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Movements of pacific bluefin tuna (*Thunnus orientalis*) in the Eastern North Pacific revealed with archival tags

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ABSTRACT

In this study, 253 Pacific bluefin tuna were archivally tagged off the coast of California, USA and Baja California, Mexico between August 2002 and August 2005. One hundred and fifty-seven fish were recaptured and 143 datasets were obtained and analyzed, yielding electronic tag datasets of up to 1203 days. Mean days at large for the 143 fish was 359 ± 248 (SD) days. A total of 38,012 geolocations were calculated from light-based longitude and SST-based latitude estimates, allowing us to examine the seasonal movement of juvenile bluefin tuna off the west coast of North America. Electronic tagged bluefin tuna showed repeatable seasonal movements along the west coast of North America. Bluefin tuna were found farthest south in the spring when they were located off southern Baja California, Mexico and farthest north in the fall when fish were found predominately off central and northern California. Fish showed latitudinal movement patterns that were correlated with peaks in coastal upwelling-induced primary productivity. Interannual variation in the locality of these productivity peaks was linked with a corresponding movement in the distribution of tagged fish. Overall geographical area occupied by tagged bluefin varied with primary productivity, with fish being more tightly clustered in areas of high productivity and more dispersed in regions of low productivity. In the spring through fall, bluefin tuna were located in areas with the highest levels of primary productivity available in the California Current ecosystem. However, in the winter months, tagged bluefin tuna were found in areas with lower productivity compared to other regions along the coast at that time of year suggesting that during the winter, bluefin tuna are feeding on aggregations of pelagic red crabs, sardines and anchovies that preferentially spawn in areas of reduced coastal upwelling.

1. Introduction

Pacific bluefin tuna (*Thunnus orientalis*) are one of three species of bluefin tuna that inhabit subtropical to subpolar seas throughout the world's oceans. Among *Thunnus*, Pacific bluefin tuna have the largest individual home range, being found throughout the North Pacific and ranging into the western South Pacific (Collette and Nauen, 1983; Bayliff, 1994). They spawn in the region between the northern Philippines and central Japan during the months of April through August and are thought to comprise a single stock (Sund et al., 1981; Bayliff, 1994). Most Pacific bluefin tuna remain in the western Pacific after being spawned but a portion make extensive migrations into the eastern Pacific late in the first or second year (Bayliff, 1994; Inagake et al., 2001). It has been hypothesized that the trans-Pacific migrations from west to east are linked to local sardine abundances off Japan (Polovina, 1996). When sardine populations are low, a greater percentage of bluefin tuna are proposed to move to the eastern Pacific. Sardine abundances in the North Pacific have been shown to fluctuate on decadal scales in concordance with large-scale atmospheric variations (Chavez et al., 2003). Likewise, bluefin tuna populations have also appeared and disappeared off the west coast of North America in phase with these decadal regime shifts (Polovina, 1996). Once in the eastern Pacific, individual bluefin tuna remain in North American coastal waters for up to 4 years before making the return migration to the western Pacific to spawn (Bayliff, 1993). Movements and distributions during certain times of the year, particularly fall and winter, are less well known as fisheries in the eastern Pacific do not encounter bluefin tuna at these times (Bayliff, 1994).

Given their expansive home ranges and migratory abilities, electronic tagging has been important in the study of the biology of bluefin tunas. The recent development of electronic tagging technologies for studying oceanic animals has provided information on movements and behavior that previously had not been possible to collect (Metcalfe and Arnold, 1997; Block et al., 2001,

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2005). Movements of juvenile bluefin tuna in the western Pacific have been studied extensively using electronic tags (Kitagawa et al., 2000, 2002, 2004; Inagake et al., 2001; Itoh et al., 2003a,b). Most juvenile and adolescent bluefin tuna have been shown to reside predominately in the Sea of Japan and along the Kuroshio Current but individual fish ranged widely. Electronically tagged fish have crossed the Pacific from west to east in as little as 66 days (Itoh et al., 2003a). Although overall geographical distributions are wide, it is thought that temperature limits the potential habitat of juvenile bluefin tuna in much of the North Pacific Ocean (Itoh et al., 2003b; Kitagawa et al., 2004). Temperatures experienced by tracked fish have consistently ranged between 14 °C and 20 °C in the western North Pacific (Itoh et al., 2003b; Kitagawa et al., 2004; Inagake et al., 2001). Limitations on bluefin tuna distribution in relation to temperature are proposed to exist both horizontally and vertically as fish spent the majority of their time on the warm side of thermal fronts as well as above the thermocline (Kitagawa et al., 2004). In addition to seasonal movements in relation to temperature, Inagake et al. (2001) have suggested movement patterns of bluefin tuna in the western Pacific relate to chlorophyll *a* concentrations, although these data were treated qualitatively.

In the eastern Pacific, several researchers have used electronic tags to study the movement patterns and behavior of bluefin tuna. Like fish in the western Pacific, juvenile bluefin tuna vertical distributions appear to be limited by the thermocline in the eastern Pacific, as fish spent the vast majority of time in the surface mixed layer (Marcinek et al., 2001; Kitagawa et al., 2007). However, tracking in the eastern Pacific has shown that bluefin tuna can tolerate extended periods of time in cooler waters of 12–14 °C, where they maintain slow-twitch swimming muscle temperatures of up to 12 °C above ambient (Marcinek et al., 2001; Kitagawa et al., 2007). Visceral temperatures in juvenile bluefin tuna in the eastern Pacific fluctuate with feeding activity and have daily maximal thermal excesses as high as 14 °C (Kitagawa et al., 2007). Although the endothermic capabilities of bluefin tuna act to minimize the range of temperatures to which the muscles and peritoneal cavity are exposed, the heart remains at ambient temperatures (Blank et al., 2004). Heart rate, stroke volume and cardiac output have all been observed to be temperature dependant and the cardiac system has been proposed to be the major limitation to thermal range expansion in tunas (Blank et al., 2004; Landeira-Fernandez et al., 2004). Marcinek et al. (2001) also proposed that high residency above the thermocline may be a way to maximize prey encounter rates even when temperatures at depth are not limiting.

Seasonal movements of bluefin tuna in the eastern Pacific have also been examined using archival tags. Domeier et al. (2005) tracked three fish and observed movement along the coast of North America between southern Baja California and the California/Oregon border. Tagged fish were found farthest north along the North American coast in the fall and farthest south in the winter through spring (Domeier et al., 2005). Similar seasonal movement patterns were observed in 18 archivally tagged fish, which were also included in the analyses presented in this manuscript (Kitagawa et al., 2007). These seasonal distributions have been correlated with shifts in sardine catch distribution along the California coast (Kitagawa et al., 2007).

The waters off the west coast of North America are one of four major eastern boundary current ecosystems. These areas are characterized by high productivity, high biomass, low biodiversity and a low number of trophic exchanges between primary production and fish production (Ryther, 1969). Middle trophic levels show particularly low diversity, being composed mainly of two clupeoid species, Northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*) in the case of the California Current. This "wasp's waist" trophic structure means that the abundance and distribution of these species exert an enormous influence on the abundances and distributions of higher trophic levels (Cole and McGlade, 1998). The distribution and abundances of clupeoid species is greatly affected by biological oceanographic parameters, particularly primary production (Smith and Eppley, 1982; Barber and Chavez, 1986). The low number of tightly linked steps between primary production and the highest trophic levels coupled with low biodiversity of the primary prey items of tunas in the California Current provide for an ideal area in which to examine the effects of oceanography on the distribution and seasonal movements of bluefin tuna. In addition, the long-term nature of this study allows for the examination of movement patterns in the context of interannual environmental variation. This allows a better assessment of how bluefin tuna movement patterns are affected the variable environment of the California Current ecosystem.

2. Materials and methods

2.1. Archival tags

In this study, we used the LTD 2310 archival tag (Lotek Wireless Inc., Newmarket, Ontario, Canada). The tag body contains pressure and internal temperature sensors and the stalk contains light level and ambient temperature sensors. Individual tags were programmed to archive depth and temperature data every 4–120 s and also recorded light level data every 60 s. Onboard tag software used pressure sensor readings to calculate the attenuation of light level with depth. These depth corrected light level readings were then used to estimate times of sunrise and sunset from which it was possible to estimate daily longitude (Ekstrom, 2004). These longitudes were stored to a "day log" along with daily sea surface temperatures (SST), both of which were used in subsequent latitude estimation. Tags released in 2002–2003 were "A" series tags with 8 MB of memory. Tags deployed in 2004–2005 were "C" series tags with 16 MB of memory.

2.2. Tagging procedure

Tagging was performed through one of two methods. Bluefin tuna tagged in July and August were captured from a long-range sport fishing vessel, the F/V Shogun, along the coast of southern California and northern Baja California. Fish were caught on rod and reel from the 22 m fishing vessel Shogun using heavy tackle (27-kg line) and barbless circle hooks to minimize trauma to the fish. The fish was then placed in a vinyl v-shaped pad and a saltwater deck hose was placed in the mouth to ventilate the gills. During surgery, a 3–4 cm incision was made in the ventral wall of the fish and a 10-cm stainless steel trocar was used to make a passageway for the tag in the abdominal cavity (Block et al., 1998). The tag was soaked in betadine antiseptic and was inserted into the peritoneal cavity. The stalk of the tag containing the ambient temperature sensor and light sensor remained outside of the fish. The tagging incision was closed by making one or two stitches with monofilament veterinary suture (Ethilon CTX-830H, Ethicon Inc.). Upon completion of surgery, two uniquely numbered conventional tags were placed in the dorsal musculature of the fish and the fish was released by sliding it off the v-pad into the water.

Fish tagged in November 2002 and March 2005 were obtained from commercial bluefin tuna pens of Mariculture del Norte, located south of Bahia Todos Santos along the coast of Baja California (31.67°N, 116.79°W). For these operations, fish were captured in the pens using a baited handline and brought aboard floating barges positioned on the edge of the pens. Fish were placed on v-shaped vinyl pads and surgery was performed in the same manner as for fish caught on rod and reel. Tagged fish were then placed in a 20-m tow pen that was then towed approximately 20 km offshore and the fish were released together by opening up the net. This was done to keep the fish from remaining in the vicinity of the penning operations where they had been held and fed for several months. It also allowed for the assessment of the health of the tagged bluefin tuna for the first day after tagging and to observe any mortality of tagged fish.

Forty-nine Pacific bluefin tuna were tagged and released in August 2002 (mean curved fork length = 101 ± 18.6 cm), 22 fish in November 2002 (mean curved fork length = 94 ± 7.4 cm), 110 in July 2003 (94 ± 4.58 cm), 8 in August 2004 (82 ± 8.0 cm) 42 in March 2005 (125 ± 6.9 cm) and 22 in August 2005 (82 ± 15.4 cm; Table 1).

2.3. Analysis

For all tags, geolocation positions were estimated using the methods reported in Teo et al. (2004). Longitudes were calculated onboard the tag using threshold light technique methods (Ekstrom, 2004). Depth sensor drift was compensated for by assuming that bluefin tuna surfaced at least once per day and then fitting a third-order polynomial to the minimum daily depth. This polynomial was then subtracted from the raw pressure readings to calculate drift-corrected depth readings. Daily longitudes were paired with tag-collected SST to estimate latitude with temperatures considered SST if the corresponding corrected pressure reading was less than 1 m. Tag-calculated longitude estimates were filtered by eliminating points that showed movement of more than 2° longitude per day. This speed was considered biologically relevant based on previous acoustic tracking studies on fish of a similar size range (Marcinek et al., 2001). For matching of tag recorded and satellite-derived SST, the latitudinal search area ranged from 20°N to 60°N and the maximum latitudinal movement between successive geoposition points was set at 1° per day. A land mask was added and movement over land was not permitted. This was particularly important in the region of the Baja peninsula. Comparisons of the calculated geolocation within a day of recapture to the reported recapture position yielded geolocation error estimates of 0.51 ± 0.47° in longitude and 1.69 ± 1.46° in latitude.

Movement and environmental preferences of bluefin tuna were examined while fish were in the California Current ecosystem. The study area was defined as the region from the southern tip of the Baja California peninsula (23–45°N) and from the coast to 5° offshore. Geolocation points outside of this region were not included in further analyses. In addition, the first month of data from fish released from holding pens was not included as these fish were released at times when wild fish were not located near the pen area. Within a month, wild fish and pen-released fish distributions overlapped considerably so data after this period were considered representative of normal behavior and were included in analyses. From these remaining points, mean latitude and tag-collected SST were calculated over all fish for every day. For comparisons of age classes, a release age was calculated from fish fork length using the conversions for Pacific bluefin tuna (Bayliff et al., 1991). Ages over the course of the track were then updated by adding release age to time at large. Comparisons of mean daily latitudes and SST among years and age classes were performed using a Wilcoxon rank sum test (Sokal and Rohlf, 1995). Age class 1 (1–2 year olds) and age class 2 (2–3 year olds) were combined, as were age classes 4 and 5 as sample sizes were small at the oldest and youngest ages.

For density maps, a temporally uniform dataset was used in order to weigh all fish and regions equally. To conduct this analysis, daily geolocations were linearly interpolated using a great circle distance for days on which it was not possible to calculate a geolocation. A total of 4518 points (10.6%) were interpolated. To calculate seasonal density maps, a kernel density with a search radius of 1.0° was used in ArcGIS v. 9.1 (Silverman, 1986). All seasons were delimited by their respective solstices and equinoxes. In addition to seasonal densities, kernel home range was determined for the period of 20 October–6 November for 2002–2004 using the least squares cross validation method (Worton, 1989). From these data, the 25%, 50%, 75% and 95% habitat utilizations were calculated using the Animal Movement Extension in ArcView 3.2.

Latitudinal movements of bluefin tuna were compared to coastal peaks in primary productivity along the west coast of North America. Primary productivity satellite data were obtained from the National Marine Fisheries Service, Pacific Fisheries Environmental Laboratory. Primary productivity measures were derived from chlorophyll *a* concentrations calculated from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) satellite and converted using the methodology outlined in Behrenfeld and Falkowski (1997). Primary productivity is the amount of photosynthetically fixed carbon available to the first heterotrophic level and therefore represents a more important measure of energy available to higher trophic levels than does chlorophyll *a* concentration. Eight-day composite satellite data were used in order to minimize the effect of cloud cover while still providing a useful time scale. Mean primary productivity from the coast to 5° offshore was calculated for each latitude from 23°N to 45°N in 0.1° latitudinal steps.

In order to examine latitudinal movements of bluefin tuna in the California Current ecosystem in relation to relative peaks in primary productivity, the latitude between 23°N and 45°N with the highest mean primary productivity was calculated for each 8-day period. This maximum value was then compared to other latitudes over that time period and the percent deviation from this maximum value was calculated for all other latitudes.

To examine the effects of localized peaks of primary productivity on fish behavior, metrics were calculated using a modified center of range analysis (Munger, 1984) to quantify aggregation and residency of tagged bluefin tuna. . A mean daily latitude and longitude were calculated over all fish for each day. The distances from this central position were calculated daily for each fish to calculate a mean distance from the center of mass. Periods of aggregation were compared to satellite-derived data to test if fish were more aggregated in areas with higher primary productivity. Values of primary productivity were extracted from satellite data for each

Table 1
Release and recapture information for Pacific bluefin tuna archivally tagged between summer 2002 and 2004.

Release dates	Number released	Release methodology	Length (cm, CFL[a])	Avg. track length (days)	# Recaptured	# Analyzed
5–11 August, 2002	49	Wild caught	101 ± 18.6	505 ± 341	32 (65%)	26
12 November, 2002	22	Pen release	94 ± 7.4	613 ± 326	9 (41%)	9
24–29 July, 2003	110	Wild caught	94 ± 4.6	350 ± 131	77 (70%)	74
20 August, 2004	8	Wild caught	82 ± 8.0	348 ± 134	4 (50%)	4
9 March, 2005	42	Pen release	125 ± 6.9	126 ± 21	33 (79%)	28
6 August, 2005	22	Wild caught	82 ± 15.4	10.5 ± 0.7	2 (9%)	2
Total	253		100 ± 16.3	359 ± 248	157 (62%)	143

[a] Curved fork length at tagging.

fish location for each day and a daily mean was calculated across all fish. These values were then compared to the mean distance from the center of mass for each day using a linear regression (Sokal and Rohlf, 1995).

Recapture rates of tagged fish were calculated separately for each year after deployment. For each successive year, the number of fish that had been recaptured was subtracted from the total number deployed. Consequently, recapture rates represent the number of fish still at large for a given year that were recaptured.

3. Results

Over the 4-year tagging period, 253 archival tags were deployed on Pacific bluefin tuna (Table 1). Fish tagged in March 2002 were significantly longer than fish tagged in other years, while fish tagged in August 2004 and August 2005 were significantly smaller than those tagged in other years (Student's *t*-test assuming unequal variance, $p < 0.01$). One hundred and fifty-seven (62%) electronically tagged fish were recaptured and datasets were recovered and analyzed from 143 fish for this study. The percent of tags that were recovered varied by deployment year and were also dependant on time at large. Most recovered tags were captured within the first year but recapture rates stayed relatively high (7–29%) for fish at liberty for over a year. From the recovered datasets, a total of 38,012 light and SST-based geolocation estimations were obtained. Time at liberty ranged from 4 to 1203 days (359 ± 248.5 days).

The geographic distribution of Pacific bluefin tuna was large with individual fish being found from the west coast of North America to the Sea of Japan in the western Pacific (Fig. 1). Seventeen fish showed movement offshore; defined as greater than 5° from the North American coast. Seven (4.5%) fish exhibited trans-Pacific movement, crossing the dateline at 180°W longitude. Two trans-Pacific fish subsequently showed movement back to the eastern Pacific with one individual traveling back to the western Pacific where it was recaptured. All other tagged fish remained in the region of the North American coast, within 5° of shore and the vast majority (37,520% or 98.7%) of daily geolocations were in this region. Offshore movements (>5° from shore) by individual fish started in the late fall through winter in all years, and the number of fish traveling offshore in the winter months varied among years with eight in 2003, six in 2004 and three in 2005.

Seasonal movements of bluefin tuna within the California Current ecosystem showed similar patterns among years with slight variations by fish and tracking year (Fig. 2). Fish were located farthest south, off the coast of southern Baja California in the spring

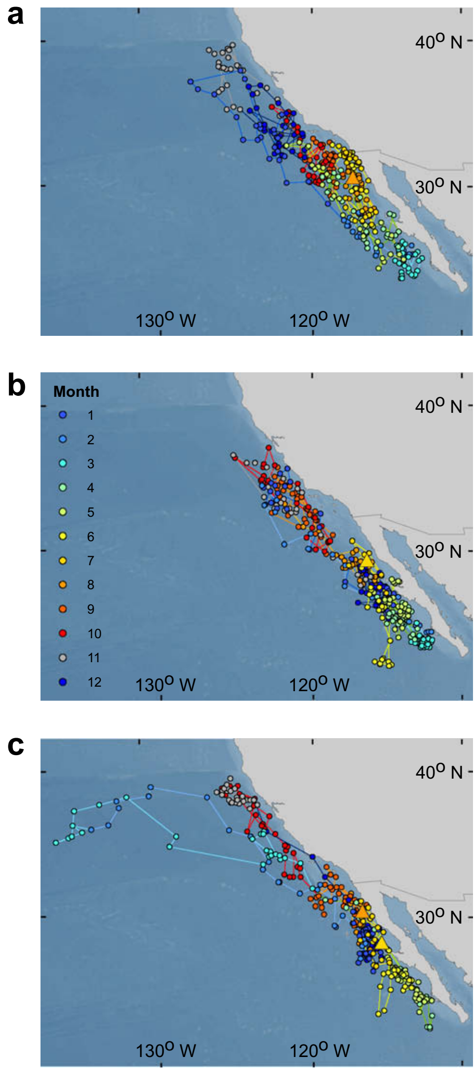

Fig. 2. Representative tracks calculated by light-based longitude and SST-based latitude, color-coded by month of tracking showing (a) 1 year of movement within the California Current ecosystem (tag A0475, 89 cm CFL at release; tagged 5 August, 2002 at 30.15°N, 116.83°W); (b) a second year of fish A0475 showing lower maximal latitude in the fall of 2003 than the previous year (recaptured 16 July, 2004 at 29.57°N, 117.25°W); (c) movement offshore in the winter before returning to the coast of North America in the spring by tag A0471, 112 cm CFL at release; tagged 5 August, 2002 at 30.15°N, 116.83°W; recaptured 22 July, 2003 at 28.58°N, 116.53°W. Release and recapture positions are shown as color-coded triangles.

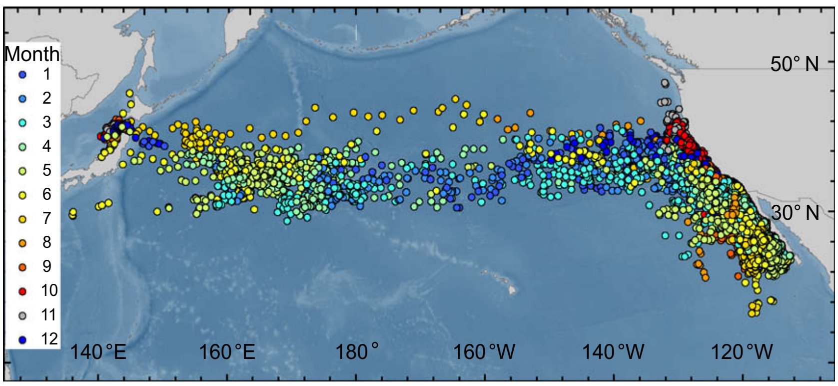

Fig. 1. Positions of all Pacific bluefin tuna tracked with archival tags, color-coded by month. Tracking data were obtained from 143 fish and 38,012 positions were obtained. Pacific bluefin tuna primarily occupy the eastern Pacific. Movement to the western Pacific ($n = 7$ fish) occurs in the winter while migrations back to the eastern Pacific occurred in the summer. Background is North Pacific bathymetry.

months. Bluefin tuna moved north into the Southern California Bight in the summer months, and extended their range farthest north along the North American coast in the fall. Winter months saw one of two patterns—movement offshore (Fig. 2c) or movement south to the waters off the coast of Baja California (Fig. 2a and b). Individual fish tracked over multiple years exhibited each of these movement patterns in different years.

Seasonal kernal density analyses of Pacific bluefin tuna distributions reveal areas of aggregation within the California Current by season (Fig. 3). Peak densities in the winter are found off the coast of Punta Eugenia, Baja California (27.8°N; Fig. 3a). The area of peak density moves south to the waters north of Magdalena Bay in the spring (24.6°N; Fig. 3b). In the summer months, most tagged fish were located in the Southern California Bight and Northern Baja, between Point Conception (34.45°N) and Punta San Antonio (27.9°N; Fig. 3c). In the fall, the range extended north with individual fish being found north of Cape Mendocino (40.45°N) but the region of highest density was in the area near Point Conception, California (Fig. 3d).

Tagged bluefin tuna showed similar latitudinal movement patterns among all tracking years (Fig. 4). As bluefin tuna within the California Current moved roughly parallel with the North American coast, plots of latitude versus time encompass the majority of the variation in movement pattern. Plots of latitude and mean daily SST over time show that tagged fish experienced the warmest mean SST (17.86–20.66 °C) during the summer months and the coldest mean temperatures (14.07–17.66 °C) during the late fall and winter (Fig. 4a). Although latitudinal movements of bluefin tuna showed the same general patterns among tracking years and age classes, some distinctions also existed. Fish tracked in 2002 moved significantly farther north in the fall (mean latitude 37.4°N) compared to other tagging years (mean latitudes 34.8–34.9°N, Wilcoxon rank sum test: $p < 0.05$; Fig. 4a and b). Sea surface temperatures experienced by tagged fish were also significantly cooler in the fall of 2002 (16.3 ± 1.4 °C) than over the same period for other tagging years (17.4 ± 1.4 °C, Wilcoxon rank sum test: $p < 0.05$; Fig. 4a). Tagged bluefin tuna also showed variation in fall distribution by age class (Fig. 4c). Fish over 4 years old (age classes 4–5) were found significantly farther north (38.3 ± 1.4°N) than fish in younger age classes (34.7 ± 2.6°N) in October of 2003 and 2004, the only years possible to make this comparison (Wilcoxon rank sum test: $p < 0.05$; Fig. 4c). Mean SST experienced by age 4–5 fish (16.2 ± 1.2 °C) were significantly colder over this time period compared to mean SST experienced by younger fish (17.8 ± 1.6 °C, Wilcoxon rank sum test: $p < 0.05$).

Latitudinal movements of tagged bluefin tuna followed the seasonal peaks in primary productivity along the California Current (Fig. 5a). Most fish were found at latitudes between 24°N and 27°N in the spring when the waters off southern Baja California, specifically the Punta Eugenia region, showed a strong peak in productivity (2811–4095 mg C/m^2/day between the coast and 5° offshore). Starting in late spring, the waters in the region of Point Conception (32–36°N) exhibited an increase in primary productivity (2059–2846 mg C/m^2/day) that lasted throughout the summer and into the fall, and most fish could be found at these latitudes at this time. The exception to this was in 2002 when the waters of Point Conception showed much reduced productivity while the area between 36°N and 40°N showed higher than average productivity (Figs. 5a and 6). Bluefin tuna distributions were similarly shifted north in 2002 in the fall compared to other years (Figs. 4–6). Throughout most of the year, bluefin tuna could be found in the region of the California Current ecosystem that showed the highest coast-wide levels of primary productivity at that time of year (Fig. 5b). This relative peak in productivity was found in the area of Punta Eugenia and southern Baja Mexico in the spring and in the region of Point Conception or Northern California in the summer and winter. The only season when bluefin distributions did not overlap with the coast-wide productivity maximum was in the winter. At this time of year the most productive waters could be found in the Point Conception region while most fish were found farther south, off central and northern Baja California (Figs. 3 and 5b).

Like the latitudinal movements, probability contours show that bluefin tuna positions overlapped with the regions of highest pri-

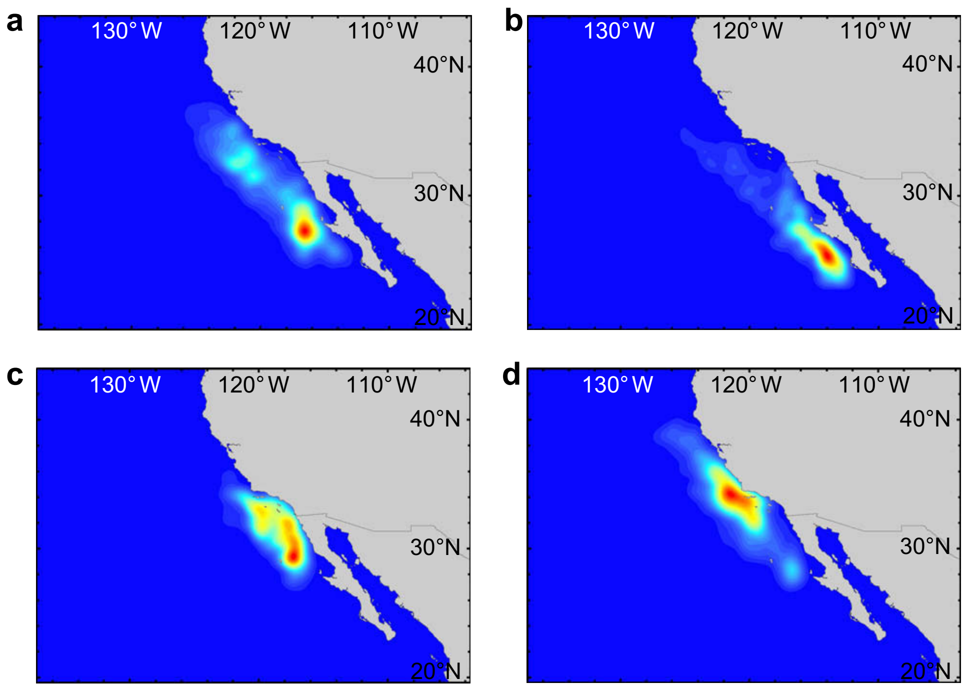

Fig. 3. Kernal density plots of Pacific bluefin tuna seasonal distributions in the California Current for: (a) winter, (b) spring, (c) summer, and (d) fall based on light and SST based geopositions. Kernal density values calculated with a one-degree search radius and an output cell size of 0.01°. Warmer colors indicate higher densities.

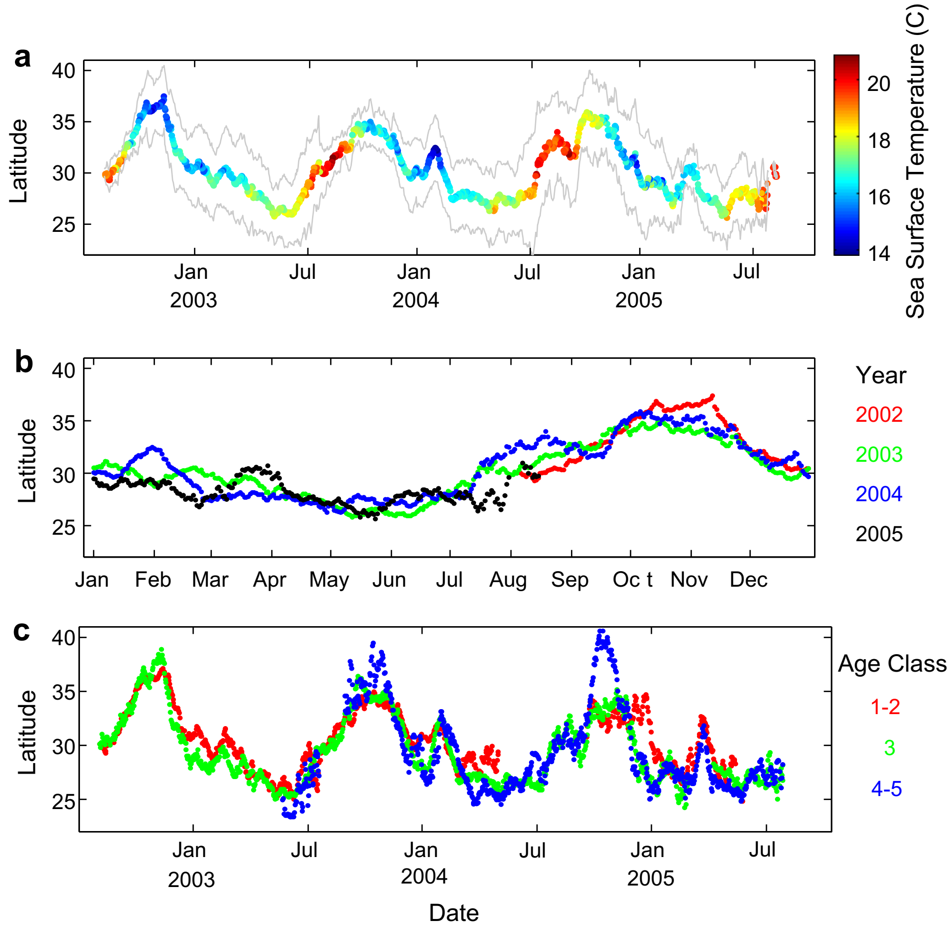

Fig. 4. Latitudinal distribution of tagged bluefin tuna in the California Current. (a) Latitude versus date with mean daily sea surface temperature recorded by the tags shown as colors. Upper and lower bounds denote one standard deviation in latitude values. (b) Latitudinal distribution by tracking year. Fish tracked in 2002 were significantly farther north in the fall. (c) Latitudinal distribution separated by age class. Bluefin tuna older than 4 years old were found at higher latitudes in the fall than fish of other age classes.

mary productivity (Fig. 6). Comparisons of bluefin tuna probability distributions over the period from 20 October to 6 November are shown over the primary productivity data for the period 8 October–24 October in Fig. 6. The peak in primary productivity was located farther north and offshore in 2002 relative to other years (Fig. 6a–c). Likewise, tagged bluefin were found farther north and offshore in 2002 (Fig. 6a). In fall of 2003, both the highest productivity and highest densities of bluefin tuna were found close to shore in regions directly north and south of Point Conception (Fig. 6b). Productivity levels were lower overall in the fall of 2004 and bluefin tuna densities did not match as well as in other years (Fig. 6c). However, both the highest concentrations of bluefin tuna and primary productivity could be found in the region around Point Conception in the fall of 2004.

Bluefin tuna also aggregated more tightly at times and in regions of higher primary productivity. Examining satellite-derived primary productivity values at all bluefin tuna positions revealed that tuna experienced the highest primary productivity in June through October (1403 ± 512.4 mg C/m^2/day; Fig. 7a). Fish experienced the lowest mean levels of productivity in the winter (687 ± 144.5 mg C/m^2/day). During the periods of high productivity, tagged bluefin tuna were found over a smaller area (mean distance from center of mass, 206 ± 78.4 km) than during the winter when productivity was low (333 ± 102.5 km; Fig. 7b). Over the entire 3-year dataset, primary productivity and mean area occupied by bluefin tuna were significantly negatively correlated ($r^2 = 0.1443$, $p < 0.001$). The association between increases in primary productivity and tighter aggregation in tunas was stronger at latitudes above 30°N ($r^2 = 0.2055$) than at latitudes below 30°N ($r^2 = 0.1255$).

4. Discussion

The area occupied by tagged bluefin tuna was large, with fish ranging throughout the North Pacific Ocean from the west coast of North America to the Sea of Japan (Fig. 1). Although total geographical area occupied was great, bluefin tuna tagged in the eastern Pacific spent the vast majority of time in the California Current ecosystem. Individual fish were observed to have remained in the coastal waters of Mexico and the United States for periods of up to 974 days. These results indicate that, although the total range occupied by bluefin tuna in the Pacific Ocean is expansive, primary habitat utilization may be much more restricted. From the age classes examined in this study, all fish were juveniles, thus residency times in the California Current are possibly higher than for older individuals. East to west trans-Pacific migration rates might be expected to be higher for older individuals since these fish may be undertaking migrations back to the spawning grounds in the western Pacific. Understanding the movement patterns, habitat preferences and ecology of juvenile bluefin tuna within this restricted area is, therefore, of great importance in understanding their biology and critical for future management.

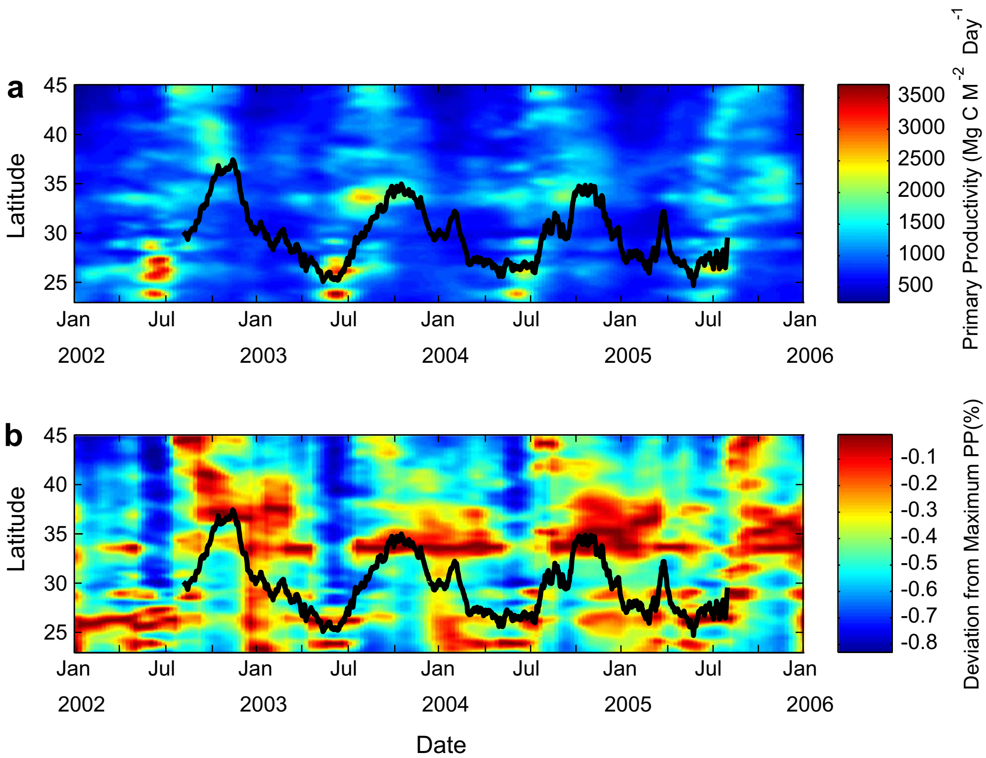

Fig. 5. (a) Latitudinal movements of tagged bluefin tuna in relation to coastal primary productivity. Mean coastal primary productivity was calculated from the coastline to 5° offshore. (b) Latitudinal movements of bluefin tuna in relation to relative weekly mean primary productivity. Maximum value of coastal primary productivity for each 8-day period is shown in red. Deviation from this maximum for each other latitude is shown as percent less than the maximum.

The limited range of bluefin tuna in the eastern Pacific can potentially expose these fish to greater fishing pressure. Recapture rates of archival-tagged bluefin tuna have been high (62%). Since most of the tagging was done in the same regions where the main commercial fisheries for bluefin tuna in the eastern Pacific are located (Bayliff et al., 1991), it is possible that recapture rates of tagged fish are an overestimate of total exploitation rate. Most recoveries have taken place within the first year after release, raising the possibility that fish were recaptured before they had time to migrate away from the main fishing areas. However, mean time at liberty for fish recaptured within 1 year of release was 256 ± 112 days, indicating that most tagged fish had enough time to depart from the tagging areas. Only seven fish were recaptured within 80 days of the release date. In addition, recapture rates remained high in the second and third year post release (20% and 29% for fish released in August 2002, and 26% and 7% for fish released in November 2002). These results suggest that true exploitation rates are high and fisheries in the eastern Pacific may catch a significant proportion of the bluefin tuna that migrate from the western Pacific. Catches in the eastern Pacific (863–9816 metric tons/year between 2000 and 2006) are generally smaller than in the western Pacific, averaging 18.6% of total Pacific catches between 2000 and 2006 (ISC, 2009). However, for some years, eastern Pacific catches may constitute over a third of the total Pacific catches, suggesting that these fisheries are an important component of fisheries mortality of Pacific bluefin tuna.

Migrations along the coast of western North America were highly stereotypical and likely determined by seasonally induced shifts in oceanography of this region. In this study, as well as in other electronic tracking studies of bluefin tuna in the eastern Pacific (Domeier et al., 2005; Kitagawa et al., 2007), fish were distributed from the southern tip of Baja California to north of 40°. All three studies saw the farthest movement north in the autumn and a concentration of bluefin tuna in the southern Baja California peninsula in the spring (Figs. 2–4). Kitagawa et al. (2007) attributed the seasonal movement into the waters north of Point Conception to an increase in seasonal upwelling that occurs in September–October in this region. As the coastal upwelling ended in the late fall and early winter, bluefin tuna moved back to the southern portion of their range. It was also during the late fall and early winter when tagged bluefin tuna exhibited the greatest amount of offshore movement (Fig. 2) and this may explain why bluefin tuna do not interact with commercial fisheries at this time of year (Bayliff, 1994). The high degree of similarity in movement patterns of bluefin tuna in the eastern Pacific among years and individuals, contrasts with similar tracking studies of bluefin tuna in the Atlantic Ocean (Block et al., 2001, 2005). Much greater variation in migration pattern was observed among individuals tracked in the Atlantic Ocean compared to fish tracked in the Pacific. This may be due to the fact that larger fish as well as a wider range of size classes were tracked in the Atlantic, as it has been seen that larger bluefin tuna range more widely than do smaller individuals (Block et al., 2005).

Although overall movement patterns were similar among all tracking years and age classes, some distinctions existed. Among age classes, bluefin tuna older than 4 years old had a significantly more northerly distribution in the fall (Fig. 4c). These fish were estimated to be between 124 and 155 cm in length. Range expansion with age has also been seen in Atlantic bluefin tuna (Mather et al., 1995; Block et al., 2005). Possible reasons for an increase in latitudinal range with age may have to do with an increased endothermic capacity with increased size allowing for penetration into colder waters due to higher thermal inertia and metabolic heat production (Kitagawa et al., 2001). In this study, fish older than 4 years old also experienced significantly colder SST in the fall compared to other age classes. Recent evidence indicates that for

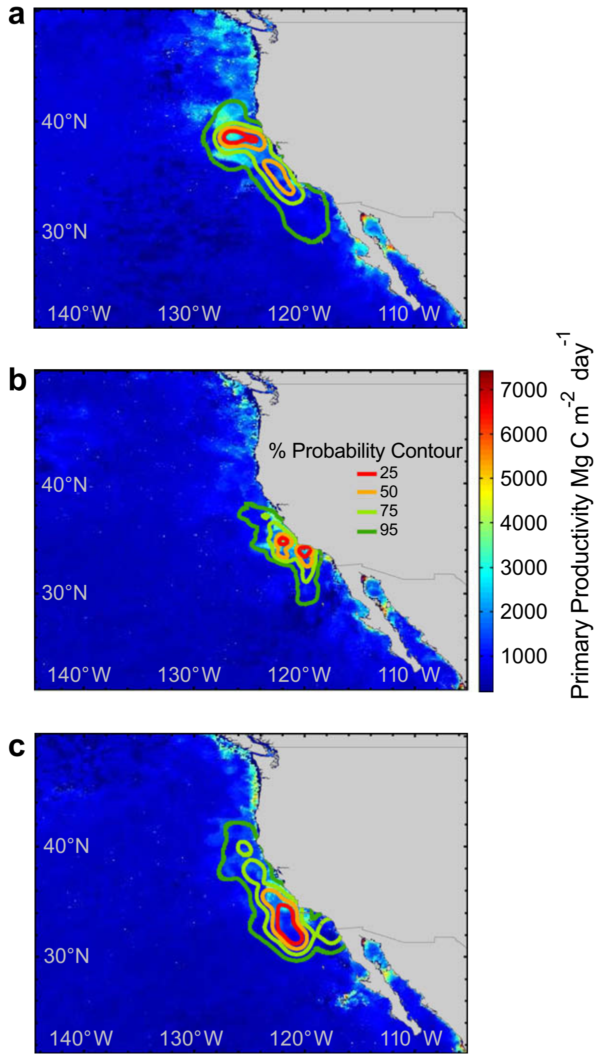

Fig. 6. Probability contours of tagged bluefin tuna for the period 20 October–6 November displayed over primary productivity data for the period 8 October–24 October. (a) Data for 2002 showing peaks in primary productivity and bluefin tuna densities offshore of Northern California. (b) Data for 2003 showing peaks in primary productivity and bluefin tuna densities close to shore in the region of Point Conception. (c) Data for 2004 showing reduced levels of primary productivity and less aggregated bluefin tuna distributions. Peak densities of bluefin and primary productivity occurred in the region of Point Conception.

Pacific bluefin tuna of the second and third year classes, the cardiac system sets the lower thermal tolerances (Blank et al., 2004). However, SST experienced by fish age four and older at the northern extent of their range (16.2 ± 1.2 °C) were still above those considered to be thermally limiting to younger fish (<15 °C; Blank et al., 2004). Shift in prey species preference with age is also a possible explanation for the observation of shifting distribution with age and size.

In addition to shifts in latitudinal preference with size and age, interannual variation within age classes was also observed. Fish tracked in 2002 shifted their distribution farther north in the fall compared to other tracking years (Fig. 4a and b). This shift was not related to the age-related shift described above, as bluefin tuna tracked in 2002 were smaller (mean length = 98.5 cm) than those tracked over any other year (mean lengths = 101.9–112.6 cm). This northward shift in the fall distribution in 2002 is also not likely to be due to differences in temperatures along the coast of North America among years. If tagged fish had been following an isotherm that had shifted north in 2002 relative to other years, it would be expected that SST experienced by fish would be similar among years. Sea surface temperatures experienced by tagged fish were significantly colder in the fall of 2002 compared to other years (Fig. 4a), suggesting that movement farther north in 2002 was due to environmental factors other than temperature.

The SST experienced by electronically tagged bluefin tuna ranged from 11.43–26.17 °C. Several studies initiated in the western Pacific have found a preference by Pacific bluefin tuna for temperatures between 14 °C and 20 °C (Inagake et al., 2001; Itoh et al., 2003b; Kitagawa et al., 2006) which was similar to the mean daily SST experienced by fish in this study (14.07–20.66 °C; Fig. 5a). Although temperatures outside of this range may not present a strict exclusionary limitation to the movements of Pacific bluefin tuna, they may add additional metabolic costs. Recent metabolic studies indicate that Pacific bluefin tuna have a U-shaped metabolic curve with an oxygen utilization minimum at 15–20 °C (Blank, 2006). Blank (2006) found that the metabolic rate in 7–10 kg Pacific bluefin tuna increased at temperatures below 15 °C and above 20 °C, indicating it was more energetically costly for bluefin in colder or warmer waters. Provided that food resources are equally plentiful across a wide range of temperatures, bluefin could be expected to reside primarily in the range that minimize their metabolic costs and maximize growth. Thus, thermal constraints may also play an important role in the movement distribution of bluefin tuna in the California Current.

The observation that juvenile bluefin tuna reside primarily in the surface waters above the thermocline in the eastern Pacific (Marcinek et al., 2001; Domeier et al., 2005; Kitagawa et al., 2007) suggests that satellite measured oceanographic variables can be useful in further examining bluefin tuna distributions. From satellite data, a strong relationship existed between the movements of bluefin tuna and the location of coastal peaks in primary productivity (Fig. 5). These regional hot spots and the timing of their appearance were correlated with the movements of bluefin tuna within the California Current, on both a seasonal as well as interannual time scale. Seasonally, movement north in the summer and fall coincided with the peak in primary productivity off the coast of California between 32°N and 37°N at this time of year (Fig. 5a). Likewise, movement back to the south occurred at a time when the waters off the coast of central and southern Baja California experienced peaks in productivity. In eastern boundary currents such as the California Current, seasonal peaks in primary productivity are caused by wind induced Ekman transport and corresponding upwelling, which brings nutrients to the surface photic zone (Bakun, 1996). This linkage between upwelling and bluefin tuna distribution has also been observed in Northern Boundary Currents such as the Great Australian Bight (Willis and Hobday, 2007). These seasonally productive areas are tightly linked to abundances of clupeoid species that form the base of the food chain for many consumers of higher trophic levels (Willis and Hobday, 2007). Previous studies of Pacific bluefin tuna found that northern anchovy made up the vast majority of stomach contents in Southern California and Baja California (Pinkas, 1971). In addition, it has been proposed that bluefin tuna migrate latitudinally in the California Current, in phase with the shifting abundances of sardines along the coast (Kitagawa et al., 2007). Sardine catch rates are generally highest in the Monterey Bay region in the fall and highest in the Southern California Bight in the winter. It is likely that both these species are important prey items for bluefin tuna in the California Current.

While tracked bluefin tuna could usually be found at latitudes with the highest levels of primary productivity along the coast at that time of year, periods existed when bluefin tuna were found in regions of lower primary productivity (Fig. 5b). During the winter months when the highest concentrations of primary productivity could be found in the region of Point Conception (33–35°N),

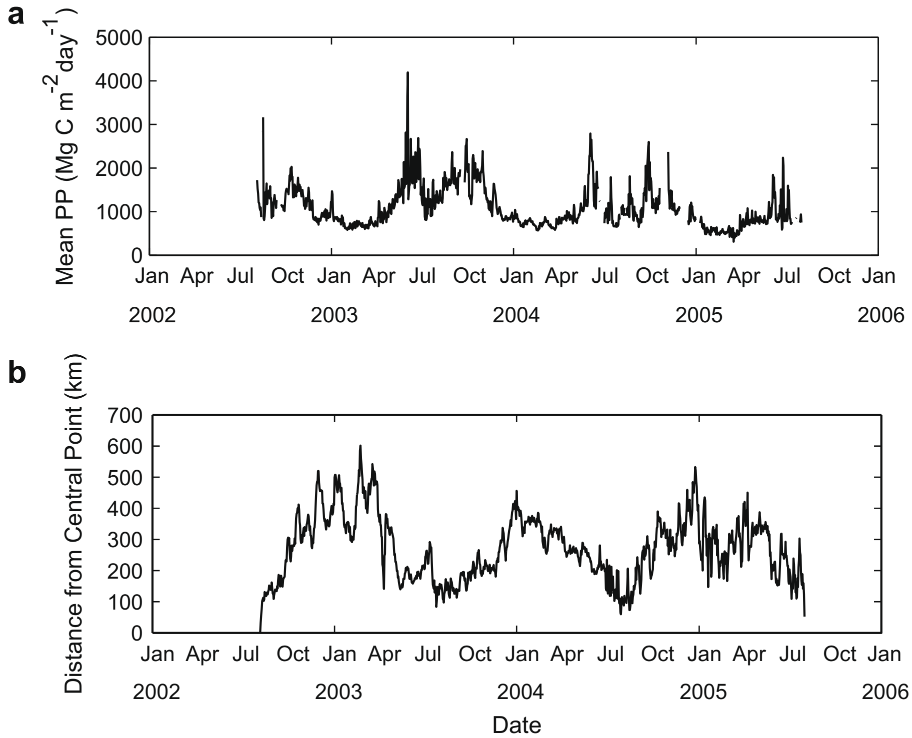

Fig. 7. Comparison between mean daily primary productivity values calculated for all tagged bluefin tuna and mean distance from the central point of all tagged fish. (a) Productivity values experienced by tagged fish show large increases in productivity the spring through early fall. (b) Mean distance from central position calculated across all fish versus date show a contraction in range in the spring through early fall and more diffusion in late fall through winter.

most bluefin tuna were found south of this region in the winter months (Fig. 5b). Possible explanations for this disconnect between bluefin tuna distribution and relative peaks in primary productivity may be: that prey species prefer areas of lower than average productivity at this time of year, that the diet of bluefin tuna shifts to other organisms, or physiological constraints push the distribution of bluefin tuna or their prey south of the most productive waters. The region where bluefin tuna are found in the winter months (peak densities in the region of Punta Eugenia and Vizcaino Bay; Fig. 3) is one of the major spawning areas for sardines in the California Current (Lluch-Belda et al., 1991). This spawning occurs primarily in the winter months when upwelling is relaxed and primary productivity decreases. Sardines in eastern boundary currents preferentially spawn in areas and at times of reduced upwelling as offshore transport of eggs and larvae will be at a minimum and survivorship of young will be maximized (Bakun, 1996; Cole and McGlade, 1998). However, a similar area of sardine and anchovy spawning occurs near the Southern California Bight (32–34°N) at this time of year (Lynn, 2003) but few bluefin tuna appear to be found at these latitudes at this time (Fig. 3).

Another possibility is that bluefin are feeding on prey items other than sardines and anchovies. Recent stomach-content analyses conducted off the coast of Baja California found a predominance of jumbo squid (*Dosidicus gigas*) in bluefin tuna stomachs (Ortega-Garcia et al., 2006). However, this study was conducted in the summer of 1 year and only 40 samples were examined, making it difficult to determine how applicable these results are to other seasons and how stable they are over multiple years. Another prey item commonly found in tuna stomachs within the California Current is the pelagic crab, *Pleuroncodes planipes* (McHugh, 1952; Alverson, 1963). During non-El Niño years, the highest concentrations of *P. planipes* could be found in the region of central and southern Baja California in the winter and early spring (Longhurst, 1969). This area overlaps significantly with the region of highest densities of bluefin tuna at this time of year. Similar to the lack of correlation between bluefin tuna and satellite-derived primary productivity during the winter months, no correlation was found between *P. planipes* and indices of upwelling in this region in the winter months (Longhurst, 1967). Bluefin tuna that were foraging predominately on this abundant prey source would, therefore, not be expected to move in relation to upwelling-induced primary productivity at this time of year. While it is possible that shifts in prey types and distribution affect the latitudinal movements of bluefin tuna in the California Current, it is also likely that physiological limitations play a role, if not in precluding bluefin tuna from northern waters then possibly in tipping the energetic balance in favor of the more southerly latitudes during the winter months. Kitagawa et al. (2007) found that bluefin tuna feeding frequency is low in the winter in the California Current, suggesting that tagged fish may be in areas with lower prey densities at this time of year. Distributions of bluefin tuna in the winter may therefore be a tradeoff between avoiding sub-optimal temperatures and maximizing prey intake within the range of temperatures available.

Although large-scale seasonal movement patterns were consistent among years, meso-scale variation existed among years, which correlated with shifts in oceanography. Over the three tracking years, the distribution of bluefin tuna in fall shifted in conjunction with the locality of relative peaks in primary productivity (Figs. 5 and 6). The highest densities of bluefin tuna could be found in the region of Point Conception in 2003 and 2004 when the highest levels of primary productivity were also in this area. In fall of 2002, the region of highest primary productivity was located at 36–40°N and core utilization areas of bluefin tuna also were found in this area. A number of pelagic species including bluefin tuna (Roberts and Paul, 1978) albacore tuna (*Thunnus alalunga*; Laurs et al., 1984), elephant seals (*Mirounga angustirostris*; McConnell et al., 1992), and basking sharks (*Cetorhinus maximus*; Sims et al., 2003) prefer areas of increased primary productivity and this has been attributed to an increase in prey availability. The corresponding shifts in both primary productivity and bluefin tuna distributions observed here show that bluefin movement patterns are not deterministic within the California Current but are influenced by environmental conditions. The high regularity of migration patterns observed over the majority of the tracking period signifies a predictable seasonal progression in the oceanography of this ecosystem (Bakun, 1996).

In addition to influencing the location of the core areas of bluefin tuna, peaks in primary productivity also influenced how tightly bluefin tuna were distributed. When in areas of higher primary productivity, bluefin tuna tended to aggregate over a smaller area (Fig. 7). This is likely due to increased prey availability in these areas; for example, clupeoid species are found at higher densities in regions of increased primary productivity (Smith and Eppley, 1982). The greater correlation between increased primary productivity and tighter aggregation above 30°N than at latitudes below 30°N may signify a change in foraging strategy throughout the year. Fish are found south of 30°N in the winter and spring. If bluefin tuna are feeding primarily on spawning aggregations during the winter, they may show a preference for lower productivity waters. Likewise, if thermal limitations during the winter months also begin to affect the distributions of bluefin tuna, we would also expect less correlation between density of tagged fish and primary productivity during this time of year.

These data reveal insight into the movements and habitat preferences of bluefin tuna in the California Current ecosystem. Movement patterns were influenced by seasonal peaks in upwelling-induced primary productivity, one of the major features of eastern boundary current ecosystems. It seems likely that movement patterns of other top-predators will show similar patterns in both the California Current as well as in other eastern boundary currents, and the repeating and predictable movement patterns of fishes in these ecosystems may make them more susceptible to fishing pressure. As some of the largest fisheries occur in eastern boundary currents, extra care should be taken to avoid over-exploitation of fish resources in these environments.

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