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ARTICLE

Size-Selective Feeding in Captive and Free-Ranging Atlantic Bluefin Tuna

Christopher M. Butler*[1]
Center for Marine Sciences and Technology, Department of Applied Ecology, North Carolina State University, 303 College Circle, Morehead City, North Carolina 28557, USA

Brian Hanrahan
Department of Natural Resources Conservation, University of Massachusetts Amherst, 160 Holdsworth Way, Amherst, Massachusetts 01003, USA

Jeffrey A. Buckel and Paul J. Rudershausen
Center for Marine Sciences and Technology, Department of Applied Ecology, North Carolina State University, 303 College Circle, Morehead City, North Carolina 28557, USA

Francis Juanes[2]
Department of Natural Resources Conservation, University of Massachusetts Amherst, 160 Holdsworth Way, Amherst, Massachusetts 01003, USA

Joseph W. Smith
National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Road, Beaufort, North Carolina 28516, USA

Abstract
We examined size-selective feeding in captive and free-ranging Atlantic Bluefin Tuna *Thunnus thynnus*. For the captive study, Bluefin Tuna were maintained in a cylindrical net-pen enclosure (30.5 m in diameter; 15.2 m deep) located 32.2 km offshore of Virginia. Tests of prey size selectivity by captive Bluefin Tuna were observed using underwater video. In free-ranging Bluefin Tuna, size selection was examined by comparing the sizes of Atlantic Menhaden *Brevoortia tyrannus* found in stomach contents with the sizes of those collected during the fall purse-seine fishery for Atlantic Menhaden off the North Carolina coast. Captive Bluefin Tuna selected larger prey when prey length : predator length ratios (PPRs) were less than 10%; however, size selectivity was not observed when the PPRs exceeded 10%. For free-ranging Bluefin Tuna, PPRs were mostly greater than 10% (12.98 ± 0.06% [mean ± SE]), and there were no significant differences in length between Atlantic Menhaden from stomach contents and those from purse-seine collections. The minimum and median sizes of Atlantic Menhaden prey increased with increasing predator size; however, the maximum size of Atlantic Menhaden prey did not change, indicating that the smallest Bluefin Tuna sampled could consume the largest Atlantic Menhaden. We conclude that the relatively small size of

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*Corresponding author: c.m.butler@usm.edu
[1]Present address: Gulf Coast Research Laboratory, Center for Fisheries Research and Development, The University of Southern Mississippi, 703 East Beach Drive, Ocean Springs, Mississippi 39564, USA.
[2]Present address: Department of Biology, University of Victoria, 3800 Finnerty Road, Victoria, British Columbia V8W 3N5, Canada.
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forage fishes commonly observed in Bluefin Tuna stomachs was likely due to the high abundance of these fishes in the environment rather than to active selection for small prey.

Multispecies models are currently employed to provide guidance for ecosystem-based fisheries management (Link 2010). An understanding of predator–prey interactions has proven useful in stock assessments when both predator and prey species are harvested commercially (Overholtz et al. 2008). Information necessary for multispecies assessments includes predators' diets and consumption rates as well as prey size.

Atlantic Bluefin Tuna *Thunnus thynnus* are highly migratory apex predators that are distributed throughout the Atlantic Ocean. In the western Atlantic, Bluefin Tuna range from Labrador to Brazil, including the Gulf of Mexico and the Caribbean Sea (Block et al. 2001, 2005). Vascular heat exchangers allow Bluefin Tuna to inhabit a wide thermal niche and therefore a wide geographic range (Carey and Teal 1969; Carey and Lawson 1973). Although Bluefin Tuna are typically considered oceanic predators, they often aggregate in nearshore waters to feed on concentrated assemblages of prey (Chase 2002; Overholtz 2006; Butler et al. 2010).

It is generally assumed that fewer prey of greater individual sizes are consumed by piscivorous fish than by planktivorous fish (Breck 1993; Juanes 1994). Chase (2002) reported that in the diets of Bluefin Tuna captured in New England waters, prey length was as much as 30% of predator body length. However, the relative prey sizes observed by Chase (2002) were the smallest reported for any northwest Atlantic piscivorous fish (Scharf et al. 2000). Although Bluefin Tuna are capable of consuming large prey items, they appear to primarily ingest a large number of relatively small forage items to meet their energetic demands (Chase 2002; Overholtz 2006; Butler et al. 2010). Thus, the feeding habits of Bluefin Tuna may differ from those of a "typical" large piscivore (Rudershausen et al. 2010). Understanding the mechanisms responsible for this pattern has implications for the management of Bluefin Tuna and their prey, which are generally pelagic forage species that are also harvested commercially (Overholtz 2006; Butler et al. 2010).

The consumption of relatively small prey could be a result of active or passive selection. A relatively large number of attacks on small prey versus large prey would result if active selection was occurring; for passive selection, attacks would occur across all size ranges, but only the smaller, more easily captured prey would be consumed (Juanes 1994). Given what has been found for other piscivores (Juanes 1994), we hypothesized that Bluefin Tuna are passively selecting for small prey. We tested this hypothesis by (1) conducting feeding trials with captive Bluefin Tuna and (2) comparing prey sizes from the stomach contents of free-ranging Bluefin Tuna to prey sizes available in the environment.

METHODS

Captive Bluefin Tuna

Collection of Bluefin Tuna.—We constructed a 30.5-m-diameter, 15.2-m-deep, cylindrical floating net-pen to observe the feeding behavior of Bluefin Tuna. A white, straight-hung mesh net (2.54-cm mesh) constituted the vertical walls and bottom of the enclosure. The enclosure was anchored 32.2 km offshore of Wachapreague, Virginia, on the southwest corner of 21 Mile Hill (~37°26′N, 75°11′W), which is a bathymetric feature that rises within 33.5 m of the ocean's surface in deeper surrounding waters. The enclosure location was relatively near to shore and was in close proximity to a temporally and spatially predictable aggregation of small (~1-m) Bluefin Tuna; this aggregation is targeted by recreational fishers during summer.

Fifty Bluefin Tuna were collected during June and July in the vicinity of the enclosure. Bluefin Tuna were captured by rod and reel using a trolled artificial lure rigged with dead natural fish bait. Bluefin Tuna were transported to the net-pen enclosure in a 2,400-L, elliptical transport tank; transport time was generally less than 3 h. All specimens were retrieved from the transport tank and individually released into the net-pen by divers to ensure that the fish recovered proper spatial orientation. Once released, individual Bluefin Tuna quickly assimilated into existing schools of captive Bluefin Tuna.

Feeding observations.—Captive Bluefin Tuna were fed twice daily to satiation with cut dead prey consisting of Atlantic Herring *Clupea harengus*, Atlantic Menhaden *Brevoortia tyrannus*, Atlantic Silversides *Menidia menidia*, and other species (e.g., American Sand Lance *Ammodytes americanus* and Bluefish *Pomatomus saltatrix*). In addition, live prey (Mummichog *Fundulus heteroclitus* and Atlantic Menhaden) were fed to Bluefin Tuna during regular feedings and as part of prey size-selectivity trials (described below). Analog 8-mm (Hi-8) video cameras in waterproof housings were used to record footage of routine daily feedings and prey size-selectivity experiments. A shutter speed of 0.0005 s was used to optimize the resolution of still frames within the constraint of available subsurface light (<15.2-m depth). All videos of feeding activity were recorded with cameras that were mounted inside the enclosure. Two video cameras were used simultaneously for each observation to ensure that their fields of view were opposed at 90° (overlapping). This strategy allowed for continuous visualization of an individual fish after it passed out of the initial camera's field of view.

Size-selectivity trials.—Two prey types—Mummichogs and Atlantic Menhaden—were used in live-prey size-selectivity trials due to morphological and behavioral differences.

Mummichogs are dorsoventrally compressed, darker-bodied, nonpelagic fish, whereas Atlantic Menhaden are laterally compressed, silver-colored, pelagic fish. Prey were collected by beach seine, sorted by species, and transported to holding tanks at the offshore enclosure. Size-selectivity trials occurred on four separate dates under similar atmospheric and oceanographic conditions (e.g., temperature and sea state) but at various times of day.

Prey size-selectivity trials consisted of the simultaneous presentation of two prey groups with differing sizes relative to predator lengths. Two feeding trials using Mummichogs with prey length : predator length ratios (PPRs) less than 10% were executed. Trial 1 occurred at 0930 hours and used Mummichog prey differing by 2 cm in mean TL (i.e., 6% PPR [prey size range = 5.0–6.0 cm] and 8% PPR [prey size range = 7.0–8.0 cm]; n = 13 successfully recorded paired presentations). Trial 2 occurred at 1500 hours on a different date and used Mummichogs that differed by 3 cm in mean TL (i.e., 6% PPR [prey size range = 5.5–6.5 cm] and 9% PPR [prey size range = 8.5–9.5 cm]; n = 29 paired presentations). Size-selectivity trials with live Atlantic Menhaden employed prey that differed by 2 cm in mean TL, and those trials occurred at 0845 and 1300 hours, respectively. Trial 3 used Atlantic Menhaden prey with PPRs of 10% or less (i.e., 8% PPR [prey size range = 7.5–8.5 cm] and 10% PPR [prey size range = 9.5–10.5 cm]; n = 3 paired presentations). Trial 4 used Atlantic Menhaden prey with PPRs that were greater than 10% (i.e., 12% PPR [prey size range = 11.0–12.0 cm] and 14% PPR [prey size range = 13.0–14.0 cm]; n = 8 paired presentations).

Prey groups were allowed to acclimate to the enclosure within a 22-L, flow-through delivery container for 5 min prior to release. Prey groups were presented in the center of the enclosure at the surface approximately 1 m apart and were released using a remote live-prey delivery system. The delivery system—a plastic, opaque-sided, 22-L cylindrical container with a removable mesh bottom—was positioned in the center of the net-pen enclosure and was submerged such that the top of the cylinder was at the water's surface. Once the container was in position, the mesh bottom was removed by using a remotely actuated trigger (i.e., a rope attached to a bungee that held the mesh over the opening). After the mesh bottom was removed, the cylinder was lifted clear of the water's surface by using the positioning ropes. The order of attack on prey was recorded as an indicator of prey size selection. First attacks were quantified only when (1) both prey sizes were visible within the video field and (2) one predator was involved during the attack. Size-selective feeding trials were analyzed using chi-square goodness-of-fit tests (Sokal and Rohlf 1995) to examine differences between observed and expected (50:50) frequencies of first attacks on the larger prey. Recorded video footage was used to determine capture success of Bluefin Tuna when attacking Mummichogs and Atlantic Menhaden. Here, capture success was defined as the number of attacks on prey that resulted in ingestion divided by the total number of attacks.

Free-Ranging Bluefin Tuna

Collection.—Bluefin Tuna stomachs were collected from the commercial Bluefin Tuna fishery off the coast of North Carolina during the winters of 2003–2006. The trolling method described above was used to capture Bluefin Tuna. The majority of Bluefin Tuna examined in this study were caught within a 28-km radius of the Cape Lookout Knuckle Buoy (~34°26′N, 76°28′W).

Bluefin Tuna were separated into two size-classes: large-medium (curved FL [CFL] = 185.4–205.7 cm) and giant (CFL > 205.7 cm; Murray-Brown et al. 2007). Stomachs were removed at sea by the fisher and were stored on ice until they could be collected by researchers (typically the same day).

Tests of size-selective feeding.—Size-selective feeding by free-ranging Bluefin Tuna was tested by comparing the lengths of Atlantic Menhaden in Bluefin Tuna stomach contents with the lengths of those harvested in the commercial purse-seine fishery for Atlantic Menhaden during winter; both types of sample were collected during the winter of 2004–2005. The fall purse-seine fishery off the North Carolina coast caught a wide size range and age range of Atlantic Menhaden, which gather in the state's coastal waters beginning in about November to spawn. For each purse-seine set, a random sample of 10 Atlantic Menhaden was measured for FL (cm). All samples were collected from the top of the fish hold and were assumed to be from the last purse-seine set location of the trip. Only purse-seine data (i.e., the last set of a trip) that could be spatially (i.e., offshore) and temporally (i.e., ±1 month) matched with the catches of Bluefin Tuna were used in this analysis (i.e., within a 28-km radius of the Knuckle Buoy; see above). Size-selective feeding patterns of Bluefin Tuna (large-medium, giant, and pooled size-classes) were examined by comparing the length-frequency histograms of ingested Atlantic Menhaden with the length-frequency histograms of Atlantic Menhaden from the commercial fishery; statistical comparisons were conducted with a median test (Zar 1999).

Quantile regression analysis and relative prey size.—Prey length–predator length relationships (using data from three winter collections) were examined by using quantile regression analysis (Scharf et al. 1998, 2000). The 5th, 50th, and 95th quantiles (selected based on sample size; Scharf et al. 1998) were used to determine the lower boundary, median, and upper boundary of the prey length–predator length scatter. Analyses were conducted on Bluefin Tuna lengths and the lengths of their prey based on (1) all fish prey types combined and (2) Atlantic Menhaden prey only. Quantile regression analyses were performed using BLOSSOM software (Cade and Richards 2001). Relative prey sizes (i.e., PPRs) were calculated for large-medium Bluefin Tuna, giant Bluefin Tuna, and Atlantic Menhaden prey.

RESULTS

Captive Bluefin Tuna

Video footage of prey size-selectivity trials yielded 53 prey attack sequences that could be quantified. Size selectivity was

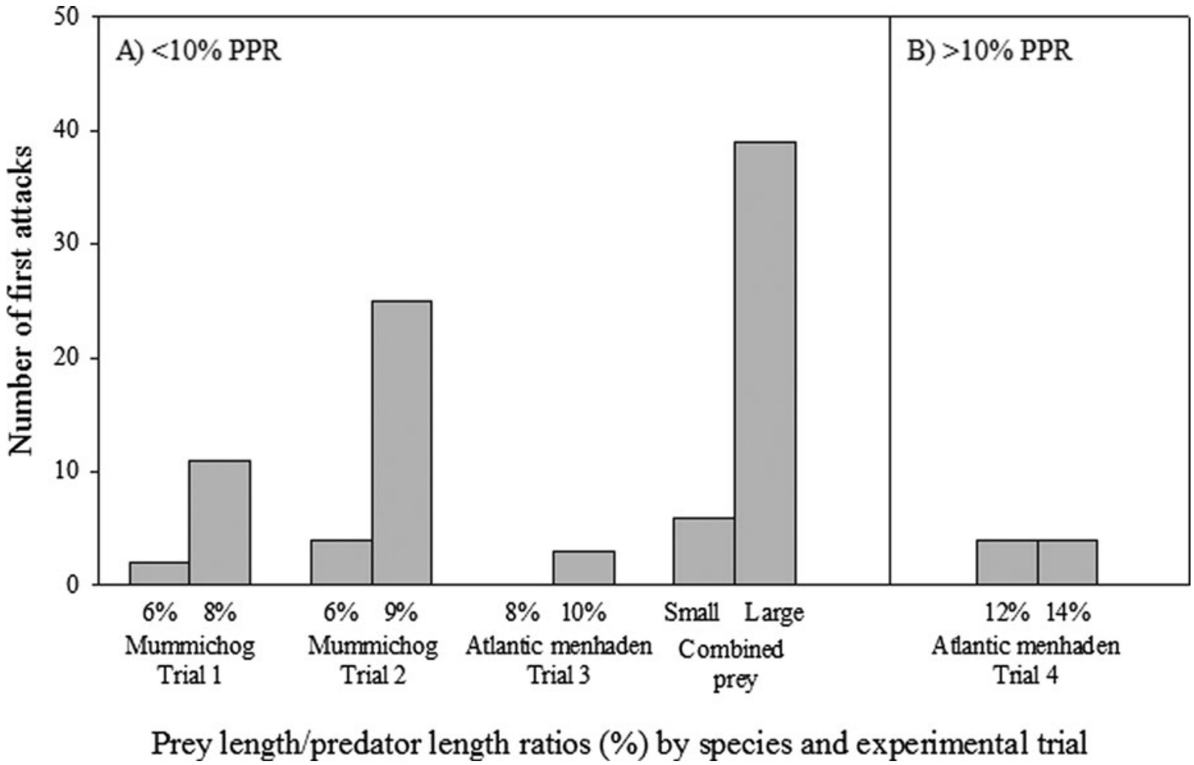

FIGURE 1. Number of first attacks by captive Bluefin Tuna on either Mummichog or Atlantic Menhaden prey with **(A)** prey length : predator length ratios (PPRs) less than or equal to 10%; and **(B)** PPRs greater than 10%.

measured in 42 attacks on paired Mummichog prey that had PPRs less than 10% (Figure 1A). In each trial, Bluefin Tuna positively selected the larger Mummichog prey over the smaller Mummichog prey (trial 1: $\chi^2 = 6.23$, $P = 0.01$; trial 2: $\chi^2 = 15.21$, $P < 0.01$).

Atlantic Menhaden prey size-selection trials yielded 11 quantifiable observations. When Atlantic Menhaden with PPRs less than or equal to 10% were used, Bluefin Tuna consumed the larger prey first in all three of the observations. However, due to low sample sizes, the selection of larger Atlantic Menhaden was not significantly greater than the selection of smaller individuals ($\chi^2 = 3.00$, $P = 0.08$; Figure 1A). When Atlantic Menhaden prey with PPRs greater than 10% were presented, we found no evidence of size-selective feeding ($\chi^2 = 0.00$, $P = 1.00$; Figure 1B).

When Mummichog and Atlantic Menhaden prey with PPRs less than or equal to 10% were considered together, the first attack was directed toward the larger prey item 87% of the time. The chi-square goodness-of-fit analysis of first attacks on large prey versus small prey revealed that the number of first attacks on the larger of the two prey presented was significantly greater than expected ($\chi^2 = 24.2$, $P < 0.01$; Figure 1A).

Capture success for Bluefin Tuna when attacking prey was extremely high for both prey types. When live Mummichogs were presented, Bluefin Tuna captured 95% of those attacked (145 of 153 fish); when Atlantic Menhaden prey were presented, the capture success rate was 97% (31 of 32 fish). No differences in capture success were detected among prey sizes.

Free-Ranging Bluefin Tuna

Test of size selectivity.—The sizes of Atlantic Menhaden consumed by free-ranging Bluefin Tuna were similar to the sizes of those captured by the purse-seine fishery (Figure 2A). Sizes of Atlantic Menhaden found in the stomachs of large-medium Bluefin Tuna (Figure 2B), giant Bluefin Tuna (Figure 2C), and pooled size-classes (Figure 2D) were not significantly different from the sizes of Atlantic Menhaden found in North Carolina waters during winter (large-medium Bluefin Tuna: $\chi^2 = 0.01$, $P = 0.90$; giant Bluefin Tuna: $\chi^2 = 0.01$, $P = 0.94$; pooled size-classes: $\chi^2 = 0.02$, $P = 0.88$).

Quantile regression analyses and relative prey size.—In total, 1,027 prey lengths were recorded from stomach samples representing 218 large-medium and giant Bluefin Tuna. The bulk of the prey length measurements were from Atlantic Menhaden, with a smaller contribution from Atlantic Needlefish *Strongylura marina*, elasmobranchs, and other teleosts. There was little change in prey size across Bluefin Tuna sizes for both minimum and maximum sizes of prey (5th quantile: $P = 0.08$; 95th quantile: $P = 0.49$; Figure 3A). However, the median size of prey increased with increasing Bluefin Tuna length (50th quantile:

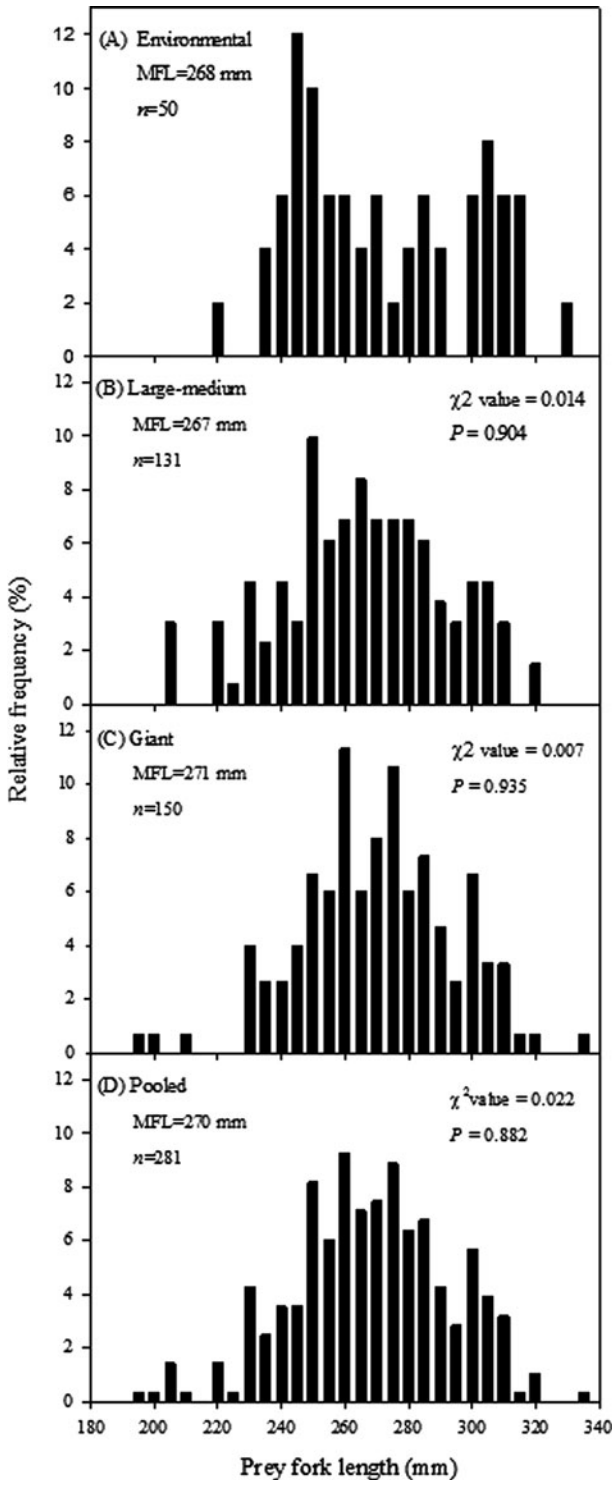

FIGURE 2. Length-frequency distributions of Atlantic Menhaden collected in **(A)** the commercial purse-seine fishery off the coast of North Carolina during winter 2004–2005 (environment) or found in the stomach contents of **(B)** large-medium Bluefin Tuna, **(C)** giant Bluefin Tuna, and **(D)** pooled size-classes of Bluefin Tuna collected off the North Carolina coast during winter 2004–2005. The P-values and chi-square statistics are from chi-square median tests comparing Atlantic Menhaden lengths in the purse-seine samples with those in stomach contents from each Bluefin Tuna size-class. The number of measured Atlantic Menhaden from purse-seine samples and stomach contents is given for each comparison (MFL = median FL).

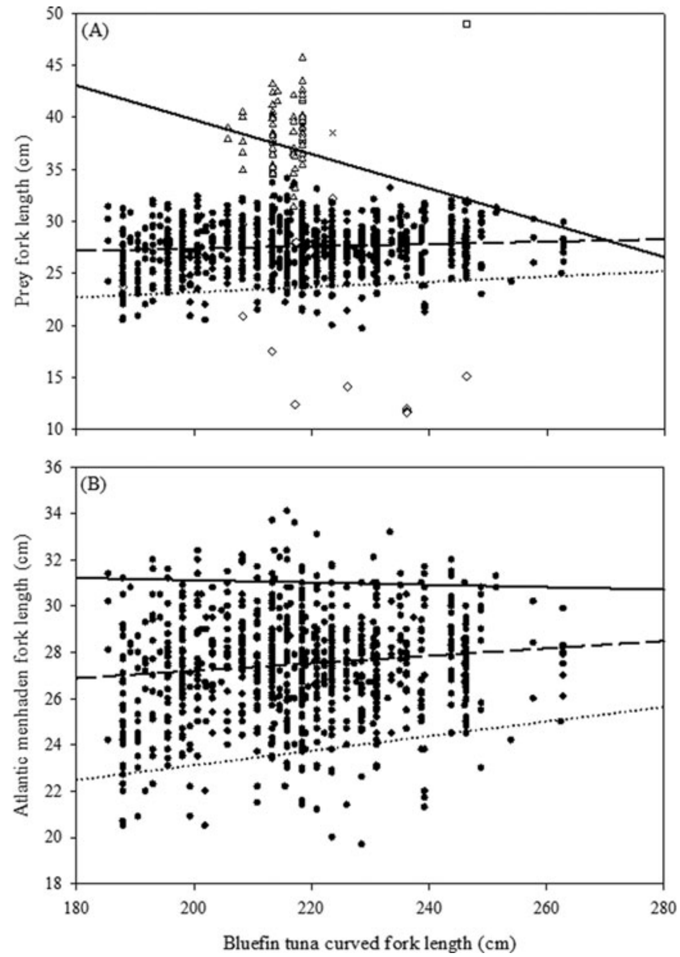

FIGURE 3. Quantile regression analysis of prey FLs in the stomach contents of Bluefin Tuna as a function of predator size: **(A)** all prey types (Atlantic Menhaden = circles; Atlantic Needlefish = triangles; other teleosts = diamonds; cephalopods = "x" marks; elasmobranchs = squares) and **(B)** Atlantic Menhaden prey only. Regression lines illustrate changes in the minimum FL (panel A: $y = 0.025x + 18.200$, $P = 0.08$; panel B: $y = 0.032x + 16.820$, $P < 0.01$), median FL (panel A: $y = 0.011x + 25.199$, $P = 0.01$; panel B: $y = 0.016x + 23.991$, $P < 0.01$), and maximum FL (panel A: $y = -0.165x + 72.770$, $P = 0.49$; panel B: $y = -0.005x + 32.125$, $P = 0.83$) of consumed prey as predator size increased. The dotted lines represent the minimum quantile; the dashed lines represent the median quantile; and the solid lines represent the maximum quantile.

$P = 0.01$; Figure 3A). When only Atlantic Menhaden prey ($n = 926$) were considered, the minimum and median sizes increased significantly with increasing Bluefin Tuna size (5th quantile: $P < 0.01$; 50th quantile: $P < 0.01$; Figure 3B). However, there was no change in the maximum size of Atlantic Menhaden prey as a function of Bluefin Tuna size (95th quantile: $P = 0.83$).

A significant ($P < 0.01$) negative relationship was observed between Atlantic Menhaden : Bluefin Tuna PPR and predator CFL (Figure 4). Large-medium Bluefin Tuna only consumed Atlantic Menhaden with PPRs less than 18% (Figure 5A). Similarly, for giant Bluefin Tuna, Atlantic Menhaden lengths were always less than 16% of Bluefin Tuna CFL (Figure 5B).

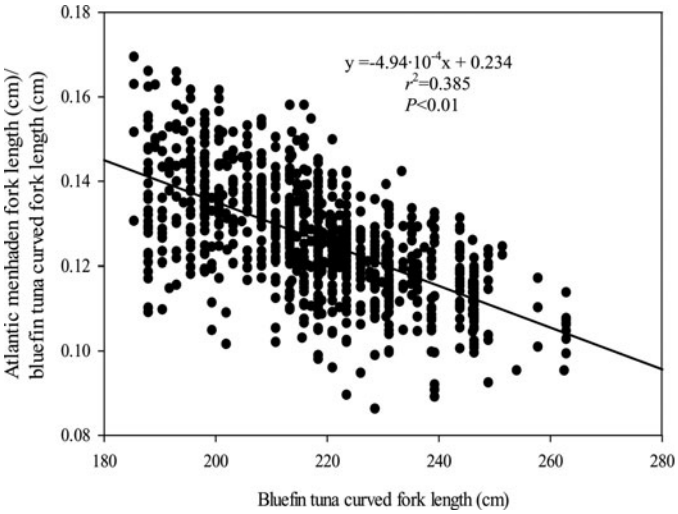

FIGURE 4. Linear regression analysis of the relative size of Atlantic Menhaden prey (i.e., prey length : predator length ratio) versus the curved FL of Bluefin Tuna.

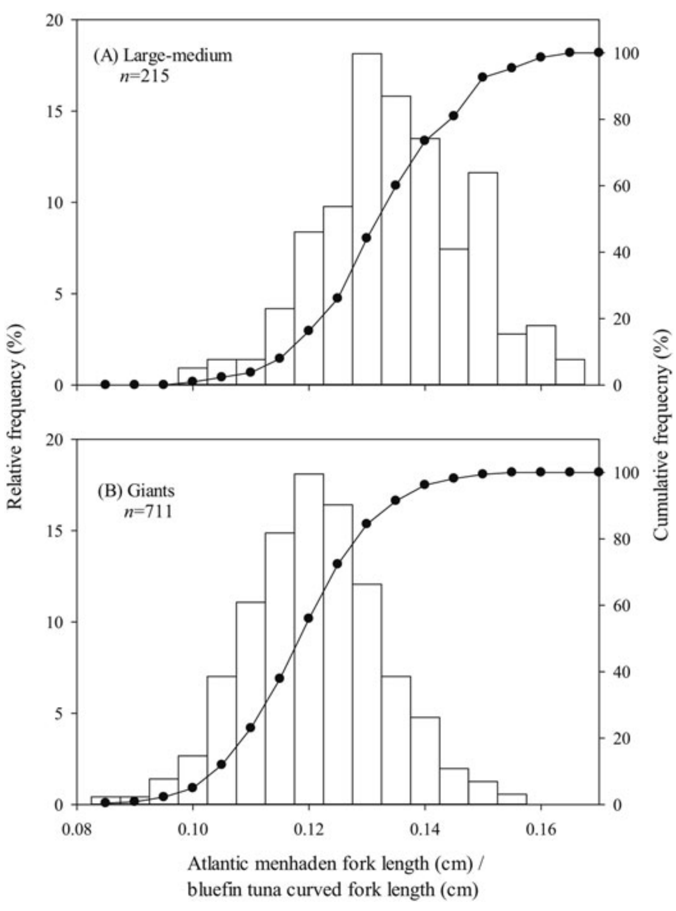

FIGURE 5. Distributions of the prey length : predator length ratios for Atlantic Menhaden prey consumed by **(A)** large-medium Bluefin Tuna and **(B)** giant Bluefin Tuna. Both relative (open bars) and cumulative (circles) frequencies are shown.

DISCUSSION

For piscivorous fishes, PPRs generally average about 20–30% (Juanes 1994; Rudershausen et al. 2010). However, Chase (2002) found that the average size of prey consumed by Bluefin Tuna sampled off New England (104–297 cm) was only about 8% of mean predator length. We examined the sizes of prey in the stomach contents of free-ranging Bluefin Tuna for which the known prey (i.e., Atlantic Menhaden) had potential PPRs nearly double that of the average prey size described by Chase (2002). We hypothesized that small PPRs for Bluefin Tuna were a result of passive selection for relatively small prey (i.e., reduced capture success on larger prey). We found no evidence of selection for smaller prey by either free-ranging or captive Bluefin Tuna. Interestingly, there was evidence for selection of larger prey by captive Bluefin Tuna when paired prey had PPRs less than 10%. This was surprising given the small differences in length between the small and large prey. To our knowledge, these are the first tests of size-selective feeding in captive or free-ranging Bluefin Tuna.

Previous studies of piscivorous fishes have found that the minimum prey size remains relatively constant with increasing predator size, whereas the median and maximum prey sizes increase significantly with predator size (Scharf et al. 2000; Bethea et al. 2004; Rudershausen et al. 2005; Young et al. 2010). These trends in prey size and predator size did not hold for free-ranging Atlantic Bluefin Tuna examined during the present study. Maximum prey size was unaffected by increasing predator size, suggesting no morphological or behavioral constraints on prey capture or handling at these predator and prey sizes. Similarly, Young et al. (1997) and Logan et al. (2011) found no evidence for a relationship between prey size and Bluefin Tuna size; however, they focused on a relatively narrow size range of Bluefin Tuna, as was the case in the present study. Chase (2002) examined the broadest length range (120–299 cm) of Bluefin Tuna and found a weak but significant relationship of prey size with increasing predator size. Future tests examining for patterns in the PPRs of Bluefin Tuna should include a broad range of predator sizes when available. We did find positive slopes for minimum and median quantiles, but this finding may have been driven by low sample sizes for the largest Bluefin Tuna or may be a real pattern wherein giant Bluefin Tuna avoid consumption of smaller prey, as predicted by optimal foraging theory (Juanes 1994). The latter conclusion is supported by the Bluefin Tuna's active selection for larger relative prey in the captive study. However, it is important to note that our captive Bluefin Tuna were much smaller than the free-ranging Bluefin Tuna from which stomach content samples were obtained.

The larger Atlantic Menhaden that were available (based on samples from the purse-seine fishery) were consumed by all sizes of Bluefin Tuna. The PPRs for these maximum-sized Atlantic Menhaden were less than 20%. The mode of Atlantic Menhaden PPRs for giant Bluefin Tuna was smaller than the mode for large-medium Bluefin Tuna. However, this shift was due to the increased size of giant Bluefin Tuna as opposed to a situation in which giant Bluefin Tuna were feeding on smaller Atlantic Menhaden. Capture success rates in the net-pen were greater than 95% for all prey types and sizes (up to 14% PPR) examined; these capture success rates are higher than those observed for other piscivorous fishes (Major 1978; Eklov and Hamrin 1989; Parrish 1993; Juanes and Conover 1994) and at least partly result from the relatively small size of the prey (Scharf et al. 2003). During winter in North Carolina waters, free-ranging Bluefin Tuna consumed mostly one prey type, the Atlantic Menhaden (Butler et al. 2010); the entire size distribution of this prey species represents relatively low PPR values for Bluefin Tuna. We believe that the low PPRs of Atlantic Menhaden make them highly vulnerable to predation. We did not find evidence for selection of small prey within a given prey type, but Bluefin Tuna appear to focus on prey types that are vulnerable across their entire size distribution.

There are several caveats that should be recognized regarding the captive Bluefin Tuna portion of the current study. First, the Mummichog is not a natural prey of Bluefin Tuna. Mummichogs were used during live-prey presentations because they could be easily collected and successfully transported live to the net-pen enclosure for feeding trials. Future feeding studies would benefit from including more types of natural prey to address questions regarding the selection of prey types and prey sizes. Second, prey sizes that were used during feeding trials were relatively small. Again, this was related to the ease of collection and transport. Because of this, identification of the maximum prey sizes for captive Bluefin Tuna was not possible based on our trials. However, the prey sizes used in our net-pen experiments represent PPRs that were similar to or larger than those found for free-ranging Bluefin Tuna in New England (Chase 2002) and allowed for realistic tests of size selectivity.

The field portion of our study relied on commercial catches of Atlantic Menhaden; during our winter study periods, these catches mostly occurred in the offshore areas where Bluefin Tuna were being captured. All sizes and ages (age 0–6) of Atlantic Menhaden are found off the North Carolina coast during winter (Nicholson 1971), but smaller fish are situated more inshore than larger fish. The larger Atlantic Menhaden spawn predominantly during December and January (Warlen 1994). Since the Atlantic Menhaden purse-seine fishery used the same gear for harvesting smaller fish (100–200 mm) inshore and larger fish (>200 mm) offshore (J. W. Smith, personal observation), it is unlikely that the gear missed smaller Atlantic Menhaden in the offshore environment. Thus, the sizes of Atlantic Menhaden caught offshore in the purse-seine fishery were assumed to represent the prey sizes available to Bluefin Tuna. However, the low sample sizes of Atlantic Menhaden lengths from the purse-seine fishery may not completely represent the size distributions found throughout the environment.

Several forage species consumed by Bluefin Tuna are also harvested commercially (e.g., Atlantic Herring and Atlantic Menhaden); multispecies models of human and fish predator "catch" have been used in stock assessments of forage fish (Overholtz et al. 2008; Garrison et al. 2010). Bluefin Tuna display extensive migration patterns related to spawning and feeding activities (Teo et al. 2007), and their focal prey species is spatially dependent on their migrations (Chase 2002; Overholtz 2006; Butler et al. 2010). The present information on prey sizes will be useful for advancing predator–prey modeling approaches and for improving assessments of both Bluefin Tuna and their primary forage species.

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