Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus orientalis*) in relation to seasons and oceanographic conditions in the eastern Pacific Ocean

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ABSTRACT

Electronically tagged juvenile Pacific bluefin, *Thunnus orientalis*, were released off Baja California in the summer of 2002. Time-series data were analyzed for 18 fish that provided a record of 380 ± 120 days (mean ± SD) of ambient water and peritoneal cavity temperatures at 120 s intervals. Geolocations of tagged fish were estimated based on light-based longitude and sea surface temperature-based latitude algorithms. The horizontal and vertical movement patterns of Pacific bluefin were examined in relation to oceanographic conditions and the occurrence of feeding events inferred from thermal fluctuations in the peritoneal cavity. In summer, fish were located primarily in the Southern California Bight and over the continental shelf of Baja California, where juvenile Pacific bluefin use the top of the water column, undertaking occasional, brief forays to depths below the thermocline. In autumn, bluefin migrated north to the waters off the Central California coast when thermal fronts form as the result of weakened equatorward wind stress. An examination of ambient and peritoneal temperatures revealed that bluefin tuna fed during this period along the frontal boundaries. In mid-winter, the bluefin returned to the Southern California Bight possibly because of strong downwelling and depletion of prey species off the Central California waters. The elevation of the mean peritoneal cavity temperature above the mean ambient water temperature increased as ambient water temperature decreased. The ability of juvenile bluefin tuna to maintain a thermal excess of 10°C occurred at ambient temperatures of 11–14°C when the fish were off the Central California coast. This suggests that the bluefin maintain peritoneal temperature by increasing heat conservation and possibly by increasing internal heat production when in cooler waters. For all of the Pacific bluefin tuna, there was a significant correlation between their mean nighttime depth and the visible disk area of the moon.

Key words: archival tag, bluefin tuna, eastern Pacific Ocean, feeding event, horizontal and vertical movements, upwelling indices

INTRODUCTION

Pacific bluefin tuna, *Thunnus orientalis*, is a highly migratory species distributed mainly in the North Pacific. The commercial value of this species exceeds that of most other species of tunas. Characteristics that contribute to its high market price include its size, reaching at the maximum about 3 m in total length (Collette and Nauen, 1983; Foreman and Ishizuka, 1990; Bayliff, 1994), and its unique taste. It is, however, universally agreed that southern bluefin, *T. maccoyii*, and Atlantic bluefin, *T. thynnus*, are overfished, and that Pacific bluefin may become overfished in the near future. Bluefin tunas are at the center of global international management concerns because of depleted populations.

The North Pacific Ocean contains one population of bluefin tuna. Pacific bluefin tuna spawn to the south of Japan and in the Sea of Japan (Sund et al., 1981). Juvenile bluefin remain in the western Pacific during the first year of life, and late in the year or early in the second year, some bluefin migrate from the Kuroshio-Oyashio transition region in the western Pacific to the eastern Pacific (Orange and Fink, 1963; Clemens and Flittner, 1969; Bayliff et al., 1991; Bayliff, 1994; Itoh
et al., 2003a). After a sojourn in the eastern Pacific, bluefin tuna are thought to return into the western Pacific (Bayliff, 1994). However, the mechanism for this east-to-west migration has not been clarified. Polovina (1996) put forward the hypothesis that migration of juvenile bluefin into the eastern Pacific increased in years when the abundance of sardines off Japan was declining.

With regard to the vertical distribution and movements of the Pacific bluefin, recent archival tagging studies in the western Pacific demonstrated that juvenile bluefin remain predominately in the surface mixed layer, with occasional dives to depths of 120 m during the period of occupation in the East China Sea (Kitagawa et al., 2000). Average swimming depths were much shallower during summer months than in winter, when the water column experiences significant mixing. In addition, Kitagawa et al. (2001, 2002) noted that juvenile bluefin (50–70 cm in fork length) used behavioral thermoregulation to thermally buffer the rapid ambient temperature drops that occur as the bluefin swims repeatedly below the thermocline for short periods. However, these studies described the bluefin behavior only in a localized area and they did not clarify the advantage of diving below the thermocline. Kitagawa et al. (2004) examined the relationship between the tuna’s vertical movement pattern for feeding and the thermocline depth during summer in the Kuroshio-Oyashio transition region, comparing it to that in the East China Sea. They conclude (as did Marcinek et al., 2001) that, in addition to the ambient temperatures, the vertical and horizontal distributions of prey species play an important role in their feeding behavior and vertical distribution, and that bluefin tuna in the Oyashio frontal area, where both the horizontal and the vertical thermal gradients are much steeper, spent most of the time on the warmer side of the front and often traveled horizontally to the colder side during the day, perhaps to feed.

Comparatively little is known about the horizontal and vertical movements of bluefin tuna in the eastern Pacific. Hanan (1983), Bayliff et al. (1991) and Bayliff (1994) have collated information about horizontal distribution off Baja California using fish catch data during the fishing season. Marcinek et al. (2001) used ultrasonic telemetry to track pressure and temperature of six bluefins of 11.8–57.6 kg mass, revealing that bluefin in the Southern California Bight have a preference for the upper mixed layer but occasionally dive through the thermocline.

This study showed that bluefin in the Southern California Bight had a preference for the upper mixed layer, but occasionally dove through the thermocline. Marcinek et al. (2001) and Farwell (2001) reported on the application of pop-up satellite archival tags to juvenile bluefin in the eastern Pacific, demonstrating movements from the Central California to the Baja region. Both authors’ results indicated a predominant use of the continental shelf waters and vertical movements in the mixed layer in tracks that ranged from 5 to 90 days. Domeier et al. (2005) analyzed the data recovered from 11 pop-up satellite archival tags and three surgically implanted archival tags to juvenile bluefin. They reported that the fish spend winter and spring off central Baja California, and summer through fall was spent moving as far northward as Oregon with a return to Baja California in the winter months.

In this paper, we report on the initial experiments involving bluefin tuna archival tagging in the Tagging of Pacific Pelagic (TOPP) research project, a pilot program of the Census of Marine Life (COML) (Block et al., 2002; Block, 2005). As a part of this project, bluefin tuna were electronically tagged off the west coast of North America beginning in August of 2002. In the present paper, we analyzed the data on vertical distribution and movement of juvenile Pacific bluefin obtained from the archival tags released in 2002. Our objectives were to examine the differences in horizontal and vertical movement patterns among seasons for the years 2002 and 2003 in relation to the oceanographic conditions in the eastern Pacific. We also examined their vertical movements through the thermocline in relation to the occurrence of feeding events. The influence of temporal and spatial movement patterns on the thermal excess observed between peritoneal cavity temperatures and ambient temperatures are examined and discussed.

MATERIALS AND METHODS

Tags and data
The archival tag used for this study was the LTD2310 (Lotek Wireless Inc., St Johns, NF, Canada). The cylindrical tag was 76 mm in length and 16 mm in diameter, with a weight (in air) of 45 g. A thin, Teflon-coated flexible stalk (270 mm long and 2.0 mm in diameter) extends from the main body of the tag. The light sensor, a 478-nm dye responsive to ambient light over nine decades, and the sensors for external temperature measurement are embedded in the end of the stalk, whereas those for pressure and internal temperature measurement are installed in the main body of the tag. The tags are designed for implantation into the peritoneal cavity with the stalk protruded outside the tag. The archival tag logs external and internal temperatures (with a resolution of 0.05°C), swimming
depth (resolution of 0.05%; this changes with depth), and ambient light levels at an interval of 60–120 s. In addition, geolocations were estimated daily using threshold-based methods based on the detection of the time of sunrise and sunset (Musyl et al., 2001; Ekstrom, 2004).

Juvenile Pacific bluefin tuna were captured by pole and line fishing off Baja California aboard the fishing vessel F/V Shogun. One hundred and sixty juvenile bluefin tuna with fork lengths of 87–125 cm, which were 2–3 yr old (Bayliff, 1993; Itoh, 2001), were tagged and released with archival tags inserted into the peritoneal cavity on 5–6 August 2002 (Fig. 1). The tagging procedure was described in detail by Teo et al. (2004) and Boustany (2006). Twenty individuals were recovered by commercial or recreational fishers and data were obtained from 18 of the archival tags placed in these fish. Fish used in this study were recaptured in the eastern Pacific after more than 3 months at liberty for analysis of diving behavior and movement patterns between seasons. The other two fish (bluefin 405 and 437) were recaptured in the same area after a very short period at liberty and were not included in the analyses.

As was pointed out by Welch and Eveson (1999), errors in geolocations estimated from archival tags can be considerable. As latitude estimation from day length was unreliable, we adjusted the latitude by using the sea surface temperature (SST), as recorded in the summary file for each day, according to the methods of Teo et al. (2004) and Block (2005). Boustany (2006) and Boustany and Block (unpublished data) provide more details on the horizontal movements of the fish tagged in the eastern Pacific.

Data analysis, and definition of feeding and diving behavior

Data analysis began with creating daily averages of the external and internal temperature data, as well as the swimming depth data, logged by the tags. The daily average data were further averaged over the period of a month for all individuals. Frequency distributions of swimming depth in relation to ambient water temperature were calculated for the month.

Figure 2 shows part of the time-series data of ambient water and peritoneal cavity temperatures as well as swimming depths for bluefin 315. In this figure, an arrow indicates a drop of peritoneal cavity temperature. Ingestion of food, which results in a decline in temperature either from the prey or from water entering the peritoneal cavity during a feeding event, provides an event marker for foraging (Carey et al., 1984; Gunn et al., 1994; Itoh et al., 2003b; Kitagawa et al., 2004). We considered the peritoneal cavity temperature drops to be an indicator of a feeding event.

only when the temperature change could not be explained by changes in the ambient water temperature, by using the method reported in Kitagawa et al. (2004). The thresholds for feeding events were established as the maximum absolute value of the rate of increase of peritoneal temperature (0.20–0.39°C per 120 s, Table 1). The threshold in only one individual (bluefin 471) could not be established because the fish dove to colder depths for longer durations compared with the other fish. In this individual the drop in temperatures caused by feeding could not be detected. A feeding depth was defined as the depth in which a feeding event occurs.

A dive was defined as starting when a descending tuna passed below 10 m and ended when it ascended to 10 m. Dive maximum depths were defined as the greatest depth reached during a dive. Dive duration was the time elapsed during one dive. In this study, data from dive depths of more than 50 m were used for dive analysis. Daily averages were calculated for dive depth, dive frequency, dive duration, feeding events and feeding frequency. The daily average data were further averaged over the period of a month for all individuals.

Oceanographic and fish landing data
In order to investigate the vertical movement of the bluefin tuna in relation to vertical thermal structure, daily or monthly vertical ambient temperature profiles were computed by estimating mean ambient temperature at 10-m depth intervals.

In the present paper, the timing of horizontal movements in relationship to oceanographic condition was examined. For these analyses fish geolocations were superimposed on the coastal upwelling indices calculated by Pacific Fisheries Environmental Laboratory, U.S. National Marine Fisheries Serves (NMFS). The data were downloaded from a web site (http://www.pfeg.noaa.gov/javamenu.html) and a daily index was calculated at nine positions from 21° to 45°N along the west coast of North America (Fig. 1), using synoptic sea level pressure gridded fields. Detailed information concerning this data set is available on the web site.

Some authors reported that juvenile bluefin tuna consumed mainly anchovies (Blunt, 1958; Bell, 1963a; Pinkas, 1971). However, recent studies have shown that climate-ocean and biological systems are not stable, but shift from one regime to another in the Pacific Ocean (Ebbesmeyer et al., 1991; McFarlane et al., 2002). This ‘regime shift’ results in oscillations of anchovy and sardine abundance cycles. An anchovy regime was in place from 1950s

<table>
<thead>
<tr>
<th>Bluefin no.</th>
<th>Duration of the data analyzed</th>
<th>Fork length (cm)</th>
<th>Sampling interval (s)</th>
<th>Threshold (°C/120 s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>315</td>
<td>Aug. 7, 2002–Aug. 5, 2003</td>
<td>91</td>
<td>60</td>
<td>0.2</td>
</tr>
<tr>
<td>333</td>
<td>Aug. 7, 2002–Jun. 6, 2003</td>
<td>102</td>
<td>60</td>
<td>0.32</td>
</tr>
<tr>
<td>340</td>
<td>Aug. 7, 2002–Jul. 17, 2003</td>
<td>88</td>
<td>60</td>
<td>0.32</td>
</tr>
<tr>
<td>345</td>
<td>Aug. 7, 2002–Aug. 23, 2003</td>
<td>104</td>
<td>60</td>
<td>0.32</td>
</tr>
<tr>
<td>364</td>
<td>Aug. 7, 2002–Aug. 11, 2004</td>
<td>91</td>
<td>60</td>
<td>0.29</td>
</tr>
<tr>
<td>403</td>
<td>Aug. 7, 2002–Aug. 12, 2003</td>
<td>92</td>
<td>60</td>
<td>0.25</td>
</tr>
<tr>
<td>411</td>
<td>Aug. 7, 2002–Jul. 23, 2003</td>
<td>91</td>
<td>60</td>
<td>0.18</td>
</tr>
</tbody>
</table>

through the early 1970s followed by a sardine cycle (Chavez et al., 2003). High sardine stocks off Japan and Chile declined in the early 1990s, but those off California have not declined yet (McFarlane et al., 2002). The tagging cruise in 2002 revealed that most of the bluefin tuna had Pacific sardines in their stomachs (B.A. Block, personal observation). In recent years, therefore, the Pacific bluefin tuna in the eastern Pacific would have primarily consumed Pacific sardines (Sardinops sagax). To look at the monthly changes in prey availability to bluefin, we downloaded Pacific sardine commercial landing data at Los Angeles and Monterey (Fig. 1) from the web site of Southwest Fisheries Science Center, NMFS (http://las.pfeg.noaa.gov:8080/las_fish1/servlets/dataset). The sum of the Pacific sardine in all ports of California in 2002 was about 58,348 tonnes, which is more than 10-fold higher than that for Northern anchovy, Engraulis mordax (4648 tonnes, California Department of Fish and Game, 2002).

RESULTS

Seasonal change in swimming depth in relation to vertical thermal structure

The time-series data for a representative individual bluefin (bluefin 315), which was released in August 2002 and tracked for 351 days, are shown in Fig. 3. Isotherms depicted in Fig. 3 were estimated from daily ambient water temperature and depth profiles acquired from the diving fish carrying the archival tag. Vertical movements for the other tagged bluefin tuna were similar to those of this fish (Table 2). The frequency distributions of the swimming depths recorded for bluefin 315 are shown in Fig. 4 together with vertical profiles of the monthly mean ambient temperature in the daytime. The average depth for all individuals in the daytime was significantly greater than that in the nighttime (Table 2), and power spectra of the swimming depth calculated by Fast Fourier Transform (FFT) had a marked peak at about 24 h for most of the

![Figure 3](image-url)
Table 2. Monthly averages of daytime depth, nighttime depth, and daytime dive duration for all individuals from 2002 through 2004.

<table>
<thead>
<tr>
<th></th>
<th>August</th>
<th>September</th>
<th>October</th>
<th>November</th>
<th>December</th>
<th>January</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth ± SD (daytime, m)</td>
<td>17.9 ± 3.9</td>
<td>22.6 ± 6.0</td>
<td>21.1 ± 9.0</td>
<td>14.8 ± 4.4</td>
<td>23.4 ± 6.6</td>
<td>34.1 ± 8.6</td>
</tr>
<tr>
<td>Depth ± SD (nighttime, m)</td>
<td>13.0 ± 2.1</td>
<td>8.6 ± 2.1</td>
<td>8.8 ± 2.8</td>
<td>10.9 ± 3.2</td>
<td>16.5 ± 4.1</td>
<td>21.7 ± 3.4</td>
</tr>
<tr>
<td>Dive duration (min)</td>
<td>17.8 ± 5.6</td>
<td>18.8 ± 7.9</td>
<td>19.1 ± 8.6</td>
<td>21.3 ± 6.6</td>
<td>27.0 ± 9.9</td>
<td>25.9 ± 8.1</td>
</tr>
</tbody>
</table>

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<tr>
<th></th>
<th>February</th>
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<th>April</th>
<th>May</th>
<th>June</th>
<th>July</th>
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<tr>
<td>Depth ± SD (daytime, m)</td>
<td>28.3 ± 6.4</td>
<td>26.5 ± 6.6</td>
<td>29.8 ± 6.4</td>
<td>26.3 ± 6.3</td>
<td>22.1 ± 2.9</td>
<td>17.9 ± 3.4</td>
</tr>
<tr>
<td>Depth ± SD (nighttime)</td>
<td>15.4 ± 2.5</td>
<td>15.6 ± 3.2</td>
<td>14.0 ± 2.3</td>
<td>13.6 ± 2.7</td>
<td>14.0 ± 2.5</td>
<td>10.1 ± 1.1</td>
</tr>
<tr>
<td>Dive duration (min)</td>
<td>19.5 ± 8.5</td>
<td>17.1 ± 5.9</td>
<td>16.2 ± 4.5</td>
<td>14.9 ± 5.3</td>
<td>11.6 ± 3.4</td>
<td>9.1 ± 2.4</td>
</tr>
</tbody>
</table>

individuals. These data indicate that bluefin make diel vertical migrations. Dive duration in the daytime ranged from about 9.1 to 27.0 min (Table 2).

In August of 2002, bluefin 315 occupied the region near the release location off the northern coast of Baja California. The horizontal movements indicate this fish was swimming in the Southern California Bight (Fig. 1). The fish remained above the thermocline most of the time while in this area, undertaking occasional, brief vertical movements below the thermocline to depths greater than 250 m (Fig. 3a). In Fig. 4a, a seasonal thermocline developed at the depth from 20 to 50 m in August, which was very stratified and stable. The swimming depths of the fish tended to be confined to the shallow mixed layer and thermocline depths (0–50 m, Fig. 4a). This suggests that a seasonal thermocline possibly regulates vertical distribution of the juvenile bluefin tuna or its prey species.

In October to November, the fish moved to the Central California coast off Monterey Bay (Fig. 1), where colder waters occurred in comparison with those in August (Fig. 3b). The temperature of surface water was 15.6 ± 0.9°C (mean ± SD, Fig. 4b). A seasonal thermocline gradient was apparent, however its depth often varied (Fig. 3b). For example before 6 November 2002, the thermocline formed at depths shallower than 50 m, while after 9 November 2002, it formed below 50 m (Fig. 3b). In addition, cold water began upwelling around 23 November 2002. These events indicate that this region dramatically changes temporally and/or spatially. In relationship to the
changes in the depth of the thermocline, the bluefin
tuna changes its diving pattern. The other fish also
took a similar tendency. That is, all bluefin (including
this bluefin) spent most of their time within the sur-
face mixed layer with a mean swimming depth of
14.8 ± 4.4 m in November during the daytime
(Table 2), and they ceased undertaking occasional
brief movements below the thermocline.

Importantly, there were temporary drops in ambi-
ent temperatures (to as cool as 13.0°C minimum at the
surface, indicated by arrows in Fig. 3b), although the
monthly surface water temperatures were relatively
constant. These temporary drops in temperature
depth of the thermocline, the bluefin
indicate daytime horizontal excursions into cooler
waters occur from warmer areas and are potentially
indicative of the bluefin tuna moving across frontal
areas in these regions. These temporary drops were
seen in most of the bluefin tunas examined.

From December to January, bluefin 315 together
with the other bluefin returned back to the waters of
the Southern California Bight and remained off Baja
California (Fig. 1). The water column had a mixed
layer above depths of around 75–100 m where the fish
spend most of the time (Figs 3c and 4c). The fish made
occasional dives to depths through the thermocline,
which was not as steep as the thermocline in Fig. 3a,b.
These horizontal and vertical migration patterns were
seen in most of the bluefin tunas examined.

In May, the fish migrated further to the south to an
area off southern Baja California, to the south of Point
Eugenia and to the north of Magdelana Bay, where

vertical ambient temperatures were comparatively
higher than those at other times of the year. When the
water column was stratified (Figs 3d and 4d), the
swimming depths tended to be confined to the shallow
depths with the maximum frequency at the 0–10 m
depth (Fig. 3d). As shown in the other panels, the fish
often repeated brief vertical movements below the
thermocline in the daytime, although the fish spent
most of the time swimming within the surface mixed
layer. Mean depth of all bluefin was 26.5 ± 6.6 m
(Table 2).

The vertical distributions of all the bluefin were
influenced by the lunar phases. A significant correla-
tion exists between the visible disk area of the moon
phase and their average nighttime depth distributions
\( r = 0.123–0.536 \), Table 3. Fish occupied signifi-
cantly greater depths for periods around the full moon,
in contrast to the other days of the lunar cycle; this
tendency was more prominent from November
through March (Fig. 5).

### Temporal and spatial variation in feeding

In order to detect temporal and spatial changes in the
bluefin tunas feeding activity, we calculated average
values for latitude, surface temperature, dive frequency
per day, feeding frequency per day, and feeding depth
in each month for all fish except bluefin 471 (Fig. 6).

During the months of August and September, we
observed high feeding frequency when the fish were
located 30°N in the Southern California Bight
(Fig. 6d,e). In these periods the bluefin dove to feeding

<table>
<thead>
<tr>
<th>Bluefin no.</th>
<th>315</th>
<th>333</th>
<th>334</th>
<th>340</th>
<th>342</th>
<th>345</th>
<th>364</th>
<th>403</th>
<th>411</th>
</tr>
</thead>
<tbody>
<tr>
<td>Correlation between lunar illumination and average nighttime depth</td>
<td>0.448</td>
<td>0.126*</td>
<td>0.406</td>
<td>0.459</td>
<td>0.495</td>
<td>0.449</td>
<td>0.470</td>
<td>0.380</td>
<td>0.469</td>
</tr>
<tr>
<td>Correlation between ambient and peritoneal temperatures</td>
<td>0.303</td>
<td>0.176**</td>
<td>0.285</td>
<td>0.322</td>
<td>0.199</td>
<td>0.367</td>
<td>0.452</td>
<td>0.224</td>
<td>0.338</td>
</tr>
<tr>
<td>Correlation between ambient temperature and thermal excess</td>
<td>-0.675</td>
<td>-0.732</td>
<td>-0.536</td>
<td>-0.472</td>
<td>-0.729</td>
<td>-0.637</td>
<td>-0.475</td>
<td>-0.768</td>
<td>-0.516</td>
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<th>412</th>
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<th>415</th>
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<th>471</th>
<th>475</th>
<th>485</th>
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</tr>
</thead>
<tbody>
<tr>
<td>Correlation between lunar illumination and average nighttime depth</td>
<td>0.217</td>
<td>0.413</td>
<td>0.403</td>
<td>0.507</td>
<td>0.184</td>
<td>0.123*</td>
<td>0.536</td>
<td>0.453</td>
</tr>
<tr>
<td>Correlation between ambient and peritoneal temperatures</td>
<td>0.399</td>
<td>0.272</td>
<td>0.603</td>
<td>0.395</td>
<td>0.472</td>
<td>0.387</td>
<td>0.337</td>
<td>0.125*</td>
</tr>
<tr>
<td>Correlation between ambient temperature and thermal excess</td>
<td>-0.680</td>
<td>-0.716</td>
<td>-0.565</td>
<td>-0.729</td>
<td>-0.511</td>
<td>-0.690</td>
<td>-0.606</td>
<td>-0.752</td>
</tr>
</tbody>
</table>

*P < 0.05, **P < 0.01, and P < 0.0001 unless otherwise stated.

depths that ranged from 36.9 to 55.4 m (Fig. 6e). The results indicate that bluefin are potentially feeding on prey items at a variety of depths and access or search for food by using repetitive vertical movements. In October to November when they migrated to around 35°N (Fig. 6a), the surface sea temperatures were lower (15.5°C in September and 15.3°C in November on average, Fig. 6b). Bluefin tunas dove less frequently and correspondingly they fed at shallower depths (Fig. 6c,e). Feeding frequencies were significantly lower than in August (P < 0.001, Sheffe test), and were also lower than in September but not significantly so (Fig. 6d). Feeding frequencies decreased during the period from December through April, although vertical movement frequency gradually increased. Mean feeding depths ranged from 38.0 to 46.4 m (Fig. 6d,e). In the months of May and June when the bluefin tuna are located around 25°N, in the south of Baja California, dive frequency was the highest and feeding events also increased (Fig. 6a,d). In July when they initiated northward migrations, the feeding frequencies increased, although the feeding depths did not vary so much (Fig. 6a,d,e).

Timing of northward migration in relation to changes in oceanography and food

In order to examine the northward migration of bluefin tuna from October to November in relationship to the potential environmental cues, we examined the relationship between daily latitude positions and coastal upwelling indices (Fig. 7). It is evident from Fig. 7 that the bluefin tuna, located around 30°N in August of 2002, initiated northward migrations just after strong upwelling events from September to October (blue) ceased in the region of 30°–45°N, and that they remained in this northern region for a while. When strong advection of surface waters (yellow to red) accompanied by a downwelling came to be dominant in the central coast of California region from November to December, almost all of the fish returned to the region around 28°–30°N. During this period a few individuals moved out into the offshore open ocean regions. During January through March, most of the bluefin were distributed in the region between 25° and 32°N once again where the upwelling indices were almost zero (green), although some individuals went on an excursion to the open ocean. From April through June, the tunas were concentrated in the vicinity of 25°N over the continental shelf, and they initiated northward migrations in July. When the

second year was represented in the track, a similar cycle of movements was revealed in 2003–04.

We analyzed time series of the monthly landing data of Pacific sardines in the ports of Monterey and Los Angeles from the months of August 1993 through July 2003. In both sets of landing data, a 1-year periodicity was detected in the fluctuations by autocorrelation analysis. This indicates that the landings fluctuated periodically within the year for these 10 yr. Figure 8 shows the average monthly landing data of Pacific sardines in the ports of Monterey and Los Angeles from August through July. In Monterey, the landings of sardines increased from August and reached the highest levels in October. Then the landings from November to April gradually decreased to almost zero. Strong downwelling along the Central California coast is clearly observed in December (Fig. 7). The landings remained low or go to zero from April through July. In Los Angeles, on the other hand, the monthly landings for all the months were significantly higher than those in Monterey (Fig. 8, Wilcoxon test $P < 0.0001$). As in Monterey, the landings in Los Angeles increased from August through October. There was a decline in November and December before reaching the highest levels from January to March. Landings of sardines decreased to the lowest levels from April to July.

**Relationship between ambient and peritoneal cavity temperatures**

The peritoneal cavity temperature showed a diel pattern often increasing in the daytime, showing small-scale temperature fluctuations corresponding to the occasional dives below the thermocline, as well as potential feeding events. Notably the peritoneal cavity temperature always decreased in the nighttime (Fig. 3a–d). According to FFT analysis, additionally, these daily temperature fluctuations for all fish showed a 24-h periodicity. This diel periodicity in the peritoneal temperatures indicates that the fish produce heat in the peritoneal cavity during the daytime potentially in association with morning feeding events and has a decay of thermal excess in the night. Mean values for ambient water and peritoneal cavity temperatures in the daytime were calculated. The relationship for bluefin 315 is shown in Fig. 9a. Positive correlations were found between the ambient water temperatures and peritoneal temperatures. This implies that ambient temperature affects peritoneal cavity thermal excesses. The results of correlation analysis for the relationships are summarized in Table 3.

Importantly, the difference between peritoneal cavity and ambient temperature (thermal excess) increased as ambient water temperature significantly decreased (Fig. 9b). The thermal excess was less than approximately 4°C when ambient temperatures were more than 18°C, while the thermal excess increased to approximately 10°C when the mean ambient temperatures were 11–14°C. This large thermal excess was especially apparent during October to December when the fish moved up to northern waters off the central coast of Monterey Bay (Fig. 9b).

**DISCUSSION**

The juvenile Pacific bluefin tuna with archival tags in the eastern Pacific show strong preferences for depths shallower than 50 m and remain above the thermocline most of the time (Figs 3 and 4, Table 2). This result agrees with previous electronic tagging studies.
Figure 9. (a) Relationship between daily mean ambient water temperature and peritoneal cavity temperature for daytime data, and (b) relationship between mean ambient water temperature and thermal excess (peritoneal cavity temperature minus ambient water temperature) for daytime data for bluefin 315.

For juvenile bluefin tuna that were similar in size or smaller (Kitagawa et al., 2000, 2002), but those studies were conducted in the western Pacific. During the daytime bluefin tuna in the eastern Pacific occasionally make vertical movements for durations of 9.1–27.0 min (Table 2). These dives are most likely foraging dives. The diving behaviors and durations at depth show distinctions from those observed in archival tagged Pacific bluefin of similar size in the East China Sea (Kitagawa et al., 2004). For example, despite the fact that the thermal structure was occasionally almost homogenous in the California Current up to 50 m depth in Fig. 3b,c, dive durations were much shorter compared with those observed in the East China Sea, which ranged from 16.7 min to more than 167 min (Kitagawa et al., 2004). Potentially, the decreased time spent at depth is due in part to the cooler temperatures of the California Current regime.

The bluefin tuna showed a cyclical pattern of movement swimming from the south off the Southern California Bight to the north and back to Baja California. During this time, the bluefin remained along the North American continental shelf (Fig. 1). In July to August, when the Ekman indices decreased in the waters north of 25°N (Fig. 7) and the ambient temperature became warm, the landings of sardines increased in both Los Angeles and Monterey (Fig. 8). These increases in landing potentially indicate the success of recruitment of sardines hatched in prior winters off the Southern California Bight. In these months, bluefin move up and into the Southern California Bight from waters off Baja California, and their feeding frequency increased to the highest levels (Fig. 6). This area is one of the regions in which bluefin tuna aggregate and actively feed: a hot spot in the eastern Pacific most likely driven by seasonal prey abundance induced by favorable environmental conditions (warm seasonal temperatures and high productivity).

From September to November, the landings of sardines increases to the highest level in Central California coincident with rising SST (Goericke et al., 2004), although the arrival of bluefin tuna in the Central California waters occurs at a period when the temperatures of surface water were $<15^\circ$C (Figs 3b and 6). This period is the beginning of the warmest SSTs in the annual cycle of the region. This suggests a likely hypothesis for why the Pacific bluefin move up the coast. The northward movement or recruitment of prey due to high productivity and warmer temperatures is accompanied by the result of weakened equatorward wind stress in the region, leading to the northward migration of bluefin (Fig. 6). A thermal window has opened for the bluefin tuna at this time – providing access to the rich prey in the region. Bell (1963b) stated that bluefin are caught by purse-seine vessels off California and Baja California waters with SST 17–23°C. However, the results shown in Fig. 9 indicate that in the eastern Pacific the juveniles experience ambient temperatures ranging from 11 to 21°C. When bluefin move to the northward point of their migration and occupy waters off the Central California coastal region, they must produce significant heat (2.5 times as much from when they are in the southern waters) as well as increase heat conservation to maintain their body temperatures.

Understanding the thermal structure in the waters offshore of regions such as Monterey Bay from September to November is important for understanding the vertical distribution of bluefin tuna. As shown in previous tuna studies (Laurs et al., 1977, 1984; Fiedler and Bernard, 1987; Block et al., 1997; Inagake et al., 2001; Kitagawa et al., 2004), bluefin aggregate in frontal regions. They make daytime horizontal excursions to the cooler coastal waters to potentially feed on schools of sardine, which might stray away from their established zone of relative abundance near the coast, and they discover the area of enhanced food concentration along the frontal region (Bakun, 2001). It is likely that the resultant abundant schools of sardines in these locations are restricted in their vertical distribution by temperature (Kitagawa et al., 2004), making foraging easier. Bluefin tuna foraging depths are very shallow in these waters potentially due to the restriction in vertical habitat of the prey species. Thus, this region appears to be another seasonal hot spot of bluefin as the elevated thermocline becomes a trap for the prey because of thermal limitations.

Strong downwelling along the Central California coast in December causes a local decrease in the productivity of the region, reducing the concentration of sardines in the zone. This change of oceanographic conditions most likely results in the bluefin tunas returning to the waters off Southern California and moving further south to Baja California. In addition, there may be an increased energy cost to feeding in these waters, as the bluefin tuna not only have to conserve heat but also potentially have to generate increased amounts of body heat to maintain their body temperatures when in waters off Central California. As shown above, ambient temperatures of 11–14°C were much lower than those around the Southern California Bight (14–18°C) (Fig. 9), yet the fish maintain significant gradients in thermal excess in the peritoneal cavity. Recent metabolic data on similar-sized Pacific bluefin tuna also demonstrate that metabolic rate goes up in cooler waters and tail beat frequency increases in the cold, suggesting a possible mechanism for increased heat production (Blank et al., 2005).

In this study, furthermore, feeding frequency was lowest in November to December off Central California in the vicinity of Monterey Bay (Fig. 6). If bluefin tuna stayed longer off Monterey Bay without acquiring food, they would pay a high energetic cost because of foraging in cooler waters. Overall, the energetic constraints of maintaining body temperature may generate a net caloric loss once the prey is less dense, when occupying these cooler regimes. We hypothesize that the motivation for the southward migration may be a tradeoff between energy acquisition off the central coast waters and metabolic costs. Migration to the south may be a mechanism for saving metabolic energy expended while in cooler waters.

From January to April, the sardine landings in Los Angeles were at a high level while they were low or zero in Monterey (Fig. 8). The landings data indicate that sardines are most likely more aggregated around the Southern California Bight and recruit to the fishery resource. The presence of the sardines is most likely the reason the bluefin tuna remain in these regions. Although the growth rate of juvenile bluefin in winter is slower than in summer (Bayliff, 1994), they are able to find sardines continuously available there during the winter months.

From April to July when the landings of Pacific sardine in Los Angeles decreased to their lowest level, they remained low in Monterey (Fig. 9). Ekman indices were high in the waters north of 25°N (Fig. 7). These months are the coldest of the year in Monterey because of strong winds (Goericke et al., 2004). There was very strong offshore transport and high levels of induced turbulence, and lower temperatures along the Central California coastal waters. The wind events and resultant upwelling do not appear to provide ideal conditions for the bluefin tuna or their prey to feed or to reproduce (Bakun, 1996). In this season, therefore, sardine populations might be depleted or migrate south because of poor environmental conditions for sardines. We hypothesize that bluefin migrate to waters around 25°N for feeding during these months, where they potentially take advantage of locally abundant species such as red crabs (Pleuroncodes planipes) or Humboldt squid (Dosidicus gigas).

The significant correlation between average nighttime depth distributions and the visible disk area of the moon all year round (Fig. 5) is consistent with similar behavior found in southern bluefin and bigeye tuna (Gunn and Block, 2001; Musyl et al., 2003). Musyl et al. (2003) suggest that the fish were mirroring the movements of nocturnally migrating organisms of the sound scattering layer, which were, in turn, attempting to occupy an isolune. However, bluefin may appear to be less active foragers during the night. From peritoneal temperatures and depth data, it appears that bluefin are not feeding as much (Kitagawa et al., 2004). Thus the behavior of moving down in the water column most likely is a behavior to hide their bullet-shaped silhouette caused by the moon light. We hypothesize that the movements with the lunar cycle are primarily to avoid predation events.

ACKNOWLEDGEMENTS

This study is part of the tuna archival tagging program in the TOPP research project, a pilot program of the COML. We thank Captain Norm Kagawa and crews of the F/V Shogun. We thank Ted Dunn for advice and support. We also thank A. Seitz, R. Schallert, K. Weng and the Stanford undergraduate assistants from the Block laboratory for assisting in the archival tagging of bluefin tuna. We thank G. Strout, D. Kohrs, H. Dewar, S. Teo, C. Perle, A. Walli and R. Matteson for assistance in data analysis. Funding is from the National Science Foundation, NOAA Sea Grant, the Sloan, Monterey Bay Aquarium, the Dave and Lucile Packard, and Gordon and Betty Moore Foundations. T. Johnson, Ocean Research Institute, University of Tokyo, provided comments that substantially improved the manuscript.

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