Understanding Environmental Influences on Movements and Depth Distributions of Tunas and Billfishes Can Significantly Improve Population Assessments

RICHARD W. BRILL

National Marine Fisheries Service, Honolulu Laboratory
Southwest Fisheries Science Center
2570 Dole Street, Honolulu, Hawaii 96822-2396, USA

MOLLY E. LUTCAVAGE

Edgerton Research Laboratory, New England Aquarium
Central Wharf, Boston, Massachusetts 02110, USA

Abstract.—The vulnerability of the highly mobile tunas (family Scombridae) and billfishes (families Istiophoridae and Xiphiidae) to various fishing gears and detection by aerial surveys is influenced by their depth distributions, travel speeds, residency times, and aggregation. As a result, understanding the effects of the physical environment on fish behavior is critical for robust population assessments. Numerous studies have attempted to understand the movements and habitat requirements of tunas and billfishes by correlating catch statistics with environmental conditions averaged over time and space. Such correlations do not necessarily elucidate the requisite relationships because the data are not gathered simultaneously, and because error terms are often too broad to demonstrate meaningful relationships. More important, using catch statistics to determine the effects of environmental conditions on catch statistics can never prove causation and result in tautology, unless independent measures of fish abundance are available. The situation is not necessarily improved when catch statistics are correlated with satellite-derived sea surface temperature data. Tunas and billfish do not always live at the surface and, more importantly, regularly move through vertical thermal gradients ($\approx 1°C$ m^{-1}) that are orders of magnitude steeper than horizontal gradients ($\approx 1°C$ km^{-1}). Sea surface temperature gradients per se are, therefore, unlikely to influence horizontal movements or aggregation. Direct observations of tuna and billfish behaviors (collected via acoustic telemetry or electronic data-recording tags) can, however, be readily combined with information on their physiologically-based environmental tolerances, forage abundance, and appropriate oceanographic data. The resulting models can correct both traditional catch-per-unit effort data and aerial survey data for differences in gear vulnerability, and thus significantly improve population assessments.

The limitations of employing nominal catch-per-unit effort (CPUE) data for population assessments have long been acknowledged (e.g., Ricker 1940; Marr 1953). Over 20 years ago, Sharp (1978) recognized that these limitations are especially acute for highly mobile pelagic fishes such as tunas (family Scombridae), and by implication also billfishes (families Istiophoridae and Xiphiidae). He stated:

> "The primary assumption in present population dynamics estimation methodologies is that fish and efforts are randomly distributed with respect to one another, and also within the prey population's habitat. This is, of course, an abiological assumption. A single example of the random phenomenon is difficult to find in any biological system. With men at the helm, fishing effort is not likely to be random with respect to anything, particularly their prey species. If tunas were truly randomly dispersed in their

habitat they would be so rarely encountered as to be virtually nonexistent."

To put this in slightly more formal terms, equating nominal CPUE with abundance involves the assumption that three situations are occurring over the time and space for which population assessments are being made:

1. Vulnerability to fishing gear is equal.
2. Fishing effort is randomly distributed.
3. Fish are randomly distributed.

As extensively discussed by Hilborn and Walters (1992) and Fréon and Misund (1999), these requirements are rarely met. Fisheries scientists, therefore, often use the terms "apparent abundance" or "relative apparent abundance" (e.g., Marr 1953) in recognition that variations in CPUE may not be associated with changes in abundance, but rather changes in "availability" or "gear vulnerability" due

to variations in environmental conditions and the fishes' responses to them.

It is, moreover, tunas' propensity to aggregate into schools, and schools' propensity to aggregate in specific areas, which render these highly mobile species an economically exploitable resource (Sharp 1978; Sund et al. 1981; Scott et al. 1999). Billfishes (i.e., marlins and swordfish) do not form schools, but they do apparently aggregate along specific oceanographic features, such as temperature fronts, which can be areas of increased productivity and relatively high prey abundance (Podestá et al. 1993; Olson et al. 1994; Bigelow et al. 1999). The recurring seaward deflection of the Gulf Stream by the Charleston Bump (the so-called Charleston Gyre; Bane et al. 2001; Legeckis and Chang 2001, both this volume) also appears to concentrate pelagic fishes and their prey and, as a result, commercial and recreational fishing effort (Cramer 1996, 2001; Sedberry et al. 2001, both this volume). Although the data and principles we describe herein have heretofore been predominately applied to ocean-basin-scale population assessments of tunas and billfish (e.g., Hinton and Nakano 1996; Hampton et al. 1998; Hinton and Deriso 1998), they are also applicable to resource assessments over smaller space scales, such as the Charleston Gyre and South Atlantic Bight.

Barkley et al. (1978), Sharp (1978), Sund et al. (1981), Brill (1994), and Fréon and Misund (1999) all describe how the horizontal movements and vertical distributions of various tuna species, and effectiveness of specific fishing gears, are influenced by oceanographic conditions. For example, vulnerability to purse seine gear requires that the fish have access to the surface, so the schools can be detected by fishing vessels. Yet the thermocline-oxycline must be shallow enough so that schools do not escape under the bottom of the net before pursing (Green 1967). Although longline fishing gear does not depend on seeing fish at the surface, the gear is deployed such that hooks target specific depths (Boggs 1992). Catch-per-unit-effort data are, therefore, as likely to be a function of gear vulnerability (e.g., related to a shallow themocline or oxycline) and effective gear targeting (e.g., placing longline hooks at depths where fish are aggregated) as they are to reflect true fish abundance (Hanamoto 1987; Punsly and Nakano 1992; Hinton and Nakano 1996; Hinton and Deriso 1998; Bigelow et al. 1999).

Fishery-independent stock assessment methodologies, such as line transect aerial surveys, are not free of these shortcomings. Although "effort" can be made systematic by surveying a grid pattern, the influences of environmental conditions on "gear vulnerability" are still problematic. In this instance, we are referring to capture either on photographic film or as a digital data stream from laser- and radar-based detection systems (LIDAR and SLAR; Lyne et al. 1992; Oliver et al. 1994; Hunter and Churnside 1995). All these systems have limited ability to detect fish at depth, so abundance estimates will depend on fish depth distribution as well as true abundance. As shown in Figure 1, depending on the geometry of the grid pattern being surveyed, schools which are highly clumped (B and C, Figure 1) could be missed entirely. Conversely, in a problem unique to fishery-independent methods, schools which move (A, Figure 1) could be counted (i.e., "captured") more than once. All these errors must be accurately corrected in order to change "apparent abundance" into a meaningful measure of true abundance. We argue that these corrections require an a priori understanding of fish movements and distribution.

The question is, therefore, how to determine the effects of environmental conditions on the depth distributions, travel speeds, residency times, propensity to aggregate, and eventually the vulnerability of highly mobile pelagic fishes to specific fishing gears. Numerous investigators have tried to delineate the habitat requirements of various tuna and billfish species by correlating catch statistics with oceanographic conditions averaged over time and space (e.g., Hanamoto 1987; Grudinin 1989). As we and other investigators have previously argued (Sharp 1978; Sharp et al. 1983; Brill 1994), such correlations do not necessarily elucidate the requisite relationships because the data are often not gathered simultaneously, and because broad error terms associated with both make it difficult to demonstrate meaningful relationships (e.g., Podestá et al. 1993). Moreover, using catch statistics to determine the effects of environmental conditions on catch statistics (i.e., calculate a measure of gear vulnerability), without an independent estimate of abundance, can easily result in tautology. The resulting conclusions have limited predictive value. In other words, as described by Brill (1994), "...we 'know' that tunas [or billfishes] are rarely or never caught under a particular set of environmental conditions because the conditions are unsuitable. How do we 'know' that the environmental conditions are unsuitable? Because tunas [and billfishes] are rarely or never caught when and where they occur. Correlations based on such circular logic eventually break down…"
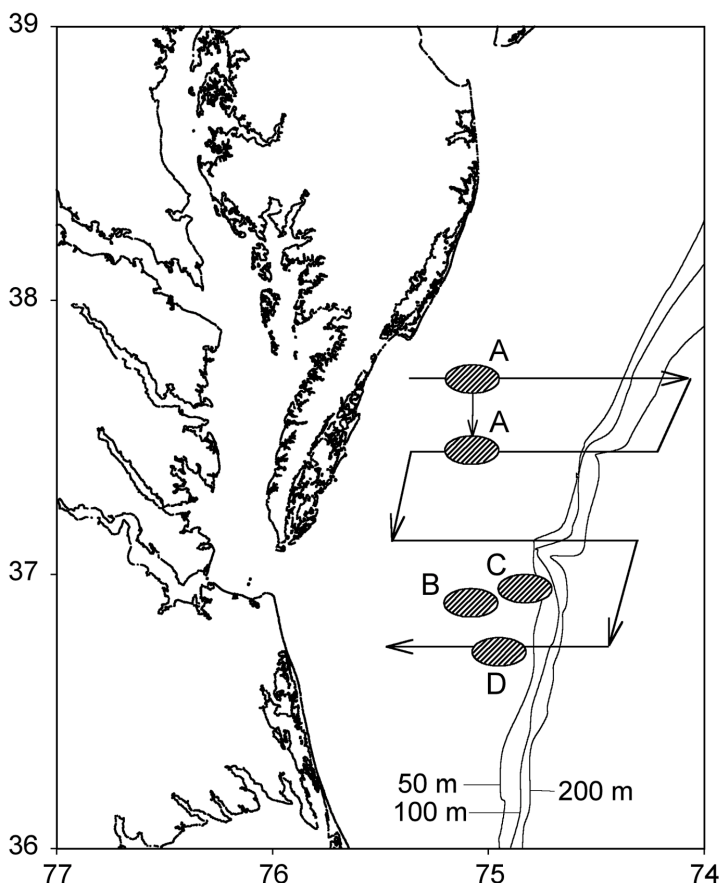
FIGURE 1. Hypothetical transect patterns flown during directed aerial surveys for population assessments and school locations (cross hatched ovals). Note that school aggregation (B and C) could result in underestimates of abundance whereas school movements (A) could result in double counting of the same fish. Population assessments for juvenile bluefin tuna by aerial surveys have been proposed for the area depicted (western Atlantic, off the eastern shore of Virginia, Delaware, and Maryland) (Polacheck et al. 1996).

We argue, as have others previously (e.g., Hunter et al. 1986), that measuring and ultimately predicting the effects of oceanographic conditions on the behaviors of tunas and billfishes requires direct observation. We contend that this can be done most cost effectively by equipping fish with either acoustic telemetry transmitters or archival (i.e., electronic data recording) tags. We disagree with the conclusions of Podestá et al. (1993) that "An experimental approach resolving the temporal and spatial scales necessary to address the questions examined here [the influence of temperature fronts on swordfish CPUE] might not be economically feasible for scarce, fast moving, large oceanic pelagic fish." Numerous studies have shown that acoustic telemetry techniques allow detailed records of both the horizontal and vertical movements of pelagic fishes, and their correlation with environmental conditions,

to be obtained (e.g., Dizon et al. 1978; Carey and Robison 1981; Carey and Olson 1982; Holland et al. 1986, 1990a,b; Carey 1990; Brill et al. 1993, 1999; Dagorn et al. 2000).

We contend, moreover, that for maximum effectiveness behavioral studies should be conducted in a way roughly analogous to a laboratory experiment; whenever possible specific hypotheses should be tested by changing only one variable at a time. To determine the effects of body size on movements and distribution requires data be gathered on fish that differ only by that variable. In other words, data should be obtained from juveniles and adults of the same species, in the same area, and under similar oceanographic conditions. Conversely, determining the effects of a particular environmental variable should involve fish of the same body size, where

behaviors are recorded in different areas or at different seasons, when oceanographic conditions differ only by the variable of interest. Such techniques have succeeded in establishing important basic principles regarding how environmental conditions limit the vertical movements of tunas and billfishes (e.g., Brill et al. 1993, 1999).

When detailed records of fish behavior are thus obtained, and combined with data gathered simultaneously on oceanographic conditions (e.g., changes in temperature or oxygen levels with depth) or forage abundance (e.g., movements of the organisms associated with the deep scattering layer), models capable of accurately predicting the movements and depth distributions of tunas and billfishes can be developed (Cayré and Marsac 1993; Josse et al. 1998). These models are now, in turn, being used to correct successfully CPUE-based population assessments of Pacific blue marlin *Makaira nigricans*, swordfish *Xiphias gladius*, and bigeye tuna *Thunnus obesus* for variations in gear vulnerability (Hinton and Nakano 1996; Hampton et al.1998; Hinton and Deriso 1998, respectively). Furthermore, we argue that behavioral studies can benefit significantly when they exist in a reciprocal relationship with laboratory research on physiological abilities and tolerances (Bushnell et al. 1990; Bushnell and Brill 1991, 1992; Lowe et al., in press). By using this approach, each technique generates hypotheses that can be subsequently tested with the other (Brill 1994, 1996). This topic will not be discussed in this brief review, however.

As do acoustic telemetry devices, newly developed archival (i.e., electronic data-recording) tags also provide horizontal and vertical movement data, as well as some basic physiological (e.g., body temperature) and environmental data (e.g., water temperature), but over long time scales (months to years) (Klimley et al. 1994). We want to emphasize, however, that archival tags complement, rather than supplant, data gathered with acoustic telemetry. Currently available archival tags have two limitations for determining the effects of environmental conditions on the movements and distribution of pelagic fishes. First, although depth records are accurate and highly detailed, the ability of archival tags to precisely fix geographic position is still limited to an area about 1° square (Welch and Eveson 1999). Although this is not a problem if the question being addressed is one of transoceanic movements, this level of accuracy makes it difficult to correlate horizontal movement data with detailed oceanographic data. As a result, acoustic telemetry remains superior for fine scale temporal and spatial sampling of environmental parameters and behavior. Second, archival tags only supply information on habitat parameters immediately surrounding the fish, because the fish itself is the data gathering platform. They supply no information on the nearby oceanographic conditions that might be occupied by the fish, or that the fish has occupied for periods too brief to be recorded by the tag. As important, there is also no information on forge abundance. In contrast, acoustic telemetry provides a data stream which is nearly continuous, and the vessel following the fish (or an accompanying vessel) can gather detailed synoptic data in real time on the surrounding oceanographic conditions, currents, and forage abundance (e.g., Carey 1990; Bertrand et al. 1999; Brill et al. 1999; Dagorn et al. 2000). Satellite data can provide environmental data for correlation with fish movement records obtained from archival tags, but as we will show, the types of satellite data employed must be carefully chosen. This is further complicated by the inability to precisely fix fish position with respect to oceanographic conditions derived from satellite data.

Archival tags do, however, have several distinct advantages over acoustic telemetry. First with acoustic telemetry, fish must be tracked individually so the number of fish from which data are obtained are generally limited to relatively few individuals. (Most published tracking studies have an "n" of less than 10.) Second, periods of observation are generally limited to a few days due to battery life of the transmitter, crew fatigue on the tracking vessel, or limited ship time. Third, acoustic telemetry studies of even the highly mobile pelagic tuna and billfish species generally take place close to shore (e.g., Holland et al. 1990a,b; Block et al. 1992; Pepperell and Davis 1999; Lutcavage et al., in press), because investigators generally do not have access to large (and expensive to operate) oceanographic vessels. Even when they do, tracking studies are still often limited to well known, relatively near-shore fishing grounds (e.g., Brill et al. 1993; Block et al. 1997). In contrast, data obtained from returned archival tags can contain information on pelagic fish movements and distributions far from any land masses and from areas previously not known as "fishing grounds."

Although simple techniques for reliable long

term attachment of archival tags to large pelagic fishes have been perfected (Brill and Cousins 1997), the fish must be recaptured and the archival tags returned in order to retrieve the data. Given the costs of archival tags (generally US$1,000–$2,000 each), and the relatively low rates of tag returns from pelagic fishes (<5%, Bayliff and Holland 1986), the cost per returned tag can easily exceed $20,000, excluding the costs of deployment[1]. Pop-up satellite archival tags, which automatically jettison from the fish and report their stored data through a satellite link, are now becoming available (Block et al. 1998; Lutcavage et al. 1999). Their current size, however, probably limits their use to fish larger than about 100 kg body mass.

In the following sections, we selectively review the use of both acoustic telemetry and archival tags to determine the effects of environmental conditions on the vertical and horizontal movements and distribution of various tuna and billfish species. In this way we intend to demonstrate the utility of comparing data where one variable at a time is changed and the applicability to population assessment issues. We will not, however, deal with the limiting effects of reductions in ambient oxygen with depth. Although this subject has received attention through both laboratory (e.g., Bushnell et al. 1990; Bushnell and Brill 1991, 1992; Brill 1994) and field studies (e.g., Cayré 1991; Cayré and Marsac 1993), there are significantly less data, from fewer pelagic fish species, than on the limiting effects of temperature.

Effects of Temperature on Vertical Movements and Depth Distribution

Data on the depth distributions of juvenile and adult bigeye and yellowfin tuna *T. albacares* around the main Hawaiian Islands, gathered with either acoustic telemetry (Holland et al. 1990b; Brill et al. 1999) or archival tags (M. Musyl, C. Boggs, R. Brill, D. Curran, and T. Kazama, National Marine Fisheries Service [NMFS], Honolulu Laboratory, and University of Hawaii, unpublished observations) are summarized in Figure 2. In brief, the depth distributions of yellowfin tuna are nearly body size invariant and

show only minor day-night differences. In contrast, the depth distributions of bigeye tuna show dramatic day-night differences and clear effects of body size. Although both adult and juvenile bigeye tuna remain relatively shallow during nighttime, adult bigeye tuna reach maximum depths during daytime of approximately 500 m (Figure 2), whereas juvenile fish reach maximum depths of less than 300 m. When these data are expressed as time spent at specific temperatures (Figure 3), it becomes clear that both adult and juvenile yellowfin tuna spend the vast majority of their time in the uniform temperature surface layer (i.e., <24°C) and expose themselves to a maximum temperature change of ≈8°C. In contrast, bigeye tuna remain in the surface layer at night but descend at dawn in behaviors that apparently allow them to exploit more effectively the organisms of the deep scattering layer as prey (Dagorn and Josse 2000). Juvenile and adult bigeye tuna thus expose themselves to significantly greater temperature changes during their daily vertical movements; ≈10°C and 18°C, respectively (Figure 3), than do yellowfin tuna.

Data are also now available from yellowfin tuna, of approximately the same body mass, tracked in areas with widely disparate oceanographic conditions (Carey and Olson 1982; Yonemori 1982; Holland et al. 1990b; Cayré 1991; Block et al. 1997). We will concentrate, however, on data obtained from only two geographic areas: near the main Hawaiian Islands and the eastern Pacific Ocean adjacent to southern California and northern Mexico. In both areas, the decrease of oxygen content with depth is not limiting at depths reached by yellowfin tuna (Block et al. 1997; Brill et al. 1999). The areas do, however, differ in surface layer temperature (the eastern Pacific being approximately 5°C colder), surface layer depth (≈50–100 m near the Hawaiian Islands and ≈20–50 m in the eastern Pacific), and the decrease in temperature with depth below the surface layer (which is significantly steeper in the eastern Pacific). The time-at-depth distributions for yellowfin tuna tracked in these areas reflect these differences. Fish in the eastern Pacific clearly remain shallower than the fish around the main Hawaiian Islands (Figure 4).

We contend, however, that Figure 5 clearly shows that yellowfin tuna depth distributions are set, not by a specific depth or water temperature, but by the relative change in water temperature with depth. Although the fish in the eastern Pacific have most likely acclimated to surface layer temperatures ≈5°C

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[1] The low return rate is for simple "spaghetti" tags where the reward for returning a tag is often a T-shirt, baseball cap, or certificate. The reward for returning an archival tag is commonly US$500–$1,000, so a higher return rate maybe achieved. To the best of our knowledge, this is yet to be documented in the peer reviewed literature.
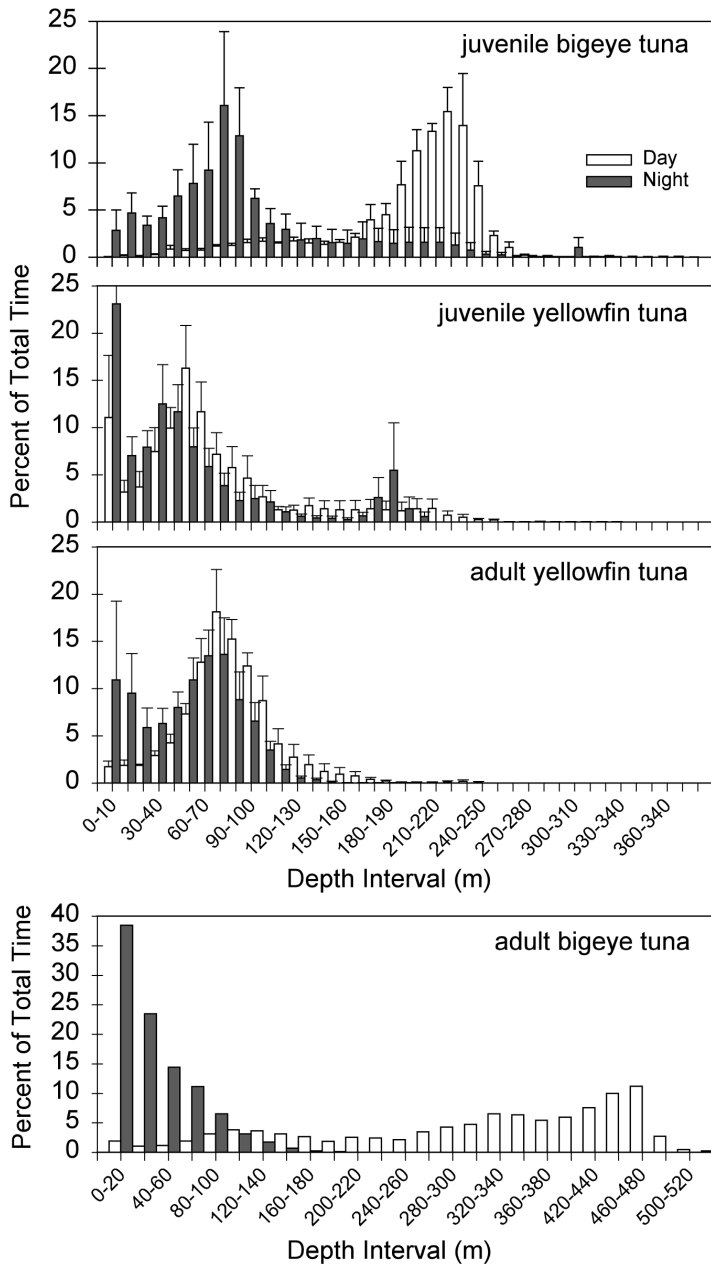
FIGURE 2.   Time spent at specific depths by juvenile bigeye tuna ($n = 4$, ≈5–10 kg), juvenile yellowfin tuna ($n = 11$; ≈5–10 kg), and adult yellowfin tuna ($n = 5$; ≈60–90 kg) carrying ultrasonic depth sensitive transmitters. The data for adult bigeye tuna (≈45 kg) come from one fish that was at liberty for three months carrying an archival (i.e., electronic data recording) tag (M. Musyl, C. Boggs, R. Brill, D. Curran, and T. Kazama, unpublished observations). All data were recorded near the main Hawaiian Islands. Note that juvenile and adult yellowfin tuna have essentially the same depth distributions. Bigeye tuna remain relatively shallow at night, but descend during the day, apparently to exploit the organisms of the deep scattering layer as prey (Josse et al. 1998). Data such as these, obtained in the same area and under very similar oceanographic conditions, allow the influence of body mass and species specific differences in depth distributions to be clearly discerned. Data for juvenile bigeye and yellowfin tunas were taken from Holland et al. (1990b), data for adult yellowfin tuna were taken from Brill et al. (1999).
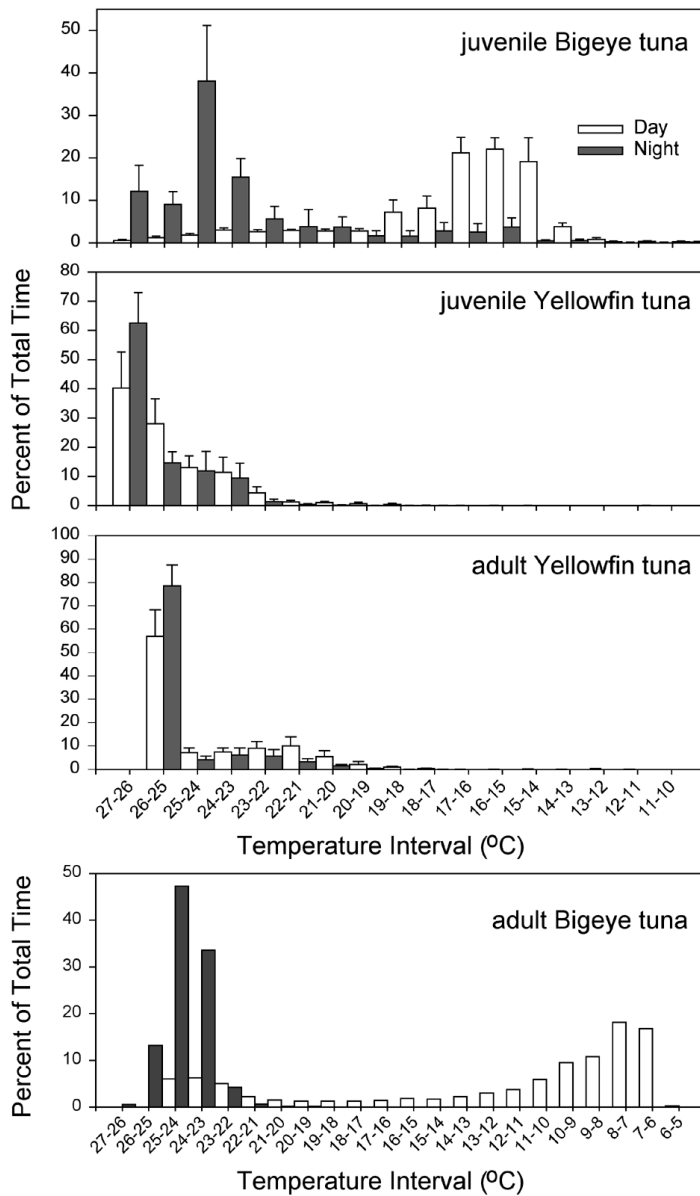
FIGURE 3. Time spent at specific temperatures by the same yellowfin and bigeye tunas shown in Figure 2. Yellowfin tuna predominantly occupy the uniform-temperature surface layer. Juvenile and adult bigeye tuna are clearly more tolerant of temperature reductions, and descend (during the daytime) to depths where water temperatures are as low as ≈15°C and 7°C (respectively).

colder, their depth distribution is limited by the same change in water temperature (≈8°C) as the fish tracked near the Hawaiian Islands. Moreover, adult yellowfin tuna (estimated body mass 64–93 kg) tracked near the Hawaiian Islands showed exactly the same temperature limitations on their vertical movements. Numerous authors have attempted to explain distributions of various fishes based on preferences for specific water temperatures (e.g., Magnuson et al. 1979; Neill 1979), including those
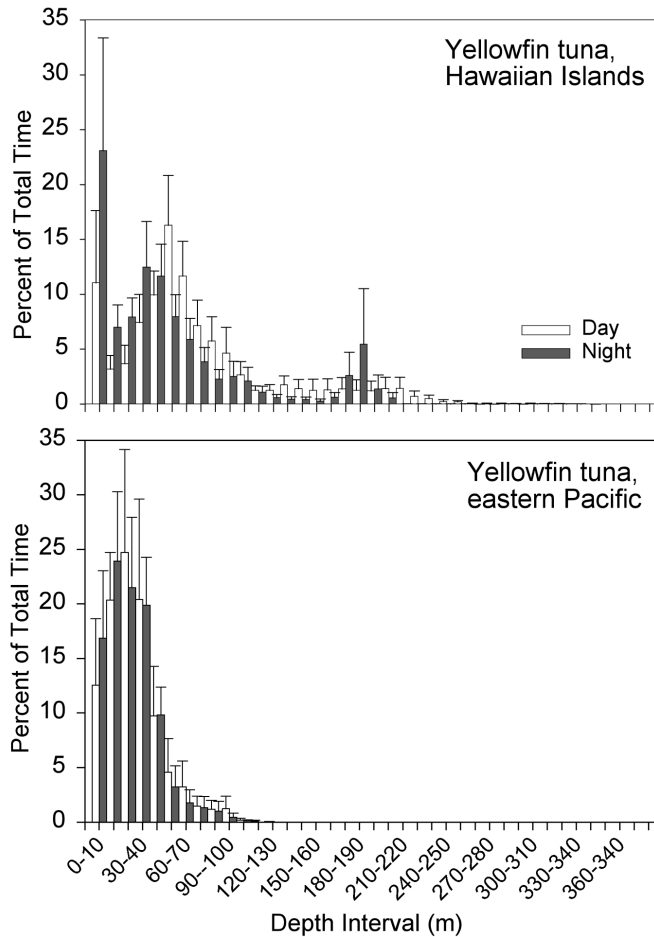
FIGURE 4. Time spent at specific depths by juvenile yellowfin tuna (≈5–16 kg), carrying depth sensitive transmitters, tracked near the Hawaiian Islands ($n = 11$) and in the eastern Pacific near southern California and northern Mexico ($n = 3$). Data for the former were taken from Brill et al. (1999) and for the latter from Block et al. (1997). Note that fish in the eastern Pacific remain relatively shallow compared to fish tracked near the main Hawaiian Islands.

of tunas (e.g., Sund et al. 1981; Roffer 1987; Grundinin 1989). However, Figure 5 also demonstrates that the concept of "temperature preference" is difficult to apply to tunas (and as we argue below, also to billfishes). Yellowfin tuna in both the eastern and central Pacific clearly occupy the warmest water available, rather than water of a specific temperature.

The concept of the change in temperature with depth limiting vertical movements is also applicable to at least three istiophorid billfish species: blue marlin (Holland et al. 1990b), striped marlin *Tetrapturus audax* (Holts and Bedford 1990; Brill et al. 1993), and black marlin *M. indica* (Pepperell and Davis 1999). As with yellowfin tuna, the depth distribution of all three species is limited by the same de-

crease in water temperature (≈8°C) that limits the depths reached by yellowfin tuna. Moreover, marlins lack counter-current heat exchangers in the vascular system supplying blood to the swimming muscles, and therefore do not have the ability to sustain swimming muscle temperature significantly above ambient water temperature, as do tunas (Lindsay 1968; Brill et al. 1994). Therefore, as explained in Brill et al. (1999), it appears to be reductions in cardiac function that are responsible for the similar (and body mass independent) limiting effects of temperature on the depth distributions of yellowfin tuna, blue marlin, striped marlin, and black marlin.

From data presented by Carey (1990), swordfish can be seen to be a clear exception. Their vertical distribution, with respect to the effect of the
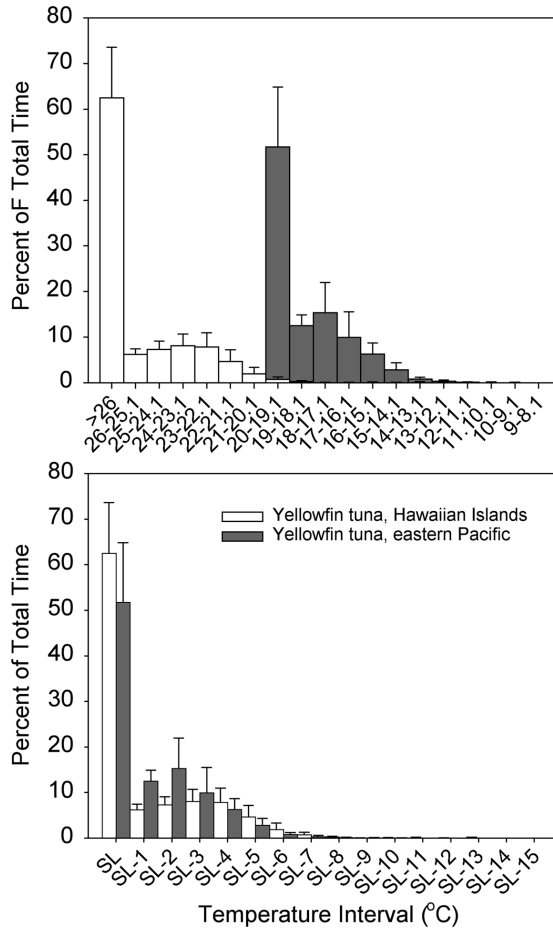
FIGURE 5. Time spent at specific temperatures (upper panel) by the juvenile yellowfin tuna shown in Figure 4. These distributions are clearly separate because the temperature of the surface layer in the eastern Pacific is ≈5°C colder than that near the Hawaiian Islands. Note, however, when the data are plotted as the change in temperature relative to that of the surface layer (lower panel), the time-at-temperature distributions for yellowfin tuna in the two areas become identical. In other words, although the fish in the eastern Pacific have most likely adapted to the lower temperatures in that area, their depth distributions are still limited by the same change in water temperature (≈8°C) that limits the maximum depths occupied by the fish tracked near the Hawaiian Islands. (Figure reproduced from Marine Biology, with permission.)

change in temperature with depth, is much closer to that of bigeye tuna than the other billfish species cited above, or to yellowfin tuna. Swordfish, like bigeye tuna, remain near the surface at night, but descend during the day following the vertical movements of the organisms of the deep scattering layer, which they apparently also exploit as prey (Carey 1990). As do adult bigeye tuna, swordfish go from the 25°C surface layer to depths where water temperatures are below 7°C. Swordfish do make upward excursions into the mixed layer to warm their muscles (Carey 1990) as do bigeye tuna. These upward movement are, however, not as regular.

Recently completed ultrasonic telemetry studies of adult (estimated body mass 134–318 kg, Lutcavage et al., in press) and juvenile (estimated body mass 7–19 kg [R. Brill and M. Lutcavage, NMFS, Honolulu Laboratory and Edgerton Research Laboratory, New England Aquarium, unpublished data]) north Atlantic bluefin tuna conducted off New England and Virginia (western north Atlantic) demonstrate further the suitability of using relative temperature change to explain and predict tuna depth distributions. The time-at-depth distributions of juvenile and adult bluefin tuna were essentially identical, although this most likely resulted from the fish

being over the continental shelf during the times they were followed. In contrast, when data are plotted as time spent at specific temperatures, juvenile bluefin tuna appear to have a clear preference for 22–25°C water, whereas no clear temperature preference is evident for the adults (Figure 6). We argue, however, that these results actually reflect the available water temperatures. The lack of a clear peak in the time-at-temperature distribution for adult bluefin tuna follows from the fact that water temperatures were highly variable over the times and areas when and where these fish were followed.

In contrast, when time-at-temperature distributions are plotted with temperatures expressed relative to surface layer temperature (i.e., the warmest water available to the fish during each track), the time-at-temperature profiles for both juvenile and adult fish become essentially identical (Figure 7). They are also similar to those for other tuna and billfish species, in that bluefin tuna spend the majority of their time occupying the warmest water available. Both adult and juvenile bluefin tuna are, however, significantly more tolerant of temperature reductions occurring with depth than are yellowfin tuna and blue, striped, or black marlin; but less tolerant of temperature change than adult bigeye tuna or swordfish. Whereas the yellowfin tuna and marlins will sub-
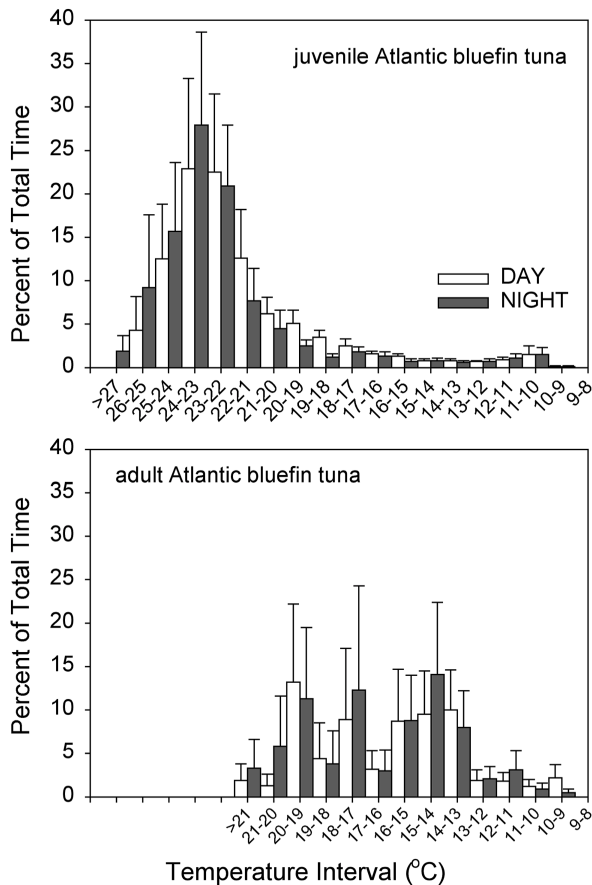

FIGURE 6.   Time spent at specific temperatures by juvenile bluefin tuna ($n = 5$, 7–19 kg) off the eastern shore of Virginia (upper panel) and adult fish ($n = 10$, 134–318 kg) in the Gulf of Maine (lower panel), carrying ultrasonic depth sensitive transmitters. The data appear to indicate juvenile fish have a preference for water temperatures of ≈22–25°C, whereas adult fish have no clear temperature preference. Data for adult fish were taken from Lutcavage et al. (2000). Data for juvenile fish from R. Brill and M. Lutcavage (unpublished observations).

ject themselves to a maximum temperature change of ≈8°C (Figures 3 and 5), bluefin tuna subject themselves to a maximum temperature change ≈14°C (Figure 7), and adult bigeye tuna and swordfish routinely subject themselves to a maximum temperature change ≈18°C (Figure 3). Note also, that these temperature limitations on vertical distribution are independent of body mass in bluefin tuna, as they are in yellowfin tuna and marlins. In brief, the depth distributions of tunas and billfishes appear to be highly predictable when they are based on the change in water temperature with depth, rather than specific temperatures.

Environmental Influences on Horizontal Movements

We now turn to factors influencing the horizontal movements of pelagic fishes. Yuen (1970) was the first to show that skipjack tuna *Katsuwonus pelamis* near the main Hawaiian Islands have precise navigational abilities, and return to the same geographic areas at the same time over several successive days. Holland et al. (1990b) and Klimley and Holloway (1999) have subsequently shown yellowfin tuna have similar abilities. Such precise navigation is conceivably based on tunas' abilities to sense
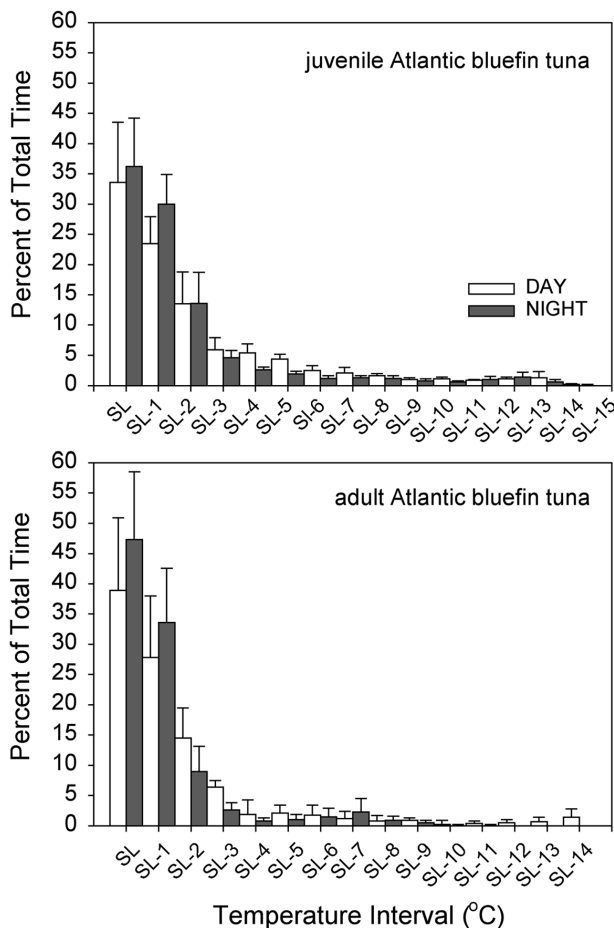

FIGURE 7. Time-at-temperature plots for the juvenile and adult bluefin tuna shown in Figure 6, with the data plotted as the change in temperature relative to that of the surface layer (i.e., the warmest water available to the fish) during each track. Note that juvenile and adult fish are now seen to have exactly the same time-at-temperature distributions. As do yellowfin tuna, bluefin tuna occupy the warmest water available. Bluefin tuna, however, are more tolerant of temperature change than yellowfin tuna, and routinely expose themselves to temperature changes of up to ≈14°C

various components of the earth's magnetic field (Walker 1984; Walker et al. 1997).

In contrast to the precise repetitive movements of tunas, blue marlin tracked near the main Hawaiian Islands (Holland et al. 1990a; Block et al. 1992), striped marlin off the coast of California (Holts and Bedford 1990), swordfish in the northwest Atlantic (Carey 1990), and black marlin near the Great Barrier Reef off northeast Australia (Pepperell and Davis 1999) all most often move over courses that are relatively straight or slowly curving. Moreover, near the main Hawaiian Islands, the horizontal movements of some striped marlin appear to have been set predominately by currents (Brill et al. 1993). In other words, the fish apparently made continuous small random movements so that their net displacements were set by the mesoscale eddies that form on the lee sides of the islands.[2] The movement of other striped marlin appeared to be a combination of active directed movement set by the fish, to which displacements due to oceanographic currents were added (Brill et al. 1993). Similar mesoscale eddies form on the seaward side of the Gulf Stream as it flows over the Charleston Bump (Legeckis 1979; Legeckis and Chang 2001). Tracking studies of billfishes, with simultaneous measurements of currents, in the area of these eddies could provide a useful comparison to the data acquired on billfishes in other areas.

Several investigators have attempted to associate the horizontal movements and aggregations of tunas with sea surface temperature, with varying degree of success. In the eastern Pacific, the movements and aggregations of albacore *T. alalunga* and skipjack tuna do appear to be correlated with temperature fronts (Laurs et al. 1977; Laurs and Lynn 1977; Fiedler and Bernard 1987). In contrast, in both the Gulf of Mexico and the eastern Pacific, the movements and aggregation of yellowfin tuna do not (Power and May 1991; Block et al. 1997).

Our recently completed ultrasonic telemetry studies of the movements of adult and juvenile bluefin tuna in the western Atlantic clearly demonstrate why tuna movements and aggregations do not correlate with sea surface temperatures, and the limita-

tion of using satellite-derived sea surface temperature data. Figure 8 shows the depth record of a juvenile bluefin tuna tracked off the eastern shore of Virginia as well as swimming speed, sea surface temperature, and mean (±SE) temperatures at specific depths. Note that, by its continuous vertical movements, the fish subjects itself to temperature gradients of $\approx 1°C$ m^{-1} over periods of minutes. In contrast, although moving through sea surface temperature gradients that are clearly visible on a satellite image (Figure 9), the maximum horizontal temperature gradient (i.e., sea surface temperature gradient) the fish could experience is $\approx 1°C$ km^{-1}; a change about three orders of magnitude less than the vertical temperature gradient. Not surprisingly, there is no apparent effect of sea surface temperature on swimming speed or direction (upper panel of Figure 8 and Figure 9), since the fish is unlikely to be able to detect the horizontal temperature gradient. Note also that the plume of water exiting the Chesapeake Bay is not clearly defined by sea surface temperature (Figure 9). (This result might be due to tidal effects because these are composite satellite images which include data from several tidal cycles.) We further argue that our hypothesis, that sea surface temperature gradients are often not detectable and have no direct influence on movements and aggregations, is relevant to other highly vertically mobile pelagic species such as bigeye tuna (Holland et al. 1990b) and swordfish (Carey 1990). Podestá et al. (1993) and Bigelow et al. (1999) reached similar conclusions with respect to the apparent concentration of swordfish along temperature fronts in the western Atlantic and central north Pacific, respectively. Both studies concluded that fish were concentrated along fronts in response to concentrations of prey species, rather than sea surface temperature.

In contrast, Figure 10 shows the movements of five juvenile bluefin tuna in relation to chlorophyll-a concentration and the diffuse attenuation coefficient (i.e., water turbidity). From these images, it is readily apparent that juvenile bluefin tuna remain within a narrow range of these parameters. Our conclusion is further supported by the locations of juvenile bluefin tuna schools recorded during aerial surveys conducted in 1997 (Lutcavage 1998). Although satellite data showing chlorophyll-a concentrations and diffuse attenuation coefficients are not available for 1997, the schools were all located near areas where the fish carrying ultrasonic transmitters

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[2] These eddies form as a result of the relatively constant northeast trade winds. Recent satellite images have shown that eddies may remain active for up to several months (D. Foley, Coast Watch Program, University of Hawaii, unpublished observations).
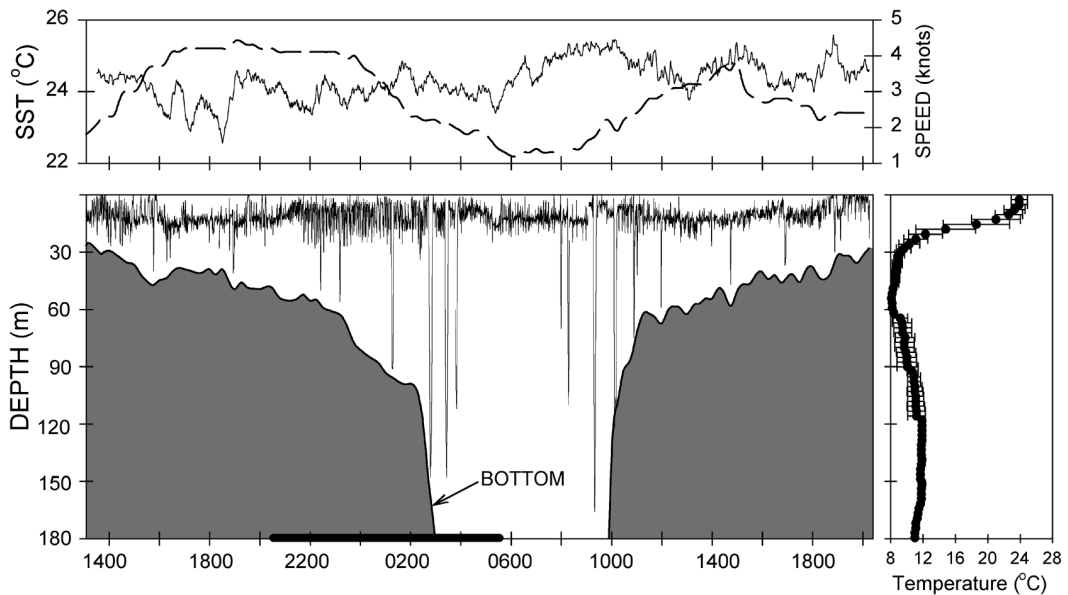
FIGURE 8. Swimming speed (solid line, upper panel) and vertical movements (lower panel) of a juvenile bluefin tuna (15 kg estimated body mass) carrying an ultrasonic depth sensitive transmitter tracked off the eastern shore of Virginia. The change in temperature in the horizontal direction (expressed as sea surface temperature, SST) is shown by the dashed line in the upper panel. The change in temperature in the vertical direction (mean ±SEM water temperatures collected at 0.6 m intervals) were obtained during the track with expendable bathythermograph probes, and are shown in the rightmost panel. 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 ($\approx 1°C$ km^{-1}) is several orders of magnitude less then that experienced moving vertically ($\approx 1°C$ m^{-1}).

remained (Figure 10). Our assertion is quantified in Figure 11, which shows that juvenile bluefin tuna during our ultrasonic telemetry study tended to remain in water characterized by narrow intermediate range of chlorophyll-a concentrations and turbidity.

We contend that chlorophyll-a concentration is a surrogate measure of tuna forage abundance, although we have no direct evidence. Moreover, quantifying tuna forage abundance is difficult because prey species exploited by tunas are not captured quantitatively with towed nets (Clarke 1983). Although acoustic surveys clearly have promise for measuring tuna forage abundance (Bertrand et al. 1999), to the best of our knowledge such surveys have never been conduced in the western Atlantic area where we tracked juvenile bluefin tuna. These shortcomings notwithstanding, we contend that our tracking results show juvenile bluefin tuna tend to remain in waters where forage density is relatively high (as shown by chlorophyll-a density), but where the water is clear enough for them to be effective visual predators (as shown by diffuse attenuation coefficient).

Local fishermen off the eastern shore of Vir-

ginia contend that the 1–2 m high irregularities in bottom topography aggregate juvenile bluefin tuna, perhaps as fish aggregating devices (FADs) do. Features of the coastal topography are known to influence the short-term movements of skipjack and yellowfin tunas around the main Hawaiian Islands (Yuen 1970; Holland et al. 1990b; Brill et al. 1999). We argue, however, that the apparent aggregation around the minor geological features is just coincidental with the water mass of appropriate productivity and clarity. It is these qualities of the water mass which, in actuality, cause the fish to remain in these areas.

In summary, we assert that sea surface temperature gradients per se are not necessarily good predictors of tuna and billfish movements or aggregations because they are undetectable by fish which routinely subject themselves to vertical temperature gradients that are up to several orders of magnitude steeper. We concede, however, that sea surface temperature gradients can be predictors of tuna and billfish movements and abundance (as noted by Fiedler and Bernard 1987 and Bigelow et al. 1999) if they are actually reflective of
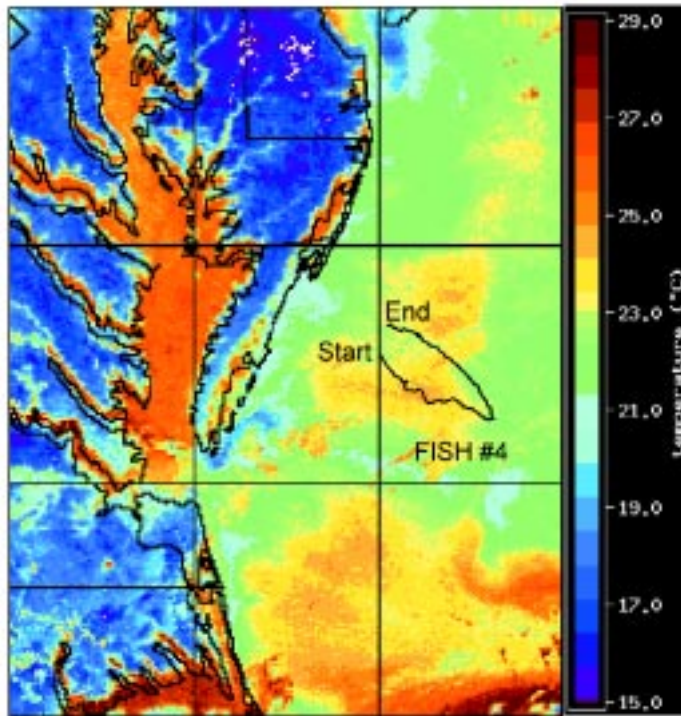
FIGURE 9.　A composite satellite image (6–7 July 1998) showing sea surface temperature (SST) and movements of the juvenile bluefin tuna depicted in Figure 8. Note that changes in SST, although clearly visible in the image, are relatively minor.

increases in prey abundance. This is an area clearly in need of further careful quantitative investigation. The unique oceanographic features created by the Charleston Bump may provide an excellent natural laboratory for testing our ideas.

Summary and Conclusions

1. Yellowfin and bluefin tunas, and blue, striped, and black marlin tend to occupy the warmest water available. In contrast, bigeye tuna and swordfish tend to remain in the surface layer only at night, and descend at dawn in behaviors that apparently allow them to exploit effectively the organisms of the deep scattering layer as prey.

2. Within reasonable temperature limits, and in areas were the decreases of oxygen concentration with depth are not limiting, the depth distribution (regardless of body size) of tunas and billfishes are set by the relative changes in water temperature with depth, rather than by a spe-

cific water temperature or depth. The relative change in water temperature with depth is, therefore, a robust predictor of the depth distribution and the vulnerability to specific fishing gears. Models constructed from these concepts have been shown to be useful for correcting population assessments (based on CPUE data) for variations in fishing gear vulnerability.

3. Bluefin tuna, bigeye tuna, and swordfish (regardless of body mass) have a greater tolerance of temperature changes occurring with depth than yellowfin tuna, or blue, striped, and black marlin. The latter species will all subject themselves to a maximum temperature change of $\approx 8°C$ during their normal daily vertical movements. In contrast, bluefin tuna will subject themselves to a temperature change of up $\approx 14°C$, and adult bigeye tuna and swordfish to a temperature change of up $\approx 18°C$ during their normal daily vertical movements.
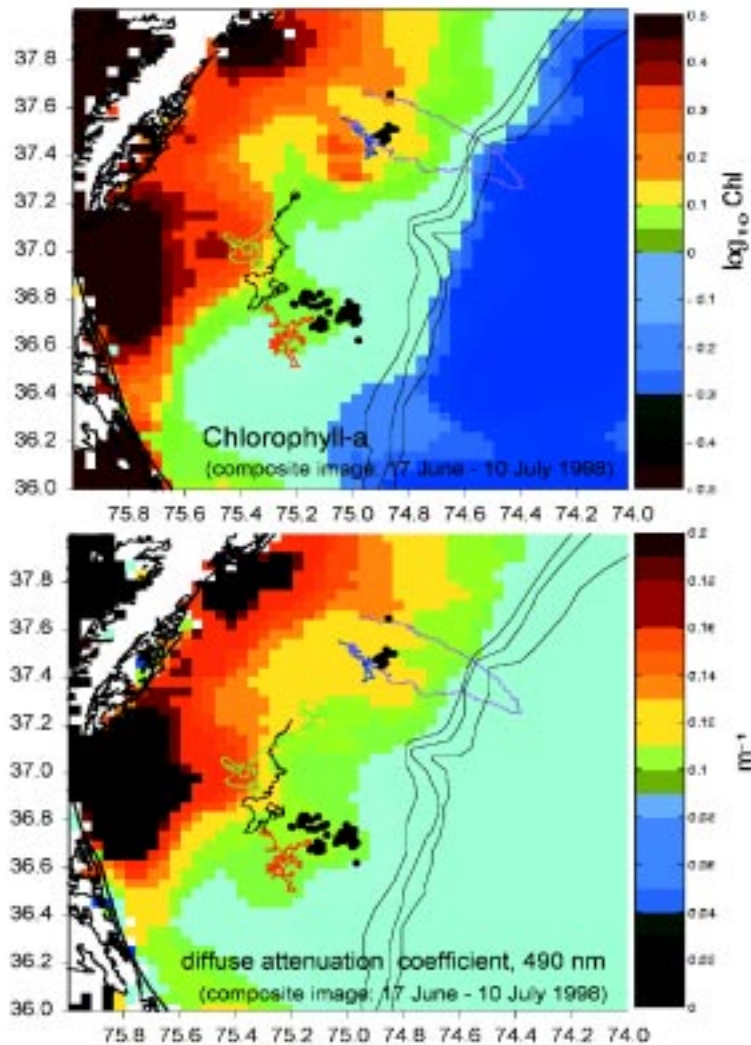
4. The short-term horizontal movements of mar-

FIGURE 10. Satellite images showing chlorophyll-a concentration (upper panel), diffuse attenuation coefficient (i.e., turbidity; lower panel), and the movements of five juvenile bluefin tuna carrying ultrasonic depth sensitive transmitters. Note that, except for Fish #4, all fish remain within a relatively narrow range of these two variables, and that the plume of plankton rich, turbid water exiting the Chesapeake Bay is clearly visible. Locations of juvenile bluefin tuna schools recorded during aerial surveys conducted in 1997 (Lutcavage 1998) are shown by filled circles. The continental shelf break is indicated by the 50, 100, and 200 m isobath lines.

lins may be strongly influenced by oceanic currents, whereas those of tunas are not. Over the continental shelf areas in the western north Atlantic, the short-term movements of bluefin tuna appear to be governed by prey concentration and water turbidity. Bluefin tuna tend to remain in intermediate water masses where prey abundance is high, but where the water mass is clear enough for them to be effective visual predators. It is yet to be demonstrated if this concept is applicable to other tuna and billfish species in other areas. The Charleston Bump and Charleston Gyre may
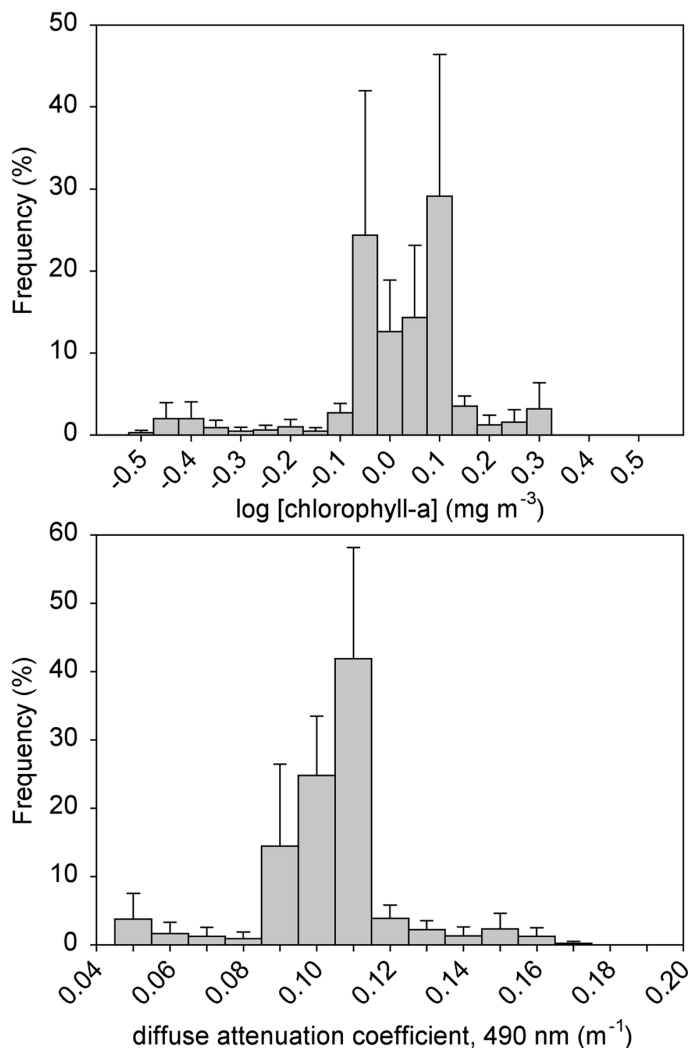
FIGURE 11.   Frequency of chlorophyll-a concentrations (upper panel) and diffuse attenuation coefficient values (lower panel) of waters occupied by the five juvenile bluefin tuna shown in Figure 10. The fish clearly spent the majority of time they were followed in water masses whose chlorophyll-a concentrations and turbidity are intermediate between those for the plankton-rich inshore water and the clear oligotrophic waters east of the continental shelf.

serve as a natural laboratory for testing these ideas.

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