

Abstract—Aerial photographic assessment is a promising technique that could be structured to yield a fishery-independent index of abundance for Atlantic bluefin tuna, *Thunnus thynnus thynnus* (ABT). The accuracy of this approach may be increased by incorporating the relationship between the surface characteristics of a school and the total number of individuals. Our objective was to develop models to facilitate the estimation of number of fish in ABT schools from aerial photographs.

Video cameras were used to observe 74 incidences of schooling for 50 captive ABT approximately one meter in length. Relationships between the surface characteristics of ABT schools and the number of fish in the school were explored by using least-squares regression. The schools ranged in number from 2 to 45 individuals. A weighted regression model incorporating the number of fish in the school at the surface as the independent variable and the number of fish in the remaining portion of the school yielded an r^2 of 0.74. A second weighted multiple-regression model incorporating the number of fish in the school at the surface and in the second depth interval (0–25% school depth below surface layer) of the school as independent variables, and the number of fish in the remaining portion of the school as the dependent variable, with $1/\text{variance}$ as the weight, achieved an r^2 of 0.70. A third model using the length and width of the surface layer of the school as the independent variables and the number of fish in the school as the dependent variable had an r^2 of 0.86. One data point from a wild school is currently available to verify model predictions. This school of 125 individuals is well outside the range of school sizes used to construct the model (2–45 individuals), yet differs from model predictions by only 7%.

We believe that these models have the potential to improve an abundance index based on aerial photographs by estimating the number of individuals in wild ABT schools from surface characteristics observed in aerial photographs.

Estimating the number of fish in Atlantic bluefin tuna (*Thunnus thynnus thynnus*) schools using models derived from captive school observations

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The bluefin tuna (*Thunnus thynnus*) is distributed worldwide in temperate and subtropical seas. It has a limited distribution in the southern hemisphere. Endothermy by means of vascular heat exchangers allows bluefin tuna to inhabit a wide thermal niche and therefore wide geographic and depth ranges (Carey and Teal, 1969; Carey and Lawson, 1973). In the western Atlantic Ocean, the Atlantic bluefin tuna (ABT), *Thunnus thynnus thynnus*, is distributed from Labrador to Brazil, including the Gulf of Mexico and Caribbean Sea. Adult ABT occur throughout the entire range, but smaller bluefin tuna (less than 45 kg) are not observed frequently above the latitude of Cape Cod, Massachusetts. The Atlantic bluefin tuna is epipelagic and usually oceanic but appears near the coast seasonally (Squire, 1962; Collette and Nauen, 1983) to feed on concentrated assemblages of prey. Adult ABT may attain a length of four meters and a body mass of 680 kg. Large medium (178–195 cm FL) and giant (>195 cm FL) bluefin tuna are targeted by commercial purse-seine, long line, and hook-and-line fisheries (Mather, 1974; Figley, 1984). A recreational hook-and-line fishery (Mather, 1974; Figley, 1984) targets all sizes of bluefin tuna as they appear along the east coast of the United States and Canada from June to October (Mather, 1962).

The combination of changes in the spatial distribution over time and associated uncertainty regarding the independence of eastern and western Atlantic stocks makes the estimation of ABT stock size particularly problematic. The stock assessment for this species

has been based upon landings data and abundance indices (Scott et al., 1993). Use of ABT landings data to generate an abundance index may lead to bias due to variability in effort, improvements in fishing technology (Lo et al., 1992), and variability in annual geographic distribution linked to prey distribution.¹ These characteristics of the northwest Atlantic bluefin tuna fishery, in conjunction with population-level behavioral characteristics observed for similar tuna species, suggest that the use of catch-per-unit-of-effort (CPUE) data to evaluate tuna population trends could lead to inaccurate estimates (Clark and Mangel, 1979). The accuracy of CPUE-based assessments in estimating the abundance of bluefin tuna in the northwest Atlantic remains controversial (Clay, 1991; Suzuki and Ishizuka, 1991; Safina, 1993). An extensive discussion of the issues involved in Atlantic bluefin tuna assessment can be found in the National Research Council report by Magnuson et al. (1994).

Recent investigations have focused on the feasibility of using aerial photographic assessment of large medium and giant bluefin tuna in New England waters and in the Straits of Florida (Lutcavage and Kraus, 1995; Lutcavage et al., 1997) as an alternative fishery-independent method of obtaining indices of abundance. The aerial survey

¹ Chase, B. C. 1995. Preliminary report of the Massachusetts bluefin tuna investigation: the diet of bluefin (*Thunnus thynnus*) off the coast of Massachusetts. Massachusetts Division of Marine Fisheries, Salem, MA 01947, 39 p.

method has been used to determine the relative abundance for other pelagic fisheries worldwide, including *Engraulis mordax* (Lo et al., 1992), *Engraulis mordax*, *Sarda chiliensis*, *Trachurus symmetricus*, etc. (Squire, 1972), *Trachurus declivis*, *Katsuwonus pelamis*, *Arripis trutta*, *Thunnus maccoyii* (Williams, 1981), *Mugil* spp. (Scott et al., 1989), and Squire (1993) has reported aerial survey data for *Thunnus thynnus orientalis* and other species. Abundance estimates derived from an aerial assessment are based on biomass or number of individuals per unit of area.

Lutcavage and Kraus (1995) concluded that the aerial method could provide area-specific minimum abundance and distribution data for large medium and giant Atlantic bluefin tuna under good viewing conditions. However, many difficulties associated with aerial photographic assessment of ABT remain to be resolved. Sea state, lighting conditions, and turbidity all play an important role in the ability to detect and produce useful photographs of schools (Lutcavage and Kraus, 1995). Rough seas, sun glare, and high turbidity may all result in reduced detection of schools, limiting the days on which this type of survey method is effective. Visual counts of individuals at the surface derived from aerial photographs are difficult to interpret without a verification count and information on behavioral factors such as surfacing frequency (Lo et al., 1992) and the proportion of the school visible at the surface (Lutcavage and Kraus, 1995). In addition, variability in population movements and distribution could lead to an inaccurate abundance estimate if an intensive, spatially expansive sampling scheme is not employed.

We propose a technique to address the problem of estimating the number of fish in a school (NFS) from the surface characteristics of a school. If the relationship between the surface structure or the surface number of fish and number fish in total school was known, school surface counts from aerial photographs or visual observations could be adjusted to include an estimate of total NFS, facilitating an improvement of area-specific minimum abundance estimates based on visual or photographic data sources.

Atlantic bluefin tuna are believed to exhibit the most rigidly defined spatial structure of schooling fishes (Partridge et al., 1983). Distinct two- and three-dimensional school structures have been described by previous authors (Partridge et al., 1983; Lutcavage and Kraus, 1995). Parabolas and echelons are the shapes of commonly observed surface-oriented two-dimensional schools, whereas the densely packed dome is the shape of a frequently observed three-dimensional school configuration (see Partridge et al., 1983 and Lutcavage and Kraus, 1995 for illustrations). The number of fish observed in two-dimensional surface schools is generally less than 15, whereas three-dimensional schools such as those forming densely packed domes usually have greater than 15 individuals (Partridge et al., 1983). Although the three-dimensional component of bluefin tuna school structure has been observed (Lutcavage and Kraus, 1995), quantitative description and analysis is lacking and little is known of the relationship between the two-dimensional surface structure and three-dimensional structure

(e.g. total count, biomass) of schools (Partridge et al., 1983; Lutcavage and Kraus, 1995). In addition, the behavioral and environmental factors that may influence tuna school structure and dynamics remain poorly described (Mather, 1962; Clark and Mangel, 1979; Partridge et al., 1983).

Our study presents a functional relationship between the surface characteristics of and the total number of individuals in ABT schools. We analyzed video-taped footage of 74 incidences of schooling in a group of captive ABT to quantify the relationship between the number of fish visible at the surface and the total number of individuals in the school (NFS), the relationships between school dimensions (e.g. length, width) and NFS, and to explore the effect of environmental conditions within the net-pen enclosure on school size and dimensions. We also analyzed the vertical distribution of individuals within schools across school size, and propose a mechanistic explanation for the limited size of the two-dimensional schools observed by Partridge et al. (1983) and Lutcavage and Kraus (1995). We then apply the predictions from one of the resultant models to the single open-ocean school size estimate available.

Methods

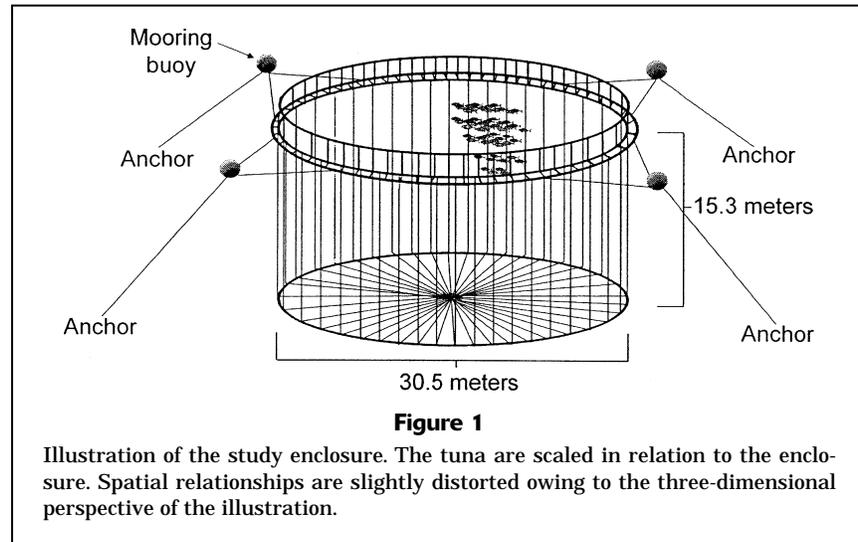
Field methods

We employed a 30.5-m diameter, 15.3-m deep, cylindrical floating net-pen enclosure (Fig. 1) to hold the tuna used in our study. This enclosure is similar to those used in tuna research and culture operations around the world. Its low cost, large internal volume (11,128.5 m³), and its resiliency to dynamic and often damaging effects of the offshore environment make this enclosure the most appropriate type for observing the behavior of large pelagic fish in captivity. The enclosure proved to be very resilient to the damaging effects of a close pass of a hurricane and a tropical storm. A white, one-inch, straight-hung mesh net constituted the vertical walls and bottom of the enclosure.

The enclosure was anchored 32.2 km offshore of Wachapreague, VA, on the southwest corner of 20 Mile Hill—a bathymetric feature that rises within 33.5 m of the ocean surface in deeper surrounding waters. This location is relatively near shore and close to a temporally and spatially reliable aggregation of small (~1 m) Atlantic bluefin tuna regularly targeted by recreational fishermen.

The vertical temperature profile (°C), dissolved oxygen (mg/L), pH, suspended solids (NTU), Secchi depth (m), and conductivity (ppt) were monitored twice daily inside and outside the enclosure at 3-m intervals to a minimum depth of 15 m.

A pattern of seven, single-hook trolling lures were fished from a 18.3-m commercial vessel on 13-kg or 22-kg class trolling gear to capture fifty bluefin tuna in the vicinity of the study enclosure in June and July 1996. Tuna were subdued as quickly as possible and landed in a specialized cloth stretcher. We recorded the fork length (cm), approximate weight (kg), and general condition of each fish and released the fish into a 2400-liter elliptical transport tank. Compressed, bottled oxygen was employed to elevate



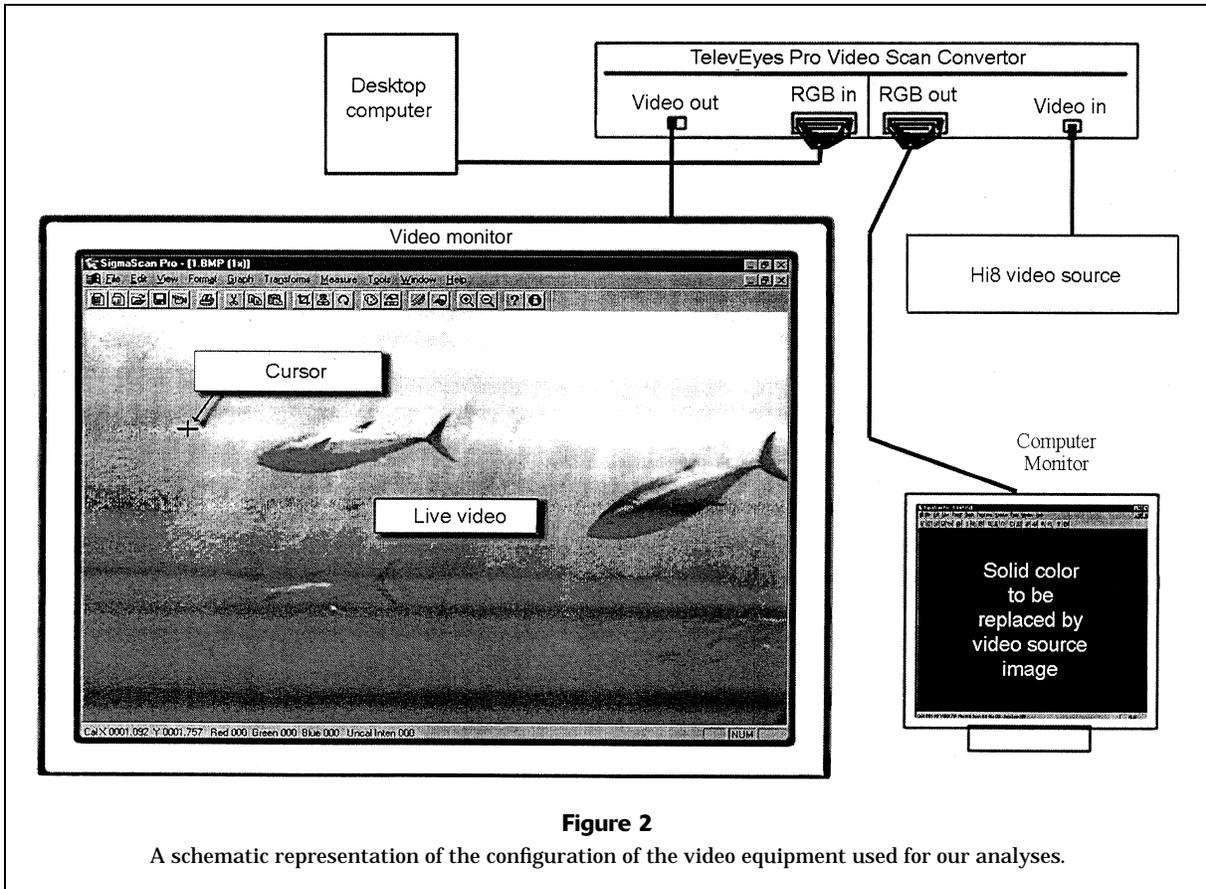
the levels of dissolved oxygen within the transport tank to ease the physiological stress associated with strenuous activity. Fresh seawater was continuously pumped into the tank to eliminate metabolic waste and maintain water quality. The tank had a padded top that minimized the potential for injury to fish during transport and reduced water loss resulting from boat movement. Viewing ports in the padded top allowed observation of the specimens while in transport. Physical contact with individual tuna was minimized, and when contact was necessary, only well-padded devices were employed. Transport time of individual fish was variable, but generally less than 3 hours. The number of fish simultaneously transported in the tank was controlled to avoid crowding and the depletion of dissolved oxygen. The tuna were recovered from the transport tank by using a cloth stretcher and released into the net-pen enclosure. Divers in the enclosure released the tuna individually, ensuring that they recovered proper spatial orientation upon release. Released specimens were assimilated quickly into the existing shoals of captive fish.

Video cameras (Hi8) in waterproof housings were used to record school structure of the captive tuna. A shutter speed of 1/2000 second was used to optimize the resolution of still frames within the constraint of available subsurface (<15.3 m depth) light. The automatic focus feature of the camera was disabled to avoid rapid fluctuations in focal depth from the intended subject to particulate matter suspended in the water column. Observations of schooling tuna were recorded with stand-alone cameras mounted inside the enclosure and with hand-held cameras during observation dives. Cameras mounted to the floating net pen on specialized polyvinyl chloride pipe structures were stabilized with elastic compensators to lessen movement caused by wave energy. Mounted cameras were positioned to provide head-on and subsequent perpendicular views in relation to the axis of motion of a school. This filming strategy allowed a more accurate observation of the characteristics of the school in three dimensions. Schooling was recorded more efficiently by using hand-held camer-

as during dives than through use of mounted cameras. During a dive, the entire internal volume of the enclosure was often visible from a given point, allowing a diver to anticipate the path of travel of a tuna school and to reposition the camera to attain the best possible images. Regardless of the apparent ease of tuna schools, divers positioned themselves against the enclosure's external wall to ensure minimal behavioral modification in the filmed schools. Video recordings from both mounted cameras and from held cameras were used in analysis.

Laboratory video analysis

Video recordings of ABT schools were reviewed, and 74 incidences of schooling in which an entire target school was visible were used for further analyses. All observations took place during daylight hours (0900 and 1600 h) and none took place during or within one hour of feeding events. An image analysis system that allowed digitization of points directly from a (paused) video source was employed for more precise quantification of school characteristics (Fig. 2). The system employed a video scan converter that overlaid the image output from a computer video source (640·480 pixel resolution) upon the video source image. The video scan converter allowed the user to select a color in the computer video overlay to be made transparent, revealing the underlying video signal (Fig.2). When employed in conjunction with an image analysis software package (SigmaScan Pro) on a personal computer, all the features of the image analysis software could be used on any still (paused) video source image without the use of a video frame-grabber. The position of each individual fish and school depth intervals were delineated by using the graphic capabilities and the Cartesian coordinate system of the image analysis software. The positions of individual fish in the school could be marked while the recording was advanced or reversed frame by frame, allowing the identification of poorly illuminated fish or fish that may have been hidden by individuals in the foreground of the school.



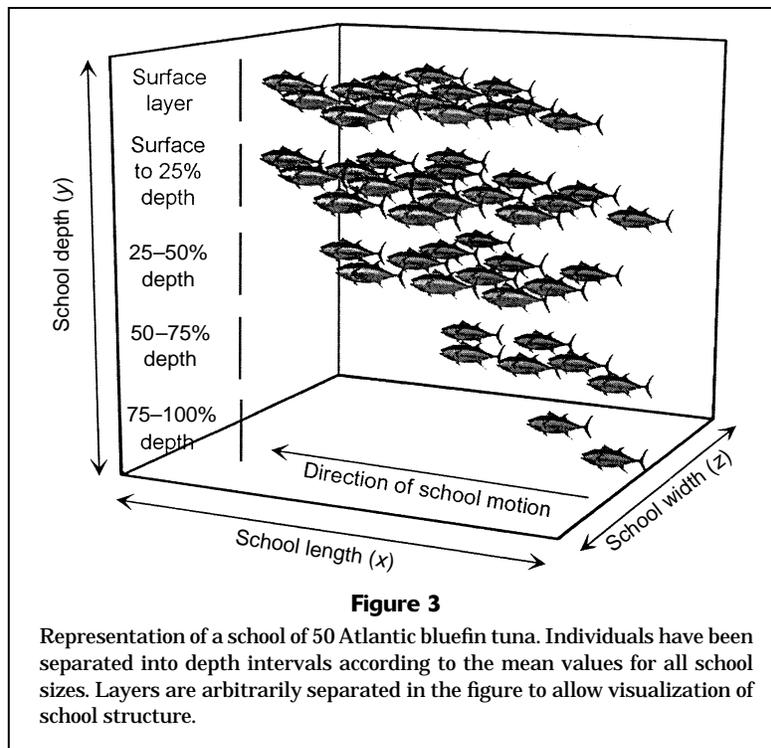
Data analysis

School size Groups of tuna were considered to be schools and were included in the analyses if they were a polarized group (multiple individuals maintaining lateral proximity to neighbors and actively maintaining the same direction of travel during an observation period). The total number of fish in each school was counted and the frequency distribution of school size was determined. Because the observations were assumed to be independent and the total sample size was less than 2000, the normality of the distribution was tested by using the Shapiro-Wilks W -test. Least-squares regression was then used to evaluate the relationship between school size (N_s) and each environmental variable.

Predicting number of fish in school from surface counts Our video footage was filmed at an oblique perspective to the upper boundary of schools occurring within two meters of the water's surface. Measurement of school characteristics in body lengths or meters was not possible because of the camera angle or because of poor image resolution due to low light or high turbidity level. The total number of individual fish (N_s) was determined and the distribution of individuals within the school was described in terms of five depth intervals (Fig. 3). The surface interval included fish that were at the immedi-

ate surface of the school or fish that overlapped other fish at the surface on the horizontal plane. Each of the four subsequent intervals encompassed 25% of the remaining depth of the school. The number of fish per interval was designated as N_j (j =the number of tuna in the j^{th} depth interval). Fish positioned at an interval boundary were assigned to the interval in which the greater portion of their body volume was positioned. Analysis of covariance (ANCOVA) (Sokal and Rohlf, 1995) was employed to detect differences in the slopes of each of the regressions of N_j on N_s in order to determine whether the distribution of individuals into school depth intervals changed in proportion to school size.

Three individual least-squares regression models were used to predict school size. The relationship between the number of individuals in the surface interval (N_1 ; independent variable) and the number of individuals in the remainder of the school (N_s ; dependent variable) was first explored using simple least-squares regression (Sokal and Rohlf, 1995). The distribution of N_s given N_1 was heteroscedastic necessitating the use of a weighted least-squares regression model by using a weight of $1/\text{variance}$ (Kleinbaum et al., 1988). A similar-weighted multiple-linear-regression relationship between N_1 , N_2 (independent variables), and N_s (dependent variable) was developed because fish below the immediate surface of the school are sometimes seen and counted in photographs.



Predicting number of fish in school (NFS) from school dimensions School length, width, and depth in number of individual fish were recorded as indicators of school shape (Fig. 3). As in the prediction of NFS from surface counts, measurements were recorded in number of fish, not metric distance, because a precise spatial scale could not be established consistently. The lack of an accurate spatial scale also precluded the measurement of fine-scale school structure such as interindividual distances. School dimension measures were recorded according to the movement axis of a school. Length in number of fish was measured along the axis of school motion (x); depth was measured vertically (y) and width (z) was measured perpendicular to x on the horizontal plane (Fig. 3). School length and width were analyzed in relation to school size by least-squares regression. Regression models employed each one or both dimensions (i.e. length, width, length and width) of school shape as independent variables, and N_S as the dependent variable. Depth data were not analyzed in relation to N_S because these data may not be collected practically from wild schools. The relationship between dimensions of each school and selected environmental variables was examined by using least-squares regression.

Results

Behavior of the specimens

The captive specimens used in our investigation exhibited a high degree of awareness of the walls of the enclosure, even during periods of excited behavior. No collision with or brushing of the net wall was observed from above the

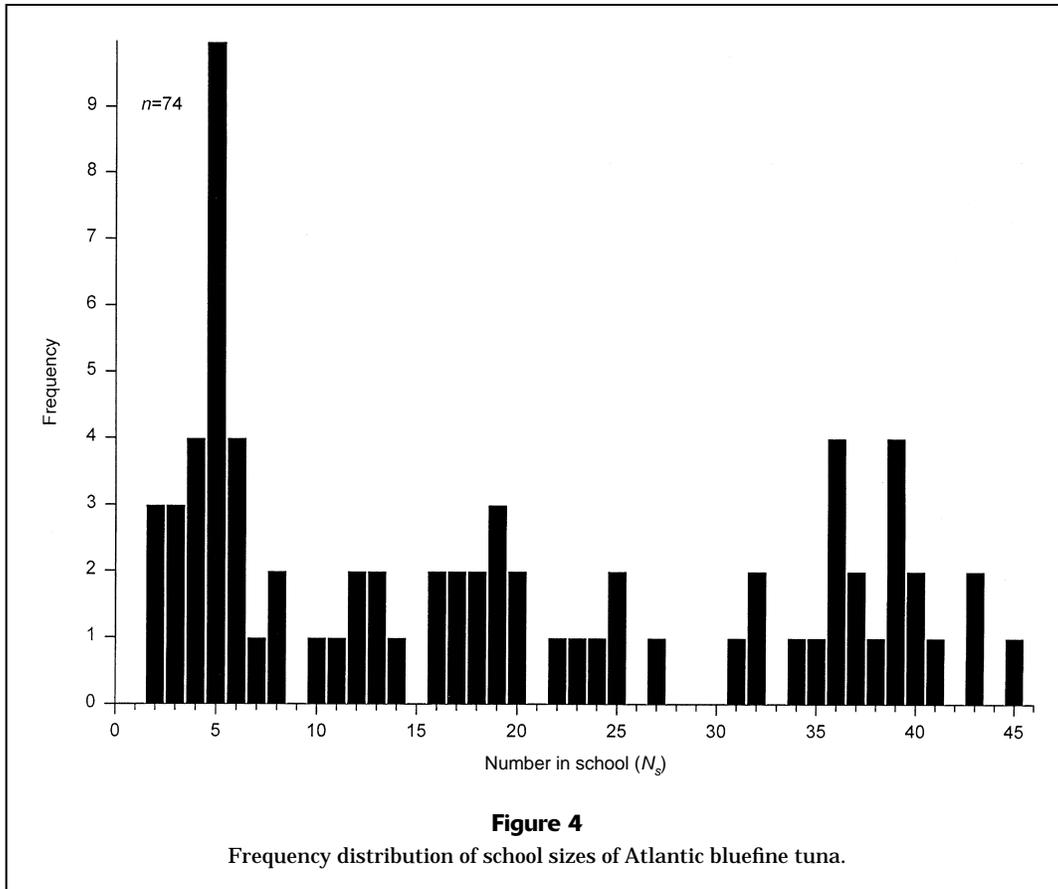
surface or in the analysis of diurnal activities from underwater video footage, and no evidence of nocturnal collisions was observed. After a brief period of acclimation, the tuna did not actively avoid divers in the enclosure; they reacted only to avoid collision.

Visualizing the model

A three-dimensional model of the typical structure of a school of ABT was constructed based on the mean characteristics of the schools analyzed and on qualitative observations of school structure (Fig. 3). The proportionate distribution of individuals within school depth intervals varied little (see ANCOVA results below), suggesting that a single model adequately describes the mean vertical distribution of individuals for schools of varying size.

Number of schools and NFS

When a single school comprised the entire group of 50 tuna, less than approximately 20% of the enclosure volume was involved in containing such a school (senior author, pers. obs.). Fish swimming within such a school were observed to travel along a slowly arcing path around the entirety of the enclosure without making sharp turns. Smaller schools (up to 25 individuals) occupied only a very small portion of the volume of the enclosure. Single large schools separated into two or more smaller schools and joined back together with fluidity. When more than one school was observed simultaneously, each school exhibited movement independent of another. If two schools came close to one another in the enclosure, they would either pass by, move through the other group, or join together to



form a larger group. While schools were remixing during such encounters, portions of one group would sometimes join another, maintaining the same number of independently acting groups, but changing the number of individuals within each group.

Particularly in larger schools, individual fish positions were observed to be dynamic, yet the overall shape of the school remained relatively constant. The mean size of schools observed was 18.88 individuals ($n=74$, $SD=13.90$). The smallest schools observed had 2 ($n=3$) individuals, and the largest had 45 ($n=1$). The frequency distribution of school sizes was not normal (Shapiro-Wilks' W , $P<0.0001$) and had two prominent modes centered at 5–10 individuals and 35–40 individuals (Fig. 4).

No statistically significant relationships between environmental variables and N_s were observed (Table 1). However, low power due to small sample sizes may have reduced our ability to detect significant effects.

Predicting NFS from surface counts

The relationship between the number of individuals in each depth interval and school size was linear in all cases. Although the r^2 values for each N_i-N_s regression were relatively low, their slopes appeared to be similar and were within a narrow range (0.14–0.23). However, ANCOVA revealed that the slopes were significantly dif-

ferent ($P<0.001$). Although the slopes were significantly different, the number of individuals in each interval remained in the same proportion except at low school sizes (<15 individuals).

The regression model incorporating the number of fish in the surface interval of the school as the independent variable and the number of individuals in the remaining portion of the school as the dependent variable had an r^2 of 0.67 ($P<0.0001$) (Eq. 1, Table 2). However, this regression model is likely biased owing to heteroscedasticity in the dependent variable. A second least-squares regression model, incorporating a weight of $1/\text{variance}$, achieved an r^2 of 0.74 ($P<0.0001$) (Eq. 2, Table 2). The third regression model incorporated the number of fish in the surface interval (N_1) and the second interval (N_2) of the school as independent variables, the number of fish in the remaining portion of the school as the dependent variable, and $1/\text{variance}$ as the weight. This model had an r^2 of 0.70 ($P<0.0001$) (Eq. 3, Table 2). Partial F -tests for these models could not be executed because the dependent variable $N_s - (N_1 + \dots + N_i)$ changed depending on the number of school depth intervals used to predict NFS.

Three least-squares regression models were used to predict school size from school length and width. The model using length as the independent variable and N_s as the dependent variable had an r^2 of 0.74 ($P<0.0001$) (Eq. 4, Table 2). The second model predicted N_s from school width, achiev-

Table 1

Mean, minimum, maximum, and standard deviation of environmental data (pH; °C=degrees Celsius; mg/L=milligrams/liter; ntu=turbidity units; ppt=parts per thousand) recorded during schooling observation periods. The r^2 and P -values for linear regressions of each school measure on each environmental variable are provided. Measurements of dissolved oxygen were discontinued due to instrument failure.

| Date | Observation start time | pH | Temp. (°C) | Dissolved oxygen (mg/L) | Total suspended solids (ntu) | Conductivity (ppt) |
|------------------------------|------------------------|-------|------------|-------------------------|------------------------------|--------------------|
| 27 Jun 1996 | 10:00 AM | — | — | — | — | — |
| 21 Jul 1996 | 3:30 PM | 8.51 | 22.90 | 9.37 | — | 27.45 |
| 6 Aug 1996 | 10:11 AM | 8.42 | 22.18 | 8.62 | 0.12 | 28.65 |
| 7 Aug 1996 | 8:45 AM | 8.43 | 24.18 | 8.39 | 0.23 | 28.98 |
| 15 Aug 1996 | 3:45 PM | 8.44 | 23.84 | — | 0.60 | 28.06 |
| 17 Aug 1996 | 10:48 AM | 8.46 | 23.86 | — | 0.77 | 28.42 |
| 22 Aug 1996 | 11:55 AM | 8.47 | 23.40 | — | 0.05 | 27.63 |
| 23 Aug 1996 | 11:15 AM | 8.50 | 23.50 | — | 0.45 | 29.63 |
| Mean | | 8.46 | 23.41 | 8.79 | 0.37 | 28.40 |
| Minimum | | 8.42 | 22.18 | 8.39 | 0.05 | 27.45 |
| Maximum | | 8.51 | 24.18 | 9.37 | 0.77 | 29.63 |
| Standard deviation | | 0.04 | 0.68 | 0.52 | 0.28 | 0.76 |
| | N_s | 0.1* | 0.15* | 0.84* | 0.09* | 0.04* |
| Coefficient of determination | School length | 0.01* | 0.19* | 0.91* | 0.02* | 0.01* |
| | School width | 0.09* | 0.22* | 0.46* | 0.1* | 0.03* |

* $P > 0.10$.

Table 2

Regression equations employed to predict school size. The results of partial F -tests indicated that model 6 is the best predictor of school size (N_s). N_1 , N_2 , school length, and school width were measured in individual fish.

| Model | Equation | n | r^2 | partial F |
|---|--|-----|-------|--------------------------|
| 1. N_1 vs. N_s | $N_s = (0.0337867 + 3.3173368 \cdot N_1) + N_1$ | 74 | 0.67* | |
| 2. N_1 vs. N_s (weight=1/variance) | $N_s = (0.2042865 + 3.1849359 \cdot N_1) + N_1$ | 74 | 0.74* | |
| 3. N_1, N_2 vs. N_s (weight=1/variance) | $N_s = (-1.412557 + 1.8516536 \cdot N_1 + 0.4190831 \cdot N_2) + N_1 + N_2$ | 74 | 0.70* | |
| 4. Length vs. N_s | $N_s = -6.769737 + 5.5334126 \cdot \text{length}$ | 74 | 0.74* | |
| 5. Width vs. N_s | $N_s = -6.70494 + 5.7894971 \cdot \text{width}$ | 74 | 0.79* | |
| 6. Length, width vs. N_s | $N_s = -9.788046 + 3.6463236 \cdot \text{width} + 2.7083604 \cdot \text{length}$ | 74 | 0.86* | (6 vs. 4)* (6 vs. 5)* |

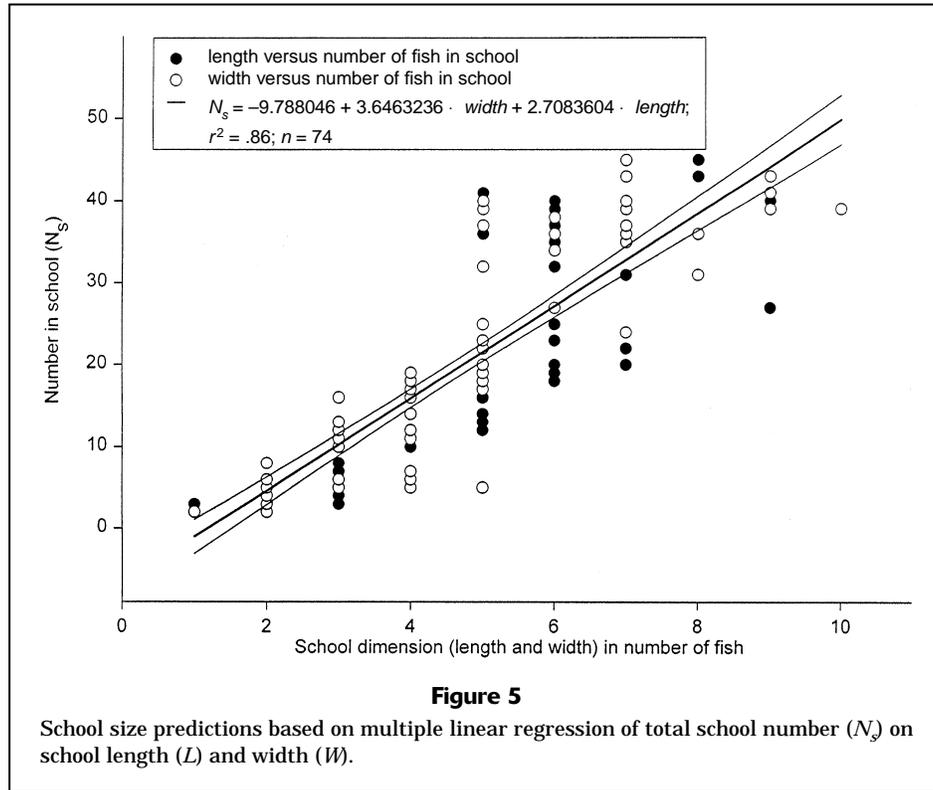
* $P < 0.0001$.

ing an r^2 of 0.79 ($P < 0.0001$) (Eq. 5, Table 2). The final, multiple regression model used school length and width to predict N_s (Eq. 6, Table 2, Fig. 5) with an r^2 of 0.86 ($P < 0.0001$). Partial F -tests revealed that the final multiple regression model explained significantly more of the variation in school size than either length or width separately. No significant relationships were seen when school dimensions were considered in terms of environmental factors (Table 1).

Discussion

School structure

The non-normal frequency distribution of NFS and the appearance of modes in our data (Fig. 4) suggest the formation of elective groups of particular number. Previous investigations in school size show that fishes actively assemble into elective group sizes dependent upon the



interaction of predation risk, food availability, migratory status, and the species' life history (Hager and Helfman, 1991; Pitcher and Parrish, 1993). Elective group size for a species differs continuously under natural conditions with varying abiotic and biotic factors. At a discrete point in time when two schools were present in the enclosure, the size of one group determined the maximum number of individuals that could be in the other. However, there were no barriers to formation of groups numbering anywhere from 2 to 50 individuals. Therefore, the modes in group number that we observed should have resulted from underlying behavioral tendencies rather than enclosure-induced limitation of group size. If elective group sizes form in response to environmental conditions, then the range of environmental conditions during the study period was probably insufficient to detect environmental influences on NFS, and therefore elective group sizes.

The range of school sizes that we observed in the enclosure was limited by the number of individuals available to join schools. Photographs of ABT in the northwest Atlantic Ocean over a 50-day period in 1993 revealed that surface school counts ranged from 5 to 1294 individuals, and that the median school size was 84 individuals (Lutcavage and Kraus, 1995). The median value is well in excess of the maximum number of fish observed in the surface layer of our schools, emphasizing the importance of verifying the accuracy of our model predictions for larger schools with field data. When very large schools occur in relatively shallow water, the vertical depth of the school would be confined by the maximum water depth. A similar effect could be imposed by physical and chemical barriers such

as vertical stratification in temperature and dissolved oxygen. Tagging studies may reveal more of the individual and group behaviors of this species in relation to the environment and assist in further understanding the way in which school structure may be affected by the physical and chemical environment.

Our results show that the vertical distribution of fish (in intervals) varies little across the range of observed school sizes. The ANCOVA of N_i on N_s illustrated that the slope of each regression was significantly different from all others (all $P < 0.001$), but the biological importance of this difference is questionable because the slopes varied by less than 10%. Although the rate at which individuals are added to each interval varies as school size increases, there is no consistent trend in slopes among intervals. Furthermore, the statistical significance of the difference in slopes may be driven by the small standard error for each regression and extremely high power (> 0.99).

The shape of large schools of bluefin tuna was less variable than that of small schools. Schools of less than 15 individuals are less vertically expansive, and generally one to three fish deep; larger (> 15 individuals) schools are more than three individuals deep (Fig. 6). The pattern of increasing vertical depth continues to the largest school sizes observed, which are nearly always more than five individuals deep. The weakly cone-shaped profile of the model school depicted in Figure 3 is representative of the shape of most schools with more than 3 intervals. Smaller schools tend to be distributed in a vertically shallow, loosely oval profile. Our findings related to school structure are consistent with the observations of other investigators who have

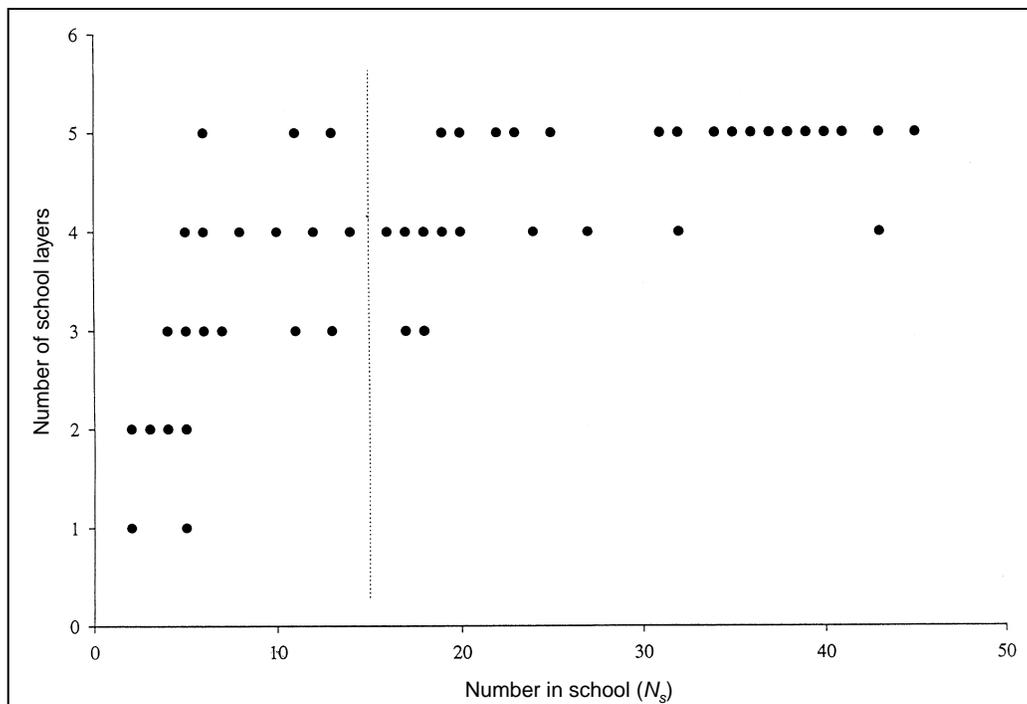


Figure 6

School depth in number of individuals plotted against total school number (N_s). The dotted line is drawn to illustrate the increase in the vertical expanse of schools coincident with the maximum number of individuals observed in parabola and echelon-shaped schools. The maximum number of depth intervals in our analysis was 5. Schools greater than 5 individuals in total depth are described by a surface layer and four 25% depth intervals.

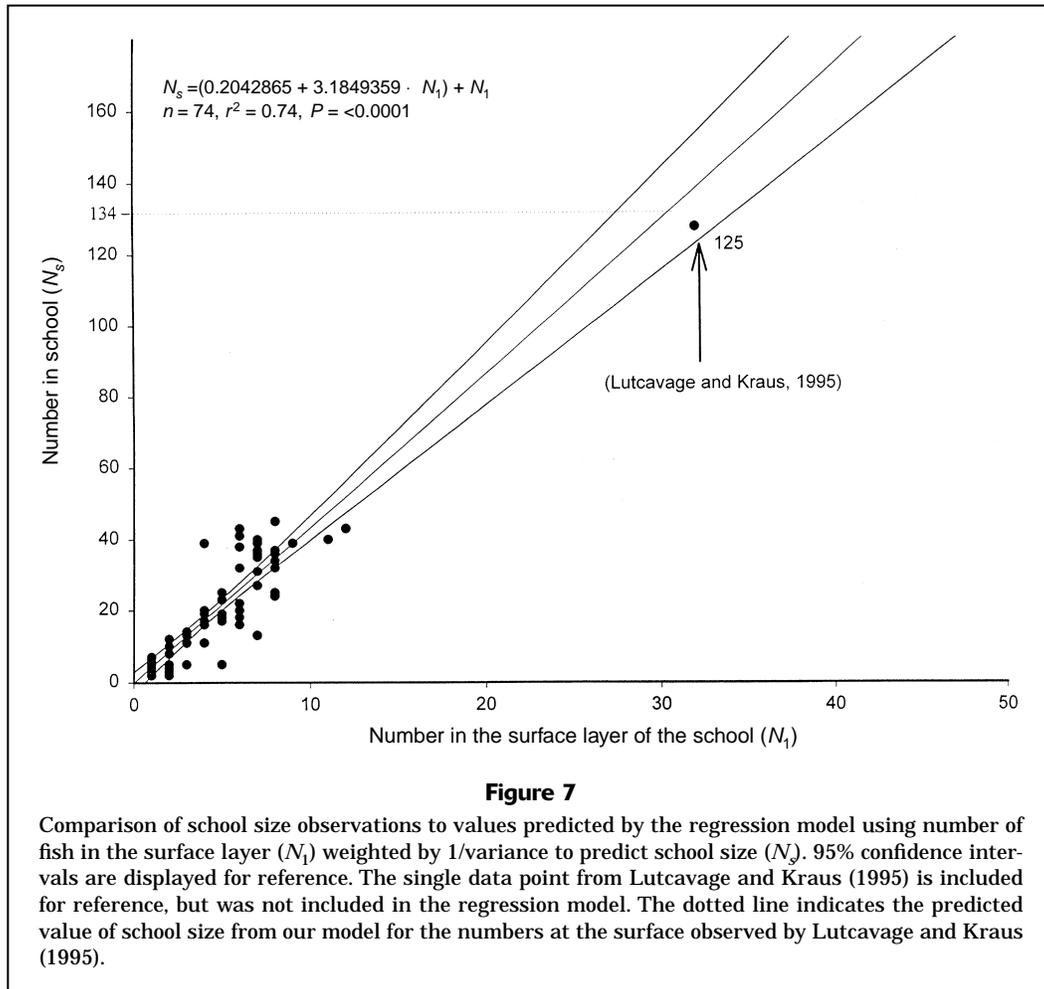
observed that small schools have a strong horizontal aspect, and little vertical expanse. For example, Partridge et al. (1983) and Lutcavage and Kraus (1995) observed that small (<15 individuals) parabola- and echelon-shaped schools of noncaptive giant ABT vary little in shape. Interestingly, parabola and echelon shapes are not observed for large (>15) ABT schools, coinciding with changes in inter-individual orientation between groups of less than 10 and 10–20 individuals (Partridge et al., 1983). This difference is similar to the shift in the depth of schools that we observed with approximately 15 individuals (Fig. 6). It is possible that Partridge et al. (1983) and Lutcavage and Kraus (1995) observed small schools in these configurations because larger schools expand vertically and adopt the semi-conical shape that we describe. These results suggest that there may be a critical minimum number of individuals that must be present in a horizontal layer before schools begin to expand vertically, which would explain the limited size of two-dimensional ABT schools.

It is possible that ontogenetic variation in school structure exists, but understanding how such changes occur is critical in determining how variability in school structure could affect our modeling approach. Because our models use numerical relationships rather than distance metrics to predict school size, neither ontogenetic shifts in inter-individual spacing or packing density changes related

to school size should substantially affect the predictive ability of our models. However, if ABT schooling behaviors change at a more basic level due to enclosure or changing fish size, then our estimation techniques may be invalid outside captivity or with larger fish. Basic changes, such as vertical distribution of individuals within schools, the three-dimensional shape of schools, and strong school structure responses in relation to environmental factors, could all have serious effects on our modeling approach. Further, we feel that schools similar in form to those described as “densely-packed domes” by Lutcavage and Kraus (1995) could be described well by our models, but that numerical estimation of other school types might require the application of a different estimation technique.

Environmental effects on school formation

The physical environment may play a role in determining the vertical position of tuna in the water column (Holland et al., 1990; Block et al., 1997) or school structure (Partridge et al., 1983; Lutcavage and Kraus, 1995). No relationship between environmental variables and the shape of schools (quantitatively determined) or the vertical position of fish (in qualitative observations) were observed in our study, perhaps because of the small range and lack of vertical structure in salinity, pH, and dissolved oxygen



measurements (Table 1), the time when school structure data were collected, or low statistical power from small sample sizes. However, on a very limited number of occasions, the thermocline became situated within the enclosure at approximately 10 m. Only a few individual fish traversed the thermal boundary, and such excursions were very brief. Entire schools were not observed to cross to the cold side of the thermal boundary. The thermal profile is an important factor in determining the vertical distribution of Pacific yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna (Holland et al., 1990). It is reasonable to assume that the thermal profile is important in the vertical distribution of Atlantic bluefin tuna as well, and that this effect was not detected in our study because of the periodicity of observations, the limited variation of environmental conditions within the enclosure, or the spatial constraints imposed by the enclosure.

Predicting NFS from surface counts

Our least-squares regression model predicts the number of fish in ABT schools from the number of individuals at the surface of the school without attempting to describe the fine-scale structure within schools in terms of interindi-

vidual spacing and orientation. The number of fish in the surface interval alone accounts for 74% of the variation in school size of three-dimensional schools similar to a densely packed dome. Because the only school type that we observed was similar to the densely packed dome, the applicability of our model to three-dimensional schools of other configurations is questionable and may be determined only by studying ocean schools of other configurations. Furthermore, the application of our model to two-dimensional schools such as parabolas, echelons, and surface sheets is not appropriate or necessary given the apparent lack of a three-dimensional component in their structure.

The only data point available to verify our model predictions is from a school described as “dome-shaped” that was photographed and subsequently captured by purse-seine (Lutcavage and Kraus, 1995). Thirty-two fish were counted at the surface of this school from an aerial photograph, and 125 “large giant” ABT were subsequently captured by the purse-seine vessel. We applied our model that predicts NFS from the number at the surface of the school to this datum to produce a NFS prediction. The prediction with our model of 134 individuals differed by 7% from the purse-seine capture of 125 individual fish, and was well within the 95% confidence intervals (Fig. 7) of model pre-

dictions. When ABT schools are captured by purse seine, it is assumed that nearly the entire school is captured.² If the net intersects an edge of the school while it is being deployed, the entire school will change its direction of travel in unison resulting in either the entire school being encircled in the net and captured or in the entire school escaping into open water. As a result, the estimate of total NFS from this data point is likely to be an accurate count of the number of individuals in the school. It is encouraging that our model so closely estimated the NFS of large giants considering that it was constructed from data for age 2+ fish that are a fraction of the size of large giant bluefin tuna. The accuracy of our prediction indicates the potential for generality of ABT school structure across both tuna size and NFS. However, substantial verification of our models is necessary before they may be applied to abundance estimation.

Predicting NFS from school dimensions

An alternative to using N_1 and N_2 to predict N_s is to use maximum school length and width. Identifying the longest and widest axis of the surface of a school and counting the number of individuals along these axes may yield more accurate estimates of the total NFS. The maximum dimensions of bluefin schools (length, width) had greater power as predictors of N_s than N_1 and N_2 (model 3 versus models 4, 5, 6, Table 2). Moreover, a combination of length and width to predict N_s produced a more confident estimate of school size than models using either variable individually. Irregularity in length and width at small school sizes likely introduced variation that reduced the individual predictive power of these variables. Inclusion of both length and width in the model to predict N_s could allow accurate prediction of small schools that are elongate or wide.

The regression diagnostics for the model using school length and width to predict school size (model 6, Table 2) suggest that it is the more reliable model for estimating NFS with aerial photographs. For the single open-ocean estimate available in the literature (Lutcavage and Kraus, 1995), the length and width of the school in number of individuals could not be determined. Model 6 may have the potential to yield a more accurate estimate of school size with a wider range of photograph qualities (as affected by sea state, water clarity, sunlight, etc.) because of its ability to predict NFS from partial surface counts. However, the utility of school length and width to predict N_s will remain uncertain until field data are available for thorough evaluation.

Enclosure effects

The effects of capture and captivity on school structure and behavior were points of concern in our study. Evaluating the effects that the enclosure had on school structure is problematic because the same factors that led to the use

of an enclosure to make the observations preclude a direct *in situ* comparison. Because tuna are highly mobile and unpredictable in their movements, it would be difficult to obtain a number of school observations comparable to that collected from the captive fish in our study. Furthermore, the ability to approach schools in nature without significantly disturbing them is questionable, and effective observation at a distance that would not cause disturbance would be unlikely because of turbidity and the normal movement of schools. In this respect, a group of tuna that has become comfortable with the presence of human observers may be a better source of accurate school structure observations than a school of noncaptive fish that may perceive a human or mechanical presence as a predatory threat and react accordingly. Evidence of the acclimation of the study specimens to the enclosure was seen in their active and aggressive feeding behavior (Hanrahan and Juanes³) that was similar to the available anecdotal accounts of their open-water feeding behavior. The relation between fish length and enclosure dimensions may cause the impression that school formation was constrained heavily by captivity and that multiple schools could not achieve meaningful separation from one another (Fig. 1 illustrates a school of tuna at a scale of 1:1 to the enclosure). However, the relatively low density of fish in the enclosure (0.05 kg/m³) allowed individuals to move in an uninhibited manner within the enclosure. Although the extent of enclosure-induced behavioral modification cannot be quantified in our study, the ability of our simple linear model to predict accurately the NFS for a noncaptive school is very encouraging.

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