

Abstract—We employed ultrasonic transmitters to follow (for up to 48 h) the horizontal and vertical movements of five juvenile (6.8–18.7 kg estimated body mass) bluefin tuna (*Thunnus thynnus*) in the western North Atlantic (off the eastern shore of Virginia). Our objective was to document the fishes' behavior and distribution in relation to oceanographic conditions and thus begin to address issues that currently limit population assessments based on aerial surveys. Estimation of the trends in adult and juvenile Atlantic bluefin tuna abundance by aerial surveys, and other fishery-independent measures, is considered a priority.

Juvenile bluefin tuna spent the majority of their time over the continental shelf in relatively shallow water (generally less than 40 m deep). Fish used the entire water column in spite of relatively steep vertical thermal gradients ($\approx 24^{\circ}\text{C}$ at the surface and $\approx 12^{\circ}\text{C}$ at 40 m depth), but spent the majority of their time ($\approx 90\%$) above 15 m and in water warmer than 20°C . Mean swimming speeds ranged from 2.8 to 3.3 knots, and total distance covered from 152 to 289 km (82–156 nmi). Because fish generally remained within relatively confined areas, net displacement was only 7.7–52.7 km (4.1–28.4 nmi). Horizontal movements were not correlated with sea surface temperature. We propose that it is unlikely that juvenile bluefin tuna in this area can detect minor horizontal temperature gradients (generally less than $0.5^{\circ}\text{C}/\text{km}$) because of the steep vertical temperature gradients (up to $\approx 0.6^{\circ}\text{C}/\text{m}$) they experience during their regular vertical movements. In contrast, water clarity did appear to influence behavior because the fish remained in the intermediate water mass between the turbid and phytoplankton-rich plume exiting Chesapeake Bay (and similar coastal waters) and the clear oligotrophic water east of the continental shelf.

Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus thynnus*), in relation to oceanographic conditions of the western North Atlantic, determined with ultrasonic telemetry

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Current estimates of spawning biomass for Atlantic bluefin tuna (*Thunnus thynnus*) remain controversial (Butterworth and Punt, 1993; Restrepo et al., 1994; Restrepo, 1996), although the most conservative predicts that a population eight times the current size would be needed to produce maximum sustainable yields (Sissenwine et al., 1998). The current strict catch quotas are based on abundance assessments for both adult and juvenile (i.e. "schooling") fish (age classes 1–5 years, body mass ≈ 6 –60 kg). Adult abundance is derived from commercial landings data; juvenile abundance has, since 1985, been based on fishing effort and landings data obtained from dockside intercepts and telephone polling of the largely recreational fishery for juvenile

bluefin tuna conducted by the National Marine Fisheries Service's Large Pelagics Survey (Turner et al., 1993, 1997). The usefulness of both data sets can be compromised, however, because the relationship between catch-per-unit-of-effort (CPUE) data and real abundance is not known with certainty (Bakun et al., 1982; Hilborn and Walters, 1992; Lauck, 1996). This problem is especially critical with highly mobile schooling fishes like tunas because of environmental influences on fish distribution and vulnerability to specific fishing gears, as well as the introduction of new fishing techniques (Sharp, 1978; Clark and Mangel, 1979; Brill, 1994; Bertrand and Josse, 2000).

Juvenile Atlantic bluefin tuna appear in the surface waters off the east coast

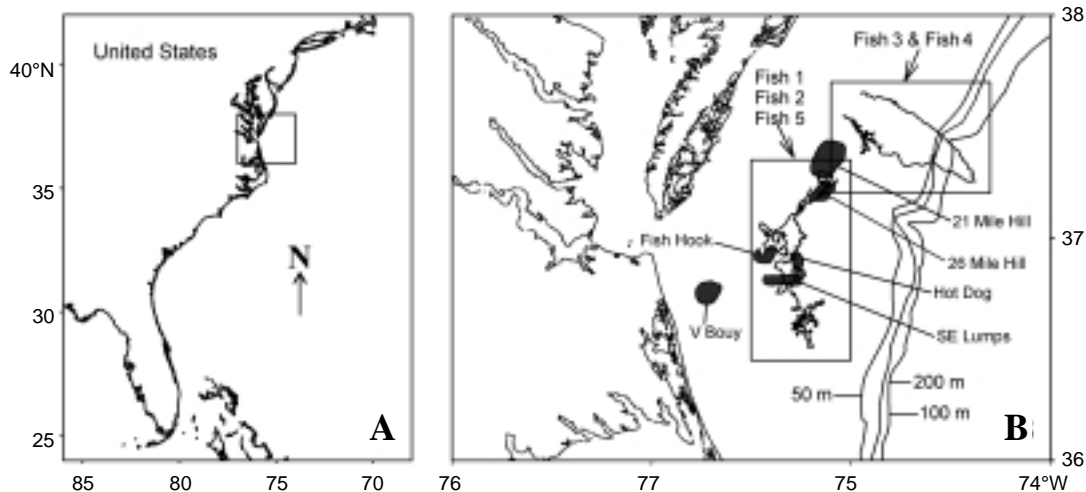


Figure 1

(A) Map of the east coast of the United States. The rectangle shows the area enlarged in panel B. (B) Movements of five juvenile bluefin tuna (*Thunnus thynnus*). The limit of the continental shelf is shown by the 50-, 100-, and 200-m isobath lines. The topographic features considered by local fishermen to aggregate juvenile bluefin tuna are shown by the shaded areas. Place names are taken from local fishing charts. The rectangles show the areas enlarged in Figures 3 and 4.

of the United States, from North Carolina to Rhode Island, usually during June and July (Rivas, 1978; Sakagawa, 1975; Roffer, 1987; Lucy et al., 1990; Mather et al., 1995). Their presence provides an opportunity for direct population assessments with aerial surveys similar to those conducted on adult Atlantic bluefin tuna (Lutcavage and Kraus, 1995; Lutcavage et al., 1997), southern bluefin tuna (*Thunnus maccoyii*),¹ and other fish species (e.g. Lo et al., 1992). Assessments of juvenile bluefin tuna abundance are considered particularly crucial for effective stock management because these will allow the forecasting of recruitment and long-term population trends (Polacheck et al., 1996; Sissenwine et al., 1998). There is, however, a need to establish the probability of detecting schools and estimating school size before aerial survey data can provide robust population assessments. This need is present regardless of whether the census techniques are simple photography (Lutcavage and Kraus, 1995; Lutcavage et al., 1997) or new laser-based digital remote sensing techniques (Oliver et al., 1994; Lo et al., 1999). As with traditional CPUE-based abundance estimates, knowledge of the effects of oceanographic conditions on depth distribution, surfacing frequency, travel speeds, and residence patterns is critical because these conditions will affect vulnerability to "capture," either on photographic film or as digital data.

To obtain the necessary data, we undertook a study of the horizontal and vertical movements of juvenile Atlan-

tic bluefin tuna using depth sensitive ultrasonic telemetry devices. Ultrasonic telemetry is a proven technique for acquiring the required precise and detailed data on the behaviors of pelagic fishes in relation to oceanographic conditions (e.g. Holland et al., 1990; Dagorn et al., 1999, 2000a; Lutcavage et al., 2000). Besides being useful for improving stock assessments (Brill and Lutcavage, 2001), the resultant data can also help clarify basic ecological relationships and provide inferences on physiological abilities and species-specific behaviors (Carey, 1983; Brill, 1994; Brill et al., 1999).

Materials and methods

Fishing operations were conducted from a 16-m commercial fishing boat (FV *Grumpy*) in the western North Atlantic off the eastern shore of Virginia (Fig. 1A) during June and July 1998. Bluefin tuna were captured with standard recreational trolling gear. The fish were brought aboard with a plastic sling and detached from hooks. Straight line fork length was measured, and a Vemco (Halifax, Nova Scotia, Canada) ultrasonic transmitter (model V32) was attached near the second dorsal fin with nylon straps as described by Holland et al. (1986, 1990). The transmitted signal was detected with a Vemco VR-60 ultrasonic receiver connected to a directional hydrophone mounted on the end of an aluminum pipe. The pipe was clamped to the side of the vessel with a custom designed aluminum bracket that allowed the hydrophone to be rotated to find the relative bearing to the transmitter. Fish depth, encoded by the interval of the transmitter's pulsed signal, was decoded by the receiver and the resultant digital data recorded by an attached laptop computer. Geographic

¹ Cowling, A., C. Millar, and T. Polacheck. 1996. Data analysis of the aerial surveys (1991-1997) for juvenile southern bluefin tuna in the Great Australian Bight. Rep. RMWS/96/4, 87 p. Recruitment Monitoring Program, CSIRO Division of Marine Research, GPO Box 1538, Hobart 7001, Australia.

Table 1

Summary of tracks of five juvenile Atlantic bluefin tuna (*Thunnus thynnus*) equipped with ultrasonic depth sensitive transmitters. Body masses were calculated from fork lengths with the weight-length regression equation provided by Coull et al. (1989).

Fish no.	Fork length cm	Body mass kg	Dates of track (1988)	Duration of track h	Total distance covered km (nmi)	Distance between start and end points km (nmi)	Mean (\pm SEM) swimming speed knots
1	74	6.7	17–19 Jun	47.2	217 (117)	52.7 (28.4)	2.8 \pm 0.03
2	91	12.1	23–25 Jun	47.8	267 (144)	11.4 (6.1)	3.0 \pm 0.03
3	79	8.0	2–3 Jul	30.0	152 (82)	7.7 (4.1)	2.7 \pm 0.04
4	99	15.4	6–7 Jul	31.2	192 (104)	14.7 (7.9)	3.3 \pm 0.03
5	106	18.8	10–12 Jul	47.9	289 (156)	32.2 (17.4)	3.2 \pm 0.03

positions were obtained by using a GPS satellite receiver and were recorded on a second laptop computer every minute. The tracking vessel's position was assumed to be the same as that of the fish. Sea surface temperature and bottom depth were recorded manually every 15 minutes by using a hull-mounted electronic temperature sensor and color fathometer, respectively. Depth-temperature profiles were taken approximately every four hours with a Sippican (Marion, MA) portable XBT system (model MK12).

Aggregate time-at-depth and time-at-temperature distributions were calculated from 10-m and 1°C bins (respectively), as described by Holland et al. (1990). These data were subsequently expressed as a fraction of the total time each fish was followed, and the fractional data bins were averaged across all fish. Speed over ground (henceforth referred to simply as “speed”) was calculated by assuming that the fish moved in a straight line between successive geographic locations.

Sea surface temperature (SST) data were recorded by the advanced very high resolution radiometer (AVHRR) carried onboard the NOAA-14 polar orbiting operational environmental satellite. High resolution picture transmission (HRPT) data were obtained from the National Coast Watch Active Access System at the National Oceanographic Data Center and had a spatial resolution of 1.25 \times 1.25 km pixels. Ocean color data were recorded by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) carried onboard the Orbview-2 spacecraft (Orbimage, Inc., Dulles, VA). The level-2 global area coverage (GAC) data were obtained from the NASA Goddard Space Flight Center's Distributed Active Archive Center. These 4-km resolution data sets included chlorophyll-*a* surface concentration and the diffuse attenuation coefficient at 490 nmi, *in vacuo*. We calculated the occupancy of waters with specific chlorophyll-*a* concentrations and light attenuations from values corresponding to and coincident with the tracks of fishes derived from satellite images. These data were subsequently expressed as a fraction of the total number of observations for each fish, and the fractional data bins were averaged across all fish. For illustrative purposes, we also generated composite images using data

from the 21-day period over which all tracking operations were conducted.

Results

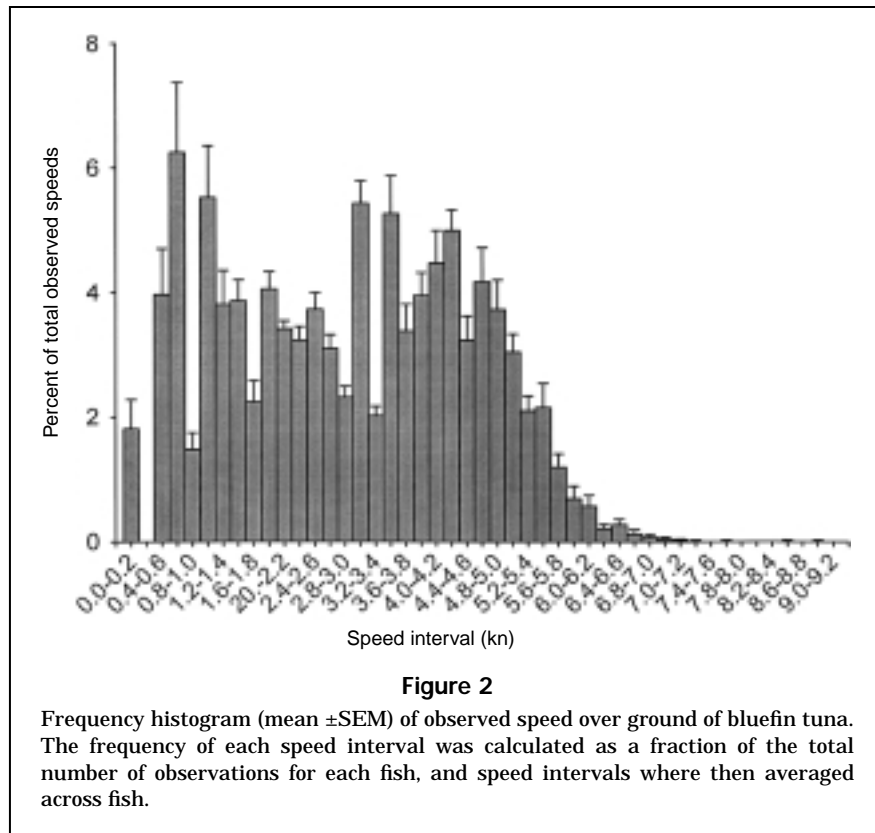
The bottom topography in the areas where the fish were tracked is generally featureless, except for small areas where the vertical relief is approximately 2 m above the surroundings. Local fishermen have named these features (Fig. 1B and subsequent figures), and the names used in this study are taken from local fishing charts.

Size of fish, starting and ending dates of tracks, duration of tracks, distances covered, distance between starting and ending points, and mean (\pm SEM) swimming speed of fish are listed in Table 1. With the exception of fish number 4 (referred to simply as “fish 4”), individuals tended to follow highly irregular courses that often repeatedly covered the same areas (Fig. 1B). The mean distance between starting and ending points for all fish was only 11% (range: 4–25%) of the total distance covered (Table 1). From tracking studies of yellowfin tuna (*Thunnus albacares*) in the Pacific, Dagorn et al. (2000a) concluded that such frequent directional changes might be characteristic of foraging behavior. The frequency of observed swimming speeds is shown in Figure 2. Although all fish reached maximum speeds of \approx 7 knots for brief periods, over 90% of the observed speeds were less than 3.6 knots.

Horizontal movements

Fish 1 was captured and released at 1340 h, approximately 1.8 km (1 nmi) west of the “26 Mile Hill” (Fig. 3). It proceeded on a southerly course for about 33 h, a direction that carried it over the “Hot Dog” and “Southeast Lumps.” After sunset on the second day, the fish reversed its course and eventually recrossed both features. The fish was approximately 5.6 km (3 nmi) south of the “Southeast Lumps,” and moving south, when the track was terminated at 1300 h.

Fish 2 was captured approximately 5.6 km (3 nmi) south of the “Southeast Lumps” (Fig. 3) at 1547 h, adjacent to where the track of fish 1 was completed four days earlier. It



proceeded south, then briefly west just before dusk. After dark it turned to the northeast, and then assumed a parallel course to the southwest. From 1000 h on the second day until the end of the track, the fish repeatedly crisscrossed an area approximately 18 km (10 nmi) southeast of the "Southeast Lumps." The fish made one brief excursion during the second day but generally remained in this area until the track was terminated at 1545 h.

Fish 3 was captured and released at 1140 h approximately 11 km (6 nmi) northeast of the "21 Mile Hill" (Fig. 4). It proceeded to the northwest for approximately 4 hours, then turned and retraced its course returning to the point where it was captured approximately 6 hours earlier. This general pattern was repeated for the remainder of the track. Fish 3 favored an area approximately 11 km (6 nmi) northeast of the "21 Mile Hill," although it moved briefly away from this area during the first night and second day.

Fish 4 was captured and released at 1300 h in the same area (northeast of the "21 Mile Hill") as fish 3 (Fig. 4). Its behavior differed significantly from all the other fish in that it swam two relatively straight courses. The first was to the southeast (from the time of release until sunrise the following day) and the second to the northwest (from sunrise until the track ended at 2015 h). (The track had to be abandoned after approximately 31 h when the fish moved into an active U.S. Navy missile test area.) It was also the only individual that moved offshore of the continental shelf.

Fish 5 was captured and released at 1330 h immediately adjacent to the "21 Mile Hill" (Fig. 3). During the first day,

the first night, and the morning of the second day the fish stayed either over or adjacent to the "21 Mile Hill" and "26 Mile Hill." It eventually followed a relatively straight course to an area approximately 5.5 km (3 nmi) northeast of the "Fish Hook," where it remained until the track was terminated after 48 hours.

Vertical movements

The vertical movements of the four fish that remained on the continental shelf are shown in Figure 5. Juvenile bluefin tuna made use of the entire water column and undertook frequent, albeit brief, forays to the bottom. Fish 4 showed similar behavior but reached maximum depths of approximately 160 m when its course carried it eastward of the continental shelf (Fig. 6). No abrupt vertical movements were apparent at dawn and dusk, as have been observed in adult Atlantic bluefin tuna (Lutcavage et al., 2000) and juvenile Pacific bluefin tuna (*Thunnus orientalis*) (Marcinek et al., 2001). Similarly, there were no dramatic and unambiguous differences in daytime and nighttime vertical movement patterns (Figs. 5 and 6), as has been observed with bigeye tuna (*Thunnus obesus*) (Holland et al., 1990; Dagorn et al., 1999).

Figure 7 presents the mean (\pm SEM) time spent at specific depths and at specific temperatures. Juvenile bluefin tuna spent \approx 90% of the time at depths less than 15 m, but less than 20% of the time at depths above 3 m. There were no clear differences in daytime and nighttime depth distri-

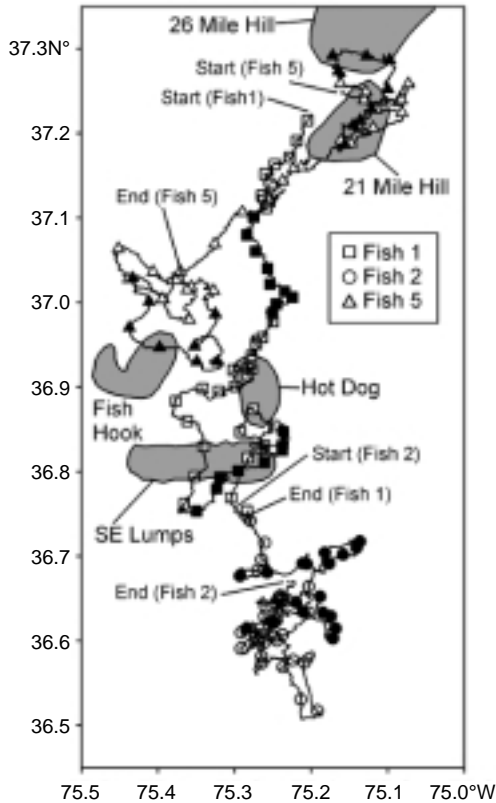


Figure 3

Movements of fish 1, 2, and 5. Symbols represent hourly intervals: open symbols indicate daytime and solid symbols, nighttime.

butions. Although they encountered water temperatures of $\approx 10^{\circ}\text{C}$ during their brief descents, fish spent $\approx 90\%$ of the time in water greater than 20°C and $\approx 50\%$ of the time in water greater than 24°C .

Occupancy of specific water masses

Figure 8 shows fish movements and sea surface temperatures (SST). Note that specific water masses (except for the Gulf Stream, a portion of which is clearly visible to the southeast) appear ill-defined by SST (Fig. 8). (During the 21-day study period, there was no evidence that an instability in the Gulf Stream resulted in discharge of warm, high-salinity water onto the Virginia continental shelf, as has been occasionally observed [Churchill et al., 1993].)

Figure 9 presents fish movements and chlorophyll-*a* concentrations (i.e. phytoplankton abundance) and water clarity measured as the diffuse attenuation coefficient (1/m) at an *in vacuo* wavelength of 490 nm (a low diffuse attenuation coefficient indicates high water clarity). Note that, in contrast to sea surface temperature data (Fig. 8), the turbid, plankton-rich water leaving Chesapeake Bay (the “Chesapeake Bay plume”) is clearly visible. The Chesapeake Bay plume flows to the south and remains trapped

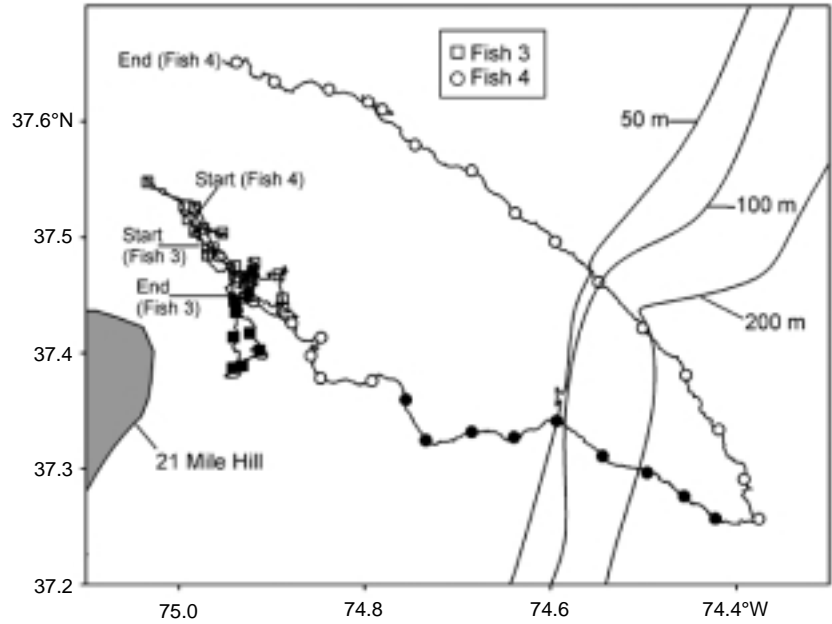


Figure 4

Movements of fish 3 and 4. Symbols represent hourly intervals: open symbols indicate daytime and solid symbols, nighttime. The edge of the continental shelf is shown by the 50-, 100-, and 200-m isobath lines.

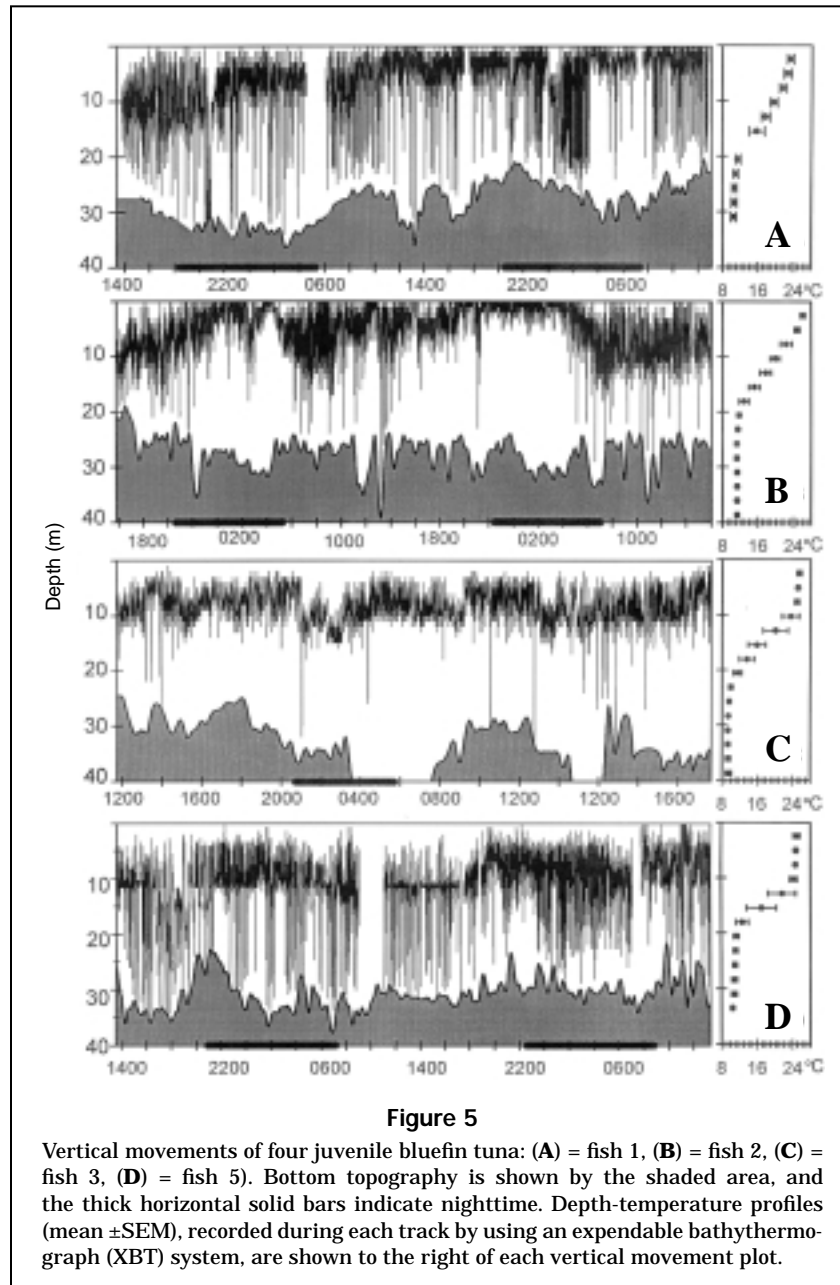
inshore because of the Coriolis effect (Reiss and McConaugha 1999), which is to the right in the Northern Hemisphere. Also visible is the clear oligotrophic mid-Atlantic slope water eastward of the continental shelf.² With the exception of fish 4, which made a brief excursion into the mid-Atlantic slope water east of the continental shelf, fish remained in the mid-Atlantic shelf water (i.e. between the extremes of water clarity and phytoplankton abundance immediately to the east and west) (Fig. 9).

Figure 10 presents the frequency histograms for the specific chlorophyll-*a* concentrations and diffuse attenuation coefficients of water occupied by juvenile bluefin tuna. These data confirm that juvenile bluefin tuna restricted their movements primarily to waters with a relatively narrow range of clarity and phytoplankton abundance.

Discussion

Although juvenile bluefin tuna remained within relatively restricted geographical ranges while being tracked (Table 1, Fig. 1), none of these fish showed the repetitive daily behaviors often demonstrated by yellowfin tuna and

² Wright, W. R. 1976. Physical oceanography. In A summary of environmental information on the continental slope Canadian/United States border to Cape Hatteras, N.C., p. 4-1-4-109. Prepared by TRICOM, The Research Institute of the Gulf of Maine, South Portland, MA, for the Bureau of Land Management, Marine Minerals Division. [Available from National Technical Information Service, U. S. Department of Commerce, Springfield, VA 22161.]



skipjack tuna (*Katsuwonus pelamis*). In the Pacific, the latter two species often spend daylight hours associated with reef drop-offs, banks, or man-made fish aggregating devices (FADs), repeatedly move up to ≈ 5 nmi away at night, then return to the same area the following day (Yuen, 1970; Holland et al., 1990; Marsac and Cayré, 1998; Dagorn et al., 2000a). The continental shelf where the juvenile bluefin tuna were followed is, however, relatively flat compared with the steep topography around the oceanic islands, where many of the yellowfin and skipjack tuna were followed. Unlike the situation in the Pacific, the small topographic features on the mid-Atlantic continental shelf probably do not possess sufficient magnetic sig-

natures that could be detected by the fish (Walker, 1984; Klimley, 1993). Moreover, the movements of the juvenile that we observed closely resembled those of bluefin tuna tracked in the eastern Pacific when they were not near the coast or any apparent significant geological features (Marcinek et al., 2001)

Juvenile bluefin tuna clearly use the entire water column and frequently interact with the bottom when over the continental shelf. Similar behaviors were observed in adult bluefin tuna in the Gulf of Maine (western North Atlantic) (Lutcavage et al., 2000). Frequent vertical movements of juvenile bluefin tuna likely reflect feeding behaviors for capturing sand lance (*Ammodytes* spp.), which

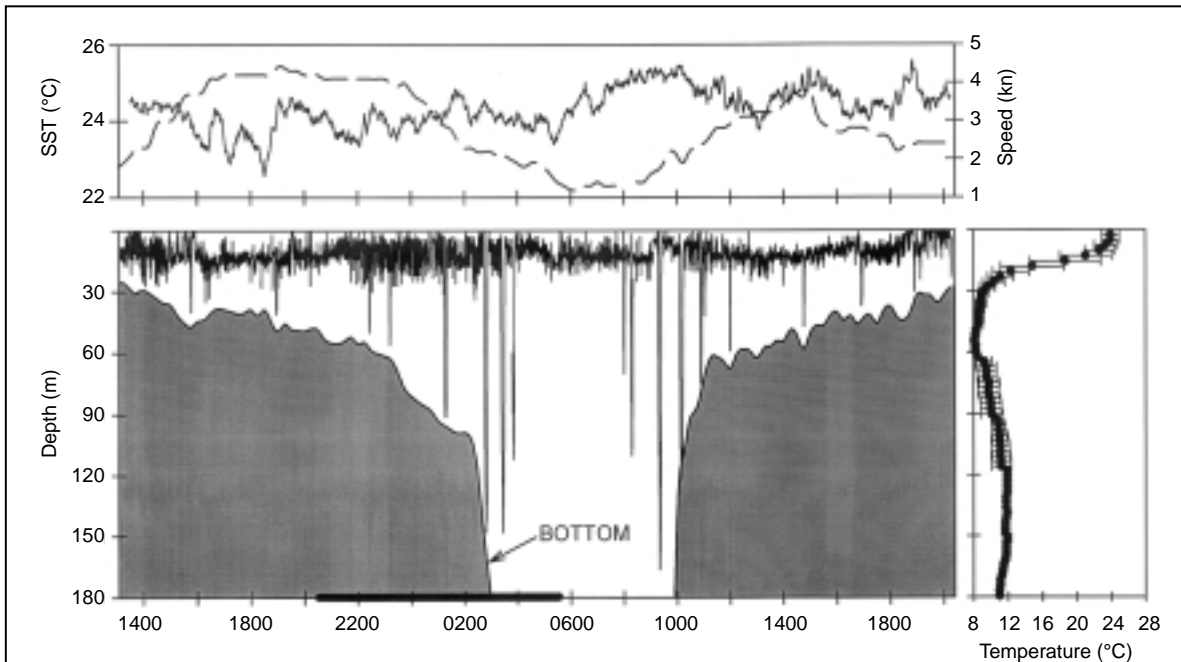


Figure 6

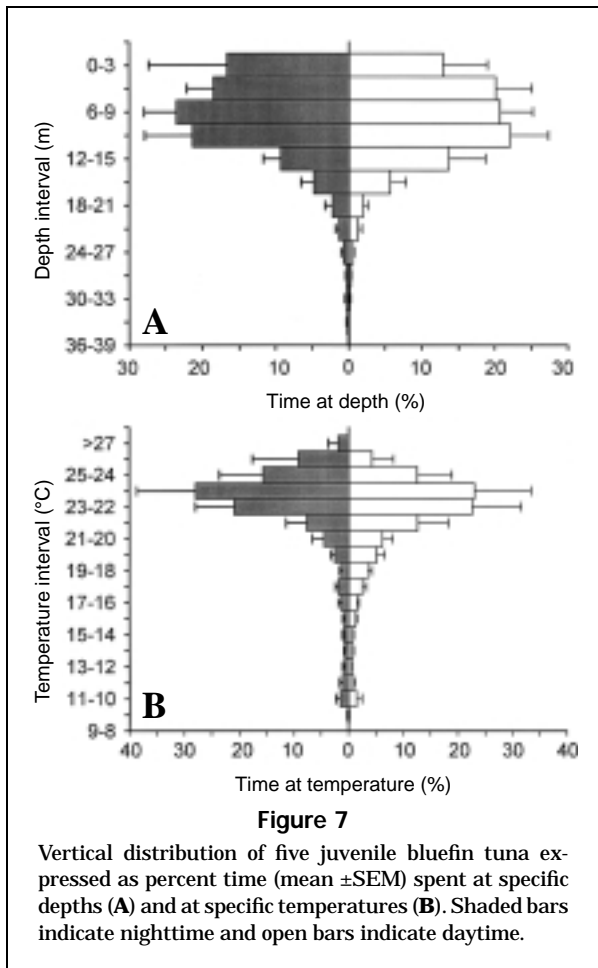
Swimming speed (solid line, upper panel) and vertical movements (lower panel) of fish 4. The change in temperature in the horizontal direction (expressed as sea surface temperature, SST) is shown by the broken line in the upper panel (Brill and Lutcavage, 2001). As in Figure 5, the change in temperature in the vertical direction (mean \pm SEM) is shown to the right of the vertical movement plot. Note that changes in swimming speed are not correlated with changes in SST, and that the steepest temperature change the fish could experience moving horizontally (generally less than $0.5^{\circ}\text{C}/\text{km}$) is several orders of magnitude less than that experienced moving vertically ($\approx 0.6^{\circ}\text{C}/\text{m}$).

occur throughout the water column during daylight, are abundant in the areas where we tracked the fish, and dominate the diet of tunas in this area (Mason, 1976; Eggleston and Bochenek, 1989). The nature of fish 4's descents up to ≈ 160 m while off the continental shelf (Fig. 6) remain unclear, although they too may be related to foraging (Dagorn et al., 2000a, 2000b). Their brevity is most likely due to the inability of Atlantic bluefin tuna to withstand temperatures below 10°C for long periods of time, rather than to an intolerance of low ambient oxygen conditions. Although no depth-oxygen profiles were obtained during our study, available data² suggest that juvenile tuna did not encounter ambient oxygen levels that were likely to be stressful (Bushnell and Brill, 1991, 1992).

The behavior pattern we observed of short oscillatory dives near the surface is similar to that of both juvenile bluefin tuna in the eastern Pacific (Marcinek et al., 2001) and adult bluefin tuna tracked in the Gulf of Maine (Lutcavage et al., 2000). In all cases, fish spent the majority of their time in the surface layer, although in the Gulf of Maine and eastern Pacific, the temperature of the warmest water available was lower (≈ 13 – 22°C) and more variable. As shown in Figure 11, when expressed as the relative change in temperature with depth (i.e. in relation to the surface water temperature occurring during each track), time-at-temperature distributions of juvenile and

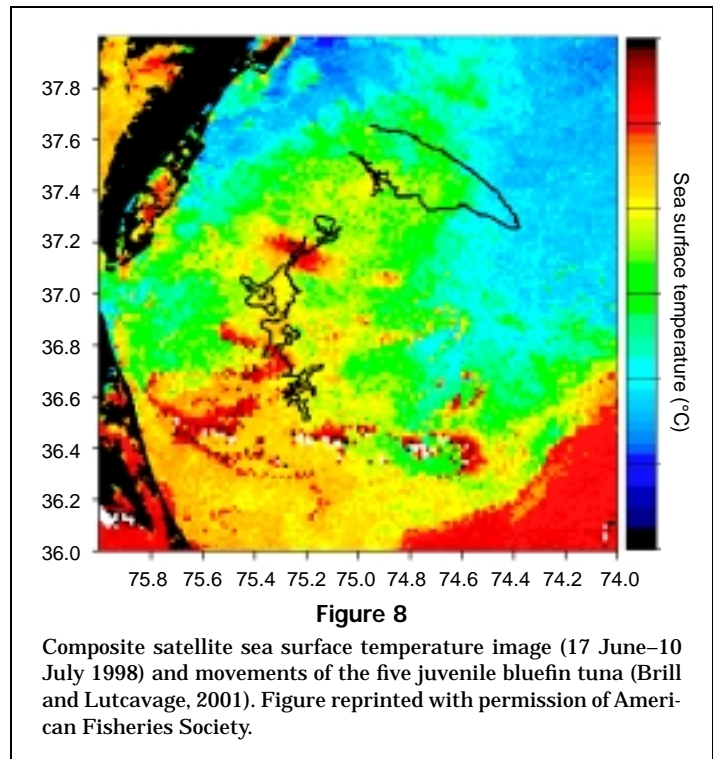
adult Atlantic bluefin tuna become essentially identical. Moreover, the limiting effects of temperature change on vertical movements are independent of body size. Similarly, yellowfin tuna tracked near the main Hawaiian Islands and off the coast of California occupy the warmest water available, regardless of body size, even though surface water temperature in the two areas differs by more than 5°C (Holland et al., 1990; Block et al., 1997; Brill et al., 1999). Atlantic bluefin tuna, however, are more eurythermal than yellowfin tuna. The latter will rarely expose themselves to more than an 8°C change in temperature, whereas the former regularly subject themselves to a temperature change of up to 13°C (Fig. 11). Surprisingly, the behavior of juvenile bluefin tuna observed by Marcinek et al., (2001) was more like that of yellowfin tuna in that these juveniles would not expose themselves to more than an 8°C temperature change.

It still remains to be conclusively demonstrated, however, whether the vertical movement patterns of tunas and other large pelagic fishes are (as suggested by Brill et al., 1993, 1999) limited by the effects of ambient temperature on cardiac function. Or whether, as suggested by Marcinek et al. (2001), that depth distributions "... may have more to do with the location of prey, and the physiological limitations of the prey, than physiological limitations of the bluefin [tuna]." Moreover, months-long observations



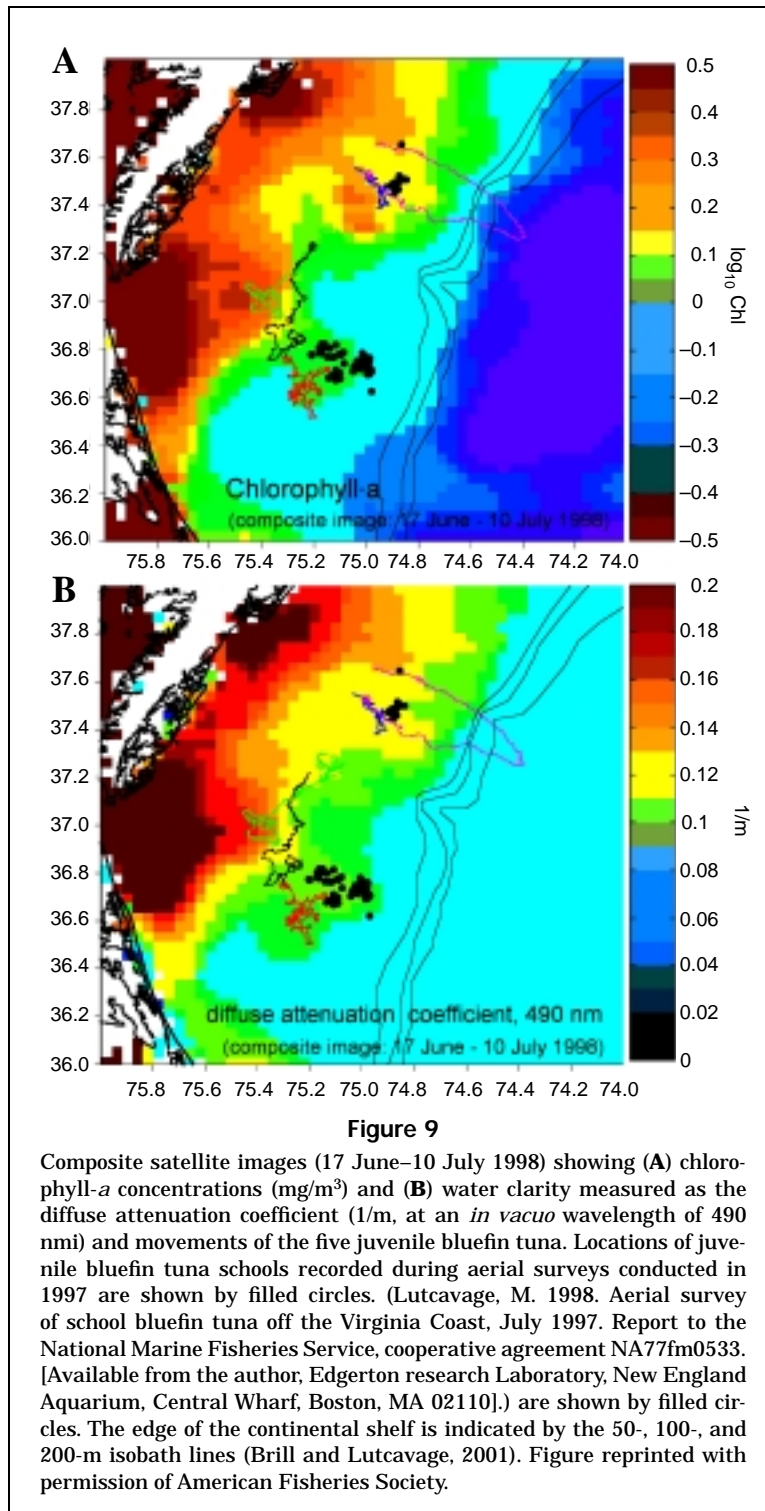
of juvenile bluefin tuna in the western Pacific recently obtained with archival (i.e. electronic data recording) tags have shown that the vertical movements of juvenile bluefin tuna can have strong seasonal and geographic components (Kitagawa et al., 2000). In areas and at times (e.g. winter) when there was a strong thermocline, bluefin tuna remained in the uniform-temperature surface layer and demonstrated vertical movement behaviors similar to those observed during the short-term ultrasonic telemetry studies. In the summer, when the thermocline was less pronounced, the fish showed very distinct diel periodicity in their vertical movement patterns. They would remain at the surface at night and make rapid vertical movements (from surface to ≈ 120 m and from $\approx 21^\circ\text{C}$ to 14°C) during the day. Kitagawa et al. (2000) concluded that the differences in behavior patterns were related to foraging. It is also still an open question as to what extent bluefin tuna's ability to conserve metabolic heat and maintain elevated muscle temperatures (Carey and Teal, 1966) enhances vertical mobility.

Roffer (1987) was apparently the first to propose that movements and abundance of juvenile Atlantic bluefin tuna are controlled by the depth and thickness of the $18.5\text{--}20.5^\circ\text{C}$ "preferred habitat" temperature layer. Likewise, Inagake et al. (2001), using archival tags implanted into juvenile



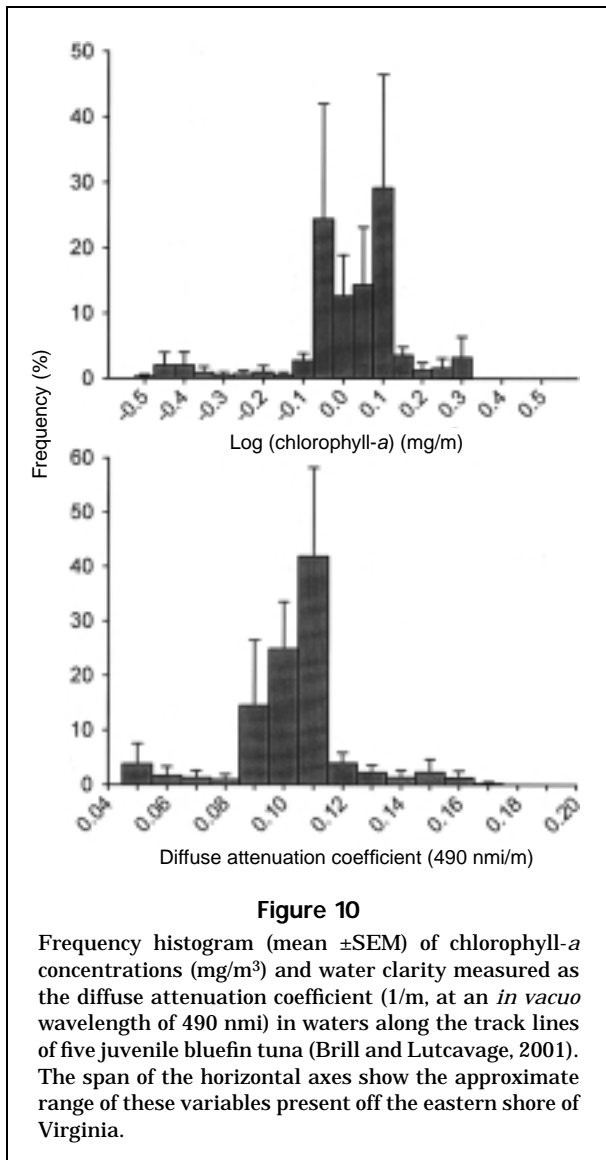
bluefin tuna in the western Pacific, found evidence that this temperature range is indeed always "preferred." During the periods of our observations, juvenile bluefin tuna spent the majority of their time ($\approx 80\%$) in water greater than 22°C . A plausible explanation is that under the conditions of our observation period, juvenile bluefin tuna simply occupy the warmest water available, although a relatively uniform temperature surface layer was evident only during tracks of fish 3, 4, and 5. We also did not find any conclusive indication that juvenile bluefin tuna avoided surface water temperatures above 26°C . Although fish spent less than 20% of time at these temperatures (Fig. 7), less than 20% of the recorded sea surface temperatures (i.e. the warmest water available) were above 26°C .

We also found no relationship between sea surface temperature and horizontal movements (Figs. 6 and 8), although this relationship has been demonstrated for other tuna species in other areas (e.g. Laurs et al., 1977; Fiedler and Bernard, 1987; Uda, 1973). We argue that our results are due to the differences in the vertical and horizontal temperature gradients occurring along the Virginia coast. Juvenile bluefin tuna routinely traveled through the thermocline, moving from the relatively warm surface layer into the mid-Atlantic cold-pool water (Houghton et al., 1982; Houghton and Marra, 1983) underlying it. The fish thus experienced temperature gradients of up to $\approx 0.6^\circ\text{C}/\text{m}$ (Figs. 5 and 6). In contrast, the steepest horizontal temperature gradient in the area where the fish were tracked was approximately three orders of magnitude smaller ($\approx 0.5^\circ\text{C}/\text{km}$). In other words, the frequent vertical movements of juvenile bluefin tuna probably prevent them from detecting and responding to SST gradients.



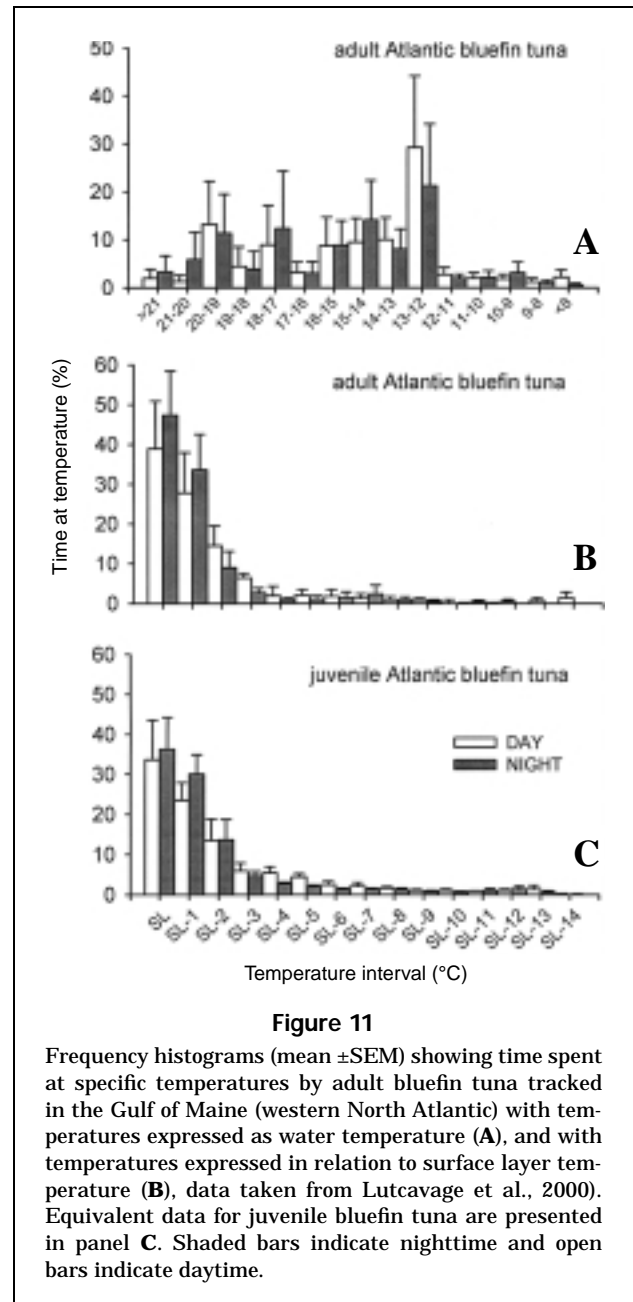
Carey (1992) was one of the first to appreciate the importance of vertical thermal structuring and stated “Temperature gradients of 15° to 20°C are not uncommon within the depth ranges of pelagic fish. By moving a few hundred meters vertically, an animal may encounter a greater temperature change than it experiences seasonally or in mov-

ing thousands of miles horizontally.” As with bluefin tuna, the vertical movements of yellowfin tuna and swordfish also result in their experiencing vertical temperature gradients orders of magnitude greater than horizontal temperature gradients (Carey and Robison, 1981; Carey, 1990; Holland et al., 1990; Cayré and Marsac, 1993). The inabil-



ity of fish to sense shallow horizontal temperature gradients in the face of the steep vertical temperature gradients they routinely experience may explain, therefore, why Power and May (1991) and Podestá et al. (1993) could find no correlation between SST “fronts” and the apparent abundance of yellowfin tuna in the Gulf of Mexico and swordfish in the western north Atlantic.

In contrast to SST, water clarity and phytoplankton abundance appear to have a strong influence on the horizontal movements of juvenile bluefin tuna (Figs. 9 and 10). Tunas are sight hunters, and possess the highest visual acuity of any teleost (Nakamura, 1968). We suspect that juvenile bluefin tuna remain in water masses with a standing phytoplankton biomass sufficient to support concentrations of prey, but where turbidity is low enough that visual prey detection and prey capture abilities are not impeded. Our conclusion is further supported by the locations of juvenile bluefin tuna schools detected in aerial



surveys conducted in 1997.³ Although satellite data showing diffuse attenuation coefficients and chlorophyll-*a* concentrations are not available for 1997, bluefin tuna schools were located in the areas where the fish carrying ultrasonic transmitters remained (Fig. 9). Olson and Podestá (1987), Olson et al. (1994), and Humston et al. (2000) have also concluded that aggregations of highly mobile species

³ Lutcavage, M. 1998. Aerial survey of school bluefin tuna off the Virginia Coast, July 1997. Report to the National Marine Fisheries Service (cooperative agreement NA77FM0533). [Available from the author, Edgerton Research Laboratory, New England Aquarium, Central Wharf, Boston, MA 02110.]

at fronts result from cues other than SST, such as changes in the photic environment associated with phytoplankton distribution, changes in prey abundance, or enhanced forage opportunities.

Aerial survey techniques and population assessments of juvenile bluefin tuna

Techniques for interpretation of aerial survey data with respect to population assessments are complex (e.g. Lo et al., 1999; Newlands and Lutcavage, 2001), and a thorough discussion is beyond the scope of our present study. We can, however, use our data on juvenile bluefin tuna's vertical movements and distribution patterns to provide some inferences as to how often they are likely to be visible at the ocean's surface or detectable at a specific depth. Juvenile bluefin tunas spent less than 13% of daylight hours at depths of 0–3 m (Fig. 7), where visual or photographic detection is possible. The depth distribution of juvenile fish was similar to that of adult bluefin tuna tracked in the Gulf of Maine (12% of daylight hours at depths of 0–4 m; Lutcavage et al., 2000). Abundance estimates based solely on photographic data will, therefore, have to be corrected to account for the significant number of fish that maybe be present, but that are beyond detection range. Fish detection systems that use lasers (the so called "light detection and range" or "LIDAR" systems) are expected to have a depth detection zone of up to 60 m (Oliver et al., 1994). This detection zone encompasses almost the entire water column over the sections of continental shelf where juvenile bluefin tuna are likely to be found. Moreover, if the behavior of the fish that moved into deeper water off the continental shelf is assumed typical, then juvenile bluefin tuna would be detected by LIDAR systems even in deep water. The relatively small net displacement distance (i.e. distance between start and end points, Table 1) may require the development of filtering algorithms to reduce errors caused by double counting if parallel transects are flown less than ~50 km apart, or if the same area is resurveyed weekly or more often. Conversely, significant fish aggregations could be missed if parallel transects are too widely spaced.

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