Abstract—The stomachs of 819 Atlantic bluefin tuna (*Thunnus thynnus*) sampled from 1988 to 1992 were analyzed to compare dietary differences among five feeding grounds on the New England continental shelf (Jeffreys Ledge, Stellwagen Bank, Cape Cod Bay, Great South Channel, and South of Martha's Vineyard) where a majority of the U.S. Atlantic commercial catch occurs. Spatial variation in prey was expected to be a primary influence on bluefin tuna distribution during seasonal feeding migrations. Sand lance (*Ammodytes spp.*), Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), squid (Cephalopoda), and bluefish (*Pomatomus saltatrix*) were the top prey in terms of frequency of occurrence and percent prey weight for all areas combined. Prey composition was uncorrelated between study areas, with the exception of a significant association between Stellwagen Bank and Great South Channel, where sand lance and Atlantic herring occurred most frequently. Mean stomach-contents biomass varied significantly for all study areas, except for Great South Channel and Cape Cod Bay. Jeffreys Ledge had the highest mean stomach-contents biomass (2.0 kg) among the four Gulf of Maine areas and Cape Cod Bay had the lowest (0.4 kg). Diet at four of the five areas was dominated by one or two small pelagic prey and several other pelagic prey made minor contributions. In contrast, half of the prey species found in the Cape Cod Bay diet were demersal species, including the frequent occurrence of the sessile fig sponge (*Suberites ficus*). Prey size selection was consistent over a wide range of bluefin length. Age 2–4 sand lance and Atlantic herring and age 0–1 squid and Atlantic mackerel were common prey for all sizes of bluefin tuna. This is the first study to compare diet composition of western Atlantic bluefin tuna among discrete feeding grounds during their seasonal migration to the New England continental shelf and to evaluate predator-prey size relationships. Previous studies have not found a common occurrence of demersal species or a predominance of Atlantic herring in the diet of bluefin tuna.

Manuscript accepted 21 September 2001.
Fish. Bull. 100:168–180 (2002).

Differences in diet of Atlantic bluefin tuna (*Thunnus thynnus*) at five seasonal feeding grounds on the New England continental shelf*

Bradford C. Chase
Massachusetts Division of Marine Fisheries
30 Emerson Avenue
Gloucester, Massachusetts 01930
E-mail address: brad.chase@state.ma.us

Atlantic bluefin tuna (*Thunnus thynnus*) are widely distributed throughout the Atlantic Ocean and have attracted valuable commercial and recreational fisheries in the western North Atlantic during the latter half of the twentieth century. The western North Atlantic population is considered overfished by the International Commission for the Conservation of Atlantic Tunas (NMFS, 1999). Bluefin tuna are the largest scombrid species, and the largest teleost occurring in the Gulf of Maine (Bigelow and Schroeder, 1953). Bluefin tuna migrate to coastal waters off New England during warmer months, feeding on local concentrations of prey. This migration supports a major component of the U.S. Atlantic commercial fishery for bluefin tuna; from 1978 to 1992 New England accounted for between 73% and 98% of annual commercial landings (Chase, 1992; and NMFS, 1995). Substantial annual variation has been seen in the harvest locations on the New England continental shelf (Chase, 1992). Spatial variation in prey populations is suspected to be the primary influence on these annual aggregations of bluefin tuna. Adaptations in the circulatory system of the bluefin tuna allow these fish to retain metabolic heat, facilitating the regulation of body temperature (Carey and Teal, 1969) and assisting in the efficient transfer of energy from consumed prey to fast growth rates and large body size. These adaptive features also allow bluefin tuna to make extensive migrations into cold-temperate waters in search of prey. Diet information is necessary to improve the understanding of seasonal movements of bluefin tuna and predator-prey relationships in the New England continental shelf region, and as a baseline for bioenergetic analyses. Information on the feeding habits of this economically valuable species and apex predator in the western North Atlantic Ocean is limited, and nearly absent for the seasonal feeding grounds where most U.S. Atlantic commercial catches occur.

Previous food habit studies have shown that western North Atlantic bluefin tuna are opportunistic feeders on a wide variety of finfish, cephalopods, and crustaceans (Crane, 1936; Krumholz, 1959; Dragovich, 1970; Mason, 1976; Holliday, 1978; Eggleston and Bochenek, 1990; Matthews et al.[1]). Pinkas (1971) reported similar results for Pacific bluefin tuna (*Thunnus thynnus orientalis*). These bluefin tuna food habit studies either reported on small numbers of samples or were qualitative studies on samples distributed over a broad geographic range. Previous studies have not evaluated size relationships between bluefin tuna and their prey and the amount of food consumed. The present study targeted regions of the New England giant tuna (>140 kg) fishery to quantitatively analyze stomach contents of bluefin tuna among discrete seasonal feeding grounds and to investigate predator-prey size relationships for this species in the Gulf of Maine.

* Contribution 3 of the Massachusetts Division of Marine Fisheries, Gloucester, MA 01930.

[1] Matthews, F. D., D. M. Damkaer, L. W. Knapp, and B. B. Collette. 1977. Food of western North Atlantic tunas (*Thunnus*) and lancetfish (*Alepisaurus*). Nat. Oceanic Atmos. Admin. Tech. Rep. NMFS SSRF-706, Washington, D.C., 19 p.

Materials and methods

Study area

Five fishery areas (Jeffreys Ledge, Stellwagen Bank, Cape Cod Bay, Great South Channel, and South of Martha's Vineyard [Fig. 1]) were selected for their traditional association with the bluefin fishery and because geographic and bathymetric differences among areas could result in distinct prey communities. The northernmost area, Jeffreys Ledge, is a major bathymetric feature in the Gulf of Maine and is important for commercial fisheries from northern Massachusetts, New Hampshire, and southern Maine. Stellwagen Bank is a distinct bathymetric ridge located on the eastern boundary of Massachusetts Bay (DOC[2]) that provides close access for ports from Gloucester to Cape Cod. Cape Cod Bay is a large, relatively shallow Gulf of Maine bay that is semi-enclosed on three sides by the land mass of Cape Cod and the south shore of Massachusetts. The two southern areas, Great South Channel and the area south of Martha's Vineyard, are larger regions with less distinct bathymetric features and are separated by Nantucket Shoals. The Great South Channel covers a wide nearshore region running east of Chatham and Nantucket and is bordered by the slopes of Nantucket Shoals on the west. The area south of Martha's Vineyard is located on the continental shelf off southern New England and is distinguished from the other areas by its warmer water, predominance of smaller bluefin tuna (<50 kg), and the seasonal occurrence of other large pelagic fish, such as marlins and tropical tunas.

Commercial catch records and trawl survey indices of abundance indicate that Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) are the principal pelagic fish species for all these study areas (Clark and Brown, 1976; and NOAA, 1998). Atlantic herring occur in lower relative abundance in the region south of New England than in northern regions. Jeffreys Ledge and Great South Channel are primary spawning locations for Atlantic herring. Catch records and trawl survey indices indicate that the following prey species have been abundant in the study areas: silver hake (*Merluccius bilinearis*), butterfish (*Peprilus triacanthus*), northern shortfin squid (*Illex illecebrosus*), and longfin inshore squid (*Loligo pealeii*).

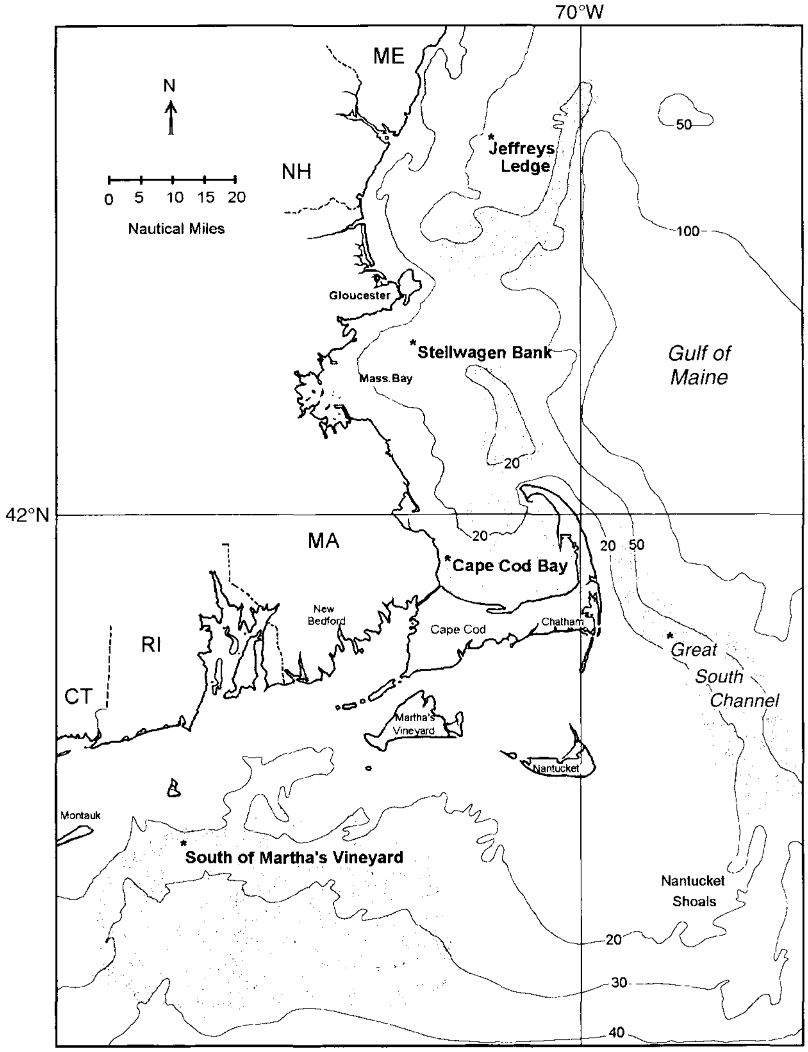

Figure 1

Map of the five bluefin tuna feeding grounds used as study areas (★) July–October 1988–92. Depths are given in fathoms.

Sample collection and analysis

Bluefin stomach samples were collected primarily from commercial landings at ports in Massachusetts during the 1988–92 seasons (July–October). Sportfishing tournaments were a secondary source of stomach samples. Handgear landings (rod and reel, handline, and harpoon) were primarily collected in Gloucester and Cape Cod. Purse-seine landings were also a large source of samples, and were collected in Gloucester, New Bedford, and Cape Cod. A majority of stomach samples was collected during 1989 and 1990. A reduced number of samples after 1990 was influenced by the increasing practice of gutting bluefin at sea to sustain a quality product for the sashimi export market.

Most samples were collected at the docks and processing locations of commercial tuna buyers. The vessel captain or tuna buyer was interviewed for location of catch.

[2] DOC (Department of Commerce). 1991. Stellwagen Bank National Marine Sanctuary, Draft environmental impact statement/ management plan. U.S. Dep. Commerce (DOC), Nat. Oceanic Atmos. Adm., Sanctuaries and Reserves Division, Washington, D.C., 238 p.

The curved fork length (CFL) and weight of the catch were recorded from the National Marine Fisheries Service (NMFS) tuna logbook. Stomachs were removed by cutting the esophagus above the pylorus and were stored on ice until analysis later that day or were frozen for analysis at a later date. Stomach samples were typically removed from bluefin tuna the day of capture, except those from purse-seine landings, where the catch was often submerged in ice for one or two days prior to landing.

Stomach contents were identified to the lowest possible taxon and weights and counts were made of individual prey species. Wet weights of prey were measured with Homs tubular scales (±5 g) after contents were rinsed through a standard testing sieve (2.00-mm mesh). Prey counts were made only when all individual prey items could be identified and counted for a given stomach sample. Because bluefin tuna consume relatively large prey items and swallow prey whole, species identification was possible for nearly all contents. Skeletal remains were compared with the skeletons of known specimens to assist with identification. Fish contents that could not be identified were categorized as "unidentified fish." Otoliths, squid beaks, and skeletal traces less than 5 g were rounded up to a minimum weight of 5 g.

Stomach-contents data were analyzed by frequency of occurrence, percent composition by number, and percent composition by weight for each prey item (Hyslop 1980; Bowen 1986). Frequency of occurrence can indicate prey composition and availability, and number and weight percentages can represent the quantity a prey item contributes to a diet. "Stomach-contents biomass" refers to all prey in stomach contents, and "prey weight" refers to the weight of individual prey species.

Stomach samples were assigned a status of "empty," "chum," "chum and prey," or "prey only." Chum refers to cut pieces of bait fish that fishermen use to attract bluefin. Both empty and chum stomach samples were eliminated from further data analysis. For "chum and prey" stomachs, chum weight was eliminated from the analysis, and prey weight was included because chum and natural prey were easily distinguished in bluefin tuna stomachs. When the status of contents, or the veracity of catch location could not be resolved, the samples were eliminated from the analysis.

Statistical analysis

Stomach-contents biomass data were analyzed to determine differences among the five fishery areas. Prey weight data were tested for normality (Shapiro and Wilk, 1965) and equality of variance (BMDP, 1990). Stomach-contents biomass data were transformed to natural logarithms and tested for area differences by using the Brown-Forsythe test for unequal variances and the Welch test for pairwise comparisons of areas (BMDP, 1990).

The species composition of stomach contents were tested among areas with the Spearman rank correlation test, under the null hypothesis of no association between species composition and feeding area. The twelve most common prey species were ranked according to frequency of occurrence for each location. The Spearman rank correlation test was applied by pairwise ranking for all locations, excluding missing cases.

Bluefin tuna size was compared with prey length and stomach-contents biomass data by using the Pearson product moment correlation coefficient (Sokal and Rohlf, 1981) to test for significant associations between prey and predator length, and to correlate bluefin tuna weight and stomach-contents biomass for all samples from the Gulf of Maine. The relationship between bluefin tuna size and food consumed was also evaluated by comparing the ratio of stomach-contents biomass and tuna weight (% kg wet weight of prey biomass/kg wet weight of tuna) to tuna length (curved fork length) (Young et al., 1997). The area south of Martha's Vineyard area was excluded from tests on size relationships because of the limited sample numbers of juvenile bluefin tuna collected there.

Results

A total of 819 bluefin tuna stomachs were analyzed during 1988–92 (Table 1) and 568 contained prey; empty stomachs (206) and "chum only" samples (45) were eliminated from further analysis. Approximately equal quantities of the samples with prey came from purse-seine landings (273) and from rod and reel and handline landings (264). The fishing method used for the hook-and-line landings was recorded for 242 samples and was evenly divided between chumming (where chum was used as bait) (123) and trolling (119). Size composition of sampled bluefin tuna was similar for the four Gulf of Maine study areas; a large majority of fish were large, mature adults, estimated to be age 10 and older (Mather and Schuck, 1960). In contrast, nearly all fish sampled from the area south of Martha's Vineyard were small juveniles, ages 2–6. Tuna sampled from Cape Cod Bay had the largest average size (251 cm CFL, and 273 kg).

Prey composition

All areas combined Stomach contents comprised at least 21 species of teleosts, two species of elasmobranchs, and at least nine species of invertebrates (Table 2). Stomach-contents biomass in terms of taxonomic composition was dominated by *Osteichthyes* (Fig. 2A). Of the invertebrates, only squid ("squid" refers to two species, *Loligo pealei* and *Illex illecebrosus*) were a consistent component of prey composition. Although squid accounted for only about 2% of the stomach-contents biomass, it was the second most common prey, occurring in a third of all stomach samples. The only other common invertebrate was the fig sponge (*Suberites ficus*) found in Cape Cod Bay. Despite the large diversity of prey items, few species made major contributions to overall prey composition. Sand lance *(Ammodytes ssp)*, squid, Atlantic herring, Atlantic mackerel, and bluefish (*Pomatomus saltatrix*) exceeded all other prey in terms of frequency of occurrence and accounted as a group for 88% of total stomach-contents biomass (Fig. 2B). In the Gulf of Maine areas, sand lance, and Atlantic herring were the major prey in the diet of bluefin tuna during

Table 1

Summary of number of bluefin tuna stomach samples collected at five study areas on the New England continental shelf, July–October 1988–92. Also included are lengths (curved fork length [CFL], cm) and weights (kg) of sampled tuna. "Other" column refers to twelve samples with prey collected at nearshore fishing areas in the Gulf of Maine that were outside the five study areas.

Sample category	Jeffreys Ledge	Stellwagen Bank	Cape Cod Bay	Great South Channel	South of Marths's Vineyard	Other	Total
By year							
1988	13	30	16	0	0	0	59
1989	13	33	28	88	13	1	176
1990	57	15	26	61	33	2	194
1991	34	8	13	34	2	8	99
1992	6	7	26	0	0	1	40
By condition of stomach							
Number with prey	123	93	109	183	48	12	568
Number with chum	19	17	6	0	1	2	45
Number empty	5	1	158	27	8	7	206
Total	147	111	273	210	57	21	819
Mean length of tuna	221	240	251	221	124	221	227
SD	32	35	19	38	30	37	44
Mean weight of tuna	186	243	273	196	36	205	215
SD	78	94	58	90	38	83	97

the study period. Twenty-one bluefin tuna stomach samples were collected outside of the five study areas; mostly at two inshore locations north of Gloucester and south of Stellwagen Bank.

Jeffreys Ledge Atlantic herring were the dominant prey in the 123 stomach samples from Jeffreys Ledge (Table 3). The frequency of occurrence for Atlantic herring (74%) was the second highest and the percentage of stomach-contents biomass (87%) was the highest for any individual prey item among areas. Squid were in nearly half of all samples, but comprised less than 2% of stomach-contents biomass. Atlantic mackerel were the third most common prey for this region (32% occurrence). All other prey species occurred incidentally. Menhaden (*Brevoortia tyrannus*) and pollock (*Pollachius virens*) were unique to samples from Jeffreys Ledge. Mean stomach-contents biomass (~2.0 kg) was the highest among study areas and few empty stomachs were found.

Stellwagen Bank As at Jeffreys Ledge, a single species dominated the stomach-contentss from Stellwagen Bank. Sand lance were found in nearly 80% of 93 stomachs and accounted for nearly 70% of the stomach-contents biomass (Table 3). Atlantic herring, squid, spiny dogfish (*Squalus acanthias*), Atlantic mackerel, and bluefish tuna were secondary prey items, with frequencies of occurrence ranging from 9% to 14%. All other prey species found in stomach contents from Stellwagen Bank occurred incidentally, and there were no species from this area that were unique to the overall study area.

Cape Cod Bay Unlike diet composition for the other study areas, diet composition for Cape Cod Bay did not indicate a dominant pelagic prey but did include the common occurrence of demersal prey. Six prey species were only found in Cape Cod Bay. Squid occurred most frequently but accounted for only 2% of stomach-contents biomass biomass (Table 3). The fig sponge was the top prey in terms of percentage by weight (27%). The diet of bluefin tuna caught in Cape Cod Bay displayed the most diversity among study areas. A total of 16 prey species were identified, of which eight were demersal species. Three species of flounder were identified, representing 9% of the stomach-contents biomass. The occurrence of bluefish tuna as prey in Cape Cod Bay (25%) was the highest among study areas. The amount of food in Cape Cod Bay stomach samples was the lowest for the four Gulf of Maine locations; 60% of the stomachs collected from this area were empty.

Great South Channel A large number of stomach samples with prey (183) were collected from the Great South Channel during 1989–91. The most abundant prey was sand lance, occurring in 62% of the stomach samples and accounting for 28% of the stomach-contents biomass. Atlantic herring was also important, with a frequency of occurrence of 27% and stomach-contents biomass of 48%. As with Stellwagen Bank and Jeffreys Ledge, squid was an important secondary prey item, and bluefish and Atlantic mackerel were secondary prey of lesser importance. Four species were unique to Great South Channel samples: shrimp (*Pandalus* spp.), finger sponge (*Haliclona oculata*), silverstripe halfbeak (*Hyporhamphus unifasciatus*), and Atlantic cod (*Gadus morhua*).

South of Martha's Vineyard Only 48 stomachs with prey were analyzed from the area south of Martha's Vineyard.

Table 2

Stomach contents of bluefin tuna caught off New England during 1988–92. Prey species are combined for all five study areas, including 12 samples from outside of the study areas. Percent frequency of occurrence (% O) and percent weight (% W) data were determined from the 568 stomach samples that contained prey.

Prey species		Frequency of occurrence	Total weight (g)	% O	% W
Sand lance	*Ammodytes* (spp.)	194	128,240	34.2	22.6
Atlantic herring	*Clupea harengus*	167	299,550	29.4	52.8
Atlantic mackerel	*Scomber scombrus*	108	18,930	19.0	3.3
Bluefish	*Pomatomus saltatrix*	55	40,830	9.7	7.2
Butterfish	*Peprilus triacanthus*	21	1685	3.7	0.3
Silver hake	*Merluccius bilinearis*	16	1490	2.8	0.3
Windowpane	*Scopthalmus aquosus*	12	1890	2.1	0.3
Hake	*Urophycis* (spp.)	11	2500	1.9	0.4
Winter flounder	*Pseudopleuronectes americanus*	8	1820	1.4	0.3
Atlantic menhaden	*Brevoortia tyrannus*	7	5500	1.2	1.0
Sea horse	*Hippocampus erectus*	7	40	1.2	<0.05
Atlantic cod	*Gadus morhua*	6	22,840	1.1	4.0
Fourspot flounder	*Paralichthys oblongus*	2	370	0.4	0.1
American plaice	*Hippoglossoides platessoides*	2	310	0.4	0.1
Wrymouth	*Cryptacanthodes masculatus*	2	1300	0.4	0.2
Pollock	*Pollachius virens*	1	940	0.2	0.2
Filefish	*Monocanthus hispidus*	1	30	0.2	<0.05
Halfbeak	*Hyporhamphus unifasciatus*	1	120	0.2	<0.05
Longhorn sculpin	*Myoxocephalus octodecimspinosus*	1	280	0.2	<0.05
Unidentified fish	Teleostei	34	605	6.0	0.1
Spiny dogfish	*Squalus acanthias*	13	10,490	2.3	1.9
Skate	*Raja* (spp.)	13	4670	2.3	0.8
Skate egg case	*Raja* (spp.)	3	20	0.5	<0.05
Squid	Cephalopoda	186	10,835	32.8	1.9
Octopus	Cephalopoda	1	30	0.2	<0.05
Shrimp	*Pandalus* (spp.)	5	25	0.9	<0.05
Lobster	*Homarus americanus*	2	230	0.4	<0.05
Argonaut	*Argonauta argo*	2	25	0.4	<0.05
Crab	*Cancer* (spp.)	2	15	0.4	<0.05
Salp	Salpidae	2	60	0.4	<0.05
Fig sponge	*Suberites ficus*	30	11,510	5.3	2.0
Finger sponge	*Haliclona oculata*	1	50	0.2	<0.05
Stomachs with chum and prey		95	107,430 (chum)		
Stomachs with chum only		45	49,040 (chum)		
Empty stomachs		206	—		
Total stomachs with prey		568	567,230		
Total stomachs sampled		819	723,700		

Giant bluefin were scarce in this area during the study period and numerous samples could not be used because the bluefin tuna were caught in association with trawler fleet discards. This area is distinguished from the others by a predominance of juvenile bluefin tuna . Four prey species were unique to this area: lined sea horse (*Hippocampus erectus*), argonaut (*Argonauta argo*), planehead filefish (*Monocanthus hispidus*), and octopus (Cephalopoda). The filefish and seahorse were associated with bluefin tuna foraging at sargassum weed communities. Squid and Atlantic mackerel were the two most important prey for this area. The frequency of occurrence and percentage of prey weight for mackerel and butterfish were the highest among study areas. Combined stomach-contents biomass for squid, mackerel, and butterfish represented nearly 80% of the stomach contents for this area.

Comparison of study areas The top 12 prey items, overall, were ranked for each area by frequency of occurrence, and area differences were tested with Spearman rank correlation. Of the ten pairwise comparisons, only Stellwagen Bank and Great South Channel showed a significant association in the ranking of prey items (r=0.98, P<0.02), attributable to a high rank of sand lance and a similar ranking of squid, Atlantic herring, and Atlantic mackerel for both areas.

Stomach-contents biomass

Comparison of study areas Large differences in stomach-contents biomass were found: Jeffreys Ledge averaged nearly 2 kg, followed by approximately 1 kg for Stellwagen Bank and Great South Channel, and less than 0.5 kg for the remaining areas. Stomach-contents biomass data from the five areas were positively skewed and heteroscedastic. The natural logarithm-transformed data for Stellwagen Bank, Cape Cod Bay, and Great South Channel were normal (Wilk-Shapiro test, P>0.05). Transformed biomass data for the other two areas still differed significantly from normality. Transformation of biomass data reduced the inequality of variances, but significant differences (Levene's test, P<0.05) remained, which precluded use of analysis of variance. The Brown-Forsythe test for unequal variances showed a significant effect of area on stomach-contents biomass (P<0.0001). Pairwise comparisons of the equality of prey weight means were made with the Welch test (Bonferroni corrected significance level of P=0.005). All area pairwise comparisons of stomach-contents biomass were significantly different except that between Cape Cod Bay and Great South Channel (P=0.816).

The similarity in the amount of food found at Cape Cod Bay and Great South Channel was also indicated by the geometric mean of stomach-contents biomass (Table 4). The arithmetic mean of stomach-contents biomass was higher at the Great South Channel than Cape Cod Bay, but this value was biased by a few samples with large amounts of prey. The stomach-contents biomass range for Cape Cod Bay did not exceed 3.0 kg, in contrast to the wider range for the Great South Channel up to 16.0 kg, including 13 samples over 3.0 kg. The use geometric means reduced the bias of skewness and indicated that samples from Jeffreys Ledge contained the most prey and that the amounts declined moving southward.

Effect of tuna size Increased stomach-contents biomass with increasing body size (due to increasing gape and stomach size) was not clearly demonstrated from these data. Correlation of stomach-contents biomass to bluefin weight was not significant for Gulf of Maine samples. A scatterplot of data for the Gulf of Maine samples revealed that a large majority of the samples contained small amounts of food, regardless of body size (Fig. 3). A size-related trend was observed in that only very large bluefin tuna (>250 kg) contained more that 6 kg of food. Size effects were also compared by using the ratio of stomach-contents biomass and tuna weight (% kg/kg, wet weight) to tuna length. The percentage of food to body mass declined with increasing bluefin tuna length (Fig. 4). Food observed in 120–149 cm bluefin tuna averaged over 1% of their body weight, and declined to approximately 0.5% for bluefin tuna over 230 cm. The high ratios primarily resulted from large meals of Atlantic herring or sand lance. Cape Cod Bay ratios were consistently the lowest among the four areas, ranging from 0.1 to 0.2%.

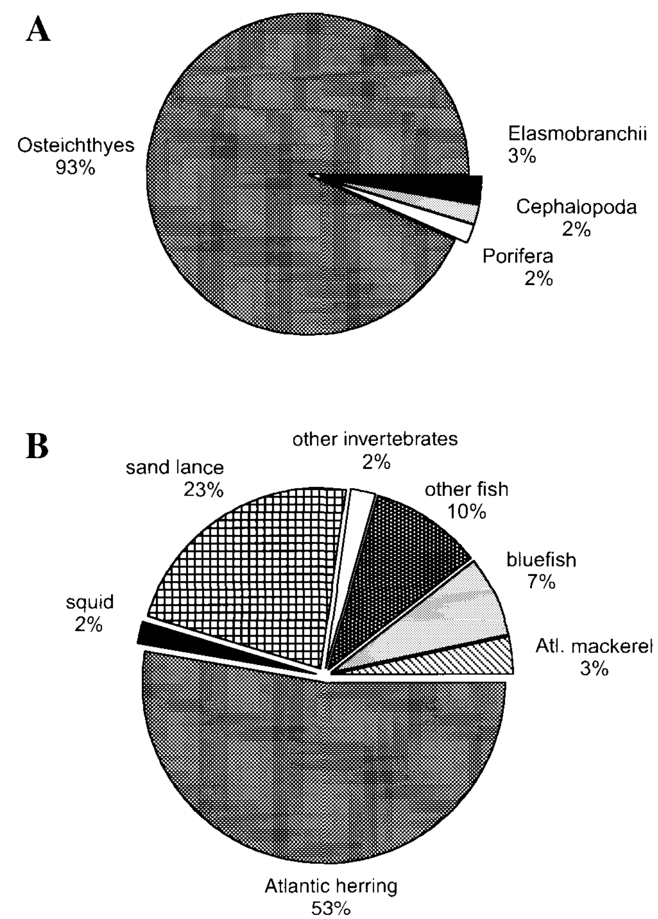

Figure 2

Percent prey weight composition in stomach contents of bluefin tuna caught off New England during 1988–92 (n=568). The taxonomic composition (**A**) includes 0.05% Crustacea and 0.01% Urochordata. The comparison by major prey type (**B**) comprises the five most common prey and all remaining fish and invertebrates.

Characteristics of prey species

Prey size Prey size was evaluated for 190 stomach samples that contained measurable prey from the four Gulf of Maine areas. A total of 1866 prey items were measured, of which 95% were either sand lance, Atlantic herring, squid, or Atlantic mackerel (Table 5). A significant positive cor-

Table 3

Stomach contents of bluefin tuna caught off New England during 1988-1992, listed by the five study areas. Percent frequency of occurrence (% O) and percent by weight (% W) were calculated for each prey species.

	Jeffreys Ledge		Stellwagen Bank		Cape Cod Bay		Great South Channel		South of Martha's Vineyard	
Prey species	% O	% W	% O	% W	% O	% W	% O	% W	% O	% W
Sand lance	3.3	1.8	79.6	69.3	0	0	62.3	28.3	0	0
Atlantic herring	74.0	87.2	14.0	6.0	8.3	3.1	27.3	48.4	2.1	2.5
Atlantic mackerel	31.7	2.0	10.8	2.6	18.3	12.7	8.2	0.6	33.3	56.2
Bluefish	7.3	3.5	8.6	17.5	24.8	14.7	4.9	5.7	0	0
Butterfish	2.4	<0.05	1.1	<0.05	5.5	1.5	1.6	0.2	16.7	10.4
Silver hake	3.3	0.2	0	0	0	0	2.2	0.3	10.4	2.9
Windowpane	0	0	0	0	10.1	4.1	0	0	0	0
Hake	4.1	0.7	1.1	0.2	0.9	0.2	0	0	8.3	9.9
Winter flounder	0	0	0	0	6.4	3.9	0	0	0	0
Atlantic menhaden	5.7	2.3	0	0	0	0	0	0	0	0
Sea horse	0	0	0	0	0	0	0	0	14.6	0.7
Atlantic cod	0	0	0	0	0	0	3.3	13.5	0	0
Fourspot flounder	0	0	0	0	1.8	0.9	0	0	0	0
American plaice	0.8	0.1	1.1	<0.05	0	0	0	0	0	0
Wrymouth	0	0	0	0	1.8	0.9	0	0	0	0
Pollock	0.8	0.4	0	0	0	0	0	0	0	0
Filefish	0	0	0	0	0	0	0	0	2.1	0.5
Halfbeak	0	0	0	0	0	0	0.5	0.1	0	0
Longhorn sculpin	0	0	0	0	0	0	0	0	0	0
Unidentified fish	4.9	<0.05	3.2	<0.05	2.8	0.1	8.7	0.1	12.5	2.9
Spiny dogfish	0	0	10.8	3.7	2.8	16.6	0	0	0	0
Skate	0	0	0	0	9.2	9.3	0.5	0.3	0	0
Skate egg case	0	0	1.1	<0.05	1.8	<0.05	0	0	0	0
Squid	48.8	1.8	14.0	0.5	35.8	1.8	22.4	2.5	60.4	12.9
Octopus	0	0	0	0	0	0	0	0	2.1	0.5
Shrimp	0	0	0	0	0	0	2.7	<0.05	0	0
Lobster	0	0	0	0	1.8	0.5	0	0	0	0
Argonaut	0	0	0	0	0	0	0	0	4.2	0.4
Crab	0	0	0	0	0.9	<0.05	0.5	<0.05	0	0
Salp	0	0	0	0	1.8	0.1	0	0	0	0
Fig sponge	0	0	0	0	27.5	27.2	0	0	0	0
Finger sponge	0	0	0	0	0	0	0.5	<0.05	0	0

relation ($P<0.001$) between prey and bluefin tuna lengths was found for all prey-size data (Fig. 5). Despite this correlation, there appeared to be little association between predator and prey length for most species. The positive correlation was influenced by 29 larger prey items (>40 cm) all consumed by bluefin tuna larger than 230 cm. The larger prey were spiny dogfish, skate, bluefish, or Atlantic cod. Size data on the four most common prey species provided evidence of the consistency of prey size across a wide range of bluefin lengths in the Gulf of Maine. A significant positive size relationship was found for sand lance and Atlantic mackerel (both $P<0.001$), although both may have contained biases. The relationship for sand lance was influenced by smaller bluefin tuna that ate smaller sand lance (t-test, $P<0.001$) in Great South Channel than at Stellwagen Bank. All mackerel were YOY or age-1, except for two large mackerel consumed by larger bluefin tuna (>200 cm). The predator-prey size relationships for Atlantic herring ($P=0.36$) and squid ($P=0.16$) were not significant. A large majority (93%) of Atlantic herring prey were 18–27 cm in length, which corresponds to age-2 to age-4 cohorts for the western Gulf of Maine (Penttila et

Table 4

Summary statistics on stomach-contents biomass (g wet weight) from bluefin tuna caught at five seasonal feeding areas off New England, 1988–92. The geometric mean, confidence intervals (CI), and coefficient of variation (CV) are backtransformed from natural logarithms.

Statistic	All areas	Jeffreys Ledge	Stellwagen Bank	Cape Cod Bay	Great South Channel	South of Martha's Vineyard
Number of stomach samples with prey	568	123	93	109	183	48
Minimum stomach biomass	5	5	5	5	5	5
Maximum stomach biomass	16100	5800	6240	2900	16100	1200
Arithmetic mean	999	1957	1012	389	925	124
Geometric mean	214	832	438	133	126	37
Lower 95% CI	180	608	324	96	91	23
Upper 95% CI	255	1140	593	184	174	60
CV	39	26	24	35	46	44

al., 1989), and the youngest were age 2. There were no young-of-the-year (YOY) sand lance. Most sand lance from Great South Channel samples were age 2, in contrast to age 3 or age 4 at Stellwagen Bank (Weston et al., 1979). Most squid were YOY or age 1.

Numbers of prey species Few prey species were found in large numbers in a given stomach sample. Only sand lance, squid, Atlantic herring, and Atlantic mackerel had sample counts higher than 20 individual fish (Table 6). Data on prey numbers are limited because prey counts were made for only 208 samples. Many samples with large numbers of well-digested sand lance were difficult to count. From this subsample, the mean number of sand lance per stomach was 159, much higher than the next highest mean of 19 for Atlantic herring. Squid and mackerel commonly occurred as prey, although typically only a few individuals were found per stomach.

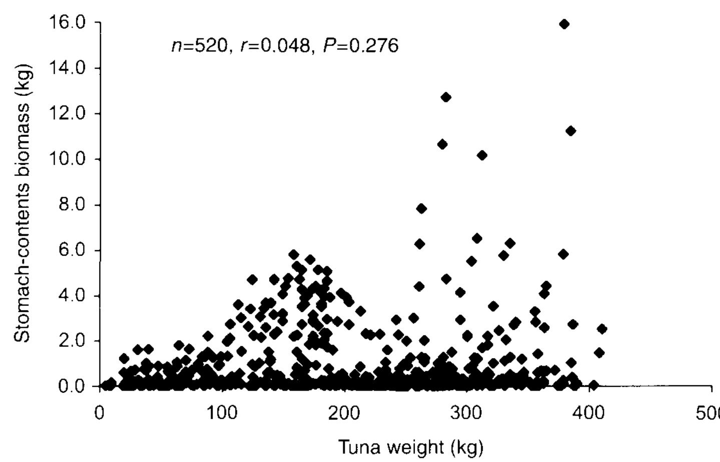

Figure 3

Scatterplot of bluefin tuna stomach-contents biomass and bluefin tuna weight for all samples from the Gulf of Maine, 1988–92.

Weight of prey species Sand lance and Atlantic herring (combined) accounted for 75% of the total stomach-contents biomass for all areas combined. The next highest species was bluefish at 7%. Despite a high frequency of occurrence, squid accounted a low percentage of overall biomass (2%) and a mean stomach prey weight of only 58 g. The highest mean prey weight was 1794 g for Atlantic herring. Only three other prey items averaged over 500 g in stomach-content weight: spiny dogfish (807 g), bluefish (742 g), and sand lance (661 g). With few exceptions, stomachs that were full or near full, contained only sand lance or Atlantic herring. Only five stomachs contained over 10 kg of prey contents: three with Atlantic herring, and one each with sand lance and Atlantic cod (16.0 kg, the largest meal observed).

In summary, five prey items occurred in frequency and mass to be considered important dietary components of the stomach contents sampled: sand lance, Atlantic herring, squid, Atlantic mackerel, and bluefish. Of these prey items, sand lance and Atlantic herring were the primary contributors to the diet of bluefin tuna sampled.

Discussion

Comparison of this study with previous west Atlantic bluefin tuna food habit studies revealed that fish prey represented a large majority of the diet, and cephalopods (primarily squid) were important secondary prey. Other prey taxa were minor components of the diet, except for Salpidae (Mason, 1976; Eggleston and Bochenek, 1990) and Amphipoda (Dragovich, 1970) for juvenile bluefin tuna. Comparisons with the four studies in which bluefin tuna were sampled prior to 1970 (Crane, 1936; Krumholz, 1959; Dragovich, 1970; Matthews et al.[1]) were limited because of small sample sizes. In pre-1970 studies, sand lance or benthic organisms were not found to be prey items. Mason (1976) was the first to record sand lance in bluefin stomach contents. In three later studies, sand lance were found to be the most frequently occurring prey, followed by squid (Holliday, 1978; Eggleston and Bochenek, 1990; and the present study).

Two limitations common to previous diet studies were the small number of samples collected and the broad geographical range over which they were collected. In contrast, large numbers of samples were collected in the present study, at discrete feeding grounds on the New England continental shelf; moreover this study is the first in which the diet of bluefin tuna in the Gulf of Maine was quantified during their seasonal feeding migration. The major contribution of Atlantic herring and the common occurrence of demersal organisms as prey have not been previously recorded for bluefin tuna in the western North Atlantic Ocean.

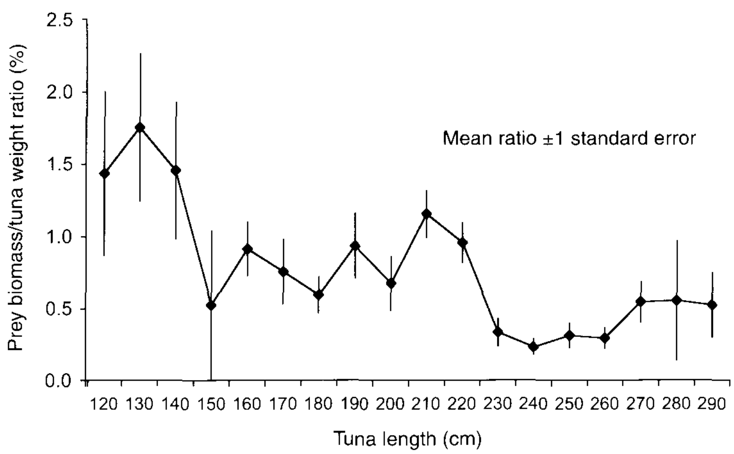

Figure 4

Relationship between the ratio of stomach-contents biomass to tuna weight (% wet weight [kg/kg]) and tuna length (curved fork length). All Gulf of Maine samples for bluefin lengths of 120–299 cm (n=519) were combined and arranged in 10-cm bins.

Sampling biases

Regurgitation, diel and seasonal effects, differential digestion rates, postcapture digestion, and predator size effects can be problematic to food habit studies and can bias data collection. (Bowen, 1986). This section discusses the potential effect that sampling biases may have on the findings of significant differences in the stomach-contents biomass and prey associations. A majority of the empty stomachs had distended stomach rugae, indicating that regurgitation had occurred. Similar observations were made during previous studies (Mason, 1976; and Dragovich, 1970), which would cause a negative bias for stomach-contents weight measurements. Diel and seasonal effects on feeding are difficult to assess and are large sources of variation. Large intersample variance can be expected given the complex interactions between predator populations and the temporal and spatial distribution of prey (Smagula and Adelman, 1982; Hodgson et al., 1989). Increasing sample size often may reduce variability, but high intra-

Table 5

Summary statistics for length data from major prey items in stomach contents and bluefin tuna sampled from Gulf of Maine (GOM), July–October, 1988–92. Prey lengths are total length, except for squid, which are mantle lengths. Bluefin tuna lengths are curved fork length (CFL). Area 1 = Jeffreys Ledge; area 2 = Stellwagen Bank; and area 4 = Great South Channel. n = number of samples taken.

		Prey				Bluefin tuna			
Species	Area	n	Mean (cm)	SD (cm)	Range (cm)	n	Mean (cm)	SD (cm)	Range (cm)
All prey	GOM	1866	17.7	7.27	3–80	190	220	38.60	104–297
Atlantic mackerel	GOM	150	15.9	3.27	10–36	40	215	42.56	132–272
Squid	GOM	89	13.8	5.63	3–24	41	224	30.81	159–295
Atlantic herring	GOM	364	24.6	2.51	18–31	57	211	30.19	119–276
Atlantic herring	1	263	24.4	2.65	18–31	42	209	27.83	119–276
Atlantic herring	4	91	25.1	1.94	21–30	9	221	42.05	130–272
Sand lance	GOM	1176	14.9	3.04	8–23	41	206	45.51	124–279
Sand lance	2	468	17.2	2.27	12–23	16	232	30.27	178–269
Sand lance	4	609	12.8	1.48	8–19	21	186	44.99	124–279

sample and intersample variation, prey weight skewness, and variance dependency are widespread findings in food habit studies that reflect natural feeding interactions (Smagula and Adelman, 1982; Amundsen and Klemetson, 1986; and Hodgson et al., 1989). Large sample variation was evident in the present study and limited the application of parametric statistics.

Differential digestion rates can result in an underestimate of the relative importance of a major prey item (Hyslop, 1980). Soft-bodied squid likely undergo digestion quicker than bony fish, and, therefore, prey weight measurements may have been negatively biased. Postcapture decomposition of prey has not been measured for bluefin tuna but may negatively bias stomach-contents weight for samples held a long time after capture (Holliday, 1978). The effect of bias on the prey weight data is suspected to be minor because of strong market incentives to chill harvested bluefin tuna and because samples were collected soon after capture.

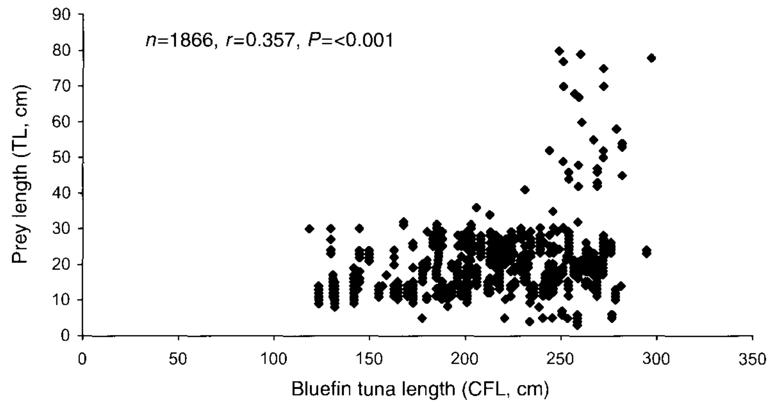

Figure 5

Relationship between bluefin tuna length and prey length for all Gulf of Maine samples during 1988–92 that contained measurable prey (190 stomach samples).

The separation of chum bait from natural prey and the exclusion of chum from diet analyses were potential minimal sources of bias. Because bluefin tuna swallow prey whole and chum is cut into small pieces, cut chum was readily separated from natural prey in stomach samples. Samples of small bluefin tuna that fed on the discards of trawlers in the area south of Martha's Vineyard did present a problem, and many of these samples were removed from analyses because natural prey and discards could not be distinguished. Other study areas did not indicate an association between tuna fisheries and trawl fishing; consequently, no evidence of discard feeding was observed. It is possible that the availability of chum could limit feeding on natural prey, although no evidence of this was found. Most chum was observed in the stomach contents of bluefin tuna from Stellwagen Bank and Jeffreys Ledge, but these areas also had the highest mean stomach-contents biomass and lowest frequency of empty stomachs.

Most of these biases were negative, possibly decreasing prey weight measurements in stomach contents, and could not easily be separated from natural conditions that lead to suboptimal feeding habits. Butler and Mason (1978) re-

Table 6

Prey number and prey weight data for the most common prey in stomach contents of bluefin tuna caught off New England during 1988–92. Both number of prey and prey weight were derived from all samples with prey (n=568), but prey number only includes samples where all prey could be counted.

	Number of prey			Prey weight (g)		
Prey species	*n*	Mean	Range	*n*	Mean	Range
Sand lance	25	159	2–557	194	661	5–10,590
Squid	76	3	1–28	186	58	5–1440
Atlantic herring	85	19	1–84	167	1794	5–12,700
Atlantic mackerel	27	6	1–30	108	175	5–1210
Bluefish	22	1	1–2	55	742	5–5800
Fig sponge	19	3	1–10	30	384	5–1250
Butterfish	10	2	1–5	21	80	5–450
Silver hake	1	17	—	16	93	5–250
Spiny dogfish	3	2	1–4	13	807	5–2900
Skate	9	1	1–2	13	359	50–810
Windowpane	11	1	1–3	12	158	40–250
Hake	5	2	1–3	11	227	40–640

ported higher daily consumption rates for pen-held bluefin tuna, an average of 28 kg per day during single feedings to satiation, and 40 kg per day during multiple feedings. Data from my study implied that naturally feeding bluefin tuna do not often reach these consumption rates: only five of 568 stomachs had prey contents over 10 kg. Regurgitation is a major confounding factor for stomach-contents biomass data and presents a serious challenge for calculations of daily rations and bioenergetic modeling of bluefin tuna feeding habits. The anatomy of the alimentary canal, combined with the stress of capture, appears to cause a high rate of regurgitation.

Cape Cod Bay

The bluefin tuna prey composition from Cape Cod Bay was unlike any prey composition previously reported for the west Atlantic, in that no individual prey item dominated nor was encountered at a high frequency of occurrence or percentage of stomach-contents biomass. In previous west Atlantic bluefin tuna food-habit studies, prey composition was dominated by a single, pelagic, schooling prey species (followed by a few secondary species of much less importance), and Pinkas (1971) reported similar results for Pacific bluefin tuna. Finding fig sponge as the highest ranked prey item in the diet of bluefin tuna in Cape Cod Bay was surprising; sessile prey organisms had not been found in previous bluefin tuna food-habit studies. Occurrence of fig sponge, locally known as "monkey dung," in the stomachs of bluefin tuna is commonly known to Cape Cod Bay fishermen who have questioned whether it is natural prey or whether it is accidentally swallowed during capture. I found the sponge at various stages of digestion; well-digested pieces as well as fresh pieces were found in the same stomach. The differential stages of digestion implies that fig sponge was ingested either as selected prey of unknown attraction and nutritional value or as incidental catch to a targeted bottom dweller.

Bottom foraging in the relatively shallow Cape Cod Bay (average depth: 25 m) was evident because eight of the 16 prey items identified were benthic or demersal species. Vertical excursions to the bottom in shallow regions were not unexpected, yet bottom foraging has not been reported for west Atlantic bluefin tuna. Bottom feeding was evident for most locations in this study, including foraging on small crabs (*Cancer* spp.) and finger sponge at Great South Channel where depths approached 100 m. In Cape Cod Bay, bottom foraging may not be the optimal feeding strategy for bluefin tuna and may simply be a response to low food availability, as suggested by the low prey biomass and higher proportion of naturally empty stomachs.

Prey size

To date, prey size in bluefin tuna food habit studies in the western North Atlantic has received little attention. Only Matthews et al.[1]) presented prey size data, a mean value based on 38 bluefin tuna stomachs. Young et al. (1997) found no relationship between prey size and size (40–192 cm) of juvenile southern Atlantic bluefin tuna (*Thunnus maccoyii*). I found only minor evidence of a predator-prey size relationship for bluefin tuna in the Gulf of Maine. A positive correlation was found between sand lance and bluefin length, although regional differences in the lengths of both species appears to bias the correlation. Smaller sand lance and bluefin tuna were found at Great South Channel than at Stellwagen Bank. A positive interaction between bluefin tuna and prey sizes was indicated by the consumption of the largest prey (>40 cm) by large bluefin tuna (>230 cm). Prey this large were not common in stomachs and were probably limited by mouth and esophagus gape. Otherwise, the sizes of prey were consistent across the range of bluefin tuna sampled in the Gulf of Maine.

The findings on prey size and numbers (per stomach) provide evidence of three selective foraging strategies used by bluefin tuna in the Gulf of Maine. Feeding on individual, fast-swimming pelagic prey was evident from consumed bluefish and Atlantic mackerel that are abundant pelagic species in the Gulf of Maine, but which occurred much less frequently in stomach contents and with few individuals per stomach. Ram feeding (swimming through a dense school prey with mouth open) of small prey may have resulted in high average number of sand lance found in stomachs and contributed to the similar prey sizes in most sizes of bluefin tuna. Bluefin tuna in Cape Cod Bay displayed a different foraging behavior, selecting larger, individual demersal prey. The variation in prey composition and different feeding strategies is consistent with previous descriptions of bluefin tuna as an opportunistic predator. However, the dominance of sand lance and Atlantic herring in the Gulf of Maine diet suggests a dependence on these species as an optimal energy source.

Trophic influences on bluefin tuna distribution

Changes in biomass and spatial availability of forage populations may affect the distribution of bluefin tuna on the New England continental shelf. Major changes in the prey community of the Gulf of Maine have occurred in recent decades. After Atlantic mackerel and Atlantic herring stocks off New England were severely overharvested in the 1960s and 1970s (NOAA, 1998), sand lance populations increased, presumably as a result of decreased predation and competition for food (Sherman et al., 1981). Atlantic herring and Atlantic mackerel stocks off New England increased steadily during the 1980s and 1990s (NEFSC, 1998). By the mid-1990s, the U.S. Atlantic coastal spawning stock biomass for these species increased to the highest levels on record (NEFSC, 1998).

Commercial bluefin tuna catches have increased in areas where Atlantic herring abundance has increased (western Gulf of Maine and Great South Channel) and diminished at traditional areas south of the Gulf of Maine (Chase, 1992). The northward shift in bluefin tuna distribution on the New England continental shelf may be influenced by improved foraging opportunities on Atlantic herring in the Gulf of Maine. I suspect that the timing of bluefin tuna migrations to the New England continental shelf are associated with seasonal spawning and feeding aggregations of Atlantic herring. Sand lance populations appear to be an important influence on bluefin tuna feeding migrations, but they occur on a limited spatial scale in relation to Atlantic herring in the Gulf of Maine, and changes in their population abundance are not well documented. Atlantic herring and sand lance are also important in the diet and distribution of marine mammals in the Gulf of Maine (Payne et al., 1990; Weinrich et al., 1997; Gannon et al., 1998).

Changes in bluefin tuna stock composition and the long-term impact of small-mesh trawling gear on commercially important prey items (squid, silver hake, and butterfish) in southern New England waters and Mid-Atlantic areas where bluefin tuna catches have diminished are two potentially confounding factors in this discussion. In the management of Atlantic bluefin tuna, care should be taken to recognize that the fluctuations in the regional abundance of this species can be influenced by more than changes in stock structure. Changes in major prey populations, produced either by environmental features or by fishery practices, can have a profound effect on regional aggregations of bluefin tuna. Investigations should be conducted on introducing forage-base information into the interpretation of catch-per-unit-of-effort indices of abundance for Atlantic bluefin tuna populations. There is also a need for future research to improve our knowledge on the bioenergetics of this warm-bodied tuna and its associated relationships with prey species.

Acknowledgments

This study was conducted by the Massachusetts Division of Marine Fisheries (DMF), Commonwealth of Massachusetts, and funded by the Federal Aid in Sportfish Restoration Program. I would like to thank the DMF and National Marine Fisheries Service staff who assisted with field sampling and the technical review of this project. I am especially thankful to Steve Cadrin for his review of the manuscript and assistance with the statistical analyses. I am very grateful to the many fishermen and tuna buyers who contributed stomach samples and catch information. Special thanks are due to the following for the contribution of large numbers of samples: Bill Raymond, Mark Godfrey, Rodman Sykes, and the crew of FV *Debra Lynn*, Great Circle Fisheries, Ralboray, Crocker and Sons, Canal Marine, and Atlantic Coast Fisheries.

Literature cited

Amundsen, P. A., and A. Klemetsen.
1986. Within-sample variabilities in stomach contents weight of fish- implications for field studies of consumption rates. *In* Contemporary studies on fish feeding (C. A. Simenstad and G. M. Cailliet. eds.), p. 307–314. Dr. W. Junk Publishers, Boston, MA.

Bigelow, H. B., and W. C. Schroeder.
1953. Fishes of the Gulf of Maine. U.S. Fish and Wildl. Serv. Bull. 74, vol. 53, 577 p.

BMDP (Biomedical Dynamic Programs).
1990. BMDP statistical software manual, vol. I. Univ. Cal. Press, Berkeley, CA, 617 p.

Bowen, S. H.
1986. Quantitative description of the diet. *In* Fisheries techniques (L. A. Nielson, and D. L. Johnson, eds.), p. 325–336. Am. Fish. Soc., Bethesda, MD.

Butler, M. J., and J. M. Mason Jr.
1978. Behavioral studies on impounded bluefin tuna. Int. Comm. Conserv. Atl. Tunas Coll. Vol. Sci. Pap. 7(2):379–381.

Carey, F. G., and J. M. Teal.
1969. Regulation of body temperature by the bluefin tuna. Comp. Biochem. Physiol. 28:205–213.

Chase, B. C.
1992. A profile of changes in the Massachusetts bluefin tuna fishery: 1928–1990. M.S. thesis, Univ. Rhode Island, Kingston, RI, 266 p.

Clark, S. H., and B. E. Brown.
1976. Changes in biomass of finfishes and squids from the Gulf of Maine to Cape Hatteras, 1963–1974, as determined from research vessel survey data. Fish. Bull. 75:1–21.

Crane, J.
1936. Notes on the biology and ecology of giant tuna *Thunnus thynnus*, L., observed at Portland, Maine. Zoologica 212:207–212.

Dragovich, A.
1970. The food of bluefin tuna (*Thunnus thynnus*) in the western North Atlantic Ocean. Trans. Am. Fish. Soc. 99: 726–731.

Eggleston, D. B., and E. Bochenek.
1990. Stomach contents and parasite infestation of school bluefin tuna *Thunnus thynnus* collected from the Middle Atlantic Bight, Virginia. Fish. Bull. 88:389–395.

Gannon, D. P., J. E. Craddock, and A. J. Read.
1998. Autumn food habits of harbor porpoises, *Phocoena phocoena*, in the Gulf of Maine. Fish. Bull. 96:428–437.

Hodgson, J. R., S. R. Carpenter, and A. P. Gripentrop.
1989. Effect of sampling frequency on intersample variance and food consumption estimates of nonpiscivorous largemouth bass. Trans. Am. Fish. Soc. 118:11–19.

Holliday, M.
1978. Food of Atlantic bluefin tuna, *Thunnus thynnus* (L.), from the coastal waters of North Carolina to Massachusetts. M.S. thesis. Long Island Univ., Long Island, NY, 31 p.

Hyslop, E. J.
1980. Stomach contents analysis—a review of methods and their application. J. Fish. Biol. 17:411–429.

Krumholz, L. A.
1959. Stomach contents and organ weights of some bluefin tuna, *Thunnus thynnus* (Linnaeus), near Bimini, Bahamas. Zoologica 44:127–131.

Mason, J. M.
1976. Food of small, northwestern Atlantic bluefin tuna, *Thunnus thynnus* (L.) as ascertained through stomach content analysis. M.S. thesis, Univ. of Rhode Island, Kingston, RI, 31 p.

Mather, F. J, III, and H. A. Schuck.
1960. Growth of bluefin tuna of the western north Atlantic. Fish. Bull. Fish Wildl. Serv. 179:39–52.

NEFSC (Northeast Fisheries Science Center).
1998. A report of the 27th Northeast regional stock assessment workshop. Stock Assess. Rev. Comm. (SARC), consensus summary of assessments. Lab. Ref. Doc 98-15, 350 p. [Available from Northeast Fisheries Science Center (NEFSC), Woods Hole, Woods Hole, MA.]

NMFS (National Marine Fisheries Service).
1995. Final environmental impact statement for a regulatory amendment for the western Atlantic bluefin tuna fishery.

National Marine Fisheries Service (NMFS), Silver Springs, MD, 142 p.

1999. Final fishery management plan for Atlantic tunas, swordfish, and sharks. *In* Chapter 3: Rebuilding and maintaining HMS fisheries, p. 1–321. [Available from NMFS, Silver Springs, MD.]

NOAA (National Oceanic and Atmospheric Administration).

1998. Status of fishery resources off the northeastern United States for 1998. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-NE-115, 149 p.

Payne, P. M., D. N. Wiley, S. B. Young, S. Pittman, P. J. Clapham, and J. W. Jossi.

1990. Recent fluctuations in the abundance of baleen whales in the southern Gulf of. Maine in relation to changes in selected prey. Fish. Bull. 88:687–696.

Penttila, J. A., G. A. Nelson, and J. M. Burnett III.

1989. Guidelines for estimating lengths at age for 18 northwest Atlantic finfish and shellfish species. U.S. Dep. Commer., NOAA Tech. Memo., NMFS-F/NEC-66, 39 p.

Pinkas, L.

1971. Bluefin tuna food habits. *In* Food habits of albacore, bluefin tuna, and bonito in California waters (L. Pinkas, M. S. Oliphant, and I. K Iverson, eds.), p. 47–63. Cal. Fish Game Fish. Bull. 152:1–105.

Shapiro, S. S., and M. B. Wilk.

1965. An analysis of variance test for normality (complete samples). Biometrika 52: 591–611.

Sherman, K. C., C. Jones, L. Sullivan, W. Smith, P. Berrein, and L. Ejsymont.

1981. Congruent shifts in sand eel abundance in western and eastern north Atlantic ecosystems. Nature 291:486–489.

Smagula, C. M., and I. R. Adelman.

1982. Day-to-day variation in food consumption by largemouth bass. Trans. Am. Fish. Soc. 111:543–548.

Sokal, R. R., and F. J. Rohlf.

1981. Biometry, 2nd ed. W. H. Freeman and Co., New York, NY, 859 p.

Weinrich, M., M. Martin, R. Griffiths, J. Bove, and M. Schilling.

1997. A shift in distribution of humpback whales, *Megaptera novaeangliae*, in response to prey in the southern Gulf of Maine. Fish. Bull. 95:826–836.

Weston, D. T., K. J. Abernethy, L. E. Meller, and B. A. Rogers.

1979. Some aspects of biology of the American sand lance, *Ammodytes americanus*. Trans. Am. Fish. Soc.108:328–331.

Young, J. W., T. D. Lamb, D. L. Russel, W. Bradford, and A. W. Whitelaw.

1997. Feeding ecology and interannual variations in diet of southern bluefin tuna, *Thunnus maccoyii*, in relation to coastal and oceanic waters off eastern Tasmania, Australia. Environ. Biol. Fish. 50:275–291.