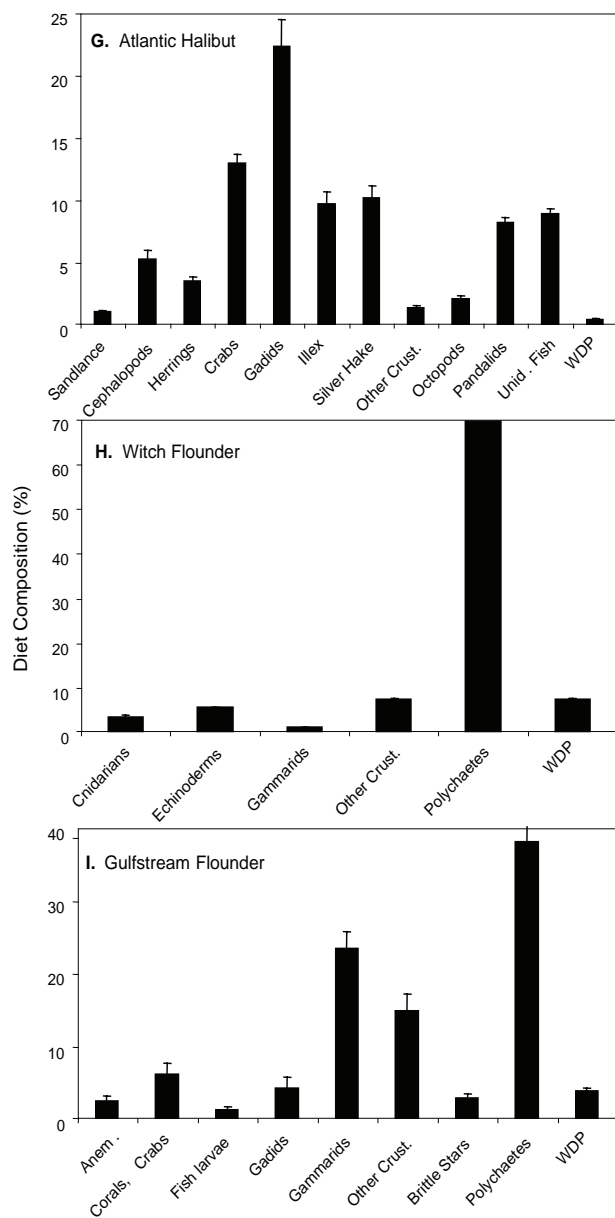


Fig. 3. (Continued). Diet composition (% weight (g)) of flatfish species in this study. WDP = well digested prey. (A) American plaice, (B) Summer flounder, (C) Fourspot flounder; (D) Yellowtail flounder, (E) Winter flounder, (F) Windowpane, (G) Atlantic halibut, (H) Witch flounder, (I) Gulfstream flounder.

spring to bivalves, pandalids and polychaetes in the summer to ophiuroids, and fish eggs in the autumn (Fig. 5, 6B).

Summer flounder

This species primarily ate fish and cephalopods (Fig. 3B). *Loligo* squid, unclassified cephalopods,

sand lance, herrings, anchovies and unidentified or other fish comprised >80% of the diet. There have been significant shifts in diet across the time series, with sand lance, unclassified cephalopods and *Illex* squids more common in the diet in the 1970s than more recently (Fig. 4B). *Loligo* squid, unidentified fish and herrings have become significantly more prominent in the diet in the 1990s.

Size and year block were the major factors determining the diet (Fig. 7). Size and five year block corresponded to the first ($r = -0.666$, $p < 0.001$) and second ($r = -0.470$, $p < 0.001$) axes, respectively. The first two axes explained 80.6% of the total explainable dietary variation (8.7%, $p < 0.001$). Major changes in diet across the year blocks were from sand lance, *Illex* and other worms in earlier periods of the time series to anthozoans, *Loligo* and pandalid shrimp in more recent years (Fig. 4B, 7). Major ontogenetic shifts in diet were from anchovies, mysids, *Crangon* and similar shrimps, to fish and squids at larger sizes (Fig. 7, 8A).

Fourspot flounder

This species had one of the broadest diets of all the flatfish studied, with an assortment of fish, squids and benthic and pelagic invertebrates comprising the diet (Fig 3C). There were significant changes in diet across the time series, with more octopods, sand lance, pandalids and amphipods in the 1970s compared to more gadids, silver hake and other crustaceans in the 1980s (Fig. 4C). Squids and other fish comprised a higher component of the diet in more recent years.

Size and year block were the major factors determining the diet, and generally corresponded to the first ($r = 0.734$, $p < 0.001$) and second ($r = -0.466$, $p < 0.001$) CCA axes, respectively (Fig. 9). The CCA ordination accounted for 8.0% ($p < 0.001$) of the total variation in fourspot flounder diets, with the first two axes accounting for 80.5% of this variation. Major changes in diet across the 5-year blocks were from octopods, other worms, sea mice and amphipods, to ophiuroids, herrings, fish larvae, *Illex* and *Loligo* in more recent years (Fig. 4C, 9). Major ontogenetic shifts in diet were similar to summer flounder; shrimps and benthic invertebrates dominated the diet of smaller fourspot flounder, whereas larger fourspot flounder, ate primarily fish and squids (Fig. 8B, 9).

Yellowtail flounder

This species ate primarily polychaetes and gammarid amphipods (Fig. 3D). Unclassified

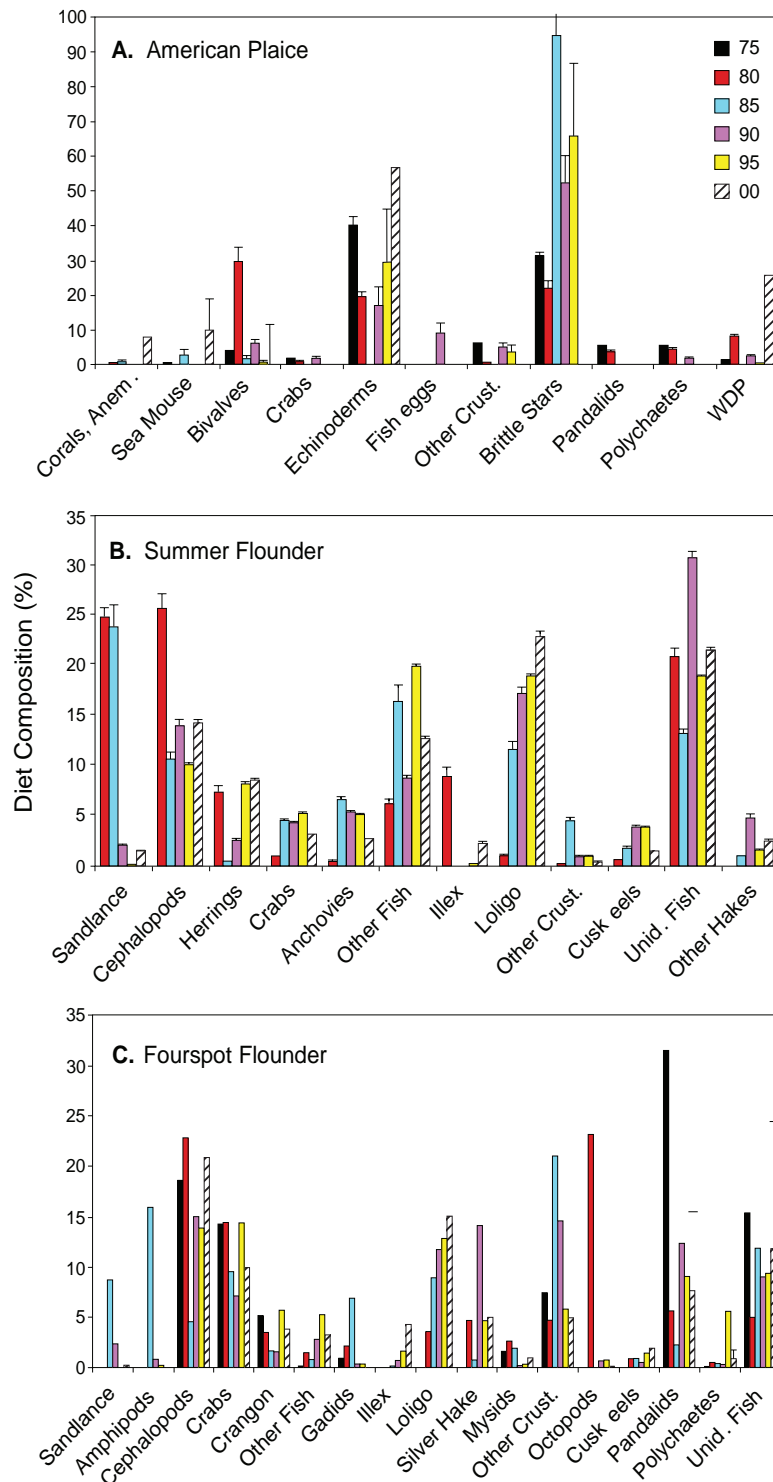


Fig. 4. Diet composition of flatfish species across the time series, presented in 5-year blocks. (A) American plaice, (B) Summer flounder, (C) Fourspot flounder, (D) Yellowtail flounder, (E) Winter flounder, (F) Windowpane. Labels for each time block are identified by the end year (e.g. 73–75=75, 76–80=80, etc.).

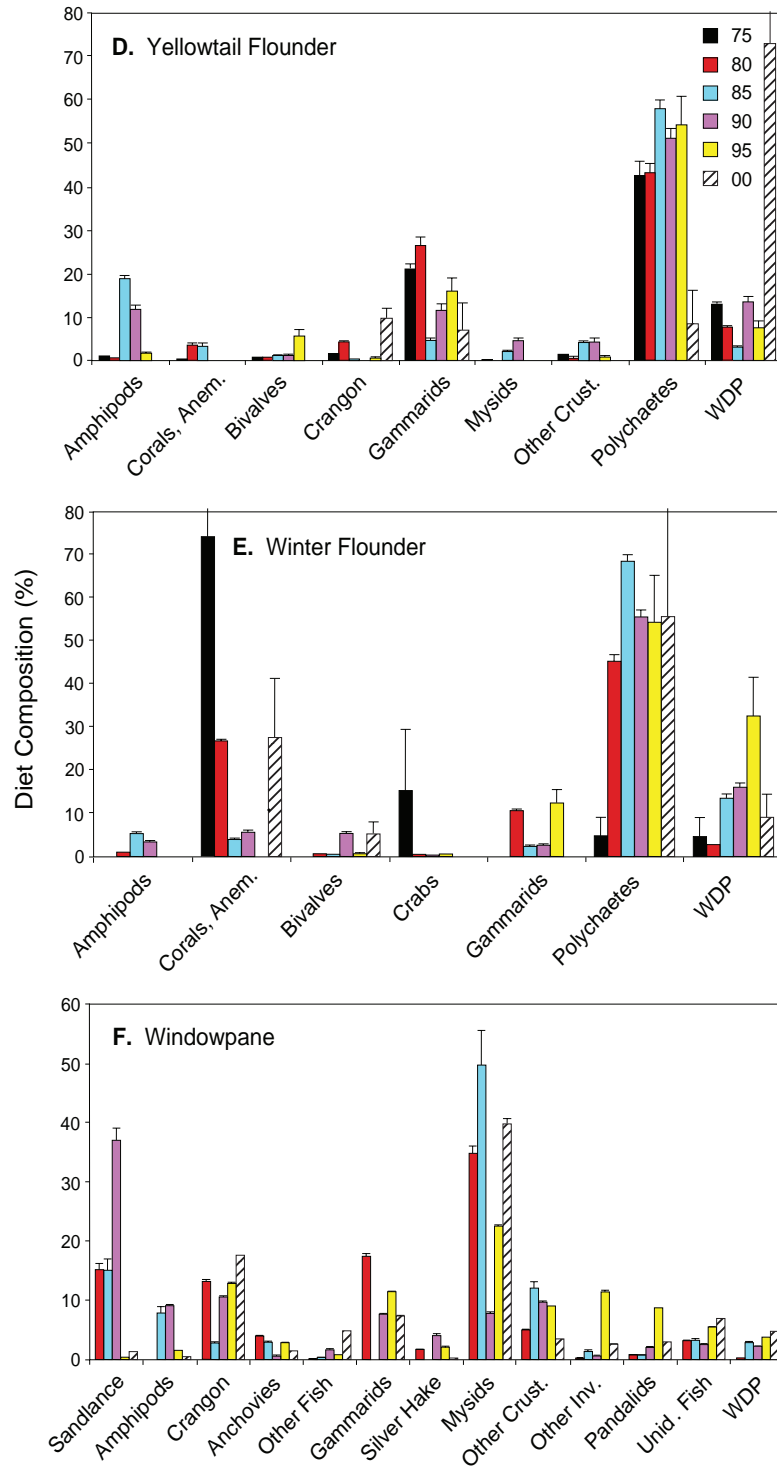


Fig. 4. (Continued). Diet composition of flatfish species across the time series, presented in 5-year blocks. (A) American plaice, (B) Summer flounder, (C) Fourspot flounder, (D) Yellowtail flounder, (E) Winter flounder, (F) Windowpane. Labels for each time block are identified by the end year (e.g. 73–75=75, 76–80=80, etc.).

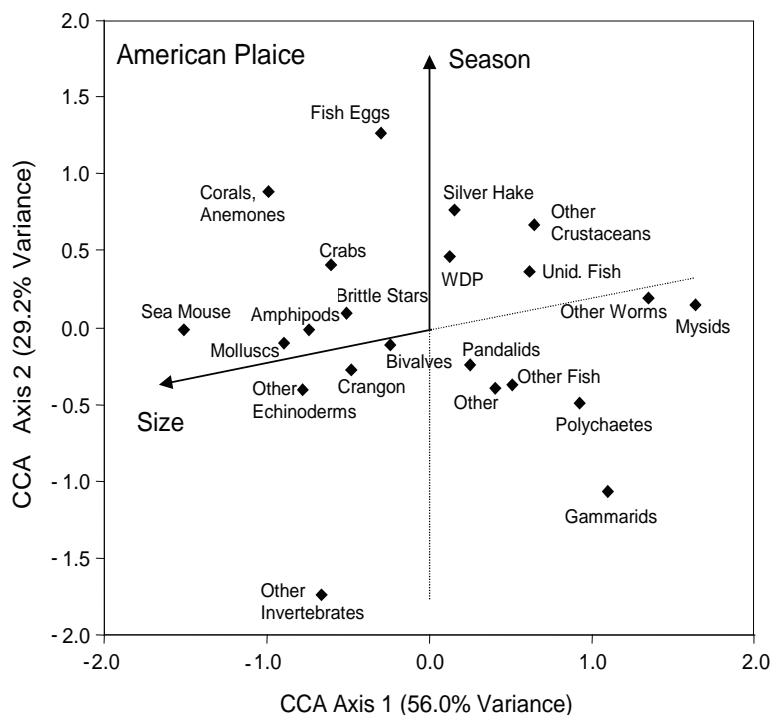


Fig. 5. Canonical correspondence analysis biplot for American plaice. The arrows indicate significant explanatory factors, with the arrowheads indicating positive values of the variable. A small angle between a variable arrow and a CCA axis indicates a high correlation between the axis and the variable. Data points indicate CCA scores of individual prey items in ordination space.

amphipods and well-digested prey (WDP) also comprised approximately 10% of the diet. There was no significant shift in the diet of this species across the time series (Fig. 4D). The slight shift from gammarids to amphipods and back to gammarids from the 1970s, 1980s and 1990s, respectively, was noted, but did not represent a shift in diet but rather a difference in taxonomic level of identification between family and class.

Although we executed a CCA ordination for this species, it did not explain a significant amount of the dietary variation; the axes had very low correlations with any of the four major factors, and did not provide any further insight into the feeding ecology of this flounder.

Winter flounder

This species exhibited a diet similar to yellowtail flounder. Stomach contents consisted primarily of polychaetes, WDP and gammarids (Fig. 3E). Winter flounder was unique among the flatfish in that 13.7% of the diet was comprised by anthozoans. There was no significant change in diet across the time series

(Fig. 4E), including moderate changes in proportion of the diet between cnidarians and polychaetes. Although we executed a CCA ordination for this species, similar to yellowtail flounder, it was not significant.

Windowpane

Similar to fourspot flounder, this species exhibited a broad diet (Fig. 3F). The major portion of the diet was comprised of shrimps (i.e., mysids, *Crangon*, pandalids) and benthic invertebrates. Fish were an important but secondary component of the diet. Like yellowtail and winter flounder, this species showed no significant change in diet across the time series (Fig. 4F), although there were small differences in the proportion of sand lance and mysids during the 1970s and early-1980s. Although we executed a CCA ordination for this species, similar to yellowtail and winter flounder, it was not significant.

Atlantic halibut

Only 229 stomachs were examined for this species, primarily from the Gulf of Maine. This small sample size precluded more detailed analysis of the

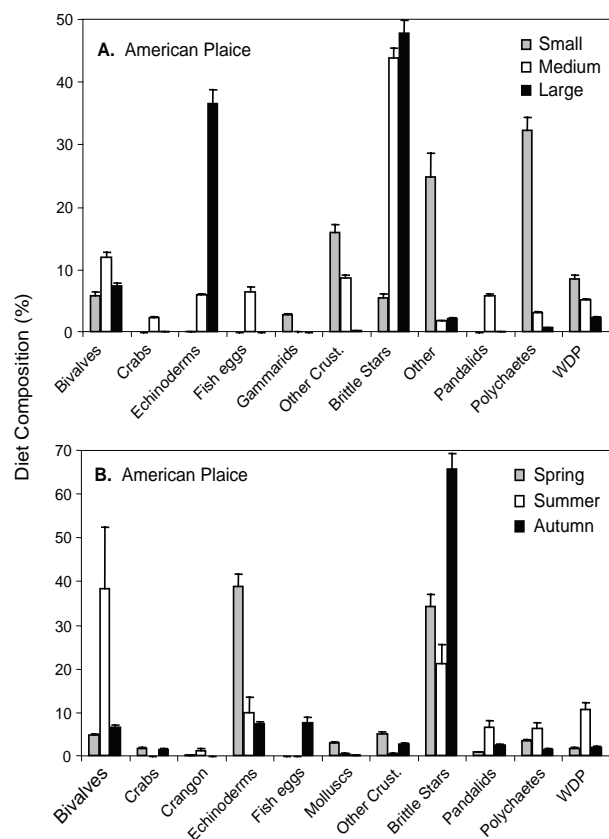


Fig. 6. (A) Diet composition of American plaice across size classes. (B) Diet composition of American plaice across different seasons.

diet. This species was primarily piscivorous, with an emphasis on gadids and small pelagic fishes (Fig. 3G). There was also a notable proportion of cephalopods (*Illex*, other squids and octopods) and crabs in the diet.

Witch flounder

There were 1 014 stomachs examined for this species, but they were not distributed evenly in time and space across our sampling period. The limited and clustered sample size precluded more detailed analyses of the diet. Approximately 70% of witch flounder diet was comprised of polychaetes, with the remainder being other benthic invertebrates (Fig. 3H).

Gulfstream flounder

There was limited sampling for this species, with only 219 stomachs examined during the study. The majority of these stomachs were sampled during the 1976–80 time period. This sampling limitation precluded more detailed diet analyses. This species exhibited typical small-mouthed flounder feeding habits, with polychaetes, gammarids and other benthic invertebrates comprising the majority of the diet (Fig.

3I).

Mean stomach contents

The mean stomach contents for the flatfish in this study have not remained constant across the time series (Fig. 10). Stomach contents of most of these fish peaked in the 1981–85 period, except summer flounder, American plaice and Atlantic halibut, which peaked in the 1986–90 period. Stomach content weights were generally lower in the 1973–80 time periods, prior to the institution of at-sea sampling in 1981. Even accounting for possible methodological differences during the 1981 field season, all eight of the fish species we examined showed declines in the amount of food eaten over the 1990s. Stomach content weights during the 1996–98 period were at or below values observed during the earliest two periods of the time series.

Discussion

Our study highlights the importance of polychaetes and gammarids in the diets of these flatfish. The large majority of flatfish are known to consume these prey items (e.g. Bowman, 1981; Langton, 1982; de Morais and Bodiou, 1984; Collie, 1987a; Livingston, 1987; Steimle and Terranova, 1991; Aarnio *et al.*, 1996; Methven, 1999). It is unlikely that flatfish predation alone regulates these prey populations, although flatfish can remove a large fraction of benthic production (Collie, 1987b). Yet declines in the abundance of polychaete or gammarid populations could strongly influence yellowtail or winter flounder population dynamics (Collie, 1987b). These small, benthic organisms are not usually considered in a fisheries context, yet perhaps should be in the broader ecosystem context for fisheries management that has been recently prescribed (NMFS, 1999; NRC, 1999).

Flatfish that ate predominately polychaetes and gammarids exhibited a consistent diet, in terms of prey composition, across the time series. This is surprising given the documented impacts to the ocean bottom from fishing activities in this ecosystem (Auster *et al.*, 1996; Collie *et al.*, 1997; Auster and Langton, 1999). We recognize that there could have in fact been changes in the species of polychaete or amphipod eaten, but the resolution of our data would not have detected such changes. Yet at a broad scale, these results imply that fishing does not affect the trophic dynamics of benthic feeding flatfish. More focused studies have demonstrated obvious short-term differences in benthic fish diets after fishing activities

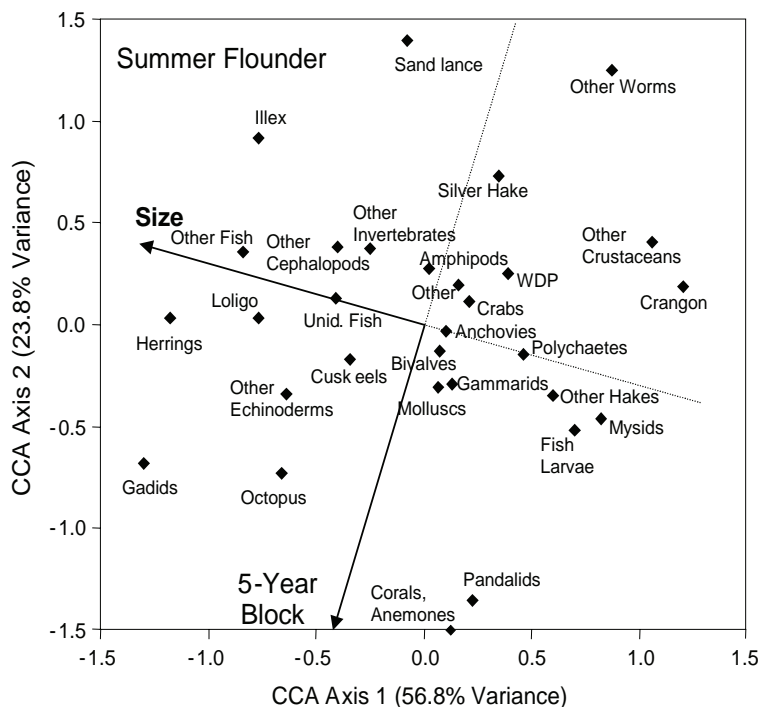


Fig. 7. Canonical correspondence analysis biplot for summer flounder. A small angle between a variable arrow and a CCA axis indicates a high correlation between the axis and the variable. Data points indicate CCA scores of individual prey items in ordination space.

(e.g. Kaiser and Ramsay, 1997; Kaiser and deGroot, 2000), yet none have documented persistent changes in diet over a large area or for an extended period of time. These results may also be reflective of the relatively fast generation times of these small benthic invertebrates, implying an ability of some of these prey organisms to rapidly recover from perturbations to the ocean bottom. Additionally, it may be that many flatfish search for, can only capture, can only ingest, or simply prefer polychaetes and small benthic crustaceans.

There is a potential for strong species interactions between some flatfish and other commercially targeted resources such as squids, scallops, other bivalves, or pandalid shrimp. Flatfish predation could affect the population size available for harvest of these molluscs or shrimp. In addition to the commercially valuable invertebrates described above, forage fish are also an important part of the diet of some flatfish (Livingston, 1993; Yang, 1995; Orlov, 1997). When a flatfish species and a fishery are removing the same size of a particular prey fish or invertebrate, the potential for strong competition between the predator and the

fishery also exists (e.g. Livingston, 1993; Overholtz *et al.*, 2000).

Piscivorous flatfish did exhibit significant diet differences over the time series. This result is not surprising because the diet composition of fourspot or summer flounder generally tracks the abundance of forage fish. The fish community of this ecosystem has undergone well-documented changes (Fogarty and Murawski, 1998). The pattern of prey switching among different forage fish across the past three decades has been documented for several species in this ecosystem (Garrison and Link, 2000b; Overholtz *et al.*, 2000; Link and Garrison, 2002). These findings demonstrate one value of long-term studies of food habits.

There was one atypical feeder in our data. American plaice ate principally ophiuroids and other echinoderms (Fig. 4A). This study is not the first to report American plaice predation on ophiuroids (Packer *et al.*, 1994), but there are only a few other flatfish species (e.g. starry flounder, Dover sole, dab) that specialize on prey such as ophiuroids (Jewett and

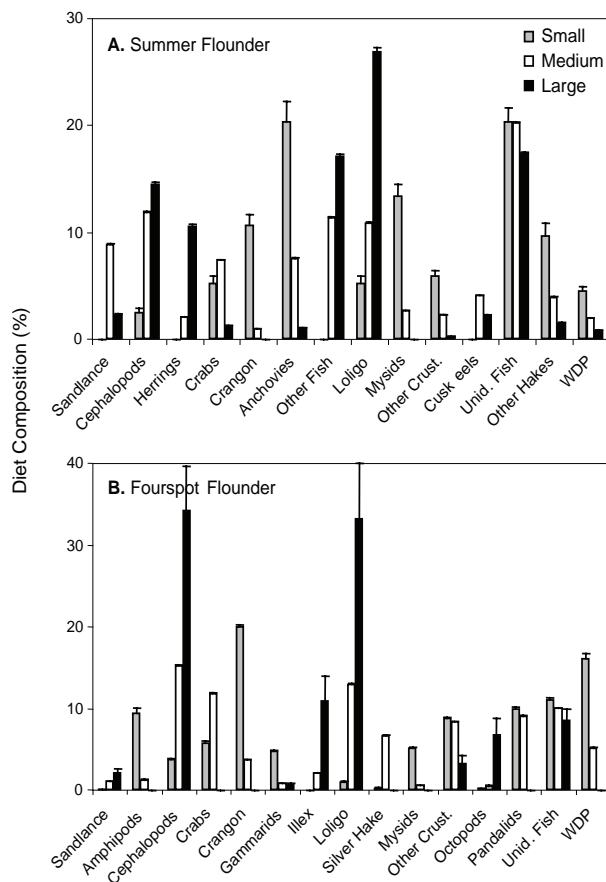


Fig. 8. (A) Diet composition of summer flounder across size classes. (B) Diet composition of fourspot flounder across size classes.

Feder, 1980; Gabriel and Pearcy, 1981; Kaiser and Ramsay, 1997). Most conspecifics, and often these species at different locations, consume a more "typical" flatfish diet of polychaetes, benthic crustaceans or small fish (Beare and Moore, 1997; Gonzalez *et al.*, MS 1998). Why certain flatfish specialize on prey items that appear to be difficult to digest and of low energy content remains an interesting question.

The vast majority of flatfish eat polychaetes during some point of their life history. Many of the flatfish that are piscivorous or specialists on larger prey items consume polychaetes and meiofauna at smaller sizes but grow out of this feeding mode (i.e. American plaice, summer flounder, fourspot flounder). This pattern is observed for many flatfish

around the world (Rodriguez-Marin *et al.*, 1995; Yang, 1995; Aarnio *et al.*, 1996). However, several small-gaped flatfish remain principally polychaete eaters throughout their life. The constancy of diet for polychaete eaters likely reflects the differences in oral morphology among the flatfish species (Podoskina, 1993). The differential shift with ontogeny in relative mouth gape and other oral morphology provides an interesting contrast among the flatfish and explains in large part why some species do not exhibit ontogenetic shifts in diet (sensu Podoskina, 1993; Piet *et al.*, 1998).

Garrison and Link (2000a, b) have shown that several of these flatfish are in the main benthivore feeding guild for the Northwest Atlantic ecosystem, and have a high dietary overlap (40–70%) and thus a high potential for competition with other benthivores such as skates. The subtle differences in oral morphology may be one mechanism whereby taxonomically and functionally similar organisms such as these flatfish can coexist by reducing the degree of competition for food. These flatfish may also minimize these potential competitive interactions via spatial segregation of habitat (Garrison, 2000; Garrison and Link, 2000b). In addition, small differences in preference for secondary prey items such as cnidarians, crabs, shrimps, or bivalves may mitigate intraguild competition. The potential for competition between flatfish and other benthivorous members of the fish community (e.g. haddock, ocean pout, sculpins, skates, etc.) merits further examination.

We view the major determinants of flatfish diet as a hierarchical sequence. First, flatfish morphology (e.g. gape width) limits what can be eaten. Second, flatfish ontogeny confines what is eaten, principally through growth and changes in size affecting morphology. Next, the abundance of all possible prey at any given place and time determines what is eaten. For example, if for whatever reason, herring in this continental shelf ecosystem were to decline and be replaced by sand lance, we would expect the diet of piscivores such as summer or fourspot flounder to reflect these changes in prey abundance, as we observed in the 1970s and early-1980s. Finally, other factors beyond the scope of this study (such as prey preferences, short-term physiological changes, spawning condition, localized oceanographic conditions, or similarly scaled processes) may also influence flatfish diet.

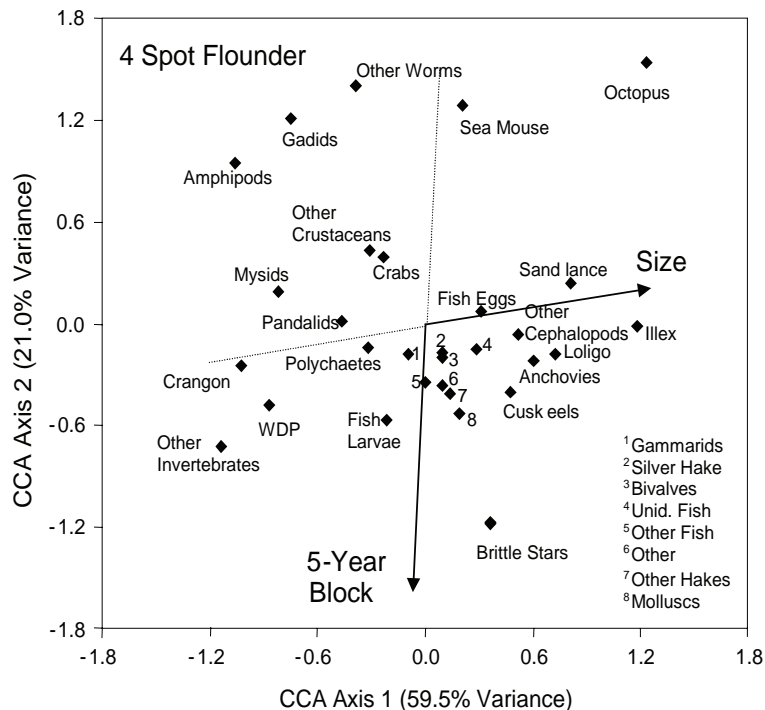


Fig. 9. Canonical correspondence analysis biplot for fourspot flounder. A small angle between a variable arrow and a CCA axis indicates a high correlation between the axis and the variable. Data points indicate CCA scores of individual prey items in ordination space.

For all flatfish species we studied, the mean stomach content has changed across the time series. Regardless of diet composition, the amount of food eaten by all flatfish peaked in the early-1980s and subsequently declined over the past 20 years. Even accounting for the methodological change in 1981, the declines have been consistent after that time period. These declines in diet are not biased by changes in fish size over the time period, as our sampling examined all size classes irrespective of abundance of a given size. Assuming there are no significant methodological differences, the current level of stomach contents may in fact represent a return to trophic conditions observed in the earlier part of the time series. The peak in the 1980s would then represent a period of increased food availability or increased feeding by flatfish due to a host of possible changes in the ecosystem. Link and Garrison (2002) observed similar patterns during the same time period for piscivorous fish on Georges Bank. From a systems perspective, the early-1980s may have been a time period when broad-scale changes occurred, leading to some form of regime shift within the fish community.

The recent declines in stomach contents imply that less benthic food was eaten, regardless of what was eaten. It is unknown whether these trophic dynamics will have any influence on flatfish populations. The decline in amount of food eaten may be a density dependent response for some flatfish populations, yet the evidence for changes in flatfish abundance, growth rates, mean size-at-age, and related parameters are either unclear or unknown and certainly merit further examination. Additionally, Link (1999) hypothesized that the Northwest Atlantic ecosystem has shifted from a vertically-oriented system, where most of the primary production and related energy is transported to the ocean bottom, to an horizontal one, where most of the energy is intercepted by organisms in the pelagia before reaching the bottom. Fogarty and Murawski (1998) hypothesized that changes to the fish community have shifted the competitive balance from groundfish to elasmobranchs. With respect to flatfish, this shift would imply that skates are out-competing flatfish for food resources. For the flatfish in the Northwest Atlantic, it is difficult to determine if the observed decline in food eaten is in response to direct impacts

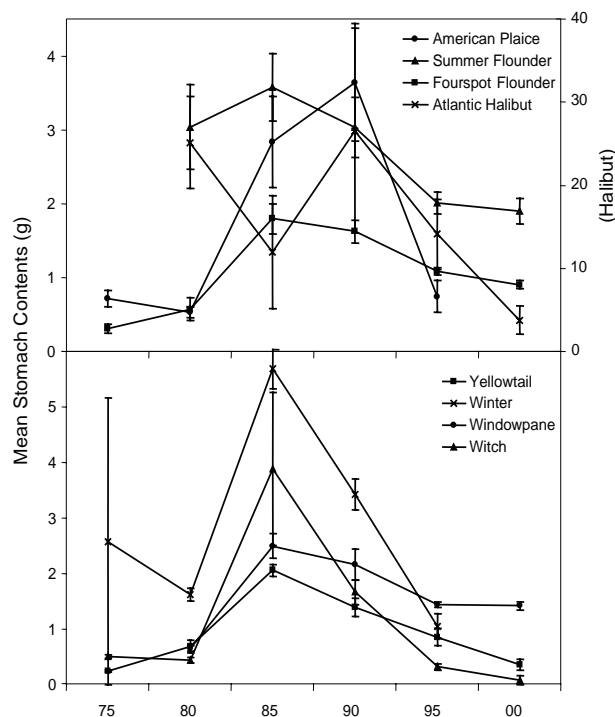


Fig. 10. Mean weight of stomach contents (g) of the flounder species in this study across the 5-year blocks of the time series. (A) American Plaice, (B) Summer Flounder, (C) Fourspot Flounder, (D) Atlantic Halibut, (E) Yellowtail Flounder, (F) Winter Flounder, (G) Windowpane, (H) Witch Flounder.

on the ocean bottom and associated benthos (i.e. less food available), is a result of the changes in energy flows within this ecosystem, is a result of the inability of flatfish to out compete more abundant skate populations, is a result of other changes to flatfish population dynamics (i.e. fishing-induced density dependence), or a combination thereof. Future and ongoing efforts should continue to evaluate the validity of these hypotheses for this and similar ecosystems.

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