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28. Thirty-five monogyne colonies of the fire ant were collected between 28 October and 10 November 1999. From these, 11 were immediately discarded either because no dealate (mother) queen was found ($n = 8$) or no sex-ratio bias occurred ($n = 3$). The remaining 24 colonies were reared under laboratory conditions, as described (*12*). The sex ratio was determined for each colony 1 to 3 weeks after collection from the field. Numerical sex ratio (proportion of males among sexuals) was estimated by sexing at least 100 haphazardly selected sexuals (adult alates + pupae) per colony and calculating the proportion belonging to each sex. Sex investment ratio, estimated as the proportional investment in males among sexuals, was determined for each colony by adjusting the number of males and females by their respective dry weights at the time of mating flights. Mean dry weights of males and females were 8.12 ± 0.68 mg and 2.6 ± 0.3 mg, respectively (*26*). Because males generally have a higher metabolic rate and, hence, on a per weight basis cost more to produce than females, investment ratios were corrected by converting female/male dry weight ratios (D) to energetic costs ratios (C), with $C = D0.7$ (*7*).
29. Eggs laid by queens for 24 hours in culture cups before the exchange experiments were collected after removal of the queen. They were incubated with workers for 3 days before they were stored for subsequent genetic analyses. For each colony, seven adult workers and five adult males (if any) were genotyped with one to six microsatellite loci (*Sol-6*, *Sol-11*, *Sol-20*, *Sol-42*, *Sol-49*, and *Sol-55*). These loci have three, seven, eight, nine, seven, and eight alleles, respectively, in the North American population of the fire ant. Primer sequences and amplification conditions are described elsewhere (*32*). The genotype of the queen and its mate were inferred at each locus on the basis of workers and male offspring genotypes, under the assumption of strict monogyny and monoandry (*33*). This is straightforward because of the haploidy of males, because, for each locus, a male gives the same allele to all his offspring. Primary sex ratio was assessed by typing 22 to 41 eggs laid per queen at one or two microsatellite loci for which the father had a different allele than that of the queen, so that all fertilized (female) eggs were heterozygous. Hence, eggs having either one or two alleles were unambiguously scored as hemizygous males and heterozygous females, respectively. Colonies for which an ambiguity remained were discarded from the analyses.
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Migratory Movements, Depth Preferences, and Thermal Biology of Atlantic Bluefin Tuna

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The deployment of electronic data storage tags that are surgically implanted or satellite-linked provides marine researchers with new ways to examine the movements, environmental preferences, and physiology of pelagic vertebrates. We report the results obtained from tagging of Atlantic bluefin tuna with implantable archival and pop-up satellite archival tags. The electronic tagging data provide insights into the seasonal movements and environmental preferences of this species. Bluefin tuna dive to depths of >1000 meters and maintain a warm body temperature. Western-tagged bluefin tuna make trans-Atlantic migrations and they frequent spawning grounds in the Gulf of Mexico and eastern Mediterranean. These data are critical for the future management and conservation of bluefin tuna in the Atlantic.

The natural history and migratory abilities of Atlantic bluefin tuna (*Thunnus thynnus*) have fascinated mankind for millennia (*1*). These fish grow to >300 cm and attain masses of 680 kg (*2*). They are powerful swimmers that range from the tropics to polar latitudes (*3*) and are renowned for their endothermic physiology (*4*). Despite a history of exploitation that spans thousands of years, little is known about the spatial dynamics of bluefin tuna movements, depth preferences, or thermal biology.

Atlantic bluefin tuna have been considered overexploited since 1982, and recent catches continue to exceed historical levels (*2, 5*). The International Commission for the Conservation of Atlantic Tunas (ICCAT) regulates the fishery and currently recognizes two management units, west and east Atlantic (separated by the 45°W meridian), the latter including the Mediterranean Sea. Larval surveys indicate two major breeding grounds, the Gulf of Mexico and the Mediterranean Sea (*2, 3, 6–8*). Eastern and western Atlantic bluefin tuna populations are presumed to reach maturity at distinct ages (*8–10*). The differences in maturity indices, coupled with isolated breeding grounds, suggest that distinct evolutionary units may exist. The west and east Atlantic populations are assumed in ICCAT stock assessments to be mixing at a low level (*2*). However, conventional tagging data have shown that Atlantic bluefin are capable of making rapid trans-Atlantic crossings (*2, 3*).

Western Atlantic breeding populations have declined in the past 30 years (*2, 5*). This has resulted in a reduction in quota for nations that fish this management unit, primarily off the North American coast, and the establishment of recovery plans for the western Atlantic fishery. Critical to a recovery is knowledge of the extent of overlap between the two management units and the level of philopatry to western and eastern breeding grounds (*2, 5*).

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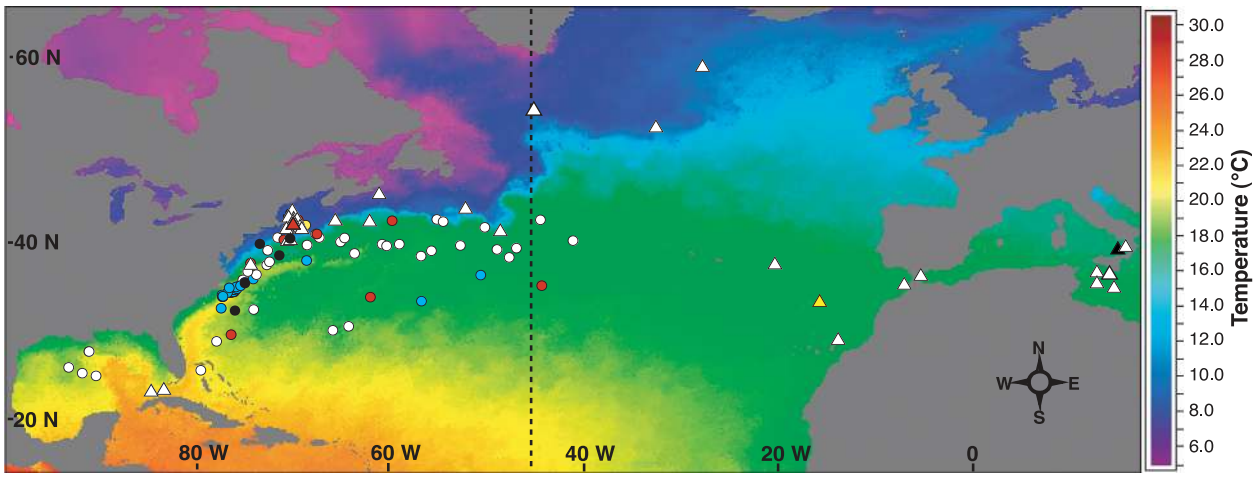

Fig. 1. Location of recapture of archival-tagged fish (white triangles). Red triangle indicates a location where 21 bluefin tuna have been recaptured. Black triangle indicates two reported recaptures of archival-tagged bluefin by Italian fishers with a complete description of the tags to local scientists but no return of the tags to the United States. Circles indicate PSAT endpoints; colors indicate the season that the tag popped up (blue, January–March; white, April–June; red, July–September; black, October–December). The two endpoints from the double-tagged fish, age ~7 upon release, are the yellow circle (June 1997) and triangle (May 2000). This image is an averaged composite SST image for December 1999 to July 2000 at 9 km resolution.

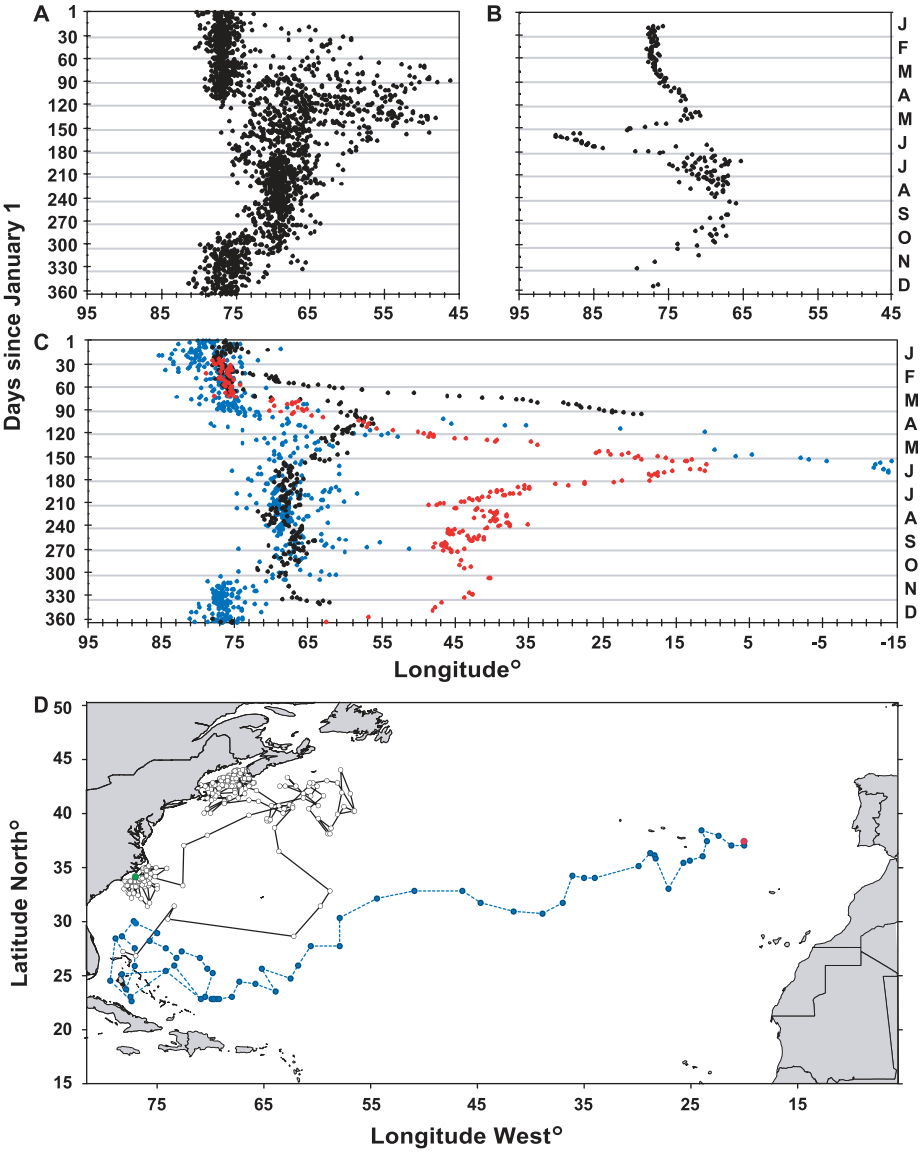

Fig. 2. Movements of bluefin tuna tagged in the west. (**A**) Longitude data from 19 fish with a western resident pattern, from implantable archival tags and PSATs with onboard geolocation. Eleven of these fish were potentially mature (≥8 years) during the first breeding season upon release (*21*). Eight were immature fish. (**B**) Longitudes for a bluefin that measured 207 cm in curved fork length (512, age ~8.5 years) that went to the Gulf of Mexico. (**C**) Longitudes for three bluefin that crossed to the eastern Atlantic or Mediterranean Sea. Black dots are bluefin 521, age ~9.3 years at release, that displayed 1 year of western residency (1999) and then moved to the east Atlantic in 2000. Individual 408 (blue) is age ~8.3 years at release. This fish remained 3.4 years (1997, 1998, 1999, winter 2000) in the western Atlantic before migrating to the Mediterranean Sea, where it was recaptured south of Malta in June 2000. Red circle is bluefin 485, an ~8.5-year-old fish that moved into the eastern Atlantic and back the year of release. (**D**) Longitudes and latitudes for 2 years (black, 1999; blue, 2000) of a bluefin that resided 1 year in the west Atlantic and moved to the eastern Atlantic in 2000, where it was recaptured. Longitude estimates were based on light-level data (*14, 20, 21, 29*). Calibration tests on oceanographic moorings indicate that the longitude estimates have an accuracy of 0.15° to ~1.2° (*11, 20, 30*). Latitude estimates were based on comparisons of SST collected on the archival tag with satellite-derived SST data along the longitude (*21*). Green circle, release point; red circle, position of recapture obtained with a GPS. The recapture position is 19.5 nautical miles from the calculated endpoint position. Additional fish have similar tracks (A to C); however, for clarity, only the above were shown.

An electronic tagging program was initiated in the western Atlantic in 1996 to examine the migrations and biology of bluefin tuna (*11, 12*). Implantable archival tags and pop-up satellite archival tags (PSATs) were used to log the movements, physiology, and oceanographic preferences of bluefin tuna (*11–20*). The relation between the movements and behaviors of organisms can be linked directly to oceanographic processes when the light-based geolocation estimates and the biology and physical oceanographic data from the tags are combined with satellite-derived sea surface temperature (SST) and ocean color images. Archival tags and PSATs (*11, 12*) were surgically implanted or externally attached in 377 bluefin tuna off the east coast of North America (*21*); four of these fish were tagged with both types. Recapture of 49 of 279 (18%) archival-tagged bluefin tuna and data acquisition from 90% of the 98 deployed PSATs provides an opportunity to examine the biology of Atlantic bluefin tuna across their range.

Recapture locations (Fig. 1) of the archival-tagged bluefin tuna primarily reflect the regions of known commercial fisheries in the western Atlantic (n = 34), eastern Atlantic (n = 7), and Mediterranean Sea (n = 8). Archival-tagged fish have been recaptured in both major spawning areas, the Gulf of Mexico and eastern Mediterranean Sea. Thirty-one percent of archival recaptures of western-tagged bluefin were in the eastern Atlantic or Mediterranean fisheries. Conventional tag-recapture data from 7065 bluefin tagged in the winter Carolina fishery (1994–2000) overlap the archival recovery locations (*22*). To date, 292 (4.1%) conventionally tagged Carolina bluefin have been recaptured; 124 (42%) were off New England, 3 (1%) in the Gulf of Mexico, and 28 (10%) in the eastern Atlantic and Mediterranean Sea. The remainder were recovered near their release locations. Both archival and conventional recapture data show that west-to-east movement is occurring.

Records obtained from the returned archival tags range from 0.2 to 3.6 years (*21*). Four behavioral trends are evident (Fig. 2): (i) western residency for 1 year or more with no visitation to known spawning areas, (ii) western residency for 1 year with Gulf of Mexico visitation during the breeding season, (iii) trans-Atlantic movements from west to east Atlantic and back in the same year, and (iv) trans-Atlantic movements to the east Atlantic or Mediterranean Sea after 1 to 3 years of western residency.

Most bluefin tuna remained in the vicinity of release off the North Carolina coast (75.5° to 76.3°W ± 0.5°) in winter and proceed offshore in early spring (Fig. 2, A, C, and D). Offshore movements were along the Gulf Stream, due east toward Bermuda or southeast toward the Bahamas. The majority of bluefin tuna displayed a western resident track the year after release, moving from the Carolinas along the Gulf Stream northern edge in spring and toward the New England and Canadian shelf in early summer (65° to 70°W). The fish remained on the continental shelf through autumn and returned to the Carolinas or Bahamas by winter (Fig. 2, A and D). These movements are corroborated by depth data (Fig. 3). Bluefin tuna show bathymetrically constrained diving while on the shallow continental shelf in the Carolinas and New England, and much deeper dives (maximum 1000 m) while offshore. The western resident bluefin tuna, which included both adolescents and adults, did not visit a known spawning ground. However, some bluefin with this movement pattern, assumed to be mature on the basis of length measurements upon release (*21*), were located in the Blake Plateau region (southeast of the Carolinas) or the Bahamas in late winter and spring.

Twelve archival-tagged bluefin tuna showed visitation to major breeding grounds during the spawning season. Four fish were recaptured in or traveled to the Gulf of Mexico. Several bluefin displayed one or more years of western residency before movement to the Gulf of Mexico. Thus, a western resident track without visitation to a known spawning ground (Fig. 2A) may be indicative of a feeding route taken by an immature fish. One bluefin (Fig. 2B) migrated into the Gulf of Mexico the year of release. This female moved from the Carolinas in winter to northern Gulf Stream waters in spring, and migrated rapidly to the Gulf of

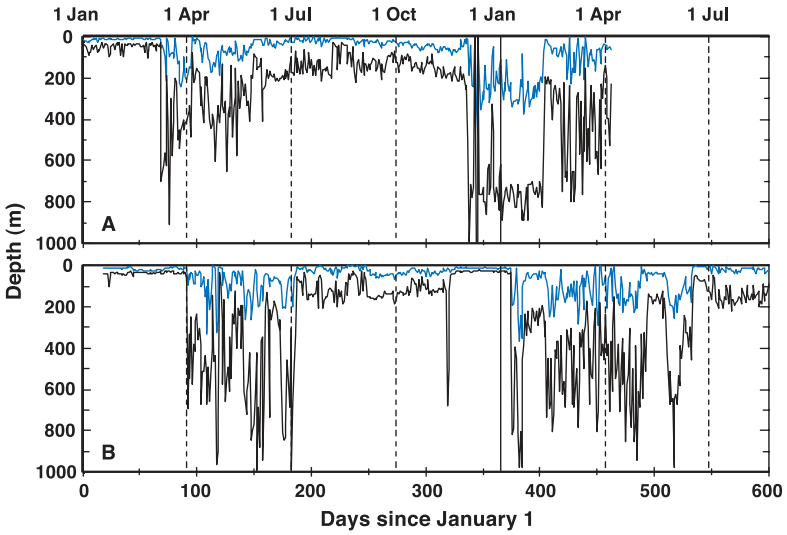

Fig. 3. Maximum (black) and mean (blue) daily depth of two bluefin in the western North Atlantic. Mean depths are calculated for each day from all pressure measurements at 120-s intervals. Maximum depth is the single deepest depth recorded in the 24-hour period. (**A**) Bluefin (521, ~9.3 years of age) that displayed western residency in 1999 before a trans-Atlantic crossing in 2000. (**B**) The ~8.5-year-old bluefin (512) that showed visitation to the Gulf of Mexico in 1999, the year of release. Breeding in the Gulf is proposed for 14 days in June where a relaxation of deep-diving behavior is evident (days 161 to 175).

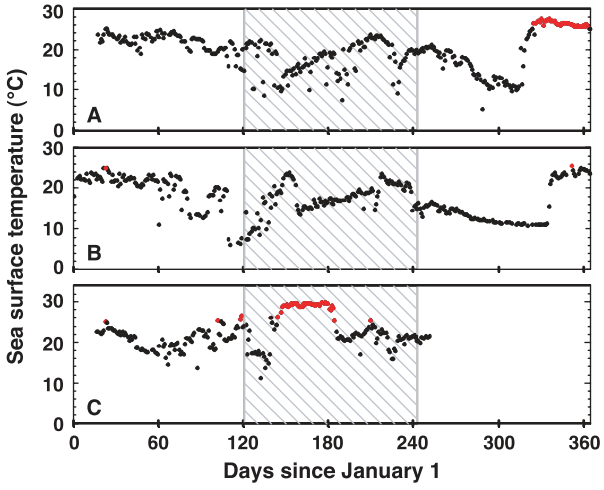

Fig. 4. A year in the life of western resident bluefin tuna, based on SST from archival tags. (**A**) Bluefin 667, (**B**) 521, and (**C**) 512 are ~9.9, 9.3, and 8.5 years of age, respectively, as assessed by length at release (*21*). Red indicates SSTs ≥25°C. The proposed duration of the western breeding season is shown in the cross-hatched area. Temperature and pressure were sampled every 120 or 128 s. The maximum daily SST recorded in the depth interval 0 to 2 m is used. Warmest temperatures during the spawning season are associated with the Bahamas in (A), a warm core ring in (B), and the Gulf of Mexico in (C). Warm temperatures in winter are in the Bahamas [(A) and (B)].

Mexico in early June 1999. For 15 days (9 to 23 June), the bluefin remained near 86° to 90°W, north of 26°N, where surface water temperatures ranged from 28.0° to 29.6°C (Figs. 4C and 5A). The fish exited the Gulf in late June and traveled toward northern waters. Seven bluefin tuna were recaptured in the eastern Mediterranean, south of Malta, or north of Sicily in mid-May and June. The positions of recapture span 4 years (1998, 1999, 2000, 2001) and overlap a region where numerous bluefin larvae are collected (*23*).

The satellite-derived endpoint positions of 88 PSATs (*12, 21, 24*) released from three locations show seasonal distribution patterns similar to the light-derived archival locations of western resident bluefin (Figs. 1 and 2A). In winter, bluefin tuna endpoints were off the Carolina coast or offshore in the western Atlantic. In spring and early summer, the fish were in the Gulf Stream, the mid-Atlantic, or the Gulf of Mexico. Three PSAT endpoint positions were east of the 45°W meridian, but no PSATs surfaced in the Mediterranean Sea. Although more than 50% of the PSAT tags were on fish long enough to show trans-Atlantic movements (>40 days), the endpoint positions were primarily in the western Atlantic, overlapping many of the implantable archival tracks.

One double-tagged Carolina bluefin tuna had a PSAT endpoint position off Massachusetts in June 1997, suggestive of western residency the year after release. However, the same fish was recaptured with an archival tag in May 2000 near Madeira (Fig. 1). This double-tagged bluefin tuna indicates the challenges of interpreting movement patterns from a single satellite-derived endpoint position and reveals the value of implantable archival tag records that span multiple years with continuous geolocation.

The recovered archival tags provide a repertoire of daily and yearly vertical movement patterns, environmental preferences, and behavioral information on breeding and feeding (Figs. 3 to 5). Bluefin tuna most often occupy the upper 300 m of the water column and occasionally dive to depths of 1000 m (Fig. 3). The SSTs were examined for periods of residency in waters considered warm enough for breeding (Fig. 4). Few individuals experience the significant warming evident in the SST record of the bluefin tuna in the Gulf of Mexico. The female tracked in Fig. 4C displayed a distinctive diel oscillatory diving behavior that may be indicative of spawning (Fig. 5A). The diving pattern consisted of regular nighttime surface intervals and short dives into the thermocline, where ambient temperatures were cooler than the 29°C surface waters. The proposed breeding activity shows up as a brief shallow period in the maximum diving record (Fig. 3B, day ~165), distinct from the deeper depths (presumed feeding dives) before and after this event.

Tuna are known to spawn in SSTs above 24°C, although for bluefin tunas there is little information (*25*). A warm ambient SST signal, indicative of potential breeding activity, was absent in most of the western resident tracks during the spawning season (Fig. 4). At least eight of the records in Fig. 2A are for immature fish, so this result is not unusual. For fish that remained in the west Atlantic for 1 year or more, and later displayed trans-Atlantic movements, the west Atlantic SSTs appear to be water masses encountered during feeding, before these fish returned to the breeding ground in the eastern Mediterranean. Alternatively, it is possible that some of western resident fish (Fig. 4A) are breeding outside the Gulf of Mexico (*3, 6, 16*). Several fish that were large enough to be considered mature display occupancy in waters warmer than 23°C for short durations throughout the year. These warm-water encounters included locations in warm core rings off New England (Fig. 4B), Gulf Stream waters off North Carolina, the Florida-Georgia Bight, the Bahamas, Bermuda, and the eastern Caribbean Sea. One bluefin tuna offshore of North Carolina in June displayed a warm SST signal and an oscillatory diving record that was similar to the Gulf of Mexico fish presumed to be breeding. Bluefin tuna larvae have been found off the Carolina coast (*6*). However, no mature bluefin with hydrated oocytes have been recorded from this region.

The elevated body temperatures of bluefin tuna increase their capacity for rapid migrations by enhancing the power output of their muscle (*4, 26, 27*). By placing the archival tags in the peritoneal cavity, it was possible to measure elevations in body temperature. Large thermal gradients between ambient and internal temperature are evident (Fig. 5B). Individuals experienced a wide range of environmental temperatures (2.8° to 30.6°C) and maintained relatively constant internal peritoneal temperature (~25°C) and a thermal excess up to 21°C above ambient.

Electronic tagging data yield important insights about bluefin movements and biology. West Atlantic bluefin tuna move to the Gulf of Mexico and the eastern Mediterranean Sea during the known breeding season. This emphasizes the need to protect both major spawning regions, as they directly influence the western fishery. Both adolescent and mature western-tagged bluefin tuna display western residency for 1 to 3 years without movement to a known breeding ground. During this period, bluefin tuna show fidelity to New England in the summer and to North Carolina, Blake Plateau, or the Bahamas in winter; they often range into the mid–North Atlantic in spring and summer, presumably following the annual cycles of productivity. Western-tagged bluefin are capable of moving from the continental shelf of North America into the eastern Atlantic in 40 days. Western bluefin tuna migrate from the west Atlantic to the east and back again in the same year. The results indicate that western-tagged bluefin are vulnerable to fishing mortality from all Atlantic bluefin tuna fisheries.

The natal origins of the western-tagged trans-Atlantic migrants remain unknown. Western fishers may be exploiting bluefin tuna of eastern Atlantic origin. Eastern migrants might be feeding in productive western

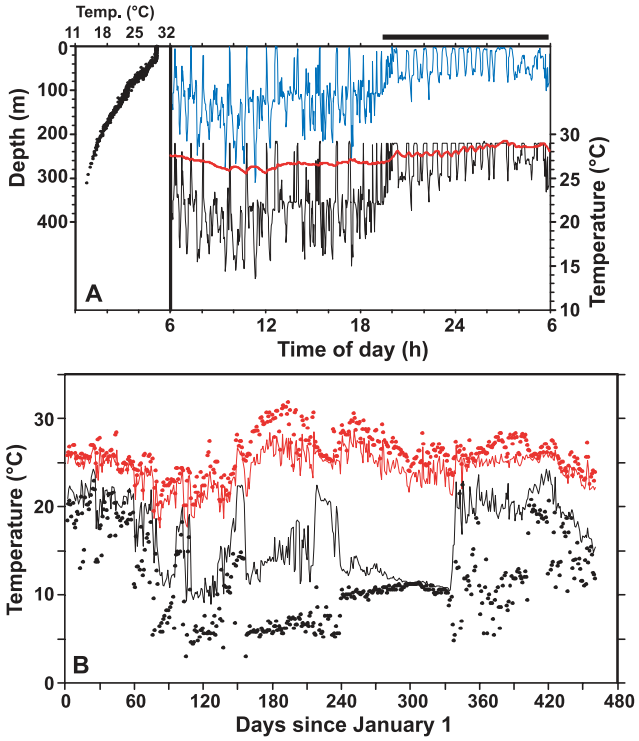

Fig. 5. (**A**) Daily depth (sampling interval, 2 min) and temperature profile of a female bluefin tuna on the Gulf of Mexico spawning grounds. A pronounced nighttime (black bar) oscillatory diving pattern with prolonged surface intervals occurs for 14 days in June. Diving before and after spawning is not diel and is associated with deeper dives (Fig. 3B). Temperature-depth profile is for a 24-hour interval on the same day. Blue, depth; black, ambient temperature; red, peritoneal temperature. (**B**) Daily mean ambient (black line) and peritoneal (red) temperatures collected in 120-s intervals for 1.5 years of fish 521. Minimum ambient temperatures (black dots) and maximum internal peritoneal temperatures over a single day's records (red dots) are shown.

North Atlantic regions but returning to the eastern Mediterranean to breed. These large-scale movements between feeding and spawning grounds are comparable to those of Pacific and Southern bluefin tuna (*13, 20, 28*). Pacific bluefin migrate from the western Pacific to the North American continental shelf and remain residents for 2 to 5 years before returning to the western Pacific to spawn (*13, 28*). Rapid movements of thousands of kilometers are common in tunas and other highly migratory species. This suggests that the metabolic costs for endothermic fish swimming across ocean basins are low in comparison to the ecological benefits.

The recovery of Atlantic bluefin tuna breeding stocks is linked to the extent of contemporary mixing of mature Atlantic bluefin, as well as to their spawning site fidelity. The electronic tagging data indicate that mixing between the two management units exists at a higher level than ICCAT has incorporated into base-case stock assessments. Although mixing occurs on western and eastern feeding grounds, bluefin tuna may be sorting to major spawning grounds in the eastern Mediterranean and Gulf of Mexico. Extensions to the western breeding area may include the Bahamas, Caribbean, and offshore Carolina waters in late spring and early summer. Future assessments of stock status should evaluate the new information and reassess the management strategies applied to Atlantic bluefin tuna.

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Infiltration of a Hawaiian Community by Introduced Biological Control Agents

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To examine the community-wide effects of introduced biocontrol agents on Kauai Island, Hawaii, we constructed quantitative food webs showing interactions among plants, moths, and moth parasitoids in a native forest. Eighty-three percent of parasitoids reared from native moths were biological control agents, 14% were accidental immigrants, and 3% were native species. Although parasitism by biological control agents reached 28% in some species of moth, all biocontrol agents reared had been released before 1945. This study highlights the importance of considering the potential damage caused by an introduced control agent, in addition to that caused by the target alien species.

The ecological impact of intentionally introduced biological control agents of insect pests is controversial. Some blame the practice for extinctions of native species (*1*), some call for increased regulation (*2*), and some insist that biological control is safe (*3*). The debate is fueled largely by anecdotal reports (*4–6*). A major point of contention surrounds the question of whether nontarget effects, such as those of the snail *Euglandina rosea* on Pacific islands (*7*) and of the lady beetle *Coccinella septempunctata* in North America (*8*), represent isolated events or more general impacts. A few studies address nontarget effects quantitatively at the community level. Louda *et al.* (*9*) measured the attack rate on native thistles by *Rhinocyllus conicus*, a weevil introduced to the United States and Canada to control exotic thistles. They concluded that the amount of seed destroyed by this biological control agent could potentially threaten some native thistles and consequently their native seed predators. The effects of the exotic moth *Cactoblastis cactorum* on native *Opuntia* species in Florida have been quantified (*10*); potential long-term effects include lower survivorship of younger plants.

Quantifying the mortality of insects from alien parasitoids and predators is more difficult because parasitoids and predators are hard to observe in the field. Boettner *et al.* (*11*) deployed, in the field, "sentinel" larvae of two native silk moth species in New England to measure the attack rate by *Compsilura concinnata*, a parasitoid fly originally introduced for control of gypsy moths. They found high levels of parasitism, up to 100% in some cases, and suggested that nontarget effects could potentially be responsible for extinctions, at least locally, of native species.

Indirect effects on native species are the most difficult to assess. An insect herbivore introduced to control a weed could be attacked by generalist native parasitoids that also have native hosts (*12*). If the weed biological control agent is abundant, then there is the potential for apparent competition (*5*, *13*) between the agent and native herbivores, mediated via shared native parasitoids. Thus, even the introduction of an entirely species-specific herbivore, presumed to have no nontarget effects, still could have a community-wide impact. Only by understanding how invasive species interact within the context of the entire community can we hope to

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