

2009

Recalculated diet and daily ration of the shortfin mako (*Isurus oxyrinchus*), with a focus on quantifying predation on bluefish (*Pomatomus saltatrix*) in the northwest Atlantic Ocean

Anthony D. Wood
University of Rhode Island, awood@gso.uri.edu

Bradley M. Wetherbee
University of Rhode Island, wetherbee@uri.edu

Francis Juanes

Nancy E. Kohler

Cheryl Wilga
University of Rhode Island, cwilga@uri.edu

Follow this and additional works at: https://digitalcommons.uri.edu/bio_facpubs

Citation/Publisher Attribution

Wood, Anthony D., Bradley M. Wetherbee, Francis Juanes, Nancy E. Kohler and Cheryl Wilga. "Recalculated Diet and Dairy Ration of the Shortfin Mako (*Isurus oxyrinchus*), With a Focus on Quantifying Predation on Bluefish (*Pomatomus saltatrix*) in the Northeast Atlantic Ocean." *Fishery Bulletin*. 107(1):76-88. January 2009. Available at <http://fishbull.noaa.gov/1071/wood.pdf>.

This Article is brought to you by the University of Rhode Island. It has been accepted for inclusion in Biological Sciences Faculty Publications by an authorized administrator of DigitalCommons@URI. For more information, please contact digitalcommons-group@uri.edu. For permission to reuse copyrighted content, contact the author directly.

Recalculated diet and daily ration of the shortfin mako (*Isurus oxyrinchus*), with a focus on quantifying predation on bluefish (*Pomatomus saltatrix*) in the northwest Atlantic Ocean

Terms of Use

All rights reserved under copyright.

Abstract—The diet and daily ration of the shortfin mako (*Isurus oxyrinchus*) in the northwest Atlantic were re-examined to determine whether fluctuations in prey abundance and availability are reflected in these two biological variables. During the summers of 2001 and 2002, stomach content data were collected from fishing tournaments along the northeast coast of the United States. These data were quantified by using four diet indices and were compared to index calculations from historical diet data collected from 1972 through 1983. Bluefish (*Pomatomus saltatrix*) were the predominant prey in the 1972–83 and 2001–02 diets, accounting for 92.6% of the current diet by weight and 86.9% of the historical diet by volume. From the 2001–02 diet data, daily ration was estimated and it indicated that shortfin makos must consume roughly 4.6% of their body weight per day to fulfill energetic demands. The daily energetic requirement was broken down by using a calculated energy content for the current diet of 4909 KJ/kg. Based on the proportional energy of bluefish in the diet by weight, an average shortfin mako consumes roughly 500 kg of bluefish per year off the northeast coast of the United States. The results are discussed in relation to the potential effect of intense shortfin mako predation on bluefish abundance in the region.

Recalculated diet and daily ration of the shortfin mako (*Isurus oxyrinchus*), with a focus on quantifying predation on bluefish (*Pomatomus saltatrix*) in the northwest Atlantic Ocean

Anthony D. Wood (contact author)¹

Bradley M. Wetherbee²

Francis Juanes³

Nancy E. Kohler⁴

Cheryl Wilga²

Email address for contact author: awood@gso.uri.edu

¹ Graduate School of Oceanography
University of Rhode Island Bay Campus
215 South Ferry Rd.
Narragansett, Rhode Island. 02882
Present address: School for Marine Science and Technology (SMAST)
200 Mill Road, ATT 211,
Fairhaven, Massachusetts 02719

² University of Rhode Island
Biological Sciences
100 Flagg Rd.
Kingston, Rhode Island 02881

³ Department of Natural Resources Conservation
160 Holdworth Way
University of Massachusetts
Amherst, Massachusetts 01003

⁴ National Marine Fisheries Service, NOAA
Northeast Fisheries Science Center
Narragansett Laboratory
28 Tarzwell Drive
Narragansett, Rhode Island 02882

Manuscript submitted 11 July 2007.
Manuscript accepted 10 September 2008.
Fish. Bull. 107:76–88 (2009).

The views and opinions expressed or implied in this article are those of the author and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

A top-down trophic system involves consumer control of the community structure and the population dynamics of an ecosystem. In many marine ecosystems many species of sharks are positioned at the top of the food chain, and through predation can potentially exert control upon their prey communities (van der Elst, 1979; Stevens et al., 2000; Heithaus and Dill, 2002). As management decisions become increasingly focused on the interactions between multiple species, it is important that the effects of predation be evaluated (Bax, 1998; Overholtz et al., 2000). One of the first steps in carrying out such an evaluation is through the examination of the food habits and daily rations of the top predators in a system (Wetherbee

and Cortés, 2004). In the northwest Atlantic Ocean ecosystem the shortfin mako (*Isurus oxyrinchus*) is an abundant apex predator. We re-examine the diet and daily ration of shortfin makos in the northwest Atlantic and quantify an important predator-prey relationship that has existed for decades.

In the northwest Atlantic, the shortfin mako ranges from the Caribbean Sea and Gulf of Mexico, north to Nova Scotia, Canada, and the Grand Banks (Compagno, 2001). Starting in the early spring (mid to late May) shortfin makos appear in abundance off the northeast coast of the United States. The annual migration to this region from the south and from offshore locales coincides

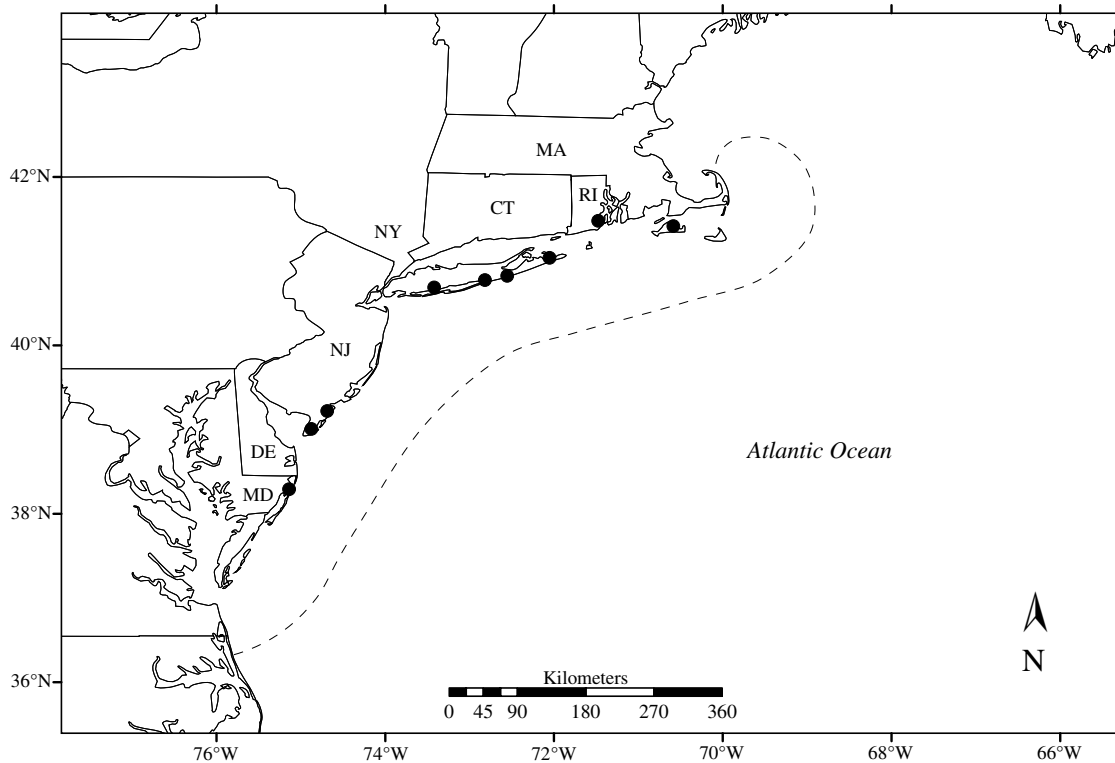


Figure 1

Map of the northeast coast of the United States showing the locations (●) of major shark fishing tournaments where shortfin mako (*Isurus oxyrinchus*) stomachs were collected from May through October of 2001 and 2002 to determine the diet of this species. An approximate boundary (- - -) indicates where fishing took place for these tournaments.

with the appearance of many teleost prey species. An early diet study from this region, during this seasonal residence, has indicated that teleosts make up 98% of the diet by volume, and that bluefish (*Pomatomus saltatrix*) account for 77.5% of prey by volume (Stillwell and Kohler, 1982). Bluefish are undoubtedly the most important prey species, but much has changed with the bluefish stocks since this initial examination of the shortfin mako diet. Throughout the 1980s and early 1990s the northwest Atlantic Ocean bluefish stock experienced a decline in both young-of-the-year abundance and spawning stock biomass (Shepherd and Packer, 2006). This decline was likely a result of many factors, including natural population fluctuation, environmental and physical stresses, fishing pressure (both commercial and recreational), and intense predation by shortfin makos and other bluefish predators.

To examine the current level of bluefish consumption by the shortfin mako, and to investigate whether predation on bluefish has changed over the past two decades, we 1) re-quantified the diet from stomach contents data collected from the late May through October of 2001 and 2002, and compared this current data with historical diet data (collected from 1972 to 1983); 2) back-calculated bluefish prey size to determine potential predator-size–prey-size relationships; 3) calculated daily ration from the 2001–02 data with a bioenergetics

model and the method of Elliot and Persson (1978). We attempt to address from our results, focusing on bluefish as the most important prey, whether shifts in prey species abundance from historical levels are reflected in the shortfin mako diet. In addition, the potential regulatory effect of intense shortfin mako predation on bluefish in this region is investigated.

Materials and methods

Stomach collection

Stomach contents were examined from shortfin mako caught in shark fishing tournaments carried out from May to October of 2001 and 2002 along the northeast coast of the United States. (Fig. 1). For the purposes of comparison with historical inshore data, these samples were considered to have been caught <45 nmi from shore and at a water depth of <91 m. Historical data on shortfin mako diet were provided by the National Marine Fisheries Service (NMFS), Apex Predators Program, located at the Northeast Fisheries Science Center (NEFSC) Narragansett Laboratory, Narragansett, RI. These data were collected from late May through October from 1972 through 1983 by NMFS staff and charter boat fishing crews at many of the

Table 1

Digestive states (1–7) of prey items found in stomachs of shortfin makos (*Isurus oxyrinchus*) caught in fishing tournaments along the northeast coast of the United States, 2001–02, and the estimated digestion time (h) and the percentage of prey items found for each digestive state.

Scale number	Description of digestive state	Estimated digestion time (h)	Percentage of prey
1	Prey maintains original shape perfectly, skin also intact, pigmentation still bright.	0 to 2	2.4
2	Original shape almost completely retained, part or all of skin missing, pigmentation faded.	2 to 4	1.6
3	Flesh still recognizable on body, skeleton nearly complete.	4 to 7	15.7
4	Skeleton partially fragmented, flesh still attached to backbone.	7 to 10	27.6
5	Skeleton fragmented into many pieces, chunks of flesh remaining.	10 to 14	35.4
6	Prey reduced to mush consisting of flesh, skeletal fragments and scales, no recognizable body parts.	14 to 18	15.0
7	Opaque liquid only.	18 +	2.4

same shark fishing tournaments where the 2001–02 data were collected.

For the 2001–02 diet data, stomachs were extracted on location, bagged, placed on ice, and brought to the laboratory for examination within 48 to 72 hours of catch. In the laboratory, stomachs were carefully removed from surrounding organs and cut open for examination of the contents. Prey were identified to the lowest taxon possible, counted, sorted, and weighed individually (± 0.01 g). When bluefish were found in stomachs, remaining bones were examined in more detail. In cases where one or more of five skull bones (maxilla, premaxilla, dentary, cleithrum, opercle) were found intact, and in good overall condition, these bones were collected for the purpose of back-calculating original bluefish size with a series of predictive equations (Wood, 2005). Unidentifiable prey items were designated as such and all prey items were given a value from 1 to 7 on a scale based on state of digestion (Table 1). This scale of digestion was used to eliminate suspicious prey items that could have been bait. All prey items were explored for clean (knife-edge) cuts, fish hook marks, and imbedded fish hooks, and any items identified as bait were removed from the samples. Typically, Atlantic mackerel (*Scomber scombrus*) pieces, butterflyfish (*Peprius triacanthus*) pieces, and bluefish are used as bait by fishermen, and menhaden (*Brevoortia tyrannus*) oil and ground menhaden are used as chum.

Diet

The diet of the sharks sampled during the current study was quantified by three basic prey indices: percentage by number (%N), percentage by weight (%W), and percentage by occurrence (%O) (Hyslop, 1980); and a compound index of relative importance (IRI) was expressed as a percentage (%IRI) (Cortés, 1997).

Comparisons between the current and historical data were based on the index of number (%N), the index of weight (%W), and the index of occurrence (%O). For a direct quantitative comparison between the current and historical data, weight was used as a proxy for volume by assuming a constant prey density of 1.0 g = 1.0 mL. The %W index from the current data was compared to an index based on prey volume (%V) from the historical diet data.

Diet overlap between the current data and the historical data was examined with two measures of niche overlap, the percentage overlap measure and the simplified Morisita index (Krebs, 1999). A contingency table (both chi-square and *G* statistic) based on prey numbers was used to investigate whether significant differences existed between the current and historical diets in aggregate. For the contingency table analyses, prey items were grouped into seven categories (Pomatomidae, Clupeidae, Scombridae, other teleosts, unidentified teleosts, invertebrates, and mammals and elasmobranchs).

Cumulative prey curves were generated for the 2001–02 and historical diet data to determine whether the overall shortfin mako diet was adequately represented by the study samples. In addition, the rate of increase of the last 10 points in both curves was analyzed to determine whether an asymptote had been reached. A rate of increase of less than 5.0% was used as the cut-off (Baremore, 2007). A jackknife estimate of species richness was also calculated to estimate how many prey species were potentially missed by sampling. The cumulative prey curves and jackknife estimate were generated with PRIMER vers. 6.0 software (Clarke, 1993).

Predator-size–prey-size relationship

Measurements of bluefish bones collected from stomach contents were used to back-calculate sizes of prey

individuals with predictive equations (Wood, 2005). To explore predator-size–prey-size relationships a shortfin mako size–bluefish size scatter plot was analyzed with least squares regression. Quantile regressions (5th and 95th) were used to determine changes in minimum and maximum prey size with increasing predator size. In addition, relative and cumulative frequency histograms were used to explore patterns in the size of prey consumed (Betha et al., 2004).

Daily ration

Two methods were used to estimate daily ration of the shortfin mako: a bioenergetics approach and the use of the average weight of stomach contents (following Elliot and Persson, 1978). These approaches were both used so that a comparison between the resulting daily ration estimates could be made. In addition, both of these methods were previously used to calculate daily ration of shortfin makos (Stillwell and Kohler, 1982).

The bioenergetics approach used by Stillwell and Kohler (1982) did not include growth information and was based on the volume of oxygen consumption (VO_2) extrapolated from four species of squaloid sharks. More recently, VO_2 has been measured directly for the shortfin mako at various swimming speeds (U) (Graham et al., 1990). Stillwell and Kohler's (1982) estimate of VO_2 (284.2 mg/kg/h) was much lower than the values of VO_2 actually measured for the shortfin mako by Graham et al. (1990), who found an average VO_2 of 369 mg/kg/h for routine metabolism.

The bioenergetics model for this study followed a form commonly used for teleost fishes which has been successfully applied to blue sharks (*Prionace glauca*) (Schindler et al., 2002). To calculate daily consumption, the model incorporates growth rates, metabolism, and other energy parameters in an energy balance equation:

$$C = M + SDA + (F + Ur) + (G_t + Rp),$$

where C = consumption rate;
 M = metabolism;
 SDA (specific dynamic action) = the amount of energy used for digestion;
 F and Ur = energy lost to waste;
 G_t = growth over time; and
 Rp = the amount of energy allocated towards reproduction.

Metabolism (M) in the model was assumed to be active metabolism because shortfin makos are obligate ram ventilators (must continually swim in order to breathe). To generate a relationship between swimming speed (U) and mean VO_2 , a least squares regression was fitted mean VO_2 data at a variety of swimming speeds taken from Graham et al. (1990)'s data. The resulting regression equation, along with observed rates of travel determined from satellite telemetry tracking of shortfin makos, was used to calculate active metabolism. An

energy equivalence of 13.6 J/mg O_2 was used to convert the VO_2 consumed into energy (Schindler et al., 2002), and a Q_{10} value for the bonnethead shark (*Sphyrna tiburo*) of 2.3 (Carlson and Parsons, 1999) was used to adjust the final metabolic rate to 18.8°C (the preferred temperature of shortfin makos in the northwest Atlantic; Stillwell and Kohler, 1982).

Specific dynamic action (SDA) was set at a fraction of consumption rate (C) equal to 0.10 C (Schindler et al., 2002), and the amount of energy lost to waste ($F + Ur$) was fixed at 0.27 C (Stillwell and Kohler, 1982; Schindler et al., 2002). For growth, sex-specific growth rates (G_t) were taken from Natanson et al. (2006) who found that growth in length was best modeled by a three-parameter von Bertalanffy growth curve for males and a three-parameter Gompertz growth curve for females. Fork length (FL) was converted to weight with the relationship $WT = 5.2432 \times 10^{-6} FL^{3.1407}$, with weight in kg and FL in cm (Kohler et al., 1996). The energy density value used for the shortfin mako was 20.6 kJ/g dry weight, which was converted to wet weight energy by assuming a 73% water content for shortfin mako flesh (Steimle and Terranova, 1985). The resulting wet-weight energy assumed for all body sizes of the shortfin mako was 5562 kJ/kg which is very close to the average estimate calculated for all sharks of 5414 kJ/kg (Cortés and Gruber, 1990; Schindler et al., 2002).

Energy allocation to reproduction (Rp) was only calculated for females and was assumed insignificant in male sharks. Reproductive growth for mature females (>18 years; Natanson et al., 2006) was calculated by assuming the following reproductive characteristics: mean litter size = 11.1, mean size at birth = 74 cm total length (TL), 24-month gestation period, and 3-year reproductive cycle (Mollet et al., 2000). This reproductive information coupled with the energy density (5562 kJ/kg) for shortfin makos gave an estimated energy cost for reproductive growth.

The overall energy content of the shortfin mako diet was determined with species-specific energy values from Steimle and Terranova (1985). The resulting value was used to calculate daily ration based on the overall energy demand from the bioenergetics model. For comparison of daily ration estimates based on the bioenergetics model, the method of Elliot and Persson (1978) was applied to the stomach contents data collected in the present study. Previously, for the shortfin mako, time for 90% evacuation of a meal was estimated at 36 to 48 hours (Stillwell and Kohler, 1982). It is now known that the VO_2 of shortfin makos is in the same range as that of tunas (Graham et al., 1990; Korsmeyer et al., 1996), which is unsurprising given the similarities that exist between these pelagic predators (i.e., body form, prey, endothermic capability). Studies have revealed that evacuation time for larger species of tuna, such as yellowfin tuna (*Thunnus albacares*), can range from 6 to 20 hours for complete evacuation depending on the prey type (Olson and Boggs, 1986). Based on similarities with tunas, as well as on a markedly higher metabolic rate than that estimated in Stillwell and Kohler (1982),

a shorter evacuation rate of 18–20 hours (higher end of the tuna scale) was used as a more realistic estimate of gastric evacuation time. This range was used to generate values for evacuation rate (R) by assuming an exponential evacuation rate according to the equation: $S_t/S_0 = e^{-Rt}$ (Elliot and Persson, 1978), where S_t and S_0 are the final and initial amounts of the prey item, respectively, and S_t/S_0 is assumed to be 0.10 (or the time when 90% of the initial food has been evacuated from the stomach). With this estimate of gastric evacuation rate, daily ration was calculated with the equation: $\Sigma C(t) = 24\hat{S}R$, where \hat{S} is the mean weight of the stomach contents data over a 24-hour period.

Results

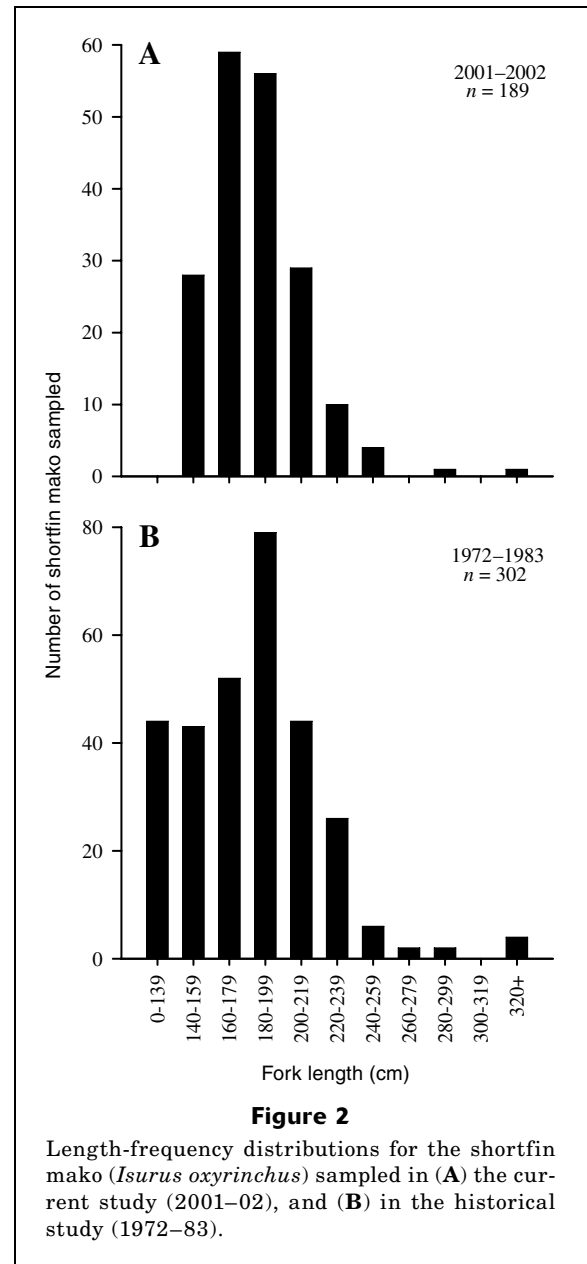
Diet

The two years of seasonal sampling for the 2001–02 diet seemed to provide a very good sample, averaging 95 sharks per year. In total, 189 sharks (108 males and 81 females) were examined that ranged in size from 146 to 335 cm fork length (FL). The majority of sharks sampled (120) contained at least one prey item in their stomach. Overall, 63% of prey items collected from stomachs were at an advanced stage of digestion (levels 4 and 5) on the digestive state scale, and only 4.0% were designated as levels 1 and 2 (Table 1). Any fresh bait that shortfin makos would have encountered and eaten on the day of the tournament would have still been fresh in the stomachs at the time of dissection. The low prevalence of fresh prey items in the digestive scale ratings would indicate that bait was not an important factor in the analysis.

The historical diet data were collected over a much longer period (11 years) and averaged fewer sharks per year (27) than the 2001–02 data. Overall, 302 sharks ranging in size from 86 to 338.5 cm FL were sampled: 148 males, 54 females, and 100 unsexed sharks. A higher percentage of the historical shortfin makos (73.8%) contained at least one prey item in their stomachs. The size distributions of sharks sampled from the two data sets were similar except for the absence of sharks <140 cm in the 2001–02 data (because of restrictions on the size of sharks taken at tournaments implemented after the historical data were collected) (Fig. 2).

Bluefish dominated the current diet of shortfin makos, accounting for 71.2% of the prey by number, 92.6% by weight, 87.5% by occurrence, and 99.2% IRI (Table 2). Other observed prey items were Atlantic mackerel, two species of squid (*Loligo pealeii* and *Illex illecebrosus*), menhaden, and Atlantic herring (*Clupea harengus*). A graphical comparison of index calculations for the three subgroupings of sharks based on the 2001–02 data illustrated the similarity in diet among groups—a similarity primarily due to the predominance of bluefish in all diets (Fig. 3, A and B).

For the historical data, bluefish also dominated the diet, but to a lesser extent, accounting for 55.6% of the



diet by number, 86.9% by volume, 78.5% by occurrence, and 97.2% IRI (Table 2). A variety of different prey items were found in the historical diet, mostly other teleosts. A comparison of prey families indicated that the current diet had prey from nine different families, plus prey from the group crustacea. In the historical diet 14 different fish families of prey were found, as well as crustaceans, mammals, and plants (Table 2). Some of the specific prey items present in the historical diet, but not found in the current diet, were saury (*Scomberesox saurus*), bullet mackerel (*Auxis rochei*), sand lance (*Ammodytes* sp.), and ocean pout (*Macrozoarces americanus*).

The 2001–02 diet data appeared to be a more accurate sample of the shortfin mako diet than the histori-

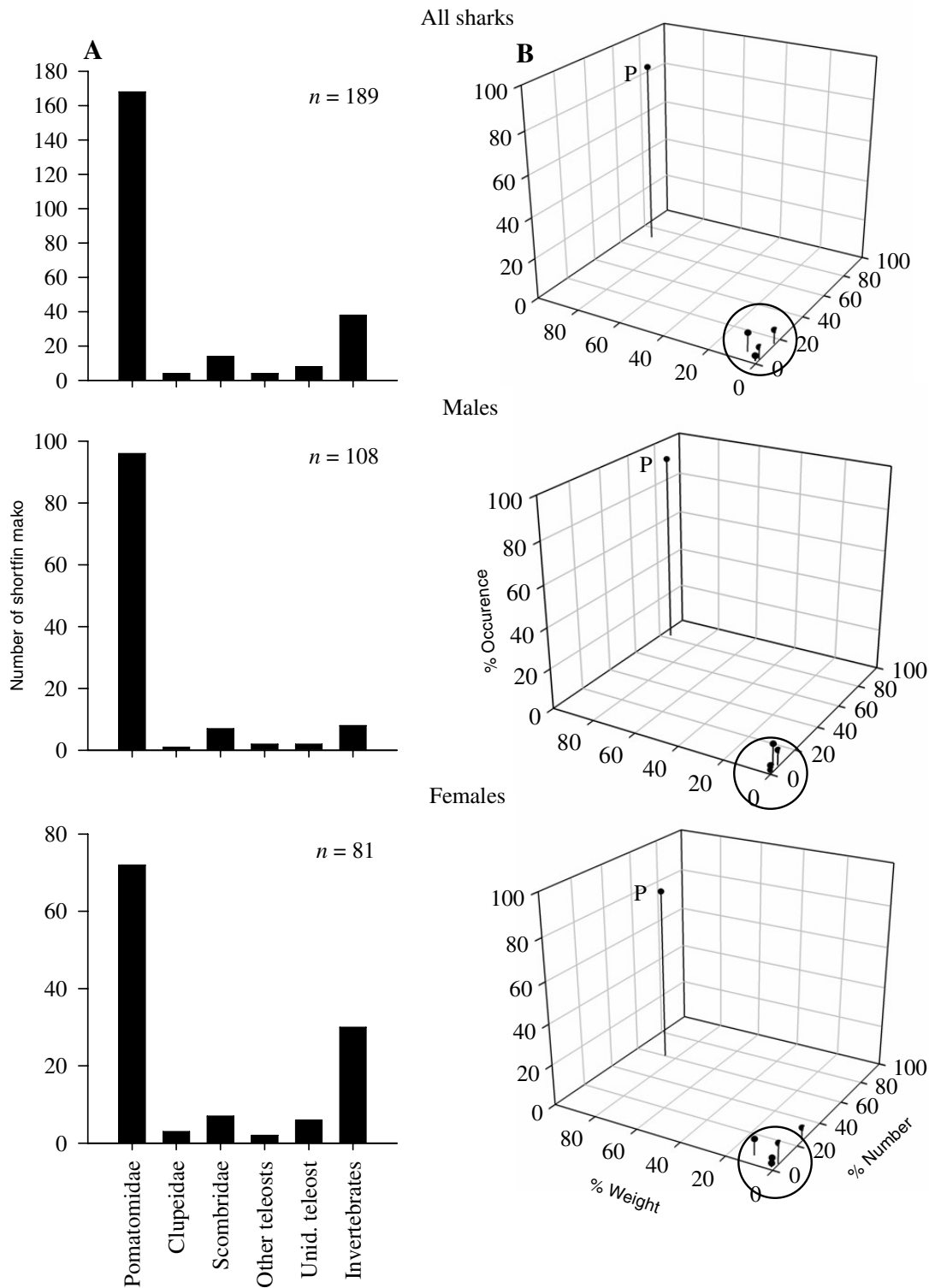


Figure 3

(A) Diet distribution by prey family for the three categories of shortfin mako (*Isurus oxyrinchus*)—all sharks, males, and females. Diet distribution was determined from the 2001–02 diet data. (B) Graphical representation of three diet index calculations for all sharks, for males, and for females. P = Pomatomidae, the predominant prey item, and the open circle surrounds a cluster of less important prey items: Clupeidae, Scombridae, other teleosts, unidentified teleosts, and invertebrates.

cal data. The rate of increase for the cumulative prey curve of the current diet was 3.0%, indicating that the diet was well sampled. Conversely, the cumulative prey curve for the historical diet showed a rate of increase of 6.24%, indicating more sampling may have

captured the diet breadth better (Fig. 4). Jackknife estimates of species richness were 16 and 36 prey species for the 2001–02 and historical diet, respectively. The two measures of niche overlap used to compare the historical and 2001–02 diet data revealed slight

Table 2

Current and historical diet data for the shortfin mako (*Isurus oxyrinchus*) expressed as a percentage by number (%N), weight (%W), frequency of occurrence (%FO), volume (%V); and the index of relative importance expressed as a percentage (%IRI).

Prey item	Current diet				Historical diet			
	%N	%W	%FO	%IRI	%N	%V	%FO	%IRI
Crustaceans	10.60	0.03	0.83	0.07	0.96	0.15	1.79	0.02
Cephalopoda								
Ommastrephidae								
<i>Illex illecebrosus</i>	2.54	0.14	1.67	0.10	6.71	2.62	4.93	0.40
Loliginidae								
<i>Loligo pealeii</i>	2.96	0.42	4.17	0.14	0.72	0.28	1.35	0.01
Unidentifiable					7.19	2.81	7.18	0.34
Elasmobranchs								
Carcharhinidae								
<i>Prionace glauca</i>					0.24	0.19	0.45	0.00
Squalidae								
<i>Squalus acanthias</i>	0.42	0.02	0.83	0.00				
Teleosts								
Ammodytidae					1.44	0.02	0.45	0.01
Clupeidae					1.20	0.02	0.45	0.01
<i>Brevoortia tyrannus</i>	0.85	0.68	0.83	0.01	0.48	0.09	0.45	0.00
<i>Clupea harengus</i>	0.85	0.35	1.67	0.02				
Gadidae					0.24	0.24	0.45	0.00
<i>Merluccius bilinearis</i>					0.24	0.03	0.45	0.00
Malacanthidae								
<i>Lopholatilus chamaeleonticeps</i>	1.27	1.07	1.67	0.03				
Pomatomidae								
<i>Pomatomus saltatrix</i>	71.19	92.62	87.50	99.21	55.64	86.90	78.48	97.24
Scomberesocidae								
<i>Scomberesox saurus</i>					10.07	0.13	2.69	0.24
Scombridae					1.44	0.88	2.69	0.05
<i>Auxis rochei</i>					0.48	0.09	0.90	0.00
<i>Euthynnus pelamis</i>	0.85	0.81	1.67	0.02	0.24	0.39	0.45	0.00
<i>Sarda Sarda</i>					0.24	0.03	0.45	0.00
<i>Scomber scombrus</i>	3.80	0.93	6.67	0.22	2.39	0.68	4.04	0.11
<i>Thunnus albacares</i>	0.85	2.51	1.67	0.04	1.20	0.63	1.35	0.02
Serraniae								
<i>Centropristis striata</i>	0.42	0.08	0.83	0.00				
Sparidae					0.24	0.06	0.45	0.00
Triglidae					0.24	0.05	0.45	0.00
Xiphidae								
<i>Xiphias gladius</i>					0.24	2.58	0.45	0.03
Zoercidae								
<i>Macrozoarces americanus</i>					0.24	0.06	0.45	0.00
Unidentifiable remains	3.39	0.34	5.83	0.15	7.19	0.94	8.52	0.60
Mammalia					0.48	0.14	0.90	0.01
Plant					0.24	0.00	0.45	0.00

differences in the diets and a percentage overlap equal to 70.3 and the simplified Morista's index equal to 0.937. The contingency table analysis indicated that the difference between the diets was significant according to a chi-square test and G -statistic ($P < 0.001$). However, a subsequent contingency table analysis with the grouping "other teleosts" removed from both diets resulted in no significant difference.

Predator-size–prey-size relationship

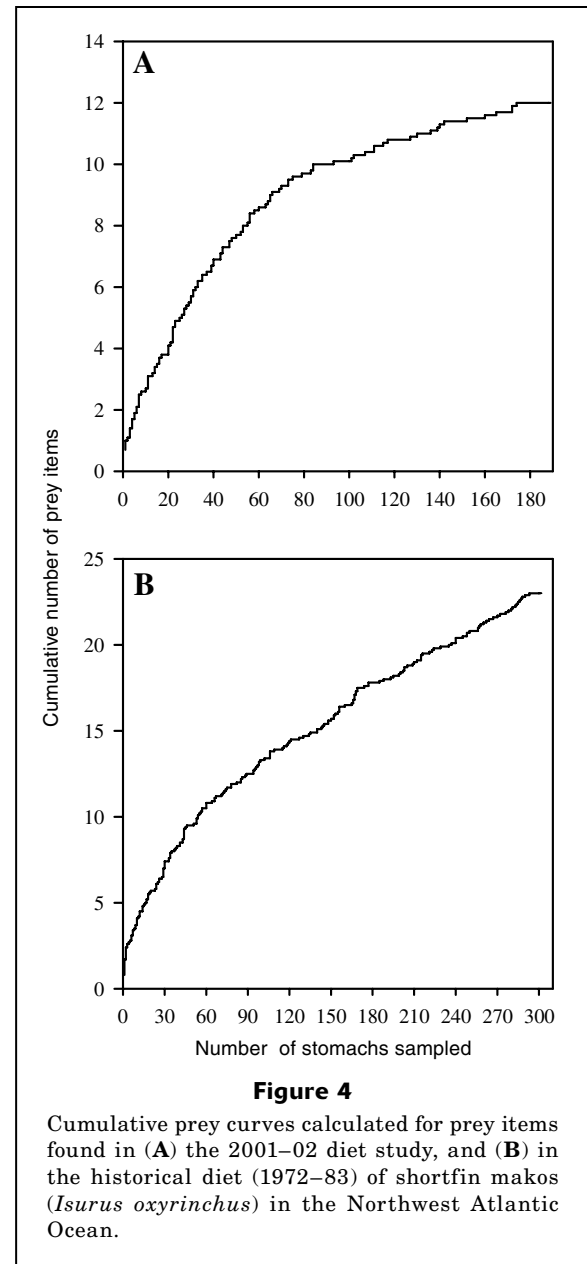
An original fork length was back-calculated for 115 bluefish prey. The average bluefish prey length was 66.7 cm FL (minimum size=36.5 cm and maximum size=82.0 cm). Over 96% of the bluefish found in shortfin mako stomachs were greater than 50.0 cm FL. There was no significant relationship between the size of bluefish prey and predator size and none of the quantile regressions was significant. Investigation of prey size indicated that shortfin makos consume intermediate-size bluefish in relative to their own body size. Overall, 100% of bluefish consumed fell in the range of 0.2 to 0.5 prey-to-predator size ratio, and the majority (35%) were at a ratio of 0.35 (Fig. 5).

Daily ration

The linear relationship between mean VO_2 and swimming speed (U) was significant ($P < 0.05$), and had a fairly good fit ($r^2 = 0.83$). The resulting regression equation was: $VO_2 = 506.42U + 201.39$. From a mean swimming speed of 0.5 body lengths per second (observed from pop-up satellite tag tracks) the active metabolic O_2 consumption rate for the bioenergetics model was calculated to be 454.4 mg/kg/h. Adjusting this value to reflect the average water temperature in which shortfin makos are found in the western North Atlantic ($Q_{10} = 2.3$), we calculated an active metabolic O_2 consumption rate of 485.7 mg/kg/h. An oxy-caloric conversion (13.6 J/mg O_2) of this metabolic demand resulted in an estimate of 6.61 kJ/kg/h of food energy for a shortfin mako to maintain active metabolism.

Total energy consumption increased with age until the onset of maturity for both sexes and slowly decreased (Fig. 6 shows energy consumption following the growth curves as they leveled off). After females reach the average age of maturity (18 years) the model calculated an average reproductive contribution of 86,299 KJ/yr.

The bioenergetic demands for the shortfin mako were higher than previously estimated, and higher than observed for any other species of shark. The average caloric value of the shortfin mako diet was calculated to be 4909 kJ/kg (Table 3). In order to satisfy the total energy demands from the bioenergetics model, shortfin makos must consume on average 4.48% of their body weight (BW) per day. Values of consumption by age ranged from 4.42–4.66 %BW/d for males and 4.42 to 4.56 %BW/d for females.



The second method applied to estimate the daily ration of the shortfin mako yielded a result very similar to that from the bioenergetics model. We assumed all but 10% of a consumed food item was evacuated after a period of 18–20 hours, and a corresponding range of evacuation rates of 0.128 to 0.115/h were calculated. This range of evacuation rates, in conjunction with an observed average stomach contents weight of 1.02 kg, resulted in daily ration estimates of 2.82 to 3.13 kg per day. Daily ration was calculated to be 4.44 to 4.93 %BW/d for a 63.5-kg shortfin mako (the median weight of sharks from the 2001–02 study) according to this model (average of 4.68 %BW/d).

Based on the estimates of daily ration, and the high proportion of bluefish in the diet, a large amount of

Table 3

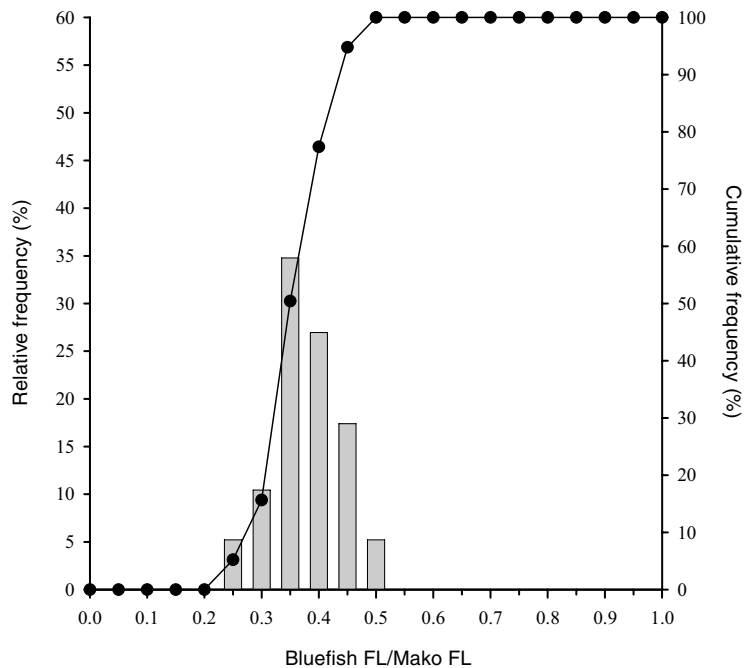
Percentage by weight and the energy content (kJ/kg) determined from the 2001–02 diet data for the shortfin mako (*Isurus oxyrinchus*) and broken down by species. All energy values were taken from Steimle and Terranova (1985).

Prey species	%W	kJ/kg	Diet contribution (kJ/kg)
<i>Brevoortia tyrannus</i>	0.68	7500	51.0
<i>Centropristis striata</i> ²	0.08	4770	3.8
<i>Clupea harengus</i>	0.35	10,600	37.1
Crustaceans ¹	0.03	4450	1.3
<i>Euthynnus pelamis</i> ²	0.81	6300	51.0
<i>Illex illecebrosus</i>	0.14	7100	9.9
<i>Loligo pealei</i>	0.42	5600	23.5
<i>Lopholatilus chamaeleonticeps</i> ²	1.07	4770	51.0
<i>Pomatomus saltatrix</i>	92.62	4800	4445.8
<i>Scomber scombrus</i>	0.93	6000	55.8
<i>Squalus acanthias</i>	0.02	8600	1.7
<i>Thunnus albacares</i> ²	2.51	6300	158.1
Unidentifiable pices ³	0.34	5535	18.8
Total			4909.0

¹ Mean energy value for crustacea was used.

² Mean energy value for benthic and pelagic fish was used.

³ Mean energy value for all fish was used.

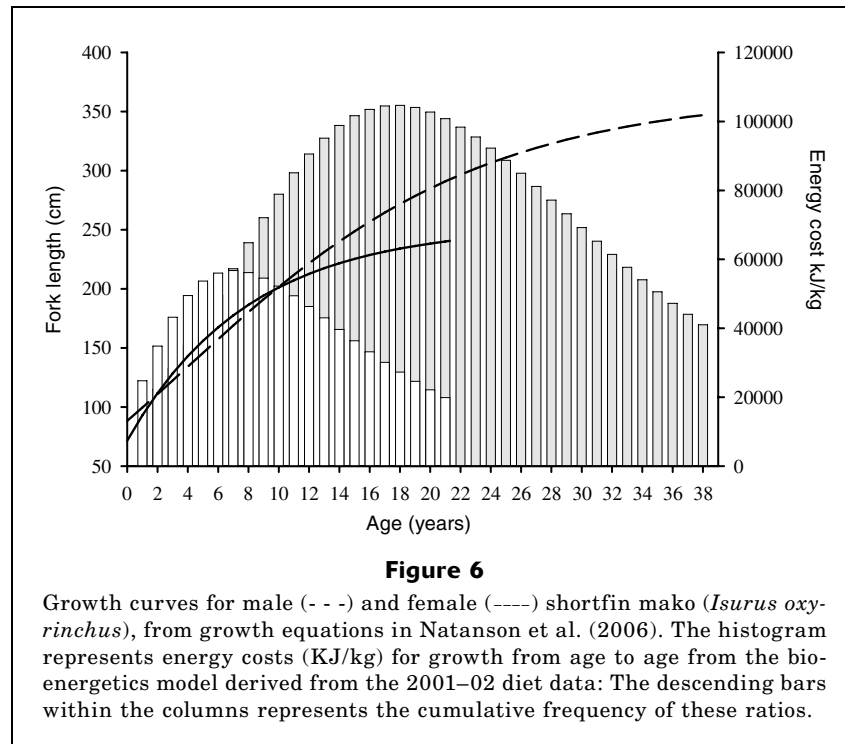
**Figure 5**

Relative frequency (bars) and cumulative frequency (line) plots showing the distribution of bluefish (*Pomatomus saltatrix*) size to shortfin mako (*Isurus oxyrinchus*) size ratios for the 2001–02 diet data.

bluefish could be consumed annually by shortfin makos in the northwest Atlantic Ocean. The average value for daily ration estimated by the two methods indicates that shortfin makos consume roughly 4.58% of their body weight per day. Considering the proportion by weight of bluefish in the diet (92.6%), an average shark (63.5 kg) could consume up to 1000 kg of bluefish per year (assuming a full year feeding cycle on bluefish).

Discussion

The level of top-down predation pressure that shortfin mako are able to exert on northwest Atlantic bluefish populations is still unclear. Quantifying this predator-prey relationship is difficult because it appears to only occur seasonally off the northeast coast of the United States. In offshore regions in the northwest Atlantic where bluefish are less abundant the shortfin mako diet is very different; the sharks focus mainly on squid species and other more prevalent teleosts (Stillwell and Kohler, 1982). It is not until these sharks migrate inshore that they shift



their diet to focus on bluefish (MacNeill et al., 2005). In diet studies from the eastern Atlantic off of Portugal (Maia et al., 2006), and the Southwest Atlantic off Argentina (Vaske-Júnior and Rincón-Filho, 2003), bluefish were not found in the diet of shortfin makos, even though their distribution covers these regions and these sharks prey mainly on teleosts. The high concentration of bluefish in the northwest Atlantic Ocean, and the presence of large schools of bluefish that could be easily located by shortfin makos, is a likely reason for the predominance of bluefish in the diet.

There have been notable changes in the perceived abundance of bluefish in the northwest Atlantic Ocean since the historical diet data were collected. Nearing the end of the historical sampling period bluefish were very abundant with a total stock biomass of 104,000 metric tons (t) in 1982 (NEFSC¹). At this time they were the most important prey species in the shortfin mako diet (86.9 %V). Since the early 1980s, fishing mortality of age-1 bluefish has increased fourfold, and recruitment for age-0 fish is thought to have declined from 75 million to 14 million (Shepherd and Packer, 2006). In addition, total stock biomass declined 72% (29,400 t) from 1982 to 1997 and was estimated to have increased since then to 40,000 t in 2004 (NEFSC¹). This

apparent decline in bluefish abundance from historical levels is not reflected in the current diet of the shortfin mako, and bluefish still represent a very high proportion of prey consumed.

The high numbers of bluefish in the 2001–02 diet indicate that even though abundance is lower than historical levels it is not limiting prey for shortfin mako. There appear to be suitable numbers of bluefish available for the shortfin mako population to prey almost solely on this species during their seasonal residence off the northeast coast of the United States. It is likely that shortfin mako abundance in this region has declined alongside bluefish since the historical diet data were collected. Therefore, although there may be a lower abundance of prey items to feed on, the predator abundance is lower as well. Unfortunately, the shortfin mako population in the northwest Atlantic Ocean has never been reliably quantified. The most recent stock assessment for large pelagic sharks was considered preliminary because of limitations on both the quality and quantity of the data, and came up short of providing reliable estimates. However, trends from catch-per-unit-of-effort indices derived from pelagic longline data for tuna and swordfish (*Xiphias gladius*) fisheries in the western North Atlantic have revealed a 43% decline in shortfin mako abundance since 1986 (Cortés et al., 2007). It is possible that any increased predation pressure on the depleted bluefish population is mitigated by a decreased abundance of shortfin makos from historical levels.

It appears that the importance of bluefish in the shortfin mako diet has not changed since the historical

¹ NEFSC (Northeast Fisheries Science Center). 2005. 41st Northeast Regional Stock Assessment Workshop (41st SAW). 41st SAW assessment report. Northeast Fish Science Center Reference Document 05-14, 237 p. Northeast Fisheries Science Center, National Marine Fisheries Service, Woods Hole Laboratory, 166 Water St., Woods Hole, MA 02543.

sampling; however, there has been an apparent decrease in species diversity in the diet. The cumulative prey curves indicate that the 2001–02 diet was well sampled, but more sampling was needed to better represent the historical diet. Additionally, the jackknife estimates of species richness indicate that 36 species would be represented in a fully sampled historical diet, and only 16 in the current diet. It is possible these results are an artifact of sampling. The total number of shortfin makos examined and the number of years over which the data were collected were both greater for the historical sampling, which likely affected prey diversity. On the other hand, some of the shift observed in the diet diversity over the past few decades could be due to temporal changes in the prey community structure of the northwest Atlantic Ocean. This ecosystem has experienced significant fluctuations in the relative abundance and biomass of many fish and invertebrate species (Overholtz et al., 2000). In addition, the community is now dominated by pelagic finfish such as Atlantic mackerel and Atlantic herring whose large concentrations draw a variety of piscivorous predators, such as bluefish (Overholtz et al., 2000). Large predatory schools of bluefish feeding on abundant pelagic finfish would themselves be easy prey for shortfin makos.

The schooling nature of bluefish is the likely explanation for their high concentration in the shortfin mako diet. Adult bluefish feed and also spawn in large schools as they migrate up the northeast coast of the United States in the spring and early summer (Juanes et al., 1996; Salerno et al., 2001). The focus of shortfin mako predation seems to be these adult bluefish. The length-frequency distribution of bluefish prey found in shortfin mako stomachs revealed that the majority (96%) of individuals fell in the 50- to 90-cm-FL size range. Bluefish at this size are around 2 years old and are likely mature individuals (Juanes et al., 1996; Salerno et al., 2001). The large feeding and spawning aggregations of these adult bluefish would be very easy to find and target for shortfin makos in the region. Intense predation on these large schools could potentially have a regulatory effect on bluefish abundance in the northwest Atlantic Ocean.

In order to quantify the level of shortfin mako predation on the bluefish population a reliable estimate of daily ration was needed. Recently available information on the metabolism, average swimming speed, and growth rate of the shortfin mako has allowed the development of a good bioenergetics model. The resulting estimates of daily ration are notably higher than those of many other elasmobranch species, which rarely exceed 3.0% BW/d (Wetherbee and Cortés, 2004). The highest published rate of consumption observed for an obligate ram ventilating shark was 3.54 %BW/d for juvenile scalloped hammerheads (*Sphyrna lewini*) (Bush and Holland, 2002). The most abundant pelagic shark in the North Atlantic, the blue shark, has a daily ration of approximately 1% BW/d, which is significantly less than that of the shortfin mako (Schindler et al., 2002). The high metabolic

and high consumption rate of the shortfin mako can be attributed to its ability to thermoregulate. The endothermic capability of the shortfin mako increases its aerobic capacity, resulting in a higher metabolism and increased energy demand.

The estimates of daily ration from this study provide a means to quantify predation on bluefish on an individual predator basis. Because there is no estimate of the shortfin mako population size, a relevant exercise is to backcalculate the number of sharks it would take to match the fishing pressure. Bax (1998) determined that predation by fish can range from 2–35 times the loss to fisheries. However, we assumed that shortfin mako predation on bluefish was set equal to the amount of bluefish taken by fisheries in 2002. The total bluefish catch (commercial+recreational) in 2002 was 11,566 t (NEFSC¹). Taking an average value of the daily ration estimates, it was determined that an average shortfin mako (63.5 kg) consumes up to 1000 kg of bluefish per year. For this estimate it is assumed that shortfin makos are feeding on bluefish all year long, which may not be the case. If shortfin makos spend around 6 months off the northeast coast of the United States (May to October), that period results in around 180 days of intense predation on bluefish. During this feeding season an average shark would consume roughly 500 kg of bluefish. At this rate of consumption it would have taken only 23,132 sharks to equal the take of the fisheries in 2002. These are very simple calculations but they serve to illustrate that the level of predation by shortfin mako on bluefish is likely much greater than the impact of the fisheries. If true, this would not be a unique case. Multiple studies have shown that predation mortality on a variety of important prey species exceeds fishing mortality, and in some cases even exceeds maximum sustainable yield of the prey population (Christensen, 1996; Bax, 1998; Overholtz et al., 2000).

The most important factor often attributed to the decline of bluefish stocks in the northwest Atlantic Ocean is fishing pressure (Shepherd and Packer, 2006), but it is evident that predation should not be disregarded. Bluefish mortality as a result of predation could exceed the loss to these fisheries, as has been shown in other predator-prey systems (Bax, 1998; Overholtz et al., 2000). It is becoming increasingly apparent that depressed fish stocks are very vulnerable to predation, but the mechanisms driving this vulnerability are still unclear. In recent studies there have been deeper probes into trophic interactions, such as efforts to quantify prey vulnerability to predation (Bundy and Fanning, 2005; Overholtz, 2006). The exact predator-prey dynamics that exist between shortfin makos and bluefish are still unclear; however, it is likely that predation has played a more important role in the decline of the northwest Atlantic Ocean bluefish population than previously thought.

Adding predation as a variable into the management of northwest Atlantic Ocean bluefish would increase the difficulty of an already complicated task. The highly

migratory nature of the bluefish, coupled with a variety of seasonal fisheries, creates a challenging situation for stock management. Bluefish in this region are currently managed as a single stock, and although the stock is still categorized as overfished, overfishing is not occurring (Shepherd and Packer, 2006). Decreases in fishing pressure have allowed biomass and abundance levels to slowly climb since 1997. However, heavily exploited fish populations tend to remain in a depressed state for a prolonged period following fishing reductions or moratoriums (Bakun and Curry, 1999; Hutchings, 2000; Bundy and Fanning, 2005). One theory offered for the lack of recovery in these populations is predation pressure (Bax, 1998; Bakun and Curry, 1999). In a depressed stock the spawning capability of the prey population is held in a depleted state by intense predation (Bakun and Curry, 1999). It is evident from this study that fisheries managers should consider predation as an important factor when managing the recovery of the bluefish population in the northwest Atlantic Ocean.

Acknowledgments

We thank the numerous fishermen and fishing tournament directors who allowed us behind the lines to collect samples. We also thank A. J. M. Wood, C. Butler, and M. Smith for their aid in the collection, transportation, and analysis of stomach contents. Funding for this study was provided by the Bluefish-Striped Bass Dynamics Research Program at Rutgers University in cooperation with the National Marine Fisheries Service (grant NA97FE0363), and the University of Rhode Island/National Oceanic and Atmospheric Administration/Cooperative Marine Education Research (grant NA03NMF4550395). Finally, we thank the many colleagues and anonymous reviewers whose suggestions helped to improve this manuscript.

Literature cited

- Bakun, A., and P. Cury.
1999. The "school trap": a mechanism promoting large amplitude out-of-phase population oscillations of small pelagic fish species. *Ecol. Letters* 2:349–351.
- Baremore, I. E.
2007. Feeding ecology of the Atlantic angel shark, *Squatina dumerili*, in the northern Gulf of Mexico. M.S. thesis, 79 p. Univ. Florida, Gainesville, FL.
- Bax, N. J.
1998. The significance and prediction of predation in marine fisheries. *ICES J. Mar. Sci.* 55:997–1030.
- Bethea, D. M., J. A. Buckel, and J. K. Carlson.
2004. Foraging ecology of the early life stages of four sympatric shark species. *Mar. Ecol. Prog. Ser.* 268:245–264.
- Bundy, A., and L. P. Fanning.
2005. Can Atlantic cod (*Gadus morhua*) recover? Exploring trophic explanations for the non-recovery of the cod stock on the eastern Scotian Shelf, Canada. *Can. J. Fish. Aquat. Sci.* 62:1474–1489.
- Bush, A., and K. Holland.
2002. Food limitation in a nursery area: estimates of daily ration in juvenile scalloped hammerheads, *Sphyrna lewini* (Griffen and Smith, 1834) in Kane'ohe Bay, Hawai'i. *J. Exp. Mar. Biol. Ecol.* 278:157–178.
- Carlson, J. K., and G. R. Parsons.
1999. Seasonal differences in routine oxygen consumption rates of the bonnethead shark. *J. Fish Biol.* 55:876–879.
- Christensen, V.
1996. Managing fisheries involving predator and prey species. *Rev. Fish Biol. Fish.* 6:417–442.
- Clarke, K. R.
1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18:117–143.
- Compagno, L. J. V.
2001. Sharks of the world: an annotated and illustrated catalogue of shark species known to date. FAO species catalogue for fishery purposes. No. 1, vol. 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes, and Orectolobiformes), 269 p. FAO, Rome.
- Cortés, E., C. A. Brown, and L. R. Beerkircher.
2007. Relative abundance of pelagic sharks in the western North Atlantic Ocean, including the Gulf of Mexico and Caribbean Sea. *Gulf Caribb. Res.* 19: 37–52.
- Cortés, E.
1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: applications to elasmobranch fishes. *Can. J. Fish. Aquat. Sci.* 54:726–738.
- Cortés, E., and S. H. Gruber.
1990. Diet, feeding habits and estimates of daily ration of young lemon sharks, *Negaprion brevirostris* (Poey). *Copeia* 1990:204–218.
- Elliot, J. M., and L. Persson.
1978. The estimation of daily rates of food consumption for fish. *J. Anim. Ecol.* 47: 977–991.
- Graham, J. B., H. Dewar, N. C. Lai, W. R. Lowell, and S. M. Arce.
1990. Aspects of shark swimming performance determined using a large water tunnel. *J. Exp. Biol.* 151: 175–192.
- Heithaus, M. R., and L. M. Dill.
2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83:480–491.
- Hutchings, J. A.
2000. Collapse and recovery of marine fishes. *Nature* 406:882–885.
- Hyslop, E. J.
1980. Stomach contents analysis – a review of methods and their application. *J. Fish Biol.* 17:411–429.
- Juanes, F., J. A. Hare, and A. G. Miskiewicz.
1996. Comparing early life history strategies of *Pomatomus saltatrix*: A global approach. *Mar. Freshw. Res.* 47:365–379.
- Kohler, N. E., J. G. Casey, and P. A. Turner.
1996. Length-length and length-weight relationships for 13 shark species from the Western North Atlantic. NOAA Tech. Memo. NMFS-NE-110, 22 p.
- Korsmeyer, K. E., H. Dewar, N. C. Lai, and J. B. Graham.
1996. Tuna aerobic swimming performance: Physiological and environmental limits based on oxygen supply and demand. *Comp. Biochem. Physiol.* 113:45–56.
- Krebs, C. J.
1999. *Ecological methodology*, 2nd ed., 620 p. Addison

- Wesley and Benjamin Cummins Publishing, New York, NY.
- MacNeil, M. A., G. B. Skomal, and A. T. Fisk.
2005. Stable isotopes from multiple tissues reveal diet switching in sharks. *Mar. Ecol. Prog. Ser.* 302:99–206.
- Maia, A., N. Queiroz, J. P. Correia, and H. Cabral.
2006. Food habits of the shortfin mako, *Isurus oxyrinchus*, off the southwest coast of Portugal. *Environ. Biol. Fish.* 77:157–167.
- Mollet, H. F., G. Cliff, H. L. Pratt, and J. D. Stevens.
2000. Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. *Fish. Bull.* 98:299–318.
- Natanson, L. J., N. E. Kohler, D. Ardizzone, G. M. Cailliet, S. Wintner, and H. F. Mollet.
2006. Validated age and growth estimates for the shortfin mako, *Isurus oxyrinchus*, in the North Atlantic Ocean. *Environ. Biol. Fish.* 77:367–383.
- Olson, R. J., and C. H. Boggs.
1986. Apex predation by yellowfin tuna (*Thunnus albacares*): independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. *Can. J. Fish. Aquat. Sci.* 43:1760–1775.
- Overholtz, W. J.
2006. Estimates of consumption of Atlantic herring (*Clupea harengus*) by bluefin tuna (*Thunnus thynnus*) during 1970–2002: an approach incorporating uncertainty. *J. Northwest Atl. Fish. Sci.* 36:55–63.
- Overholtz, W. J., J. S. Link, and L. E. Suslowicz.
2000. Consumption of important pelagic fish and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons. *ICES J. Mar. Sci.* 57:1147–1159.
- Salerno, D. J., J. Burnett, and R. M. Ibara.
2001. Age, growth, maturity, and spatial distribution of bluefish, *Pomatomus saltatrix*, off the northeast coast of the United States, 1985–96. *J. Northwest Atl. Fish. Sci.*, 29:31–39.
- Schindler, D. E., T. E. Essington, J. F. Kitchell, C. J. Boggs, and R. Hilborn.
2002. Sharks and tunas in the Central Pacific: fisheries impacts on predators with contrasting life histories. *Ecol. Appl.* 12:735–748.
- Shepherd, G. R., and D. B. Packer.
2006. Essential fish habitat source document: Bluefish, *Pomatomus saltatrix*, life history and habitat characteristics, 2nd ed. NOAA Tech. Memo. NMFS-NE-144, 68 p.
- Steimle, F. W., and R. J. Terranova.
1985. Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. *J. Northwest Atl. Fish. Sci.* 6: 117–124.
- Stevens, J. D., R. Bonfil, N. K. Dulvy, and P. A. Walker.
2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES J. Mar. Sci.* 57:476–494.
- Stillwell, C. E., and N. E. Kohler.
1982. Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* 39: 407–414.
- van der Elst, R. P.
1979. A proliferation of small sharks in the shore-based Natal sport fishery. *Environ. Biol. Fish.* 4:349–362.
- Vaske-Júnior, T., and G. Rincón-Filho.
2003. Stomach contents of blue sharks (*Prionace glauca*) and anequim (*Isurus oxyrinchus*) from oceanic waters of southern Brazil. *Rev. Brasil. Biol.* 58:445–452. [In Spanish].
- Wetherbee, B. M., and E. Cortés.
2004. Food consumption and feeding habits. *In* Biology of Sharks and their Relatives: Food Consumption and Feeding Habits. (J. C. Carrier, J. A. Musick, and M. R. Heithaus, eds.), p. 223–244. CRC press, Boca Raton, FL.
- Wood, A. D.
2005. Using bone measurements to estimate the original sizes of bluefish (*Pomatomus saltatrix*) from digested remains. *Fish. Bull.* 103:461–466.