J. Northw. Atl. Fish. Sci., Vol. 36: 55–63 Publication (Upload) date: 4 Jan 2006

Estimates of Consumption of Atlantic Herring (*Clupea harengus*) by Bluefin Tuna (*Thunnus thynnus*) During 1970–2002: an Approach Incorporating Uncertainty

W. J. Overholtz
Northeast Fisheries Science Center, NOAA Fisheries Service
166 Water St, Woods Hole, Massachusetts 02543, USA

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. Northw. Atl. Fish. Sci.*, **36**: 55–63. doi: 10.2960/J.v36.m572

Abstract

Bluefin tuna (*Thunnus thynnus*) are a major apex predator in the Gulf of Maine-Georges Bank region and Atlantic herring are a keystone prey item in the diet of bluefin as well as the majority of other apex predators, seabirds and piscivorous fishes in this ecosystem. Key variables for the calculation of consumption of herring by bluefin tuna are uncertain, necessitating a modeling framework that can utilize scant and variable information. Input distributions for bluefin tuna biomass, percent of the Northwest Atlantic bluefin stock in the region, percent daily ration of bluefin, and percent of herring in the bluefin tuna diet were developed and used in a model that incorporates uncertainty. Consumption of Atlantic herring by bluefin tuna in the Gulf of Maine-Georges Bank region peaked at 58.0 kt in 1970, dropped to a series low of 2.2 kt in 1982, and increased steadily to 24.4 kt in 2002. Changes in abundance of bluefin tuna and herring, combined with substantial fishery removals on both species caused major fluctuations in herring consumption by tuna during 1970–2002. Sensitivity analysis indicates that tuna diet composition and daily ration are the most important variables affecting the estimates of herring consumed by bluefin tuna.

Key words: Atlantic herring, Bluefin tuna, consumption, uncertainty

Introduction

Recent emphasis on ecosystem management necessitates a requirement for more information on the biological interactions, energy transfer, consumption, and production among trophic levels in ecosystems (Christensen and Pauly, 1995; Pauly *et al*., 2002; Link *et al*., 2002a). Bluefin tuna (*Thunnus thynnus*) are a key apex predator in the Northwest Atlantic, feeding on a variety of fishes and invertebrates (Dragovich, 1970; Mason, 1976; Holliday, 1978; Chase 2002). These large pelagic predators frequent the waters off New England during a summer feeding season that generally occurs during July–October (Lutcavage *et al*., 2000; Chase, 2002; Schick *et al*., 2004). During this time tuna feed voraciously on the small fishes in the region, particularly on sand lance (*Ammodytes americanus*), Atlantic mackerel (*Scomber scombrus*), butterfish (*Peprilus triacanthus*), and Atlantic herring (*Clupea harengus*).

Herring are a keystone prey species in the diets of many of the demersal fishes, marine mammals, seabirds, and large pelagic predators in the Gulf of Maine-Georges Bank region (Fig. 1) (Powers and Backus, 1987; Gannon *et al*., 1998; Overholtz *et al*., 2000; Chase, 2002; Lutcavage *et al*., 2000; Schick *et al*., 2004). The fishery on herring in the region is one of the largest on the east coast of the USA (Overholtz *et al*., 2004). To account for biological interactions and assess the Atlantic herring resource properly, it will be necessary to quantify and include removals by predators in stock assessments for this species.

Consumption of herring by demersal predatory fish in the region can be readily quantified because time series of empirical data on the diets of these predators have been collected routinely since 1963 (Link *et al.*, 2002A). The diet composition of many of the other predators of herring such as harbor porpoise (*Phocoena phocoena*) and large pelagic fishes such as bluefin tuna and the blue shark (*Prionace glauca*), have generally been quantified, but only for brief periods of time, usually only one or several years (Gannon *et al*., 1998; Chase, 2002; Kohler and Stillwell, MS 1981). Hence the need for developing methods that can be used to provide estimates of consumption, but that also address the limited nature of the available data and the greater uncertainty in the estimation process. Probabilistic methods are particularly well suited to this type of problem because they allow uncertainty in the input variables to be represented as distributions (Shelton *et al*., 1997). A probability based estimation approach was developed to estimate the

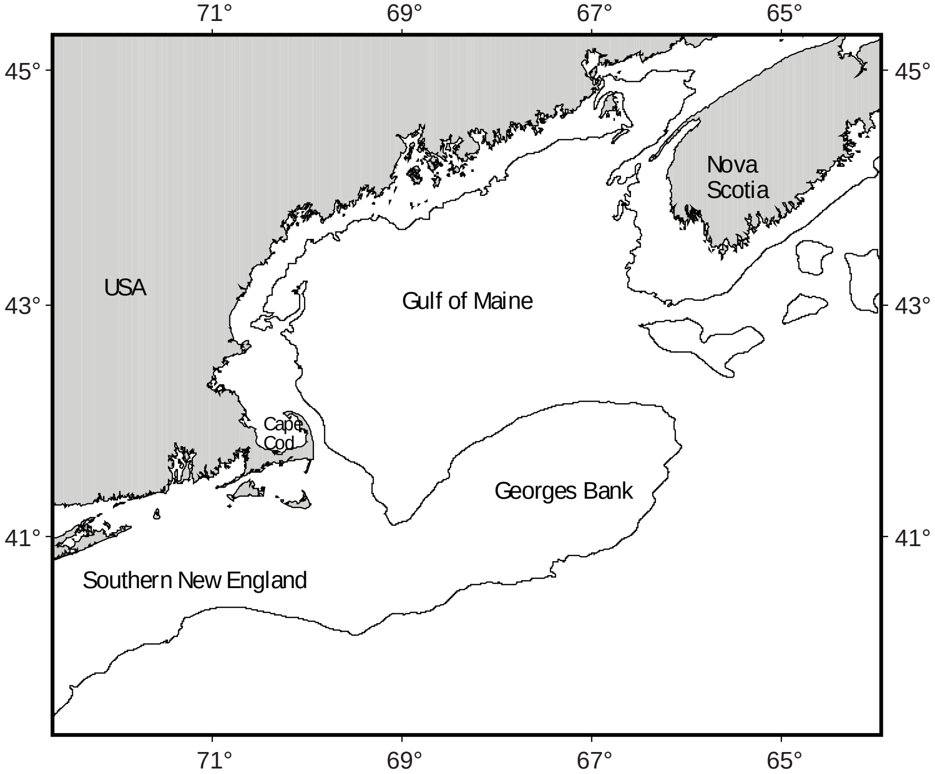

Fig. 1. Gulf of Maine-Georges Bank region with 100 m contour line.

consumption of Atlantic herring by bluefin tuna during 1970–2002.

Materials and Methods

Stock Size

The four important input variables that were considered in the analysis were bluefin tuna biomass, the proportion of the tuna in the region during the summer period, the daily ration of tuna, and the proportion of the tuna diet composed of Atlantic herring. Stock size estimates for bluefin tuna during 1970–2002 were available from the most recent VPA (ICCAT, 2003). Age 3+ biomass was calculated using these estimates of stock size-at-age and mean weight-at-age data from the same source (Fig. 2). Only age 3+ tuna were considered for analysis since younger fish are frequently found in Southern New England waters during the summer and their prey generally does not include herring (Mason, 1976; Holliday, 1978; Chase, 2002). A distribution for tuna biomass was constructed for each year from 1970–2002 by assuming a 30% CV on the annual biomass data and using a pert distribution (modified beta distribution) (Palisade, 2002) to describe the data (Fig. 3a). The density function for the pert distribution can be written as:

$$f(x) = \frac{(x-\min)^{\alpha 1-1}(\max - x)^{\alpha 2-1}}{B(\alpha 1,\alpha 2)(\max - \min)^{\alpha 1+\alpha 2-1}} \qquad (1)$$

where the distribution is based on inputs, pert (min, *m.likely*, max), *B* is the Beta function and:

$$\mu = \frac{\min + 4 * m.likely + \max}{6} \text{ and} \qquad (2)$$

$$\alpha 1 = 6\left[\frac{\mu\text{-min}}{\text{max - min}}\right] \text{and } \alpha 2\text{-}6\left[\frac{\text{max-}\mu}{\text{max-min}}\right]$$

The distribution for each year was centered on the estimate of annual biomass (*m.likely*) and a minimum (min) and maximum (max) value were determined such that the minimum value was one standard deviation less than the mean and the maximum was one standard deviation greater than the mean with the 30% *CV*, or:

$$\text{for } CV = {}^{SD}\!\big/_{m.likely} \text{ or } SD = m.likely \times CV$$
$$\text{then } \min = m.likely - SD \text{ and } \max = m.likely + SD \qquad (3)$$

This distribution was chosen because it is simple, is easy to make symmetrical, can be easily fit, and has insignificant tails.

Proportion in Region

The Northwest Atlantic bluefin stock migrates into the region and distributes into the waters off New England, the Nova Scotian shelf, and the Gulf of St Lawrence during July to October. During this time tuna are actively feeding on prey fishes that probably follow temperature

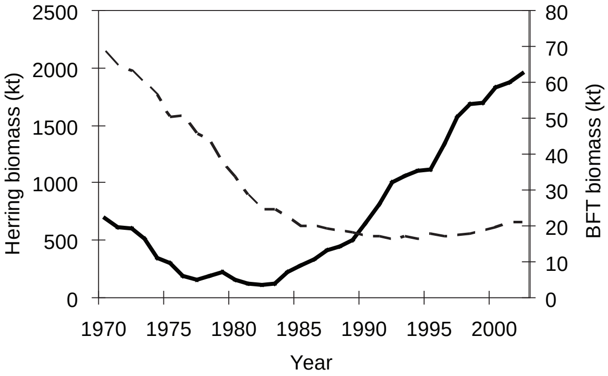

Fig. 2. Biomass of Atlantic herring (2+, kt, solid line) and bluefin tuna (3+, kt, dashed line) during 1970–2002.

frontal zones in areas of high productivity (Schick *et al*., 2004). Some of the bluefin tuna stock (3+) is also distributed in the Bay of Fundy, on the Nova Scotian shelf, in the Gulf of St Lawrence, and offshore during this time.

An examination of available information suggests that on average about half of the adult stock is in the Gulf of Maine-Georges Bank region during the summer feeding season. This assumption was based on the relative catches of western bluefin tuna off the USA, Canada and offshore during 1950–99 (ICCAT, 2003). Additionally an examination of relative catch rates by Japanese vessels for bluefin tuna in the US EEZ during 1978–88, Canadian EEZ during 1986–95, and offshore, suggests that CPUE was more than twice as high in the US region (Hoey *et al*., 2002; ICCAT, 2003). The proportion of tuna resident in the region was assumed to be 50% of the 3+ biomass with a 30% CV; a pert distribution was constructed with a range between 0.35 and 0.65 (Fig. 3b).

Daily Ration

A meta-analysis approach was used to estimate the daily ration size for bluefin tuna in the region. Observational and empirical data on the daily ration size of bluefin tuna are available from several regions worldwide (Tiews, 1978; Young *et al*., 1997; Chase, 2002). Data on the average weight of bluefin tuna from Chase (2002) and ICCAT (2003) are also available and were used in an energetics equation to predict daily ration (Innes *et al*., 1987). The consumption equation is written as:

$$c = .123M^{0.80} \tag{4}$$

where C is consumption (kg) and M is the weight of the predator (kg) (Innes *et al*., 1987). This equation was originally used to predict consumption by marine mammals, but since bluefin tuna are functionally homeothermic and hence very similar to marine mammals, the approach is useful and in this case was used only for the data from Chase (2002) and ICCAT (2003). Theses sources (empirical and estimated) were used to produce six estimates of daily ration size for bluefin tuna with a mean estimate of 3.2% body weight (% BW), an SD of 1.4%, and a range between 1.0–4.7% BW (Table 1). A pert distribution was used to model the proportional daily ration with a mean of 0.032 and a range between 0.018 and 0.045 (Fig. 3c). These results for ration size are also in general agreement with data for yellowfin tuna (*Thunnus albacares*), another large highly mobile apex predator (Olsen and Boggs, 1986; Maldeniya, 1996).

Percent Herring in Diet

Diet compositions of predatory fish largely reflect prey abundance (Overholtz *et al*., 2000; Link and Garrison, 2002b). Marine predators be they fish, mammal, or seabird, generally feed on prey resources that are abundant, but they may readily change their diets when a

TABLE 1. Daily ration size (percent body weight, % BW), and average % BW for bluefin tuna by source of information and study.

Study	Source	% BW
Chase (2002)	energetics equation, average size of large fish	4.19
Chase (2002)	empirical data	1.00
Tiews (1978)	observations	2.40
Tiews (1978)	observations	4.00
ICCAT (2003)	energetics equation, average size from VPA	4.70
Young *et al*. (1997)	stomach contents	2.69
	Average	3.16

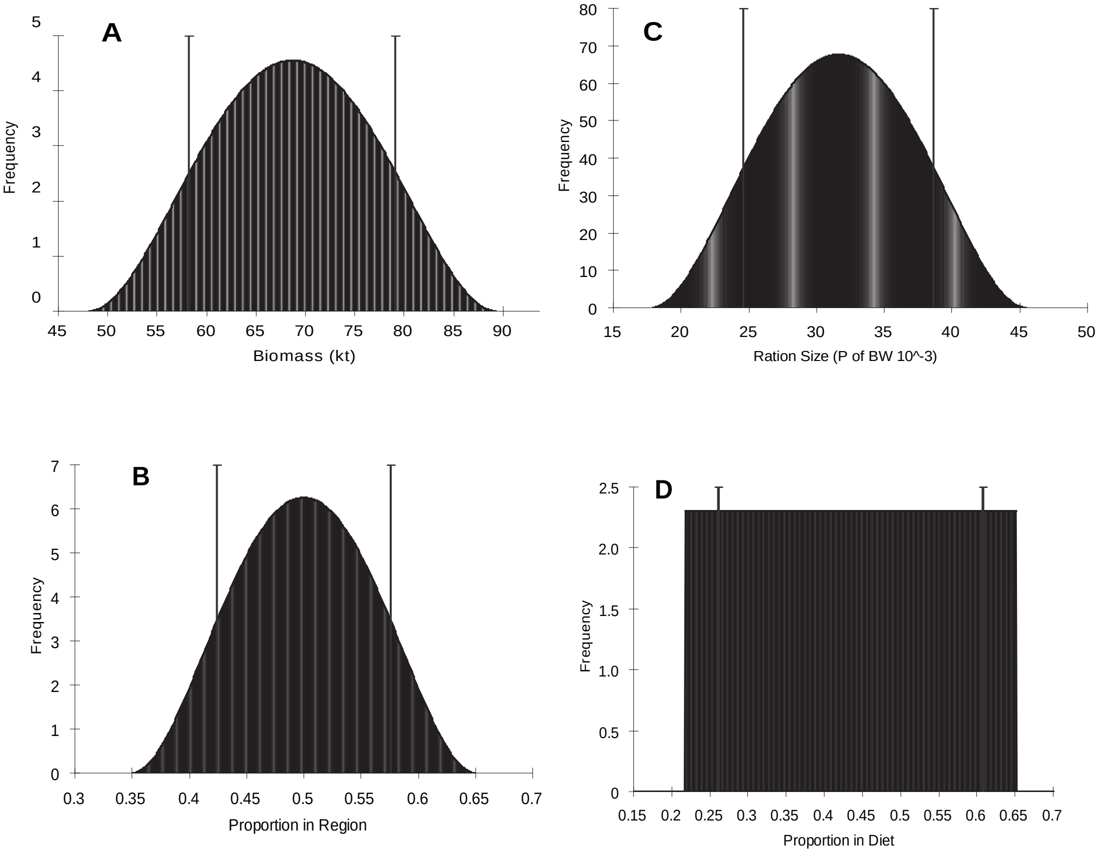

Fig. 3. (**A**) Bluefin tuna biomass in 1970 with 80% CI's, (**B**) proportion of bluefin tuna biomass in the New England region during 1970–2002, (**C**) daily proportion of bluefin tuna body weight that is consumed, and (**D**) the proportion of herring in the bluefin tuna diet in 1970.

preferred prey item declines and another prey source becomes more abundant (Kawamura, 1980; Mitchel, 1974; Payne *et al*., 1986; Payne, 1989; Hain *et al*., 1995; Haug *et al*., 1996; Weinrich *et al*., 1997; Gannon *et al*., 1998; Link and Garrison, 2002b). Also, although vertebrate predators may have a preponderance of one item in their diet, the percentage is seldom greater than 40 to 60%, in complex ecosystems with multiple linkages (Kawamura, 1980; Haug *et al*., 1996; Gannon *et al*., 1998; Overholtz *et al*., 2000). This phenomenon is probably due to a variety of factors such as the general euryphagous nature of predators, predator satiation, and the patchy distribution of prey. It may also be adaptive since intense specialization can be a dangerous evolutionary strategy. Exceptions to this rule are boreal or simple ecosystems such as the Arctic and Antarctic, where few prey items reside (Kawamura, 1980; Mitchel, 1974).

Information on the diet composition of bluefin tuna is available for both school and larger fish (Mason, 1976; Holliday, 1978; Eggleston and Bochenek, 1990; Chase, 2002). Holliday studied bluefin tuna diets during 1978, concluding that 9% by volume was composed of herring, while sand lance (27%) and silver hake (24%) were much more important. The stomach contents of bluefin tuna were analyzed by Eggleston and Bochenek (1990); they found that the diets of small tuna in the Mid-Atlantic Bight were dominated by sand lance during 1986. Chase (2002) studied the diet of bluefin tuna in the New England region during 1988–92, finding that about 50% of the diet by weight was comprised of herring. Since there is no consistent long-term time-series of diet composition data available for bluefin tuna in the region, a logistic model relating the proportion of herring in the diet to herring abundance during 1970–2002 was constructed as:

$$P = \frac{a}{1 + be^{-cx}} \tag{5}$$

where P is the relative proportion of herring in the bluefin diet, a (0.6) is the maximum value, b (25.0) is a shape parameter, and c (6.0) is a control parameter for the value of x at the inflection point of the curve, and x is herring biomass (million mt). Data on herring abundance (x)

were taken from Overholtz *et al*. (2004), and used to parameterize a logistic model where the proportion of herring in the diet was at a maximum of 0.60 at the highest abundance in the time-series, roughly 2 000 kt (Fig. 4). The other two parameters were set so that values of *P* were roughly 50% during the early 1990s as suggested by Chase (2002) and 10% or less in the late 1970s and 1980s (Holliday, 1978; Eggleston and Bochenek, 1990). All the years were predicted then, using herring abundance data from 1970–2002 to estimate the diet composition in each of those years (Fig. 5). Predicted values ranged from about 0.040 to 0.60 (Fig. 5), closely matching the trend in diet composition observed for bluefin tuna in the aforementioned studies and the diet composition of many demersal and semi-pelagic fish during most of this period (Overholtz *et al*., 2000).

Finally since these data are the most uncertain of the four input distributions used in the analysis, a uniform distribution was used to model the proportion of herring in the bluefin tuna diet. The trajectory of the proportion of herring in the bluefin tuna diet (Fig. 5) during 1970–2002 was used to center the uniform distribution for each year and a minimum (-50%) and maximum (+50%) value (uniform(min,max)) for the distribution was calculated for each year. An example of this approach can be seen in Fig. 3d for the proportion of herring in the diet during 1970.

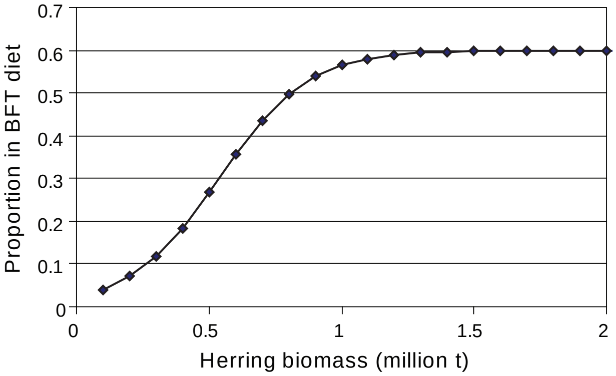

Fig. 4. Herring biomass (million t) and proportion of herring in the bluefin tuna diet.

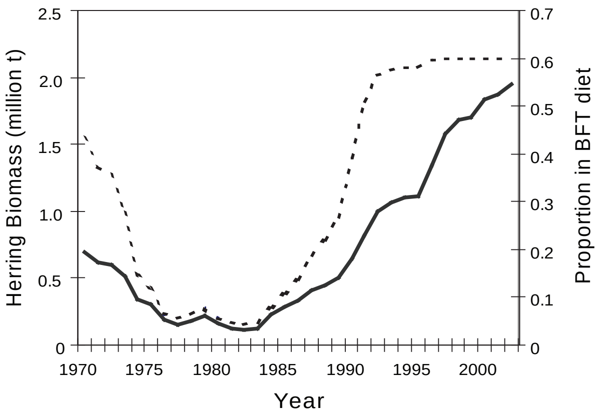

Fig. 5. Herring biomass (million t, solid line) and proportion of herring in the bluefin tuna diet (dotted line) during 1970–2002.

The distributions were constructed using @RISK software (Palisade, 2002), interfaced with an EXCEL (Microsoft, 2002) spreadsheet and used to estimate the consumption of herring by bluefin tuna during 1970–2002. Outputs from the model were the distribution of consumption each year, the time series of consumption, and a sensitivity analysis for the most important contributing factors in the consumption estimates. The overall consumption for any particular year was a linear combination of the four components as:

$$C_t = B_t A_t R_t P_t \tag{6}$$

where *B* is the bluefin tuna biomass, *A* is the portion of the stock in the region, *R* is the daily ration size, *P* is the proportion of herring in the diet, and *t* is the year. A Monte Carlo approach was used to resample the input distributions and 5 000 iterations were completed. Simple percentile confidence intervals (80%) were used as a measure of uncertainty around the estimated annual consumption distributions and the 1970–2002 consumption trajectory.

Results

Bluefin consumption of herring declined steadily from a high of 58 kt in 1970 to a low of 2.2 kt in 1982 (Fig. 6). Herring declined tremendously during this time and the offshore component of the stock was extirpated (Fig. 5) (Overholtz and Friedland, 2002; Overholtz *et al*., 2004). Consumption of herring slowly increased starting in 1983, reaching 24 kt in 2002 as bluefin tuna biomass reached a historic low during this period (Fig. 2). Confidence intervals (80%) around the mean estimate of herring consumed were very wide during the early 1970s and moderately large from 1991 onwards to 2002 (Fig. 5).

Estimates of consumption were quite different during the beginning and end of the time-series from 1970 to 2002. Consumption of herring by bluefin tuna ranged between 16.7 and 132.8 kt, averaged 58 kt, and had an 80% CI of 32.2 kt–86.2 kt during 1970 (Fig. 7a). Bluefin tuna were abundant and herring moderately so during

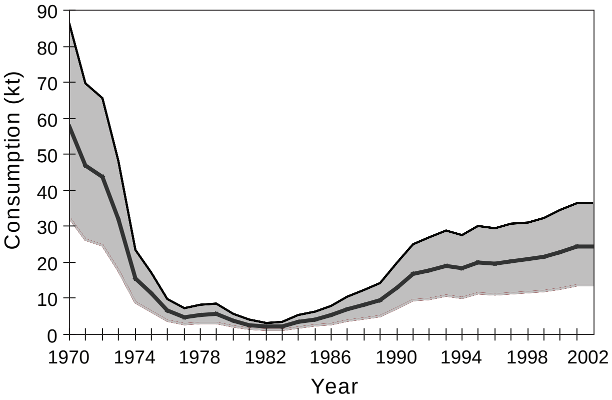

Fig. 6. Consumption of herring (kt) (dark line) and 80% CI (gray shaded area) by bluefin tuna during 1970–2002.

the early part of the 1970–2002 time-series when consumption estimates were relatively high (Fig. 2). Bluefin consumed an average of 24 kt during 2002, with a range between 7.4 and 63.5 kt and an 80% CI of 16 kt–38 kt (Fig. 6 and 7b). Herring were very abundant, but bluefin tuna biomass had declined to one of the lowest values in the series in 2002 (Fig. 2).

The sensitivity analysis showed that estimates of consumption are most influenced by the percent of herring in bluefin tuna diets (Fig. 8). This input had a correlation of 0.63 with estimated consumption during 2002. The percent of daily ration and percent of the bluefin stock in the region were the next most important contributors to consumption with correlations of 0.58 and 0.41, respectively, in that year. Finally, bluefin tuna biomass had a correlation of roughly 0.1 (Fig. 8). The sensitivity analysis was repeated for 1970 and 1982 with the same results as in 2002.

Discussion

Bluefin tuna are an important predator of herring in Gulf of Maine-Georges Bank region as evidenced by historical and recent patterns of consumption. This species consumes herring biomass in roughly the same proportion as the minke whale, harbor porpoise, and white-sided dolphin (*Lagenorhynchus acutus*) (Read and Brownstein, 2003) or Atlantic cod (*Gadus morhua*) and white hake (*Urophycis tenuis*) (Overholtz *et al*., 2000). Only fin whale (*Balaenoptera physalus*), humpback whale (*Megaptera novaeangliae*), silver hake (*Merluccius bilinearis*) and spiny dogfish (*Squalus acanthias*) consume more herring from this ecosystem (Overholtz *et al*., 2000; Read and Brownstein, 2003). Although the current impact of bluefin tuna on herring is only about 7% of the total herring consumption in the region, a recovery of the western bluefin tuna stock would make this species one of the dominant herring predators in the region.

The trend in consumption of Atlantic herring by bluefin tuna was related to the abundance of both species and the fishery that occurred during 1970 to 2002. During the early 1970s herring and tuna were both relatively abundant and herring consumption was relatively high. By the early 1980s both herring and tuna had markedly declined and consumption was very low. Most predators switched to sand lance (*Ammodytes* sp.) during this time period (Overholtz *et al*., 1991; Overholtz *et al*., 2000; Link and Garrison, 2002B). The fishery for herring during the mid to late 1970s had seriously depleted the herring resource overall and caused a collapse of the offshore component. Bluefin tuna were also seriously overfished during this time (ICCAT, 2003). Consumption by bluefin increased, but only to moderate levels in the late 1990s because although herring had recovered, bluefin tuna biomass had reached historic lows. Fishing rates on herring declined sharply during this period, but the condition of the bluefin tuna resource remained depleted.

This analysis assumes that the proportion of the stock in the region, the daily ration and the percentage of herring in bluefin tuna is constant for age three and older fish. Age specific data are not available for use in a more detailed analysis. Small or school bluefin tuna are generally found further to the south and have different diets than the larger fish that frequent the Gulf of Maine-Georges Bank region, so they were not included in the analysis (Mason, 1976; Holliday, 1978; Eggleston and Bochenek, 1990; Chase, 2002). Chase (2002) found that there was little relationship between stomach contents (kg) and bluefin tuna size in the region after the fish reached 100 kg. In a study of 4 181 yellowfin tuna stomachs, Maldeniya (1996) concluded that several variables such as the percentage of fish in the diet and ration size (% BW) increased with fish size, but the rate of change slowed greatly after the fish reached 50 cm. These results suggest that excluding the younger tuna because they eat few herring and generally do not inhabit the area and aggregating at age 3+ because the dynamics are similar, is probably a reasonable assumption. Low herring abundance in the region may have caused changes in the distribution of bluefin tuna during 1970–2002, so the proportion of the stock in the Gulf of Maine-Georges Bank region might have been lower at times. If age specific estimates of ration size, diet composition

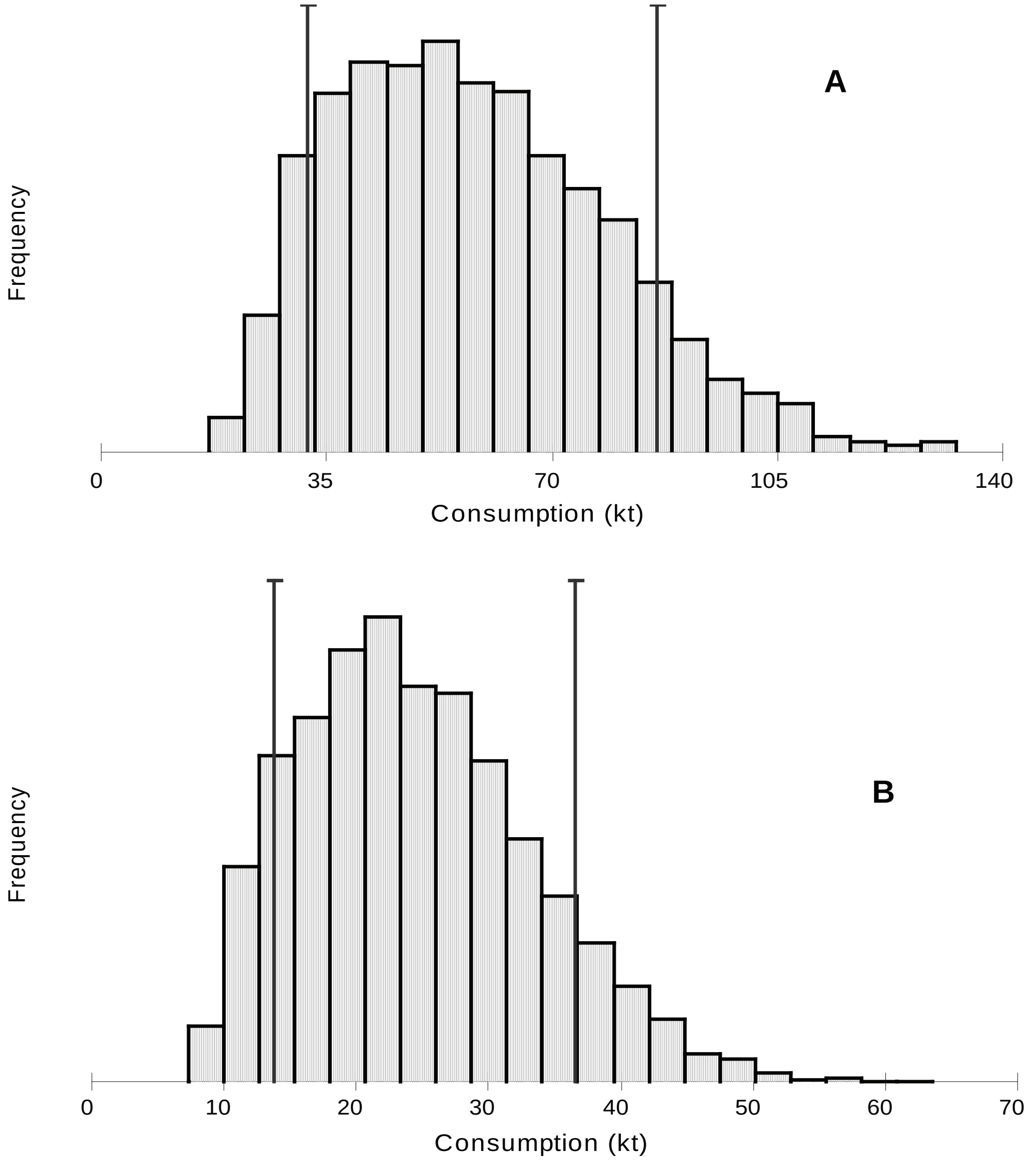

Fig. 7. Distribution of consumption (kt, with 80% CI) of herring by bluefin tuna in (**A**) 1970 and (**B**) 2002.

and age-specific and time-specific residency were available, more detailed estimates of herring consumption could be produced.

The approach used in this analysis allowed for the available data on bluefin tuna to be incorporated into the analysis in a manner that included uncertainty. The point estimate can serve as the best estimate of herring consumption by bluefin tuna given the assumptions made on the input distributions and the 80% CI's as an envelope around this estimate (Fig. 6). During the early 1970s, when herring and tuna were both relatively abundant, the 80% CI was relatively wide. In the late 1970s and early 1980s, the 80% envelope was compact because the proportion of herring in the bluefin diet was minor and tuna were much less abundant. As herring recovered in the 1990s, the proportion of herring in the diet increased again and the 80% CI was again relatively wide. Coefficients of variation for three example years in the series, 1970, 1982, and 2002, were equal (0.2780, 0.2784, 0.2734), but the magnitude of the uncertainty on the earliest and latest years in the series was the greatest. Interestingly, bluefin biomass, an apriori choice for the most influential input variable, was the least important of the four inputs, in determining consumption in any given year.

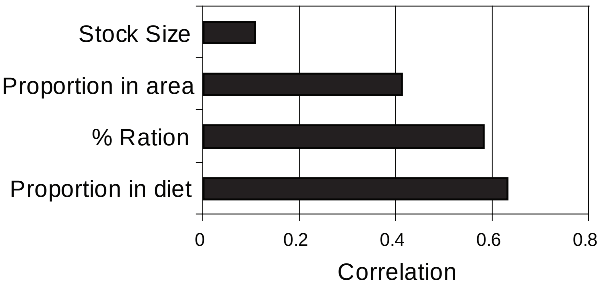

Fig. 8. Sensitivity analysis (correlations) of input variables and estimate of consumption in 2002.

Additional work on estimating bluefin tuna daily ration is necessary to better understand the general role that this species plays in the regional ecosystem and specifically on the dynamics of Atlantic herring. More research would be of value since this daily ration estimate is still not well determined (Olsen and Boggs, 1986; Young *et al*., 1997; Essington *et al*., 2001). The current study used an average of 3.2% BW to estimate bluefin tuna total consumption. A 300 kg tuna would require 10 kg of food on a daily basis to maintain a ration of 3.3% BW. In the several hundreds of fish in this size range sampled by Chase (2002), only five fish contained 10 kg or greater of prey in their stomach. If tuna feed during only a portion of the day, as some researchers believe, then the empirical estimate of daily ration of 0.5–1.5% from Chase (2002) based on average stomach contents alone may be a reasonable estimate of daily ration. Estimates of daily ration from energetics model approaches tend to be larger on average than estimates from field conditions. If field estimates are correct, this would make a very large difference in estimates of consumption by bluefin tuna (Olsen and Boggs, 1986). Other methods of estimation based on growth considerations suggest that bluefin daily ration may be in the range of 1–2% BW (Essington *et al*., 2001)

The sensitivity analysis results from this study will be helpful in planning future research on bluefin tuna. Results from this analysis were most sensitive to the diet composition data because this information was the most uncertain of the four input variables. A longer time-series of annual sampling of the diet composition of bluefin tuna would be very useful to ascertain how variable the diet of tuna is and if factors such as environmental forcing or spatial effects are important. Research using stable isotope methods could also help to better define the diet of bluefin tuna in the region. Some studies have successfully used this approach on bluefin tuna and other apex predators (Estrada *et al*., 2003; Estrada *et al*., 2005). Additional methods such as mercury and cesium budget analysis might also prove useful and help in understanding the trophic role of bluefin tuna in regional ecosystems (Olsen and Boggs, 1986; Trudel *et al*., 2000).

References

CHASE, B. C. 2002. Differences in diet of Atlantic bluefin tuna (*Thunnus thynnus*) at five seasonal feeding grounds on the New England continental shelf. *Fish. Bull*., **100**: 168–180.

CHRISTENSEN, V., and D. PAULY. 1995. Fish production, catches and the carrying capacity of the world's oceans. *Naga* (*ICLARM Qtr*), **18**(3): 34–40.

DRAGOVICH, A. 1970. The food of Bluefin tuna (*Thunnus thynnus*) in the western North Atlantic Ocean. *Trans. Am. Fish. Soc*., **99**(4): 726–731.

EGGLESTON, D. B., and E. A. 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.

ESSINGTON, E. T, J. F. KITCHELL, and C. J. WALTERS. 2001. The von Bertalanffy growth function, bioenergetics, and the consumption rates of fish. *Can. J. Fish. Aquat. Sci*., **58**: 2129–2138.

ESTRADA, J. A., A. N. RICE, M. E. LUTCAVAGE, and G. B. SKOMAL. 2003. Predicting trophic position in sharks of the northwest Atlantic Ocean using stable isotope analysis. *J. Mar. Bio. Assoc. UK*., **83**: 1347–1350.

ESTRADA, J. A., M. E. LUTCAVAGE, and S. R. THORROLD. 2005. Diet and trophic position inferred from stable carbon and nitrogen isotopes of Atlantic bluefin tuna (*Thunnus thynnus*). *Mar. Biol*., **147**: 37–45.

GANNON, D. R., 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.

HAUG, T., U. LINDSTROM, K. T. NILSSEN, I. ROTTINGEN, and H. J. SKAUG. 1996. Diet and food availability for Northeast Atlantic Minke Whales, *Balaenoptera acutorostrata*. *Rep. Int. Whales Comm*., **46**: 371–382.

HAIN, J. H. W., S. L. ELLIS, R. D. KENNEY, P. J. CLAPHAM, B. K. GRAY, M. T. WEINRICH, and I. G. BABB. 1995. Apparent bottom feeding by humpback whales on Stellwagen Bank. *Mar. Mammal Sci*., **11**: 464–479.

HOEY, J. J., E. PRITCHARD, C. BROWN, and M. SHOWELL. 2002. Pelagic shark abundance indices based on fishery-dependent and fishery-independent data from the Western North Atlantic. *Col. Vol. Sci. Pap. ICCAT*, **54**(4): 1199–1211.

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 University, Long Island, NY, 31 p.

ICCAT. 2003. Report of the 2002 Atlantic bluefin tuna stock assessment session. *Col. Vol. Sci. Pap. ICCAT*, **55**(3): 710–937.

INNES, S. D., M. LAVIGNE, W. M. EARLE, and K. M. KOVACS. 1987. Feeding rates of seals and whales. *J. Anim. Ecol*., **56**: 115–130.

KAWAMURA, A. 1980. A review of food of Balaenopterid whales. *Sci. Rep. Whales Res. Inst.*, **32**: 155–197.

KOHLER, N. E., and C. E. STILLWELL. MS 1981. Food habits of the blue shark (*Prionace glauca*) in the Northwest Atlantic. *ICES C.M. Doc.*, No. 1981/H:61, 12 p.

LINK, J. S., J. K. T. BRODZIAK, S. F. EDWARDS, W. J. OVERHOLTZ, D. MOUNTAIN, J. W. JOSSI, T. D. SMITH, and M. J. FOGARTY. 2002A. Marine ecosystem assessment in a fisheries management context. *Can. J. Fish. Aquat. Sci.*, **59**: 1429–1440.

LINK, J. S., and L. P. GARRISON. 2002B. Changes in piscivory associated with fishing induced changes to the finfish community on Georges Bank. *Fish. Res.*, **55**: 71–86.

LUTCAVAGE, M. E., R. W. BRILL, G. B. SKOMAL, B. C. CHASE, J. L. GOLDSTEIN, and J. TUTEIN. 2000. Tracking adult North Atlantic bluefin tuna (*Thynnus thynnus*) in the northwestern Atlantic using ultrasonic telemetry. *Mar. Biol.*, **137**: 347–358.

MALDENIYA, R. 1996. Food consumption of yellowfin tuna, *Thunnus albacares*, in Sri Lankan waters. *Environ. Biol. Fish.*, **47**: 101–107.

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

MICROSOFT CORP. 2000. Microsoft EXCEL 2000. Microsoft Corporation.

MITCHEL, E. 1974. Trophic relationships and competition for food in Northwest Atlantic whales. *Proc. Can. Soc. Zoo.* Ann. Meeting, June 2–5, 1974, 123–133 p.

OLSEN, 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**: 1760–1175.

OVERHOLTZ, W. J., S. A. MURAWSKI, and K. L. FOSTER. 1991. Impact of predatory fish, marine mammals, and seabirds on the pelagic fish ecosystem of the northeastern USA. *ICES. Mar. Sci. Symp.*, **193**: 198–208.

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.

OVERHOLTZ, W. J., and K. D. FRIEDLAND. 2002. Recovery of the Gulf of Maine-Georges Bank Atlantic herring (*Clupea harengus*) complex: perspectives based on bottom trawl survey data. *Fish. Bull.*, **100**: 593–608.

OVERHOLTZ, W. J., L. D. JACOBSON, G. D. MELVIN, M. CIERI, M. POWER, D. LIBBY, and K. CLARK. 2004. Stock assessment of the Gulf of Maine-Georges Bank Atlantic herring complex, 2003. *NEFSC Ref. Doc.*, No. 04-06, 290 p.

PALISADE CORP. 2002. @ RISK advanced risk analysis for spreadsheets. Version 4.5, February 2002.

PAULY, D., V. CHRISTENSEN, S. GUENETTE, T. J. PITCHER, U. R. SUMAILA, C. J. WALTERS, R. WATSON, and D. ZELLER. 2002. Towards sustainability in world fisheries. *Nature*, **418**: 689–695.

PAYNE, P. M., J. R. NICOLAS, L. O'BRIEN, and K. D. POWERS. 1986. The distribution of the humpback whale, *Megaptera novaeangliae*, on Georges Bank and in the Gulf of Maine, in relation to densities of the sand eel, *Ammodytes americanus*. *Fish. Bull.*, **84**: 271–277.

PAYNE, M. P. 1989. The distribution, abundance and selected prey of the harbor seal, *Phoca vitulina* concolor, in Southern New England. *Mar. Mammal Sci.*, **5**: 173–192.

POWERS, K. D., and E. H. BACKUS. 1987. Energy transfer to seabirds. *In*: Georges Bank. R. H. Backus and D. W. Borne (eds.), MIT Press, Cambridge, p. 372–374.

READ, A. J., and C. R. BROWNSTEIN. 2003. Considering other consumers: fisheries, predators, and Atlantic herring in the Gulf of Maine. *Cons. Ecol.*, **7**(1): 2.

SCHICK, R. S., J. GOLDSTEIN, and M. E. LUTCAVAGE. 2004. Bluefin tuna (*Thunnus thynnus*) distribution in relation to sea surface temperature fronts in the Gulf of Maine (1994–96). *Fish. Oceanogr.*, **13**(4): 225–238.

SHELTON, P. A., W. G. WARREN, and G. B. STENSON. 1997. Quantifying some of the major sources of uncertainty associated with estimates of harp seal prey consumption. Part II: Uncertainty in consumption estimates associated with population size, Residency, Energy requirements and diet. *J. Northw. Atl. Fish. Sci.*, **22**: 303–315.

TIEWS, K. 1978. On the disappearance of bluefin tuna in the North Sea and its ecological implications for herring and mackerel. *ICES Rapp. Proc.-Verb.*, **172**: 301–309.

TRUDEL, M., A. TREMBLAY, R. SCHETAGNE, and J. B. RASMUSSEN. 2000. Estimating food consumption rates of fish using a mercury mass balance model. *Can. J. Fish. Aquat. Sci.*, **57**: 414–428.

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.

YOUNG, J. W., T. D. LAMB, D. LE, R. 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**(3): 275–291.