**Abstract**—The northern bluefin tuna (*Thunnus thynnus*) is a highly mobile apex predator in the Gulf of Maine. Despite current stock assessments that indicate historically high abundance of its main prey, Atlantic herring (*Clupea harengus*), commercial fishermen have observed declines in the somatic condition of northern bluefin tuna during the last decade. We examined this claim by reviewing detailed logbooks of northern bluefin tuna condition from a local fishermen's co-operative and applying multinomial regression, a robust tool for exploring how a categorical variable may be related to other variables of interest. The data set contained >3082 observations of condition (fat and oil content and fish shape) from fish landed between 1991 and 2004. Energy from stored lipids is used for migration and reproduction; therefore a reduction in energy acquisition on bluefin tuna feeding grounds could diminish allocations to growth and gamete production and have detrimental consequences for rebuilding the western Atlantic population. A decline in northern bluefin tuna somatic condition could indicate substantial changes in the bottom-up transfer of energy in the Gulf of Maine, shifts in their reproductive or migratory patterns, impacts of fishing pressure, or synergistic effects from multiple causes.

# Decline in condition of northern bluefin tuna (*Thunnus thynnus*) in the Gulf of Maine

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The Gulf of Maine is a highly productive region of the northwest Atlantic where substantial aggregations of forage fish attract northern bluefin tuna (*Thunnus thynnus*) and other top predators, including sharks, marine mammals, and seabirds. Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scomber*), and sand lance (*Ammodytes dubius*) form a major part of this prey base (Bigelow and Schroeder, 1953). As seasonal migrants, northern bluefin tuna arrive in the Gulf of Maine in limited numbers in late May and early June (Bigelow and Schroeder, 1953; Mather et al., 1995). Fish landed in the Gulf of Maine during June and early July are typically lean and have little to no perigonadal or body fat reserves (Estrada et al., 2005; Goldstein et al., in press). Presumably, energy stores of mature northern bluefin tuna entering the Gulf of Maine have been exhausted after spawning, a time when shifts in fat and energy stores are pronounced (Mourente et al., 2001) and mesenteric lipid stores are used for gametogenesis and for subsequent migration to feeding grounds.

Given its size, speed, and wide thermal tolerance, the northern bluefin tuna is a formidable predator, capable of exploiting diverse prey species. Having visceral retes that warm the stomach (Carey et al., 1971) and digestive enzymes with fast turnover rates, northern bluefin tuna can rapidly process prey (Stevens and McLeese, 1984). During the 1950s and 1970s, individual northern bluefin tuna gained 7% (Rivas, 1955) and 10% (Butler[1]), respectively, of their body mass per month on the northwest Atlantic feeding grounds. The majority of this mass gain was reflected in the accumulation of intramusculature and perigonadal fat stores, which presumably provide the necessary reserves for migration to the spawning grounds and subsequent gamete production following their departure from the Gulf of Maine in late September to mid November (Lutcavage and Kraus, 1995; Wilson et al., 2005).

Recent observations by fishermen, brokers, and co-operative managers have identified two declining trends in the Gulf of Maine commercial northern bluefin tuna fishery. First, there appears to be fewer mature fish now than in the last decade. Hundreds of surface schools were detected

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annually between 1994 and 1996 in aerial surveys (Lutcavage and Kraus, 1995), but catches in 2004 and 2005 decreased dramatically, and only 30% of the commercial quota was landed in the New England region. Second, coincident with the reduction in catch, over the past decade fishermen and dealers have reported a decline in fish quality irrespective of season. Fish landed in September and October had the same somatic condition as those landed in June, indicating that northern bluefin tuna are not establishing the fat reserves they once did. Given that energy allocation is a key factor in growth, maturation, reproduction, and migration in long-lived fishes (Marshall et al., 1999; Rideout et al., 2005; Jørgenson et al., 2006), a decline in the somatic condition of northern bluefin tuna would be expected to affect the population.

Catch rates of highly migratory species, especially northern bluefin tuna, have fluctuated over the years in many different regions of the world (Anderson and Piatt, 1999; Ravier and Fromentin, 2001). These top pelagic predators may have altered their distribution because of environmental shifts (Anderson and Piatt, 1999), or may have suffered localized depletion because of fishing pressures (Tiews, 1978; Fromentin and Powers, 2005). Although these causes may explain why northern bluefin tuna distribution or abundance in the Gulf of Maine has changed, they do not account for the apparent decline in quality of those fish remaining in the area. In this study, we examined records of the fat and oil content and shape of northern bluefin tuna captured in the Gulf of Maine from 1991 to 2004 in order to investigate whether the observations of a decline in quality (as advanced by commercial fishermen and dealers) represents a significant change in somatic condition of these fish.

## Materials and methods

Fish condition is most often assessed through the use of Fulton's K or linear regression, both of which give a quantitative value to the physical condition of fish. Such analyses were not possible in this study because individual lengths and weights were not recorded for many of the fish. As a substitute, we used grade data from brokers in the commercial northern bluefin tuna fishery who grade every fish before purchase. This procedure is quite involved and often requires schooling or an apprenticeship to learn the trade. Grading involves a qualitative assessment of the condition of fish, defined by the characteristics of freshness, color, fat and oil content, and fish shape (Bestor, 2004). Fat grade is assessed by evaluating the amount of marbling in a tail cut sectioned between the third and fourth finlet, the thickness of the midsection, and the amount of fat present in a small core of muscle (near the mid-line) extracted for biopsy. Shape grade is determined by the overall appearance of the fish, the more rotund the better. A good quality fish will receive high marks in all categories. Even though different graders may use different terms, ranking of fish quality is consistent between experienced graders (Foote[2]).

We used two of these characteristics, fat and oil content and fish shape, as proxies for fish condition. Fish with large fat reserves and rotund appearance are presumably feeding in excess of their daily metabolic requirements and hence, are in good condition. Fat and oil content and fish shape are reasonable proxies to assess condition because, unlike freshness and color, they cannot be altered by either the time fishermen are at sea or type of gear used.

Detailed logbooks were obtained from a local fishermen's co-operative that consisted of 3834 observations of fat and oil content and 3082 observations of shape from fish landed between 1991 and 2004. Fish ranged in size from the commercial minimum of 185 cm curved fork length (CFL) to 300 cm CFL and weighed from 54 kg to 351 kg dressed (i.e., after head, gill plate, and internal organs were removed). All of the grading was carried out by the same individual using the same grade scale for the entire 14-year period.

To examine temporal trends in fish quality, as defined separately by fat and oil content and fish shape, we used multinomial logit regression with fat and oil grade or shape grade as the dependent variable, and month and year as independent variables. The multinomial logit model estimates the probability of a fish being in grade $j$ in month $m$ and year $y$ as

$$\pi_j(m,y) = \frac{\exp\big(\eta_j(m,y)\big)}{\sum_{\forall i} \exp\big(\eta_i(m,y)\big)}.$$

where $\eta_j(m,y)$ is a linear equation consisting of the variables for month ($m$) and year ($y$) and any month-year interactions.

The coefficients for these variables can take on different values for each grade (McCullagh and Nelder, 1989). For example, if we treat month as a categorical variable, $n_j(m,y)$ can be written as

$$\eta_j(m,y) = \beta_{0,j} + (\beta_{1,k,j} \times m_k) + (\beta_{2,j} \times y) + (\beta_{3,k,j} \times m_k \times y)$$

where $B_{0,j}$ = the intercept for grade $j$;
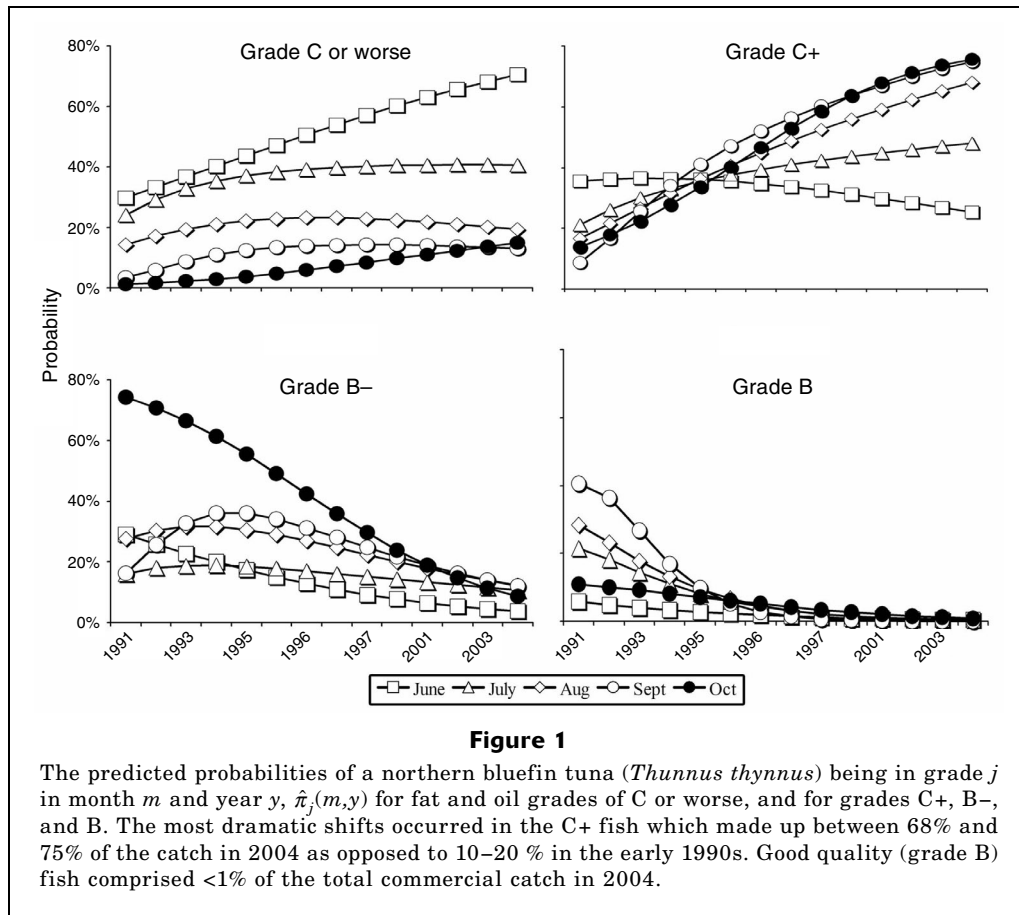$B_{1,k,j}$ = the coefficient for the effect of month $k$ on grade $j$;
$m_k$ = an indicator variable denoting the month as a categorical variable;
$B_{2,j}$ = the effect of year on grade $j$; and
$B_{3,k,j}$ = the interaction between month $k$ and year $y$.

The model was fitted by using the multinomial command in the NNET library of S-PLUS vers. 6.2 (Insightful Corporation, Seattle, WA). The significance of each variable was tested by using likelihood ratios for nested

**Figure 1**

The predicted probabilities of a northern bluefin tuna (*Thunnus thynnus*) being in grade $j$ in month $m$ and year $y$, $\hat{\pi}_j(m,y)$ for fat and oil grades of C or worse, and for grades C+, B−, and B. The most dramatic shifts occurred in the C+ fish which made up between 68% and 75% of the catch in 2004 as opposed to 10–20 % in the early 1990s. Good quality (grade B) fish comprised <1% of the total commercial catch in 2004.

models, and Akaike's information criterion (AIC) for non-nested models.
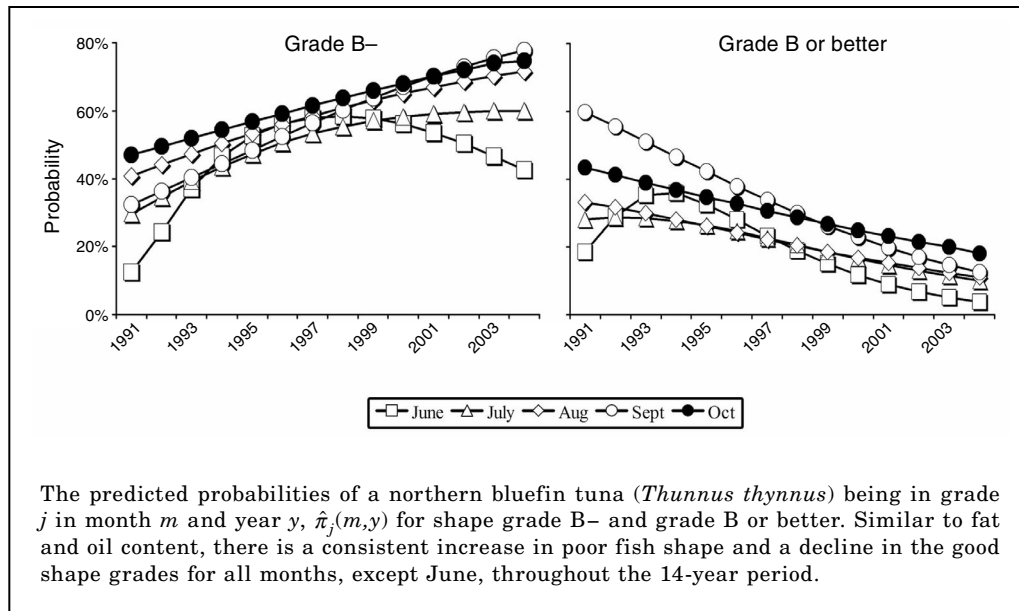
## Results

Our analysis identified significant declines in the somatic condition (fat and oil content and fish shape) of northern bluefin tuna in the Gulf of Maine. For fat and oil content, the effect of month, year, and the month-year interaction were each significant (all $P<0.0001$; $\chi_4^2=429$, $\chi_4^2=1088$, and $\chi_4^2=29.95$, respectively). Fish landed in the month of June arrived in poorer condition than they did in the early 1990s (Fig. 1). For example, the probability of landing a poor quality fish (grade C or worse) in June 1991 was 30% compared with 70% in 2004. Similar, but more striking results were observed in the C+ category during August and September (Fig. 1). In 1991, the probability of landing a fish in the C+ category was 16% and 9% for August and September, respectively. In 2004, the probability increased to 68% and 76% in the C+ category for August and September, respectively. Good quality fish, such as B or better now comprise <1% of the commercial catch at this particular co-operative (Fig. 1).

For fish shape, the effect of month, year, and the month-year interaction were each significant (all

$P<0.0001$; $\chi_3^2=207$, $\chi_3^2=388$, and $\chi_3^2=47.18$, respectively). Results for shape were similar to fat and oil content, likely because shape and fat and oil content are closely related (fat fish should have a more rotund shape). The probability of landing a fish that received a B− (lesser quality) grade for shape increased by 30%, 32%, 43%, and 28% from 1991 to 2004 for the months of July, August, September, and October, respectively (Fig. 2). For the same time period, fish with a good shape (B or better) decreased by 18%, 22%, 47%, and 25% for the months of July, August, September, and October, respectively (Fig. 2).

## Discussion

Our multinomial regression analysis demonstrated highly significant declines in the fat and oil content and shape of northern bluefin tuna landed in the Gulf of Maine over the last 14 years, corroborating the observations of fishermen. Northern bluefin tuna arrive in leaner condition and are not increasing their fat stores on the feeding grounds as they did in the early 1990s. This was particularly true in late summer and early fall, when fish usually fatten and become more rotund (Butler[1]).

The predicted probabilities of a northern bluefin tuna (*Thunnus thynnus*) being in grade *j* in month *m* and year *y*, $\hat{\pi}_j(m,y)$ for shape grade B– and grade B or better. Similar to fat and oil content, there is a consistent increase in poor fish shape and a decline in the good shape grades for all months, except June, throughout the 14-year period.

Seasonal migrations of adult northern bluefin tuna are believed to be bound by reproduction and feeding constraints: spawning in warm (>24°C) regions in spring and early summer followed by dispersal to continental shelves at higher latitudes for intensive foraging through late fall (Rivas, 1955; Clay, 1991). Their body condition also varies through this cycle: feeding periods presumably put individuals into positive lipid balance, creating energy stores for gonadal development and metabolism (Medina et al., 2002; Carruthers et al., 2005). Since the mid 1990s, mixed size classes of northern bluefin tuna appeared in North Carolina coastal waters from December to February (Block et al., 2001), extending the range of their inshore foraging on Atlantic menhaden (*Brevoortia tyrannus*) and possibly other species. If the temporal or spatial aspects of migration, reproduction, and feeding patterns have changed over the past decade, alterations in the somatic and bioenergetic condition of fish feeding in the Gulf of Maine could be expected. Other possible explanations for changes in somatic and bioenergetic condition of fish include increased growth rates due to selective fishing pressure (Polacheck et al., 2004), or skipped spawning to increase growth (Jørgensen et al., 2006), but the general declines in condition in fish of such large body size are difficult to explain based on intrinsic changes in growth. This is particularly true in this study where every fish was larger than 110 cm, the size at which the seasonal length-weight relationship begins to decrease (Mather et al., 1995) and northern bluefin tuna gain more in mass than length.

In pelagic fishes, migrations require a substantial energetic cost (Harden Jones, 1984), and migration distance has been linked to body size and available fat stores (Nøttestad et al., 1999). The longstanding migration paradigm is that western Atlantic northern bluefin tuna spawn in the Gulf of Mexico and Straits of Florida from April to June and then migrate northward along the continental shelf to New England and Canadian waters (Rivas, 1955; Mather et al., 1995; Block et al,. 2005). A substantial increase in migrants from the Eastern Atlantic may explain why the condition of fish in this region has declined. Northern bluefin tuna migrating to the Gulf of Maine from the eastern Atlantic would have to swim a greater distance, travel against major currents and through unproductive waters using more stored energy than individuals coming from western Atlantic spawning grounds. To date, there is insufficient data to confirm that such a shift has occurred (Fromentin and Powers, 2005). Another possibility is that the timing and location of spawning has shifted. The long held assumption that the New England assemblage spawns exclusively in the Gulf of Mexico and adjacent regions (Rivas, 1955; Block et al., 2005) may be incorrect (Lutcavage et al., 1999; Fromentin and Powers, 2005; Goldstein et al., in press). If fish are spawning outside of these traditional spawning grounds during May and June (Mather et al., 1995; Lutcavage et al., 1999; Wilson et al., 2005), or at different times, their somatic condition and lipid allocations would be expected to shift from historical patterns (Rajasilta, 1992).

Given that northern bluefin tuna spend up to five months on the feeding grounds, a decline in somatic condition intuitively points to changes in the forage base and energy transfer within the Gulf of Maine. Northern bluefin tuna exploit several trophic levels, including krill, before arrival in the Gulf of Maine (Estrada et al., 2005), but while there, they forage extensively on herring (Chase, 2002), which has the highest energy density of prey in the region (Lawson et al., 1998). The observed decline in condition could result

from a decrease in the amount, quality, or availability of herring (Marshall et al., 1999; Diamond and Devlin, 2003), or an increase in the energy required for northern bluefin tuna to acquire and process sufficient amounts of prey (Marshall et al., 1999; Nøttestad et al., 1999; Carruthers et al., 2005).

Atlantic herring spawning stocks in the Gulf of Maine and Georges Bank-Nantucket Shoals are at historically high levels (Overholtz et al.[3]); this fact argues against a reduction in herring abundance as a causal factor for the declining condition in northern bluefin tuna. A reduction in the energy density of herring itself, as seen in seabird-herring-copepod ecosystem studies (Diamond and Devlin, 2003; Durant et al., 2003) are other possible reasons for the decline. A coincident decline in northern bluefin tuna and Atlantic herring condition in the Gulf of St. Lawrence indicate that similar changes are occurring in other Northwest Atlantic shelf systems. In view of changes also detected in other predators, such as seabirds, and in the distribution and abundance of baleen whales, there appears to be a major shift in energy transfer and dynamics across the Gulf of Maine ecosystem over a period when oceanographic changes linked to the North Atlantic Oscillation were also evident (Greene and Pershing, 2003).

If the abundance of forage fish has been reduced, dispersed into smaller schools, or shifted, northern bluefin tuna would have to expend more energy in search of prey, shift their diet to less energetic prey (i.e., the junk food hypothesis [Piatt and Anderson, 1996; Golet et al., 2002]), or move to regions with a greater biomass of forage fish (Anderson and Piatt, 1999). Northern bluefin tuna are arriving in poorer condition than they were 10–14 years ago, and despite long residency in the area they are no longer attaining the good condition of previous decades. Of additional concern is that after disappearances in the North Sea and in some historic locations on the Canadian Atlantic shelf, northern bluefin tuna have not returned to these areas (Tiews, 1978; Clay and Hurlbut, 1989).

Condition data alone do not allow us to identify the cause of observed declines in this top predator, but decreased energy stores on feeding grounds could reduce energetic allocations to growth and reproduction, as observed in gadids in the northwest Atlantic and elsewhere (Marshall et al., 1999; Lambert and Dutil, 2000), and may have unexpected and detrimental consequences for rebuilding the northern bluefin tuna population. Given that northern bluefin tuna are currently overexploited throughout most of their range, it is essential to identify root causes for these declines on one of their most important foraging grounds in the western Atlantic.

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