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Food web ecology of Gulf Stream flounder (*Citharichthys arctifrons*): a continental shelf perspective

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Abstract

Gulf Stream flounder, *Citharichthys arctifrons*, are regularly observed in fish diets of the northeast U.S. continental shelf, yet lack commercial value and are often ignored. Similarly, Gulf Stream flounder diets of the Northwest Atlantic have remained largely unexamined, except for a brief period from 1976 to 1980. To better understand their role in the ecosystem, juvenile through adult Gulf Stream flounder were examined both as a predator and prey, and the magnitude of their feeding footprint (removal of prey biomass) was quantified for the northeast U.S. continental shelf. Their stomachs were sampled from 2005 to 2010, with the majority examined in the field macroscopically. Due to large proportions of unidentifiable prey, the effort was expanded in 2011–2012, and all stomachs were processed in the laboratory microscopically. Gulf Stream flounder were consumed by 15 fish, and what they eat (percentage mass and percentage frequency of occurrence) was documented by season, spatial region and year. Highly benthivorous, Gammaridea and Polychaeta dominated the diet in all years, seasons and regions, but Ophiuroidea (brittle stars) were also prominent in Southern New England during the spring. Gulf Stream flounder diets remained consistent across regions and time, with only a few feeding differences between seasons and one region. Relative to the productivity of benthos for this shelf ecosystem, the feeding footprint of Gulf Stream flounder was minor for their predominant benthic prey with a maximum percentage of benthos production eaten of 0.01% m^{-2} in Southern New England. With an ecosystem perspective, this feeding information offers a foundation for improving fisheries management among shared living marine resources considering benthic habitat and prey availability.

KEYWORDS
benthic production, benthivore, fish diet, flatfish, Northwest Atlantic, trophic ecology

1 | INTRODUCTION

Gulf Stream flounder (GSF; *Citharichthys arctifrons*; Goode, 1880) are widely distributed along the northeast U.S. continental shelf from Georges Bank east of Massachusetts to Florida, typically in 46–365 m (Gutherz, 1967), but occasionally in as little as 21 m of water (Bigelow & Schroeder, 1953). A relatively small ovate-shaped, left-eyed flatfish, with a maximum length of 17.7 cm (Bigelow et al., 2002) they lack commercial value, yet many of their consumers are fished commercially. Characterized by an osseous protuberance on their snout that increases with fish length (Gutherz, 1967) and large cycloid or feebly ctenoid scales (Collette & Klein-MacPhee, 2002), they are a commonly identified flatfish in the stomachs of finfish examined by the Northeast Fisheries Science Center (NEFSC; Smith & Link, 2010).

Despite GSF's wide distribution and presence as prey, few published reports of their diet and consumptive removal of prey biomass by them exist. Four studies examine their diet through samples collected between 1969 and 1980. With sample sizes ranging from 219 to 809 stomachs, these studies looked at diet patterns overall (Link *et al*., 2002), diet in relation to size class (Bowman *et al*., 2000; Sedberry, 1983), diet by region (Bowman *et al*., 2000; Langton & Bowman, 1981) and diet by season (Sedberry, 1983). The general consensus that polychaetes and amphipods are GSF's primary prey warrants further examination with more recent data. GSF appear as notable prey for four species in Smith and Link (2010), yet publications targeting species consuming GSF in the broader food web are lacking. This study expands the existing knowledge of GSF's prey and predators with more recently collected samples, larger sample sizes and greater geographic coverage.

As fisheries management continues to move forward with ecosystem approaches, the need for understanding interactions between fish populations and their prey has increased (Christensen, 1996; Langton & Bowman, 1981; Link *et al*., 2020). "Understanding trophic interrelationships among the majority of fish species within an ecosystem is necessary to define more precisely the role that predation plays in determining ecosystem structure and the possible long-term effects of various fisheries exploitation regimes" (Bowman *et al*., 2000). Many flatfish primarily consume benthic prey, converting their energy into a form more accessible to higher trophic levels (Link *et al*., 2015). GSF, in particular, primarily consume polychaetes and gammarids, which may have a direct impact on the productivity of these preferred benthic prey resources in the Northwest Atlantic. With ongoing plans to rebuild managed fish stocks for this continental shelf and globally (*e.g*., Murawski, 2010; Wiedenmann & Mangel, 2006; Worm *et al*., 2009,), it's critical to have an understanding of the feeding footprints and magnitude of predation on benthos considering a system with many shared benthic prey resources (Smith & Link, 2010; Smith & Rowe, 2021). In addition, the importance of GSF as prey to multiple species, several of which are managed, warrants an understanding of their ecological role in the food web.

The objective of this study was to better understand the functional role of GSF in the food web of the northeast U.S. continental shelf ecosystem with three approaches. First, species eating GSF: examined through an analysis of diets from 679,557 finfish on the northeast U.S. continental shelf. Second, what do GSF eat, and describe any seasonal, regional or annual feeding trends from 1716 stomachs sampled from 2005 to 2012 and 225 historic samples dating 1976 to 1980. Third, examine the feeding footprint of GSF with estimates of annual biomass of prey removed for several regions within the northeast US continental shelf and derive the percentage of benthic production consumed for the primary prey of GSF.

2 | MATERIALS AND METHODS

2.1 | Data

The diet and predators of GSF were determined with data from the Northeast Fisheries Science Center's (NEFSC) seasonal bottom trawl surveys, which sample the entire northeast U.S. continental shelf (Figure 1a): Mid-Atlantic Bight, Southern New England, Georges Bank and Gulf of Maine (>290,000 km^2). These surveys use a standardized, stratified random sampling design to monitor fish distribution and abundance (since 1963), primarily occurring in the spring and fall (Azarovitz, 1981; NEFC, 1988; Politis *et al*., 2014). Currently, 350–400 stations are sampled each spring and fall by towing a standardized bottom trawl net for 20 min. Since 1973, systematic fish diet sampling has occurred on these surveys (24 h a day). Detailed species-specific diet sampling protocols are available in Link and Almeida (2000), Smith and Link (2010) and Smith and Rowe (2021). For GSF, diet sampling occurred from 1976 to 1980 and from 2005 to 2012. Prior to 1981, all stomach samples were returned to the laboratory for microscopic examination and weighed to the nearest 0.01 g. Since 1981, macroscopic sampling at sea has been the primary method. This includes estimating the total volume of all stomach contents to the nearest 0.1 cm^3, then identifying prey to the lowest taxonomic level possible, followed by estimating prey percentages respective to total content. A small proportion (0.09) of sampled GSF stomachs were examined microscopically from 2005 to 2010, while the rest were examined at sea. From 2011 to 2012 all GSF samples were classified to the lowest taxonomic resolution microscopically and weighed to the nearest 0.001 g. A summary of GSF sampling information including examination methods applied for this study relative to prior studies is available in Table 1. A conversion factor of 1.1:1 (volume-to-mass) was applied based on linear regression ($r^2 = 0.906$; $P < 0.0001$) by Link and Almeida (2000) to include diet data throughout the time series.

2.2 | Diet analyses

All occurrences of GSF as prey through 2019 were queried from data of the NEFSC bottom trawl survey. For each predator of GSF, species, date and station location (latitude/longitude) were obtained. A list of predators containing GSF in stomach contents was compiled, including counts of the number of observations as prey per species. To assess the importance of GSF in the diet relative to other flatfish, queries were run to determine the number of times left-eyed flatfish, right-eyed flatfish (Pleuronectidae), unclassified flatfish (Pleuronectiformes) and flatfish identified to species were recorded as prey items. Station locations where GSF were identified in the catch, as prey, and sampled for stomach contents were obtained from NEFSC bottom trawl survey data and plotted with ArcGIS 10.7 (ESRI, 2018).

To examine what GSF eat, data were queried for all GSF stomachs examined on bottom trawl surveys. All prey of GSF were grouped at the class, order or family level to adjust for differences in resolution between stomachs examined macroscopically at sea and microscopically in lab. Unidentifiable prey were classified as Animalia. Prey data were then examined for seasonal, regional or annual trends by estimating the percentage of each prey by mass and percentage of prey frequency of occurrence in GSF stomachs and focusing on the four predominant and identifiable prey: Gammaridea, Polychaeta, other Crustacea and Ophiuroidea. For percentage diet by mass the

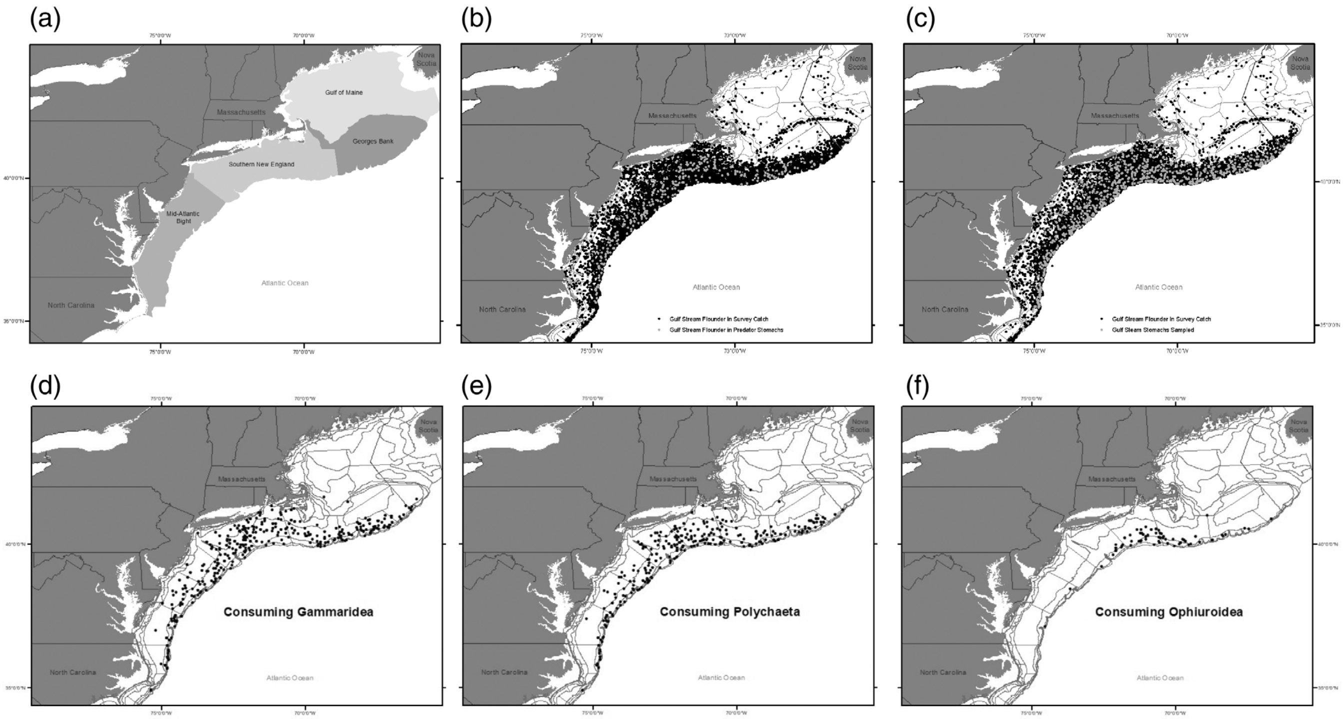

FIGURE 1 (a) Northeast Fisheries Science Center Bottom Trawl Survey Regions. (b) Locations where Gulf Stream flounder (*Citharichthys arctifrons*) were present in the catch throughout the entire survey range over the time series, overlaid by locations where Gulf Stream flounder were identified as prey. (c) Locations where Gulf Stream flounder were present in the catch, overlaid by locations where their stomach contents were examined. Locations where Gulf Stream flounder consumed (d) Gammaridea, (e) Polychaeta and (f) Ophiuroidea

TABLE 1 Summary of prior and current studies examining Gulf Stream flounder (*Citharichthys arctifrons*) diet for the northeast U.S. continental shelf and their methods of diet examination

Study	Sampling years	Number of stomachs	Number of tows	Regions sampled[a]	Sampling overlap	Methods
Langton and Bowman (1981)	1969–1972	387	69	MAB, SNE, GB	No, but from NEFSC BTS[b]	Microscopic
Sedberry (1983)	1976–1977	809	528	NJ, Delaware Bay	No	Microscopic
Bowman *et al.* (2000)	1977–1980	224	30	MAB, SNE, GB	Yes, NEFSC BTS[b]	Microscopic
Link *et al.* (2002)	1976–1980	219	31	MAB, SNE, GB	Yes, NEFSC BTS[b]	Microscopic
This study	1976–1980 and 2005–2012	2212 (225 from 1976–1980)	887	MAB, SNE, GB, GOM		Macro- and microscopic

[a]Geographic regions labelled as GB, Georges Bank; GOM, Gulf of Maine; MAB, Mid-Atlantic Bight; NJ, New Jersey; SNE, Southern New England.
[b]Northeast Fisheries Science Center Bottom Trawl Survey.

data were weighted by the total number of GSF caught per station to account for the two-stage cluster sampling of diet data within the stratified random sampling design of the NEFSC bottom trawl survey (Buckel *et al.*, 1999; Cochran, 1977; Latour *et al.*, 2008; Link & Almeida, 2000). A minimum number of 40 stomachs per factor level (*e.g.*, Georges Bank region or year) was considered sufficient to report comparisons based on cumulative trophic diversity curves (Belleggia *et al.*, 2008; Koen Alonso *et al.*, 2002). Seasonal comparisons were made only for spring and fall (*i.e.*, primary sampling seasons). To assess statistical differences in diet variation by season, region and year, a canonical correspondence analysis (CCA; Ter Braak, 1986) was first considered; nonetheless, a permutation test (R function anova.cca; VEGAN package; R Core Team, 2021) was used to see if the CCA axes (explanatory factors) would explain more variance of prey amounts (response variables) than expected by chance for the four predominant, identifiable prey and a separate prey category for everything else. A non-significant result suggests these factors explain minimal diet variation.

2.3 | Consumption rates for feeding footprint

Estimates of consumption (biomass removed by GSF) of Gammaridea, Ophiuroidea, Polychaeta and total prey per region (Mid-Atlantic Bight, Southern New England and Georges Bank) were made with the gastric evacuation rate method (Eggers, 1977; Elliot & Persson, 1978). A daily *per capita* consumption rate of benthos by region (r) and season (s), $C_{r,s}$, was calculated as follows:

$$C_{r,s} = 24 \cdot E_{r,s} \cdot D_{r,s}, \tag{1}$$

where 24 is the number of hours in a day. E is the seasonal evacuation rate (proportion of prey evacuated per hour) modelled for each region, and D is the seasonal mean amount of benthos eaten by region, assuming a continuous rate of feeding with 24 h sampling. D was weighted to account for cluster sampling of diet data within the stratified random sampling design of the NEFSC bottom trawl survey (Buckel *et al*., 1999; Latour *et al*., 2008; Link & Almeida, 2000), and regions with <40 GSF stomachs per season were excluded from analyses as done previously. The evacuation rate, $E_{r,s}$ was modelled as follows:

$$E_{r,s} = \alpha e^{\beta T_{r,s}}, \tag{2}$$

with ambient temperature ($T_{r,s}$) as the stratified mean bottom temperature associated with the presence of GSF from the NEFSC bottom trawl surveys per region and season (Taylor *et al*., 2005; Taylor & Bascuñán, 2000). The parameters α and β and their standard deviations in parentheses were set as 0.004 (0.00157) and 0.115 (0.022) and chosen from the literature for this general area (Durbin *et al*., 1983; Temming & Herrmann, 2003; Tsou & Collie, 2001a, 2001b).

2.4 | Scaling consumption

Following the estimation of *per capita* daily consumption rates for each region and season, those estimates were scaled up to seasonal and finally annual estimates by multiplying the number of days in each half year (182.5) and summing the half-year estimates. Data were primarily collected in the spring and fall; nonetheless, winter data (2006–2007; 201 stomachs) were included, and it was assumed that the spring/winter and fall adequately represented the entire year. Annual *per capita* consumption was scaled to a population level by including GSF population abundance. Regional population abundance was estimated as swept area abundance from survey indices (stratified mean numbers per tow) of the NEFSC seasonal bottom trawl survey assuming each tow swept an area of 0.0384 km^2 (0.0112 nautical mile^2; see also Azarovitz, 1981; NEFC, 1988; Politis *et al*., 2014). These indices accounted for vessel and gear changes over time based on calibration coefficients for GSF from Miller *et al*. (2010). Without a known catchability coefficient (q) for GSF, it was assumed to equal 1.0. Population abundance by region was represented by data collected in the fall season. Total consumption of benthos was presented as annual tonnes per region by multiplying annual *per capita* consumption by population abundance for each region.

2.5 | Benthic production

Values of benthic production (g m^{-2} year^{-1}) were obtained from production:biomass (P:B) ratios for specific benthos detailed in Collie (1985), Hermsen *et al*. (2003) and references therein (Table 2). When a range of P:B ratios were available per taxon, an average was used. For the Gammaridea, Ophiuroidea and Polychaeta considered here, P:B ratios were matched by taxonomic class, order or suborder of benthos available in the referenced literature. Mean biomass per square metre of benthos for Georges Bank and Southern New England regions of the northeast U.S. continental shelf were available in Theroux and Wigley (1998). Biomass per square metre for the suborder Gammaridea was represented by order Amphipoda. Although these data were collected seasonally from 1956 to 1965, they were assumed to be time invariant given the three shelf regions were not sampled annually. In addition, no other sampling of this scope and scale has occurred on this shelf since this effort; thus, it was assumed these data have had minimal departure from this reference. There has been minimal evidence of benthos biomass variability over time considering fish stomachs as benthic samplers of this continental shelf (Link, 2004). Notably, several benthivores of this continental shelf indicate time as the least important factor influencing diet variability (Byron & Link, 2010); thus, the authors felt this assumption was reasonable for this approach. The static values of production across time and region permitted estimates of total percentage of benthic production per square metre consumed by GSF by region.

2.6 | Uncertainty of consumption for feeding footprint

Error associated with consumption and percentage production consumed per square metre was quantified with a randomization approach. Gamma distributions for each input parameter of Equations 1 and 2 [*i.e*., amount of prey ($D_{r,s}$), α, β, temperature ($T_{r,s}$)] and

TABLE 2 Estimates of biomass (g m^{-2}), production:biomass (P:B; year^{-1}) ratios and production (P; g m^{-2} year^{-1}) for benthic prey of Gulf Stream flounder (*Citharichthys arctifrons*) by regions with available information

Benthos	Region[a]	Biomass (g m^{-2})	P:B (year^{-1})	P (g m^{-2} year^{-1})
Gammaridea	GB	5.55	2.80	15.54
	SNE	8.34	2.80	23.35
Ophiuroidea	GB	1.26	0.48	0.60
	SNE	5.41	0.48	2.60
Polychaeta	GB	7.93	2.15	17.05
	SNE	29.60	2.15	63.64

Note: Sources included: Biomass (Theroux & Wigley, 1998), and P:B (Collie, 1985; Hermsen *et al*., 2003).
[a]Regions denoted as GB, Georges Bank, and SNE, Southern New England.

GSF population abundance were simulated from 1000 random observations. Standard deviations for literature values of benthos biomass per square metre (Theroux & Wigley, 1998) were assumed to be two times mean biomass per square metre based on similar efforts for this continental shelf (ICES, 2019). Production estimates were assumed to be without error. These methods provided mean estimates of consumption with 95% C.I. The same methods were applied when considering total percentage of benthic production consumed per square metre across regions.

3 | RESULTS

3.1 | Gulf Stream flounder as prey

There were 2894 occurrences of flatfish as prey out of 679,557 stomachs sampled by the NEFSC trawl survey from 1973 to 2019. Breaking these records down, there were 1478 left-eyed flounders, 560 Pleuronectidae and 856 only identified at the level of Pleuronectiformes. GSF were the most frequently identified species of flatfish prey – accounting for 529 of the 1478 left-eyed flounder records (Figure 1b). Spiny dogfish *Squalus acanthias* (85), little skate *Leucoraja erinacea* (84), spotted hake *Urophycis regia* (71), goosefish *Lophius americanus* (61) and fourspot flounder *Paralichthys oblongus* (44) were the top-five consumers with frequency of occurrence of GSF positively identified in their diet in parenthesis. GSF were also identified in the stomachs of red hake *Urophycis chuss* (28), summer flounder *Paralichthys dentatus* (23), silver hake *Merluccius bilinearis* (23), windowpane flounder *Scophthalmus aquosus* (19), smooth dogfish *Mustelus canis* (14), white hake *Urophycis tenuis* (14), Atlantic cod *Gadus morhua* (12), winter *Leucoraja ocellata* (11), barndoor *Dipturus laevis* (9) and clearnose *Raja eglanteria* (8) skates. The second most frequently identified species of flatfish in stomachs was smallmouth flounder (*Etropus microstomus*) occurring just over half as many times as GSF with 278 positive identifications.

3.2 | What Gulf Stream flounder eat

Two hundred twenty-five GSF stomachs collected from 1976 to 1980 and 1987 stomachs collected from 2005 to 2012 were examined for a total of 2212 stomachs from GSF with standard lengths ranging from 2 to 20 cm (average 11.3 cm) (Figure 1c). By season, 1105 of the total stomachs were obtained during the fall, and 826 during the spring (Table 3). Stomachs examined during summer (49) and winter (232) were not included in this analysis due to inconsistent coverage during those seasons. Regionally, 576 samples came from the Mid-Atlantic Bight, 1223 from Southern New England, 395 from Georges Bank and 10 from the Gulf of Maine (excluded from regional analysis due to small sample size). The total number of stomachs sampled was greater due to some samples falling outside of these designated factor levels. For all samples analysed together, the top-five prey categories by percentage diet by mass were 24.97% unidentifiable Animalia, 24.14% Gammaridea, 22.49% Polychaeta, 9.58% Crustacea and 3.7% Ophiuroidea. The same five prey categories comprised the top-5 % frequency of occurrence in a slightly different order: 23.73% Gammaridea, 17.18% Polychaeta, 16.37% Animalia, 5.43% Crustacea and 4.34% Ophiuroidea.

Table 3 lists percentage diet by mass and frequencies of occurrence for prey categories by season, region and year. Animalia, Gammaridea and Polychaeta were the dominant prey categories (by mass and frequency) during both spring and fall seasons and in all three regions. In spring, Ophiuroidea was the fourth most common prey category. Nonetheless, in fall, Crustacea was the fourth prey category with Ophiuroidea of lesser importance. Gammaridea and Polychaeta were consumed throughout GSF's range (Figure 1d,e), whereas the majority of Ophiuroidea were found in stomachs from the Southern New England region (Figure 1f). Annual trends in prey composition had high percentages of Gammaridea and Polychaeta for most years, with some variation in the other predominant prey between years (Table 3). Figure 2 shows the top-five prey categories by percentage diet composition by mass and percentage frequency of occurrence over the time series. The data show Animalia percentages were higher from 2005 through 2010, whereas the rest of the categories change little from year to year. Permutation test results for running canonical correspondence analysis (full model) revealed that these factors did not significantly explain more variance than variance due to random chance for diet by mass (999 permutations; DF $= 4, 12$; $F = 2.93$; $P = 0.06$) and frequency of occurrence (999 permutations; DF $= 4, 12$; $F = 2.34$; $P = 0.08$).

3.3 | Quantity of benthos consumed

The total annual amount of prey consumed by GSF was 72.74 (+123.39, −52.68) t for Georges Bank, 98.61 (+167.53, −72.29) t for Mid-Atlantic Bight and 559.67 (+797.35, −399.29) t for Southern New England (Figure 3). Consumption of predominant prey: Gammaridea [159.79 (+279.05, −122.22) t], Ophiuroidea [23.56 (+49.83, −19.53) t] and Polychaeta [136.82 (+269.67, −106.07) t] in Southern New England were higher by comparison with the two other regions. On Georges Bank and the Mid-Atlantic Bight, GSF consumed a total of 55.61 t per year of these three predominant prey taxa. Considering the distribution of GSF on this continental shelf, the population abundance used to scale these consumption estimates was 2.1 times greater in Southern New England (35,532,381 individuals) *vs*. Mid-Atlantic Bight (16,737,062 individuals) and 4.0 times greater than the population abundance on Georges Bank (8,894,645 individuals). Relative to the production (g m^{-2} $year^{-2}$) of Gammaridea, Ophiuroidea and Polychaeta available on Georges Bank and Southern New England, the percentage of production consumed per square metre per year by GSF was a maximum of 0.01 (+0.03, −0.01) % each for gammarids and ophiuroids consumed in Southern New England and minimums of 0.001 (+0.002, −0.001) % each for gammarids and

TABLE 3 Number of stomachs sampled, and percentage prey composition by mass followed by percentage frequency of occurrence in parentheses for each factor level with at least 10 Gulf Stream flounder (*Citharichthys arctifrons*) stomachs

	Fall	Spring	Gulf of Maine *	GeorgesBank	Southern New England	Mid Atlantic Bight	1978	1979 *	1980	2005	2006	2007	2008	2009	2010	2011	2012	All samples
# Stomachs	1105	826	10	395	1223	576	122	26	67	143	351	255	125	342	251	161	359	2212
Amphipoda	3.19 (1.27)	0.23 (0.36)		0.99 (1.52)	2.38 (0.74)	0.09 (0.69)	4.13 (1.64)				4.19 (1.42)	0.3 (1.18)	0 (0.8)	6.27 (1.17)		0.34 (0.62)	0.02 (0.84)	2.07 (0.86)
Anthozoa	0.01 (0.18)	0 (0.12)			0 (0.08)	0.07 (0.35)	4.58 (1.64)										0 (0.28)	0.01 (0.14)
Animalia	14.53 (14.12)	37.45 (18.04)	0 (30)	61.04 (18.23)	19.46 (15.54)	43.78 (16.67)	5.5 (9.02)	0 (3.85)	5.19 (16.42)	15.84 (15.38)	54.4 (20.23)	37.51 (22.75)	39.55 (21.6)	32.32 (23.98)	74.56 (19.12)	2.02 (7.45)	0.84 (3.9)	24.97 (16.37)
Arthropoda		0.01 (0.12)		0.06 (0.25)												0.02 (0.62)		0 (0.05)
Asteroidea	1.53 (0.36)	0.04 (0.36)		0.02 (0.25)	1.06 (0.49)								0.18 (0.8)	3.17 (0.88)	0.11 (1.2)			0.88 (0.32)
Bivalvia	0 (0.18)	3.52 (1.21)		0.03 (0.51)	1.67 (0.74)	0.05 (0.17)		4.58 (3.85)					0.8 (0.8)	4.62 (0.29)	0.83 (2.39)	0.05 (0.62)	0 (0.56)	1.4 (0.54)
Cancridae	0.06 (1.45)	0 (0.12)		0.17 (0.76)	0.01 (0.9)	1.21 (0.69)	5.34 (5.74)	6.71 (19.23)	0 (1.49)	0.06 (0.7)	1.49 (0.57)					0.04 (0.62)	0.02 (0.28)	0.12 (0.81)
Caprellidae	0.03 (0.36)	0.52 (0.85)		0 (0.25)	0.27 (0.65)	0 (0.35)	0 (0.82)		0 (1.49)		0.17 (0.28)	0.51 (0.78)		0.71 (0.58)		0.02 (0.62)	0.02 (0.84)	0.22 (0.5)
Cephalopoda		0 (0.12)			0 (0.08)								0.1 (0.8)					0 (0.05)
Copepoda	0.01 (1.09)	0 (0.36)		0 (1.52)	0 (0.74)	0.05 (0.17)	0 (5.74)	0 (3.85)		0.14 (0.7)		0.05 (0.39)				0 (0.62)	0 (1.39)	0.01 (0.72)
Crangonidae	2.35 (1.9)	0.43 (1.33)		0.79 (1.77)	1.62 (1.64)	1.28 (1.22)		0 (7.69)		38.39 (2.8)	0.34 (0.57)	1.67 (1.57)	8.74 (4)	0.41 (0.58)	0.09 (0.8)	0.36 (3.73)	0.31 (1.95)	1.52 (1.54)
Crustacea larvae		0 (0.12)				0 (0.17)											0 (0.28)	0 (0.05)
Crustacea shrimp	1.4 (3.8)	0.41 (1.21)		3.79 (2.28)	0.81 (2.37)	2.52 (3.82)					4.58 (2.85)	1.01 (0.78)	2.41 (4)	0.27 (2.05)	0.22 (1.2)	1.7 (3.73)	1.6 (7.52)	1.2 (2.71)
Crustacea	14.03 (6.79)	4.15 (5.08)	19.28 (10)	3.7 (6.08)	10.84 (5.07)	2.73 (5.73)	2.1 (2.46)	0 (11.54)	1.31 (5.97)	1.51 (4.2)	1.01 (4.27)	3.08 (3.14)	1.94 (5.6)	0.01 (2.92)	6.08 (5.58)	28.28 (9.94)	5.14 (8.64)	9.58 (5.43)
Cumacea	0.57 (2.71)	0.25 (2.78)		0.12 (3.29)	0.47 (2.78)	0.24 (2.26)	4.58 (7.38)	4.58 (23.08)	0 (11.94)	0.01 (0.7)	0.01 (0.28)	0.16 (0.39)	0.57 (2.4)	1.03 (1.46)	0.07 (0.8)	0.07 (4.35)	0.51 (5.01)	0.43 (2.76)
Decapoda	0.26 (0.63)	0.01 (0.12)		0.13 (1.27)	0.17 (0.33)		0 (0.82)				0.02 (0.28)	0.65 (2.35)			1 (0.4)			0.16 (0.41)
Decapoda crab	3.98 (2.62)	0.38 (0.48)		1.62 (1.77)	2.55 (1.88)	1.68 (1.04)	5.82 (4.92)	1.78 (23.08)	0 (4.48)	0.19 (0.7)		2.36 (0.78)	1.04 (1.6)	0.64 (0.88)	0.12 (0.4)	7.88 (3.11)	0.13 (1.95)	2.4 (1.63)
Decapoda larvae	0.02 (0.54)	0 (0.12)		0.09 (0.76)	0 (0.25)	0.04 (0.52)	0.2 (1.64)	13.74 (7.69)	0 (1.49)				0.27 (0.8)	0 (0.29)			0 (0.56)	0.01 (0.41)
Decapoda shrimp	0 (0.18)	0 (0.12)		0 (0.25)		0.03 (0.52)	0 (0.82)		0 (1.49)					0 (0.29)				0 (0.18)
Euphausiidae	0.88 (1.54)	0.13 (0.24)		0.72 (1.01)	0.57 (1.23)	1.73 (0.69)	0.81 (0.82)			3.29 (1.4)	0.13 (0.28)	5.05 (1.96)	0.24 (0.8)	1.22 (2.05)	0.43 (0.8)	0.02 (0.62)	0.23 (0.84)	0.68 (1.04)
Fish larvae					0 (0.08)		0.81 (0.82)											0 (0.05)

TABLE 3 (Continued)

	Fall	Spring	Gulf of Maine *	GeorgesBank	Southern New England	Mid Atlantic Bight	1978	1979 *	1980	2005	2006	2007	2008	2009	2010	2011	2012	All samples
Fish scales	0.04 (0.18)			0.07 (0.25)		0.2 (0.17)									0.12 (0.4)		0.03 (0.28)	0.02 (0.09)
Gadidae					0 (0.08)			6.24 (3.85)										0 (0.05)
Gammaridea	28.76 (24.16)	18.41 (23.73)	8.43 (10)	12.81 (28.1)	26.38 (21.42)	12.95 (25.87)	17.31 (38.52)	17.45 (73.08)	14.68 (47.76)	23.43 (16.78)	10.55 (12.25)	22.28 (18.43)	26.09 (21.6)	19.84 (16.37)	3.65 (17.53)	43.82 (30.43)	22.37 (37.6)	24.14 (23.73)
Gastropoda		0.01 (0.12)				0.04 (0.17)				0.11 (0.7)								0 (0.05)
Hydrozoa	0 (0.09)	0 (0.12)			0 (0.08)	0 (0.35)	0 (0.82)									0 (0.62)	0 (0.28)	0 (0.14)
Hyperiidae	0.3 (1.45)	0 (0.61)		0.02 (0.25)	0.03 (0.74)	1.9 (2.08)	0 (1.64)			0.33 (1.4)	0.11 (0.57)	5.72 (1.96)		0.02 (0.88)			0.03 (2.23)	0.18 (0.99)
Isopoda	0.01 (0.45)	0.56 (1.09)	19.28 (10)	0 (0.25)	0.21 (0.74)	1.6 (0.69)				2.98 (0.7)	1.19 (0.28)		0.08 (0.8)			0.03 (1.24)	0.7 (2.79)	0.3 (0.68)
Miscellaneous materials	0.11 (1.27)	0 (1.57)	9.64 (10)	0 (0.25)	0.06 (0.98)	0.16 (2.43)			0 (1.49)	0.64 (1.4)	0 (0.57)		0.08 (1.6)	0.11 (1.75)	0 (1.2)	0 (0.62)	0.06 (3.06)	0.06 (1.27)
Mollusca	0.01 (0.09)	0.01 (0.24)			0.01 (0.25)					0.19 (0.7)	0.03 (0.28)					0.01 (0.62)		0.01 (0.14)
Mysidae	0.3 (1.81)	1.59 (1.82)	33.73 (30)	0.51 (1.52)	0.51 (1.55)	4.27 (1.56)	0 (0.82)			1.75 (0.7)		1.77 (1.96)	2.15 (1.6)	0.23 (0.29)	0.03 (0.8)	0 (1.24)	3.19 (6.41)	0.81 (1.67)
Ophiuroidea	0.55 (1.99)	7.91 (7.63)		1.79 (2.28)	4.21 (6.95)	0.35 (0.35)	5.49 (9.02)	0 (3.85)	12.43 (11.94)	1.27 (3.5)	6.84 (4.84)	1.28 (3.53)	2.35 (2.4)	8.77 (4.39)	1.57 (3.59)	0.86 (2.48)	1.69 (3.9)	3.7 (4.34)
Osteichthyes	2.95 (0.36)	0.02 (0.24)			2 (0.33)	0.12 (0.35)						0.11 (0.39)	0.72 (1.6)			6.25 (0.62)	0.01 (0.56)	1.68 (0.27)
Other	0.25 (4.16)	1.78 (3.75)		0.19 (2.53)	0.87 (2.04)	1.34 (7.12)							0.36 (2.4)	0.1 (4.97)	0.04 (2.39)	0.43 (9.94)	3.57 (9.75)	0.85 (3.48)
Paguridae	0 (0.09)			0 (0.25)												0 (0.62)		0 (0.05)
Pandalidae	0.05 (0.18)	0.06 (0.12)			0.06 (0.25)					0.62 (0.7)	0.49 (0.57)							0.05 (0.14)
Plankton	0 (0.09)					0 (0.17)										0 (0.62)		0 (0.05)
Polychaeta	23.73 (14.93)	22.11 (21.79)	9.64 (10)	11.3 (14.18)	23.75 (18.4)	21.32 (16.84)	22.42 (29.51)	44.91 (46.15)	66.4 (31.34)	9.13 (6.99)	14.43 (7.41)	15.93 (10.59)	12.33 (12)	20.27 (14.04)	11.09 (15.14)	7.8 (22.98)	59.52 (30.36)	22.49 (17.18)
Thecosomata	0.01 (0.09)			0.04 (0.25)						0.12 (0.7)								0 (0.05)
Stomatopoda	0.07 (0.36)				0.03 (0.25)	0.26 (0.17)	20.91 (2.46)					0.55 (0.39)						0.04 (0.18)

Note: Factor levels marked with an * were excluded from analyses. Prey category "Other" includes unidentified invertebrata and "Miscellaneous materials" includes rock, sand, Animalia tubes.

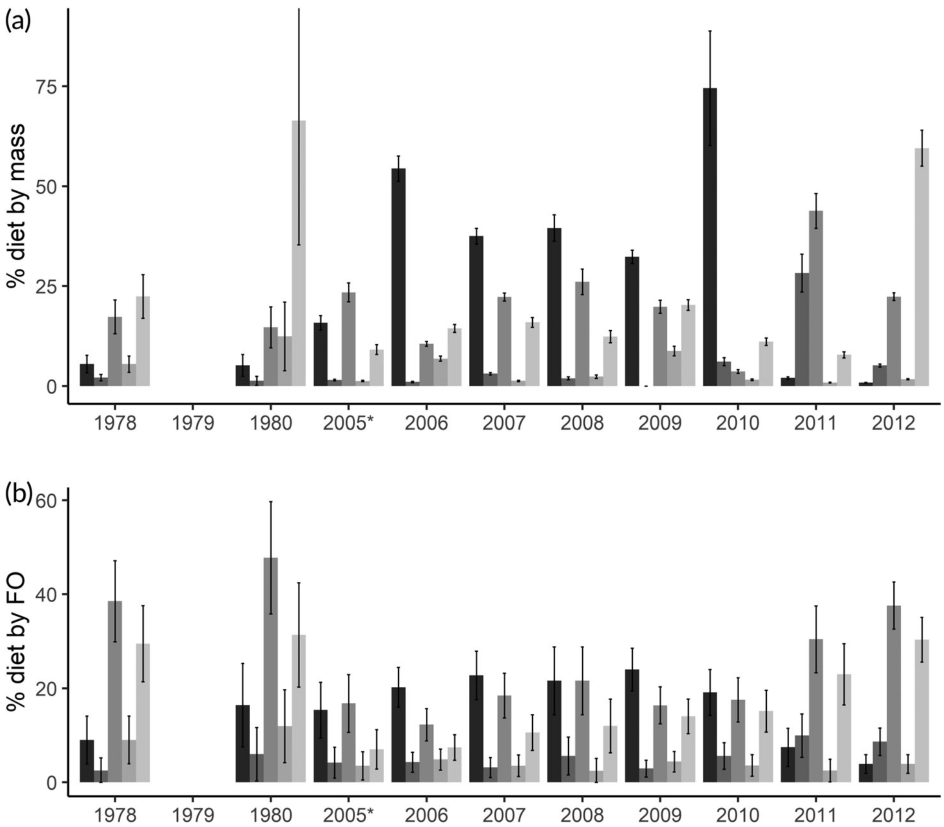

FIGURE 2 Annual comparison of the top-five prey categories consumed by Gulf Stream flounder (*Citharichthys arctifrons*) by (a) percentage diet by mass and (b) percentage diet by frequency of occurrence (FO). Error denoted by 95% C.I. Break in time series between years 1980 and 2005 denoted by "*". Animal remains, Crustacea, Gammaridea, Ophiuroidea, Polychaeta

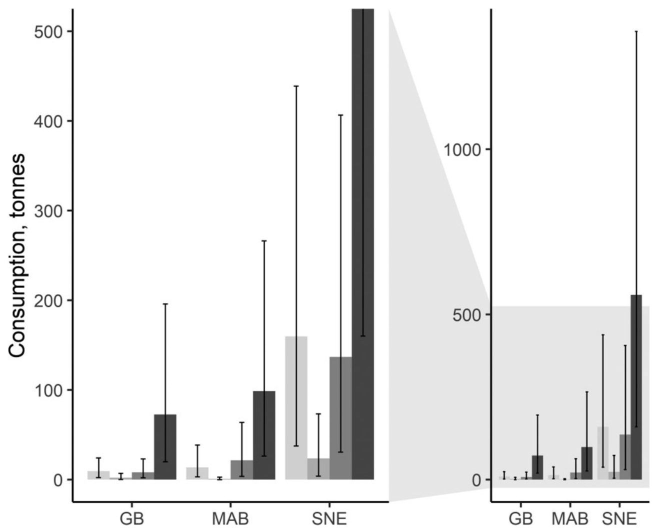

FIGURE 3 Estimates of annual consumption (tonnes) of prey removed by Gulf Stream flounder (*Citharichthys arctifrons*) for benthic taxa and the total prey consumed by region. Regions labelled as GB, Georges Bank; MAB, Mid-Atlantic Bight; and SNE, Southern New England. Error denoted by 95% C.I. Gammaridea, Ophiuroidea, Polychaeta, Total prey

polychaetes consumed on Georges Bank. For reference, GSF consumed 0.008 (+0.019, −0.007) % of the production m^{-2} $year^{-1}$ of ophiuroids on Georges Bank and 0.003 (+0.007, −0.003) % of polychaete production m^{-2} $year^{-1}$ in Southern New England.

4 | DISCUSSION

4.1 | Gulf Stream flounder as prey

Unidentified and miscellaneous fishes are the fourth most frequently identified prey category by occurrence in the NEFSC Food Habits database (Smith & Rowe, 2021). The unique body shape of flatfish can make identification beyond that of unidentified bony fish (Teleostei) possible, even in a well-digested state. GSF account for 18.3% of identified flatfish prey on the northeast U.S. continental shelf, indicating GSF are a notable flatfish prey for groundfish predators sampled in this ecosystem. Considering their relatively small body size which permits capture and may digest faster than other flatfish in the survey range, more GSF were likely to have been present as prey but only confidently identified to the level of left-eyed flounders or Pleuronectiformes. In fact, very well-digested GSF may have only been identified to the level of Teleostei and were therefore excluded entirely from the estimate of flatfish in diets. On the contrary, their bony snout withstands digestion to some degree, providing a means for easier identification over other flatfish in the same state of digestion under ideal dissection conditions. Regardless, the percentage of GSF prey relative to other flatfish in this ecosystem illustrates their importance as a food source to higher-level fishes while their 17.7 cm maximum standard length keeps them in an easily consumed size class for much, if not all, of their life history. Sedberry (1983) noted in the summer, offshore Mid-Atlantic Bight and Southern New England, GSF were a primary diet component for large red hake (>300 mm SL). The present study documents a wide variety of commercially valuable fish that feed on GSF. Although spiny dogfish was the species with the most documented predation, collectively gadids (spotted hake, red hake, silver hake, white hake and cod) were regular GSF consumers. Collectively, skates (little, clearnose, winter and barndoor) had over 100 occurrences of GSF in stomachs. Left-eyed flounders of the northeast U.S. continental shelf are often piscivorous (Smith & Link, 2010); therefore it also wasn't surprising to find fourspot, summer and windowpane among the top GSF consumers.

4.2 | What Gulf Stream flounder eat

Gammarids, polychaetes, other crustaceans and brittle stars were the prey most frequently consumed by GSF. Link *et al*. (2002) noted prey composition was consistent across time for flatfish that consumed primarily polychaetes and gammarids, so it was not surprising gammarids and polychaetes were top prey for GSF in this study across all three regions, seasons and years sampled. This study found GSF diets to be in general agreement with results of previous studies (Bowman *et al*., 2000; Langton & Bowman, 1981; Link *et al*., 2002; Sedberry, 1983).

Considering GSF's small body size, it wasn't surprising well-digested Animalia was commonly recorded as prey during macroscopic identification as the experience level of the examiner, size of prey, digestive state, time constraints and at-sea working conditions during 2005–2010 may have led to lower taxonomic resolutions. It is reasonable to assume a portion of the Animalia prey category included other important prey such as gammarids and polychaetes. Similar prey categories were reported by Link *et al*. (2002) with a subset (late 1970s) of the data included here: polychaetes and gammarids were the dominant prey items followed by other crustaceans. Other studies document similar results, but with more Annelids (Langton & Bowman, 1981) or leading with Polychaeta followed by non-decapod crustaceans (Bowman *et al*., 2000). Although the top-prey categories in this study coincide with that of previous studies, the authors observed less Polychaeta. It is possible well-digested small polychaetes were observed in this study but classified as Animalia during macroscopic examination.

Geographic, seasonal and year-to-year variation in GSF diet was mostly low as documented here with minimal variation explained by these factors relative to random chance. Gammarids were eaten throughout the sampling range. Polychaetes were consumed through the majority of the range with a shift towards more in offshore waters. Ophiuroidea consumption primarily occurred offshore Southern New England in spring at depths from 71 to 155 m, often nearing the shelf edge. Similar to the results of this study in Southern New England, Langton and Bowman (1981) and Bowman *et al*. (2000) observed polychaetes more frequently than gammarids, whereas Bowman *et al*. (2000) also documented Ophiuroidea as prey. This is not surprising as Theroux and Wigley (1998) documented the Southern New England region as good Ophiuroidea habitat in the 1950s to 1960s. Increased availability of Ophiuroidea may explain their increase in GSF's diet in the Southern New England region and further supports the use of fish stomachs as a form of benthic sampler (Frid & Hall, 1999; Lilly & Parsons, 1991; Link, 2004). GSF's small mouth limits the size of prey they are capable of consuming. The average length of those consuming Ophiuroidea was 13.3 cm, and it's possible the Ophiuroidea size class most suitable as prey for GSF's gape size is most abundant in spring when they were consumed in noticeably greater amounts. Increased Ophiuroidea consumption in spring may be due to a combination of seasonal recruitment patterns, as demonstrated for *Ophiura* spp. in the North Sea (Reiss & Kroncke, 2005), and possible habitat shifts of adult GSF offshore. Link *et al*. (2002) note that there are few flatfish (*e.g*., American Plaice *Hippoglossoides platessoides*) that specialize in the consumption of ophiuroids, and document them as comprising 3%–4% of GSF's diet. In the Mid-Atlantic, Langton and Bowman (1981) and Bowman *et al*. (2000) agreed polychaetes and gammarids were prey of high importance with polychaetes representing a greater proportion of the diet than gammarids. On Georges Bank, gammarids and polychaetes were the dominant identifiable prey in all three studies although Langton and Bowman (1981) found more Amphipoda and Bowman *et al*. (2000) found higher percentages of polychaetes. It would be worthwhile to further examine GSF feeding by depth (*e.g*., inshore *vs*. offshore), but to some degree this may be reflected in seasonal variation in GSF distribution and may require additional sampling to address feeding with greater detail. Few annual trends were observed in the current study primarily due to prey taxonomic resolution being higher in lab with the aid of a microscope. An annual comparison of the five most prevalent prey categories indicates Animalia as the dominant prey both by mass and frequency of occurrence from 2005 to 2010. For 1978, 1980 and 2012, Polychaeta was the dominant prey category as percentage composition by weight, whereas Gammaridea was the most frequently observed prey during the same period. Ophiuroidea was a relatively consistent prey category of lower importance throughout the entire sampling period.

Diet sampling of small fish predators presents many challenges. Over 85% of GSF in this study were 7–16 cm which represented adequate sampling given their limited size range, but with a narrow window of variation in mouth gape width, GSF size was not included as a factor in addressing diet variation. It would be worthwhile to examine diet by GSF size, although it is suggested one use a higher level of prey taxonomic resolution than that considered here. Another challenge was visually identifying small, digested invertebrate prey. Animalia was recorded less often during the early and late years coinciding with time periods where contents were preserved and analysed microscopically. The increase in Animalia along with the decrease in Polychaeta and Gammaridea from 2005 to 2010 is an artefact of prey taxonomic resolution. During this period, the majority of stomachs were examined macroscopically at sea, making it less likely that the small prey of GSF were able to be positively identified. In the lab, microscopic analysis of preserved fish stomachs allowed classification to a finer taxonomic level, decreasing the occurrence of Animalia and subsequently increasing the percentage diet composition of finer taxonomic classification levels as seen in 1978, 1979, 2011 and 2012. During the same period the authors saw a decrease in Gammaridea, which was not entirely unexpected, as gammarids were occasionally identified to the level of family (Corophiidae) and even species (*Byblis serrata*) with a microscope. Interestingly, Ophiuroidea was present in all years with no observable trend. The arms of Ophiuroidea tend to quickly break apart into individual shields after consumption, yet maintain a unique texture that can assist with macroscopic identification. Even though taxonomic resolution and mass precision were greater for minute prey in the lab, diets determined macroscopically at sea were similar to diets determined in the lab. Nonetheless, for small predators such as GSF with mainly minute benthic invertebrate prey, in-lab microscopic examination of stomachs is ideal for greater precision with prey mass and greater taxonomic resolution.

Rebuilding managed fish stocks for the northeast U.S. continental shelf and around the world is a long-term objective (Murawski, 2010; Wiedenmann & Mangel, 2006; Worm *et al*., 2009). With this come questions regarding overlapping resources such as availability of prey and habitat for fishes (ecological pressures) and commercial harvesting (anthropogenic pressures). As documented here, GSF is a strict benthivore, consuming mostly small benthic invertebrates on the order of tens and hundreds of tonnes of benthos eaten each year within several regions of this continental shelf. Relative to estimates of benthic production of their primary prey for Georges Bank and Southern New England, the percentage of production consumed by GSF was minimal at 0.01% or less. It is understood that these estimates are likely minimums based on the assumptions made regarding GSF catchability for population abundance and subsequent modelling of consumption and percentage of production consumed. Even so, GSF is not believed to be a substantial driver of benthic biomass per square metre for this continental shelf; nonetheless, this metric was quantified for a larger predator field of benthivores (including GSF) resulting in >5% of production eaten per square metre for Ophiuroidea, >15% of Isopoda and >30% of Anthozoa for specific geographic regions (ICES, 2019). With existing plans to rebuild managed fish stocks, understanding ecosystem demands (*i.e*., predation) is critical, particularly with potential increases in sharing marine benthic habitat associated with commercial harvesting (*i.e*., bottom fishing), fish prey and changes to prey biogeography relative to climate or other environmental drivers (Roberts *et al*., 2017; Spalding *et al*., 2014).

Although challenging, understanding the food web roles of specific species or large trophic groups within a marine community plays an important role in understanding the northeast U.S. continental shelf ecosystem (see Link *et al*., 2010; Smith *et al*., 2016; Smith & Smith, 2020). GSF is unique in that it is a notable flatfish prey, a benthivore with narrow feeding preferences, and has previously received little attention. This study further defines the role of GSF within the food web of the northeast U.S. continental shelf, and given major ecological (climate; Nye *et al*., 2009, 2013) and anthropogenic (fishing; Blenckner *et al*., 2015; Litzow *et al*., 2014) drivers of ecosystems, this information can provide a stronger footing for managing overlap among living marine resources.

AUTHOR CONTRIBUTIONS

S.R. and B.E.S. made equal contributions to all aspects of this work including concepts, data handling, analysis and manuscript preparation.

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