Swimming depth, ambient water temperature preference, and feeding frequency of young Pacific bluefin tuna (*Thunnus orientalis*) determined with archival tags

Tomoyuki Itoh
Sachiko Tsuji
National Research Institute of Far Seas Fisheries
5-7-1 Shimizu-Orido, Shizuoka
Shizuoka, 424-8633, Japan
Email address (for T. Itoh): itou@fra.affrc.go.jp

Akira Nitta
Japan NUS Co., Ltd.
Loop-X Bldg.
3-9-15 Kaigan, Minato
Tokyo, 108-0022, Japan

Abstract—We investigated the migration and behavior of young Pacific bluefin tuna (*Thunnus orientalis*) using archival tags. The archival tag measures environmental variables, records them in its memory, and estimates daily geographical locations based on measured light levels. Of 166 archival tags implanted in Pacific bluefin tuna that were released at the northeastern end of the East China Sea from 1995 to 1997, 30 tags were recovered, including one from a fish that migrated across the Pacific. This article describes swimming depth, ambient water temperature, and feeding frequency of young Pacific bluefin tuna based on retrieved data. Tag performance, effect of the tag on the fish, and horizontal movements of the species are described in another paper.

Young Pacific bluefin tuna swim mainly in the mixed layer, usually near the sea surface, and swim in deeper water in daytime than at nighttime. They also exhibit a pattern of depth changes, corresponding to sunrise and sunset, apparently to avoid a specific low light level. The archival tags recorded temperature changes in viscera that appear to be caused by feeding, and those changes indicate that young Pacific bluefin tuna commonly feed at dawn and in the daytime, but rarely at dusk or at night. Water temperature restricts their distribution, as indicated by changes in their vertical distribution with the seasonal change in depth of the thermocline and by the fact that their horizontal distribution is in most cases confined to water in the temperature range of 14–20°C.

Manuscript approved for publication 22 October 2002 by Scientific Editor.

Manuscript received 3 January 2003 at NMFS Scientific Publications Office.

Fish Bull. 101:535–544 (2003).

Swimming behavior of *Thunnus* species and its relation to various environmental factors have been examined mainly by acoustic tracking (e.g. Carey and Lawson, 1973; Laurs et al., 1977; Carey and Olson, 1982; Holland et al., 1990b; Cayré, 1991; Cayré and Marsac, 1993; Block et al., 1997). Acoustic tracking has also been applied to young Pacific bluefin tuna (*T. orientalis*): to one fish tracked for three hours around Japan (Hisada et al.[1]), and to six fish tracked for several days each in the eastern Pacific Ocean (Marcinek et al., 2001). Acoustic tracking can monitor fish movement, behavior, and even physiological conditions on a time scale of seconds. However, the duration of monitoring any one fish is generally limited to several days at most because of the short life of the tracking transmitter. This limitation, together with the high cost of adequate ship-time, generally makes it difficult to monitor the behavior of a large number of fish over a long period of time.

An archival tag is an electronic device that measures environmental variables and records raw or processed data in its memory. The archival tag can monitor animal behavior, its physiological conditions, and the several environmental factors that the animal is actually experiencing, simultaneously. Data can be collected for a much longer period than with acoustic tracking, if the tags are successfully retrieved. Recently, a type of archival tag that can estimate geographical locations has been developed. This type of tag has been applied to southern bluefin tuna *T. maccoyii* (Gunn and Block, 2001) and Atlantic bluefin tuna *T. thynnus* (Block et al., 1998a, 1998b). These reports show the remarkable value of the archival tag data for investigating fish migration and behavior.

We have implanted archival tags in young Pacific bluefin tuna since 1994 to investigate their migration and behavior. This article describes the results obtained from recovered tags and places special emphasis on vertical swimming behavior, preferred water temperature, and feeding frequency. Some insights regarding vertical swimming depth have already been reported in Kitagawa et al. (2000) who used some of the same data. We have described in another paper (Itoh et al., 2003) the performance of the archival tag used in the present study and the characteristics of young Pacific bluefin tuna migration based on data from these same tags.

---

[1] Hisada, K., H. Kono, and T. Nagai. 1984. Behavior of young bluefin tuna during migration. *In* Progress report of the marine ranching project 4, p. 1–7. Nat. Res. Inst. Far Seas Fish. Pelagic Fish Resource Division, 5-7-1 Shimizu-Orido, Shizuoka, 424-8633, Japan. [In Japanese, the title is translated by the authors.]

Materials and methods

The archival tag used in the present study (Northwest Marine Technology, Inc., Shaw Island, WA) had four sensors—for external temperature, internal temperature, pressure, and light intensity. The external and internal temperature sensors had a 0.2°C resolution and response times of three seconds and 20 seconds, respectively. Resolution of the pressure sensor was 1 m of depth between the surface and 126 m, then 3 m down to the scale limit of 510 m. The tags measured data every 128 seconds.

Two types of data files were created within the tag memory. One data file stored daily records containing date, estimated times of sunrise and sunset, water temperatures at 0 m, plus two other selectable depths (we selected 60 m and 120 m), and other information required or produced in the course of location estimates for each day. This file is referred to as the "summary file" in this article, and it stored daily data from the time the memory was last cleared.

The second data file contained unprocessed time series data records taken at 128-second intervals. The tag could record at any integer multiple of its measurement interval and a multiple of one was chosen. Each record consisted of external temperature, internal temperature, pressure, and light intensity, and corresponded to a known time. This file is referred to as the "detail file" in this article. It can hold about 54,000 records, or about 80 days of steady data at the high rate chosen—a small fraction of the tag's lifetime. The time-series memory was divided into two sections, and the size allocation between the two sections was determined by the user. The first section filled first and did not change thereafter. The second section filled next, but once full, it is then continually overwrote old data. Thus the first section always contained the earliest data seen in a tag deployment and the second always contained the latest data. We divided the detail file into two 40-day sections for releases in 1995 and 1996, and into 20- and 60-day sections for releases in 1997. Most of the analyses in this study were conducted with the detail file.

Prior to experiments on wild fish, we applied archival tags to three pen-held Pacific bluefin tuna from 93 to 97 cm in fork length (FL) at Kasasa in Kagoshima Prefecture (31°25′N, 130°11′E) in November 1994 to observe the effect of archival tag attachment and implantation on fish. One of the fish that had an archival tag inserted in its abdominal cavity was recovered 453 days after tag implantation, when the fish was caught for sale in the market.

Experiments on wild young bluefin tuna were conducted near Tsushima at the northeastern end of the East China Sea every November and December from 1995 to 1997. A total of 166 fish, ranging from 43 to 78 cm FL (age 0 or 1), were caught by chartered trolling vessels, tagged on the vessel by inserting archival tags into their abdominal cavities, and released immediately. Details of the tag, its performance, and the manner of tagging are described in Itoh et al. (2003).

Thirty of the 166 archival tags (18.1%) were recovered. The durations of the tags at sea were 50 days or less for 13 fish, 96–211 days for 13 fish, and 359–375 days for three fish, all recaptured around Japan. One additional fish was recaptured off the west coast of Mexico, on the east side of the Pacific Ocean, 610 days after release. Data could not be downloaded from one archival tag released in 1995 and recovered 30 days after release; all other tags yielded data.

Results

Sample records of swimming depth, water temperature, and temperature of fish viscera as recorded in the detail file are shown in Figure 1 for three days in winter and three days in summer. The fish changed swimming depth frequently with rapid dives and ascents. The water temperature changed little in winter, but it changed frequently and substantially corresponding to dives in summer. Visceral temperature changed gradually.

Diurnal and seasonal change of swimming depth

Differences between daytime and nighttime swimming depth, water temperature, visceral temperature, and the temperature difference between water and fish viscera (thermal excess) were examined by using the Mann-Whitney *U* test ($P=0.05$) with data in the detail file. Data taken during the hour before and the hour after both dawn and dusk (four hours in all) were excluded from the test in order to distinguish clearly between daytime and nighttime. For this purpose, dawn and dusk were taken as the times the tag sensed the first or final light of the day. The average swimming depth was significantly deeper during daytime for 70% of all recorded days, which accounts for the additional observation that the water temperature was significantly lower during daytime for 66% of the days. The visceral temperature was significantly higher during daytime for 71% of the days, and thermal excess was significantly larger during daytime for 85% of the days.

Fish spent about 40% of their time within a 0–9 m depth range and the time spent within each depth interval decreased as depth increased. This concentration in the 0–9 m depth range was observed at both daytime and nighttime, but was more pronounced at night (Fig. 2).

The vertical thermal profiles (Fig. 2) show the change of depth range of the surface mixed layer, the ocean layer that lies above the seasonal thermocline, for one year. Although young Pacific bluefin tuna aggregated in the 0–9 m depth range for almost all months, swimming depth was more broadly distributed in winter when the depth range of the mixed layer was greater (e.g. January and March). When the depth range of the mixed layer became less in summer (e.g. May and July), fish tended to concentrate near the sea surface. Then as the depth range of the mixed layer became greater in autumn (e.g. September and November), the vertical distribution of the tuna gradually expanded toward deeper water.

Vertical swimming behavior at dawn and dusk

The fish commonly showed a distinctive vertical movement at dawn and dusk. At dawn, after a slow and steady descent for about 40 minutes to reach to a maximum depth of 82 ±28 m (average ±SD), fish suddenly and rapidly ascended

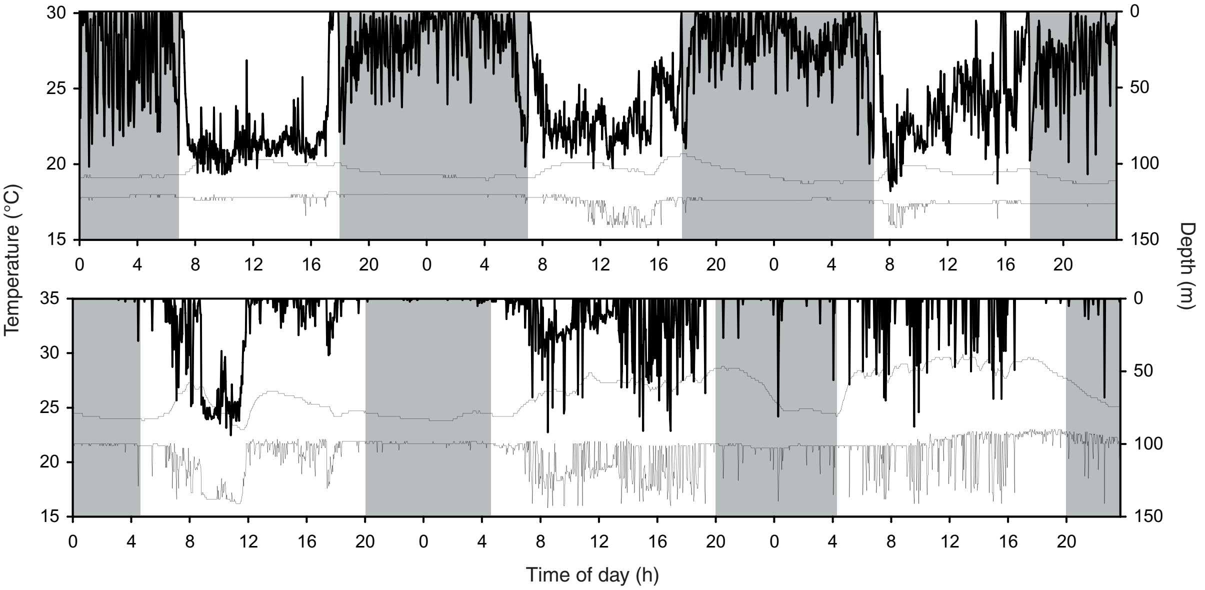


Figure 1

Sample records of swimming depth (thick solid line), water temperature (lower thin solid line), and temperature of viscera (upper thin solid line) for Pacific bluefin tuna from the detail files of two archival tags. Upper panel: records of a fish from 23 to 25 December 1995 in the East China Sea. Lower panel: records of another fish from 15 to 17 June 1997 in the East China Sea. Shadows indicate nighttime.

to near the sea surface (upper panel in Fig. 1, and Fig. 3). At dusk, after a rapid descent from near the sea surface to the maximum depth of 89 ±34 m, fish slowly and steadily ascended for about 40 minutes. The time that maximum depth was recorded was most frequently at four minutes before (or after) the time when the archival tag sensed the first (or final) light at dawn (dusk) for 29% (37%) of cases where this behavior was observed. The end (onset) of rapid ascents (descents) occurred most frequently at the time when the tag sensed the first (final) light, that is to say for 68% (49%) of all cases. The light detection threshold for the tags used in our study corresponded to an intensity in the blue-green transmission window of seawater (470 nanometers (nm) center, 60 nm width of the filter) of about 3×10^{-6} times the surface noon solar intensity on a clear day in that same spectral band. Because the light-sensitive region of the measurement stalk was located below the animal's body, we assumed that the eyes encountered a somewhat higher intensity than did the light sensor. Quick examination of tags in air in the early October revealed that the time when the archival tag sensed the first light at dawn or the final light at dusk was about 40 minutes before sunrise or about 40 minutes after sunset, respectively. Some combination of these vertical swimming behaviors was observed in 1081 of 1452 days (74%) during which the detail file data were available for both dawn and dusk. They occurred at both dawn and dusk in 679 days (47%), only at dawn in 77 days (5%), and only at dusk in 325 days (22%).

Occurrences of these behaviors differed by area and season (Table 1). The area was determined by using fish locations estimated as described in Itoh et al. (2003). The average occurrence of these depth excursions at dawn and dusk was as high as 87–88% in the East China Sea from November to January but decreased to 15–49% from February to June and October. In the Sea of Japan, the average occurrence was 4–39% in April, May, and September to November. In the Pacific Ocean, the behaviors were observed in 75–90% of days from May to July, in contrast to the relatively low occurrences within the East China Sea in the same season.

Water temperature

Water temperatures recorded in archival tags ranged from 8.3° to 28.4°C at 0 m depth, and 1.4° to 28.4°C when all depths were combined. A range of water temperatures that appeared to be preferred by young Pacific bluefin tuna was estimated. A simple frequency distribution of recorded water temperatures was inappropriate because fish could be forced to tolerate water out of their preferred temperature range because of a lack of water with a more favorable temperature within the geographical range accessible to the fish. Instead we compared the range of water temperature within the geographical area accessible to the fish with the frequency distribution of actual recorded water temperatures, grouped by year, month, and sea. We assumed that the accessible areas in each sea were those areas that a tag reported as its position. These include areas along the Japanese coast between 35° and 45°N in the Sea of Japan, 30–45°N in the western Pacific Ocean west of 160°E, and 25–45°N in the eastern Pacific Ocean east of 160°E. In

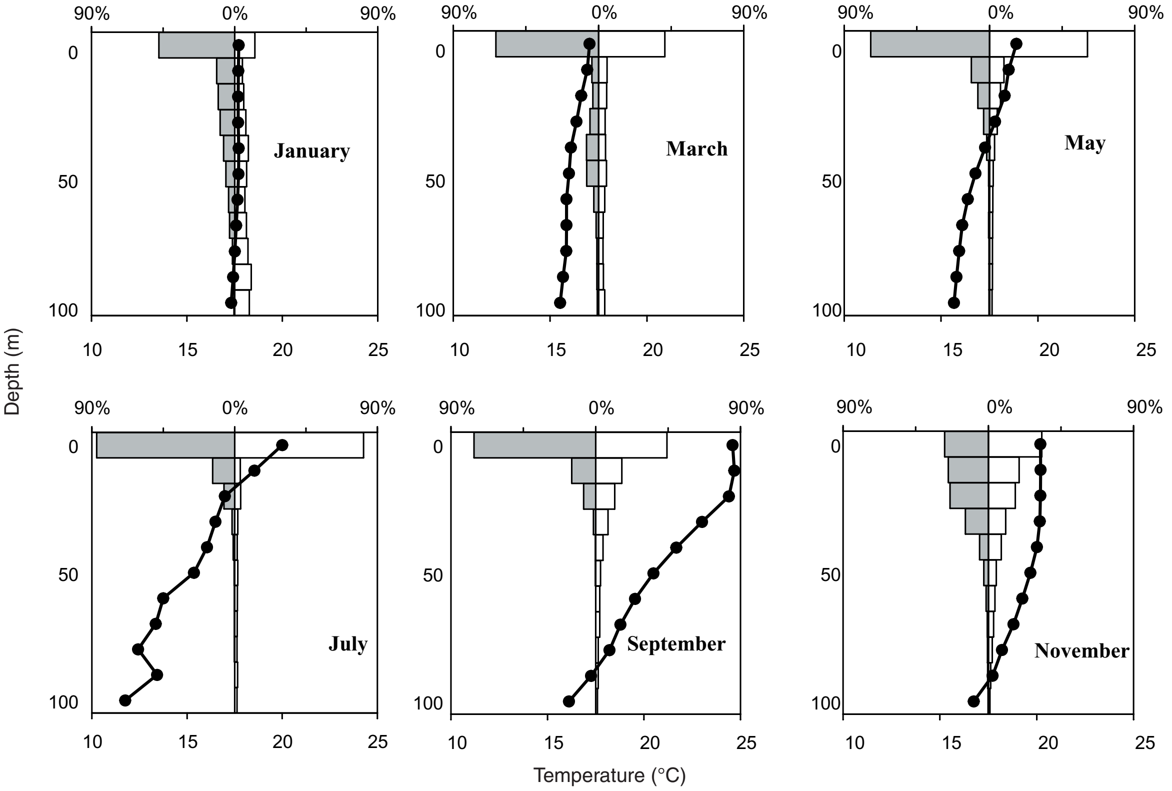


Figure 2

Vertical occurrence frequencies of young Pacific bluefin tuna in daytime (clear bar) and nighttime (shaded bar) and vertical thermal profile (line with dots) by month.

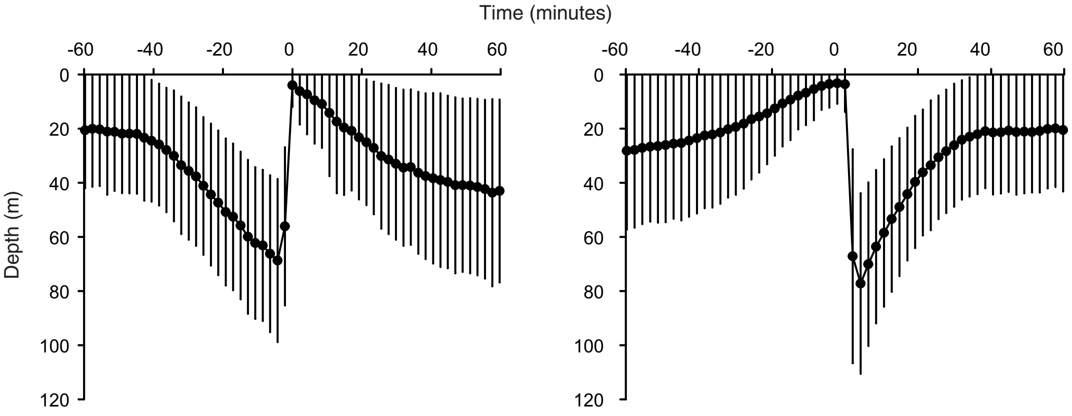


Figure 3

Average swimming depth of young Pacific bluefin tuna recorded by archival tags at dawn (left panel) and dusk (right panel). Times marked as 0 are the time just after the end of rapid ascent at dawn and just before the onset of rapid descent at dusk. All of records in which a rapid ascent or rapid descent occurred were averaged. Bar shows standard deviation.

the East China Sea, the area considered was enclosed by four points of 29°N–126°E, 29°N–128°E, 35°N–130°E, and 33°N–126°E, where the majority of estimated tag locations occurred. The temperature range in each area was derived from the sea-surface temperature maps published by the Japan Fisheries Information Service Center.

Table 1

The number of days during which swimming behaviors with rapid ascent at dawn and rapid descent at dusk were observed by area and month.

			Dawn			Dusk			
Area	Month	Number of fish	Total days	Observed days	Observed rate	Total days	Observed days	Observed rate	Average observed rate
East China Sea	1	7	87	73	84%	86	77	90%	87%
	2	1	23	6	26%	22	16	73%	49%
	3	2	36	11	31%	37	12	32%	31%
	4	7	66	24	36%	67	41	61%	49%
	5	10	220	51	23%	221	128	58%	41%
	6	8	182	17	9%	176	37	21%	15%
	10	1	24	4	17%	24	6	25%	21%
	11	23	132	109	83%	153	142	93%	88%
	12	29	487	388	80%	489	457	93%	87%
Sea of Japan	4	1	13		0%	12	1	8%	4%
	5	1	9	1	11%	9	1	11%	11%
	9	1	12		0%	12	4	33%	17%
	10	2	61	10	16%	61	22	36%	26%
	11	2	43	15	35%	42	18	43%	39%
Pacific Ocean	5	1	16	11	69%	16	13	81%	75%
	6	2	26	19	73%	26	25	96%	85%
	7	1	31	25	81%	31	31	100%	90%
Total			1468	764	52%	1484	1031	69%	61%

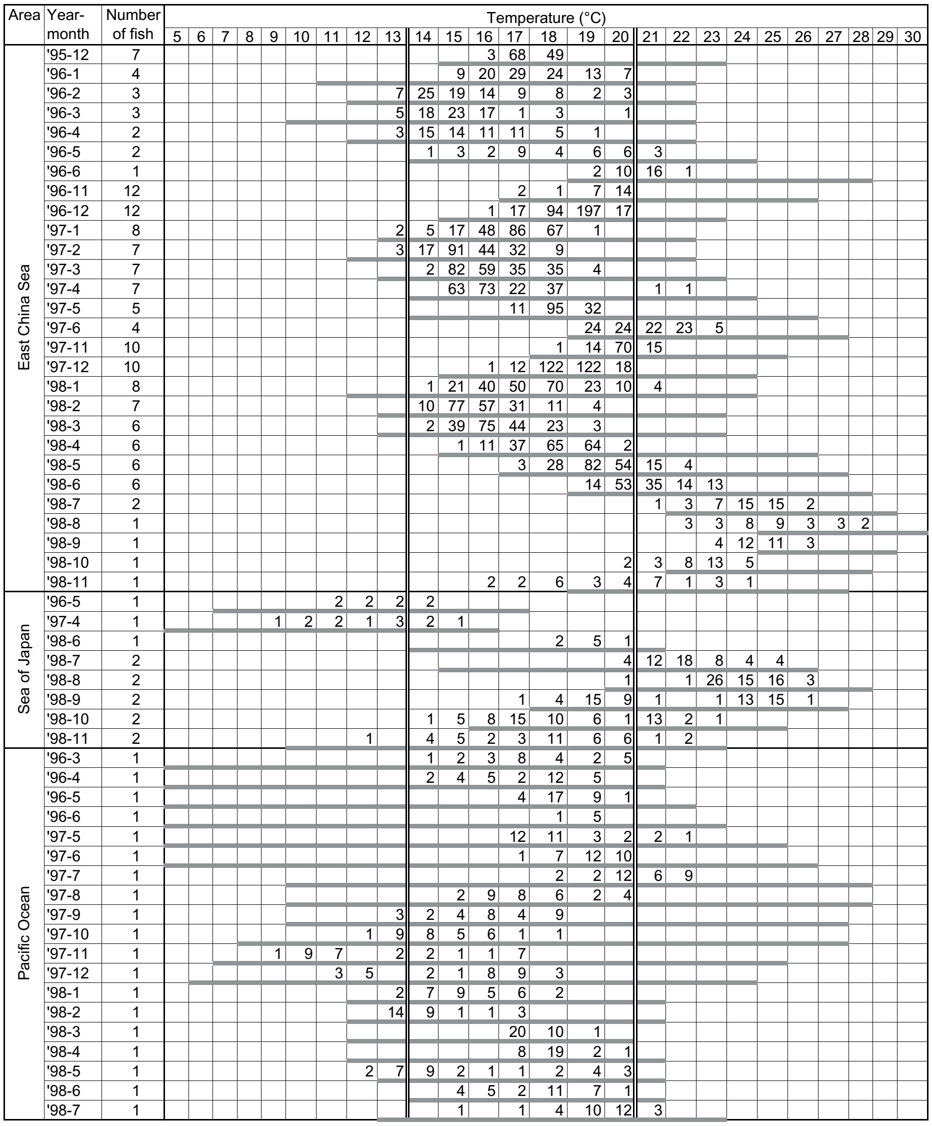
The tag temperature used in our comparison was the temperature at 0 m depth recorded in the summary file because that file contained a much larger number of days than that of the detail file. In support of this, we confirmed that the average water temperature over all depths for a day in the detail file had only slight differences of −0.1 ±0.7°C in average (range: −4.0−+4.3°C) from the temperature at 0 m recorded for the day in the summary file. Because the fish swam near the surface, the temperature recorded to represent 0 m depth also represented well the temperature at all depths where the fish actually swam. Frequencies of days were summed from the data for all individuals in one-degree temperature bins separated by year, by month, and by area, such as the East China Sea, the Sea of Japan, and the Pacific Ocean.

The water temperature recorded by archival tags commonly ranged from 14° to 20°C (Fig. 4). When water of this temperature range was located within an accessible area (e.g. many months in the East China Sea and the Pacific Ocean, and November in the Sea of Japan), almost all fish were found in such water. Where water temperature was higher (e.g. June 1996, June 1997, and between June and October 1998 in the East China Sea) or lower (e.g. May 1996 and April 1997 in the Sea of Japan), fish tended to choose water that was close to this range. However there were a few cases in which fish stayed in water with a temperature outside of this range (e.g. between July and September 1998 in the Sea of Japan) even when water of the 14–20°C range was accessible to them.

Visceral temperature and feeding events

Temperature of the fish viscera ranged from 13.0° to 30.9°C. It was usually higher than the water temperature and the thermal excess for a given individual ranged from 1.3° to 4.6°C, and averaged 3.0° ±1.0°C. The visceral temperature changed in parallel with the water temperature all year (Fig. 5).

In preliminary experiments, pen-held fish were fed completely thawed mackerel of 20–30 cm FL twice a day at approximately 900 h and 1500 h. The following changes in visceral temperature before and after feeding were generally observed (Fig. 6). All figures given below regarding thermal excess and timing after feeding are average values. The visceral temperature in a stable state just before feeding (n=5) was 3.7°C higher than ambient water temperature. This thermal excess decreased to 2.3°C at 22 minutes after feeding, and then increased to 7.6°C at 7.7 hours after feeding. Then it slowly decreased again and reached a stable thermal excess of 3.1°C at 21.0 hours after feeding. When the fish fed again before the visceral temperature stabilized (n=7), with the thermal excess still as high as 6.8°C, the thermal excess reached a high of 8.5°C but the increase after feeding was 1.7°C, much smaller than that observed in the previous case (3.9°C). The time required to reach the highest visceral temperature and the time to change back to a stable state were similar to the previous case. When the fish were not fed, because of rough sea conditions, the visceral temperature stayed stable all day (e.g. 16 January on Fig. 6).



Area	Year-month	Number of fish	Temperature (°C)																									
			5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
East China Sea	'95-12	7												3	68	49												
	'96-1	4											9	20	29	24	13	7										
	'96-2	3									7	25	19	14	9	8	2	3										
	'96-3	3									5	18	23	17	1	3		1										
	'96-4	2									3	15	14	11	11	5	1											
	'96-5	2										1	3	2	9	4	6	6	3									
	'96-6	1															2	10	16	1								
	'96-11	12													2	1	7	14										
	'96-12	12												1	17	94	197	17										
	'97-1	8									2	5	17	48	86	67	1											
	'97-2	7									3	17	91	44	32	9												
	'97-3	7										2	82	59	35	35	4											
	'97-4	7											63	73	22	37			1	1								
	'97-5	5													11	95	32											
	'97-6	4															24	24	22	23	5							
	'97-11	10														1	14	70	15									
	'97-12	10												1	12	122	122	18										
	'98-1	8										1	21	40	50	70	23	10	4									
	'98-2	7										10	77	57	31	11	4											
	'98-3	6										2	39	75	44	23	3											
	'98-4	6											1	11	37	65	64	2										
	'98-5	6													3	28	82	54	15	4								
	'98-6	6															14	53	35	14	13							
	'98-7	2																	1	3	7	15	15	2				
	'98-8	1																		3	3	8	9	3	3	2		
	'98-9	1																			4	12	11	3				
	'98-10	1																2	3	8	13	5						
	'98-11	1												2	2	6	3	4	7	1	3	1						
Sea of Japan	'96-5	1							2	2	2	2																
	'97-4	1					1	2	2	1	3	2	1															
	'98-6	1														2	5	1										
	'98-7	2																4	12	18	8	4	4					
	'98-8	2																1		1	26	15	16	3				
	'98-9	2													1	4	15	9	1		1	13	15	1				
	'98-10	2										1	5	8	15	10	6	1	13	2	1							
	'98-11	2								1		4	5	2	3	11	6	6	1	2								
Pacific Ocean	'96-3	1										1	2	3	8	4	2	5										
	'96-4	1										2	4	5	2	12	5											
	'96-5	1													4	17	9	1										
	'96-6	1														1	5											
	'97-5	1													12	11	3	2	2	1								
	'97-6	1													1	7	12	10										
	'97-7	1														2	2	12	6	9								
	'97-8	1											2	9	8	6	2	4										
	'97-9	1									3	2	4	8	4	9												
	'97-10	1								1	9	8	5	6	1	1												
	'97-11	1					1	9	7		2	2	1	1	7													
	'97-12	1							3	5		2	1	8	9	3												
	'98-1	1									2	7	9	5	6	2												
	'98-2	1									14	9	1	1	3													
	'98-3	1													20	10	1											
	'98-4	1													8	19	2	1										
	'98-5	1								2	7	9	2	1	1	2	4	3										
	'98-6	1											4	5	2	11	7	1										
	'98-7	1											1		1	4	10	12	3									

Figure 4

Frequencies of sea-surface water temperatures for young Pacific bluefin tuna with archival tags. The number given is the sum (over all individuals) of days in the category based on temperature at 0 m depth from the summary files. Gray, thick bars indicate the sea-surface temperature range that appeared to be accessible to the fish in each month.

In the detail files obtained from wild fish, the following three types of visceral temperature changes were identified as indicators of feeding (Fig. 7). Type A: a sharp decrease of 1–2°C followed by an increase above the initial temperature. Type B: an increase above the initial temperature, preceded by either no decrease or a slow decrease. Type C: a sharp decrease of 1–2°C followed by a return to the initial temperature. In addition, in only cases where the visceral temperature changes could not be explained by water temperature changes were they counted as being caused by feeding. For example, a slow decrease of visceral temperature when the fish dived into cold water was not counted as a feeding event. Cases where the water temperature changed frequently were also excluded as too difficult to interpret.

Feeding events were observed in 942 days out of 1494 total recorded days (63%). Because it was found that fish did not feed normally for approximately the first 30 days after release (Itoh et al., 2003), data from the first 60 days after release were excluded in the following description. After exclusion of data for the first 60 days, feeding events were observed in 726 out of the remaining 807 recorded days (90%). The number of daily feeding events ranged from zero to ten, with an average of 1.8 ±1.4. Feeding events occurred most frequently in the daytime (69% of all observed feeding events more than 60 days after release), followed by dawn with 27% (Fig. 8). Feeding events rarely occurred at dusk and at night, accounting for only 1% and 3% of the total feeding events, respectively. For this analysis, dawn and dusk were defined as explained above, a one-hour period centered on the time of first or last detected daylight. Changes in visceral temperature of "type B" (increase only) were observed most frequently (51.4% of total observed feedings), followed by "type C" (decrease only, 45.2%). Bipolar events (type A) were as few as 3.5%.

When averaged over individual months, the number of feeding events per day per individual ranged from 0.9 in January to 2.2 in June and averaged 1.5. Feeding events were observed all year, although they were slightly more frequent in May and June than in other months (Fig. 9).

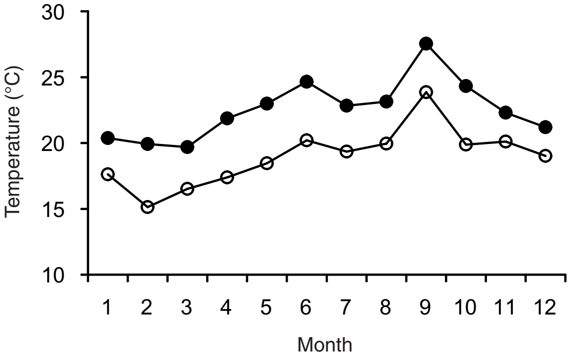


Figure 5

Monthly change of average water temperature (○) and average visceral temperature (●) in young Pacific bluefin tuna with archival tags. Average values of each individual were averaged.

Discussion

Diurnal and seasonal change of swimming depth

Young Pacific bluefin tuna were previously assumed to swim near the sea surface based on the fact that most of the catch was made by surface fishing gear and fish schools were observed at the sea surface (Yabe et al., 1953). However, details of their vertical swimming behavior and relationships between their behaviors and oceanic structures have not been well investigated. Recently, Marcinek et al. (2001) observed during an acoustic tracking experiment over several days that Pacific bluefin tuna in the eastern Pacific Ocean spent the majority of their time in the top portion of the water column. Our archival tag data showed that young bluefin tuna in the western Pacific Ocean also ordinarily stayed within the surface mixed layer and most frequently near sea surface, regardless of the time of day or the season. The vertical distribution of fish changed according to the seasonal change in depth range of the surface mixed layer and appeared to be controlled by the depth of the thermocline. Restriction by the thermocline was also observed for yellowfin tuna (*T. albacares*) and bigeye tuna (*T. obesus*) (Carey and Olson, 1982; Holland et al., 1990b; Cayré and Marsac, 1993; Block et al., 1997). Occasionally young Pacific bluefin tuna dived through the thermocline into deep, cooler water, but they returned to the surface mixed layer after a short period.

Diurnal change in swimming depth, i.e. deeper swimming depth during daytime, was reported by acoustic tracking studies not only for *Thunnus* species, such as yellowfin tuna (Carey and Olson, 1982; Holland et al., 1990b; Cayré, 1991; Yonemori[2]) and bigeye tuna (Holland et al., 1990b), but also for other large pelagic species, such as skipjack tuna, *Katsuwonus pelamis* (Yuen, 1970; Dizon et al., 1978); swordfish, *Xiphias gladius* (Carey and

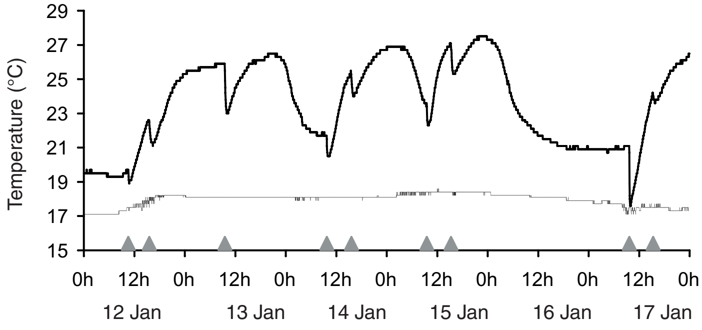


Figure 6

Visceral temperature (thick line) and water temperature (thin line) of a pen-hold young Pacific bluefin tuna recorded by an archival tag. Triangles indicate the time of feeding.

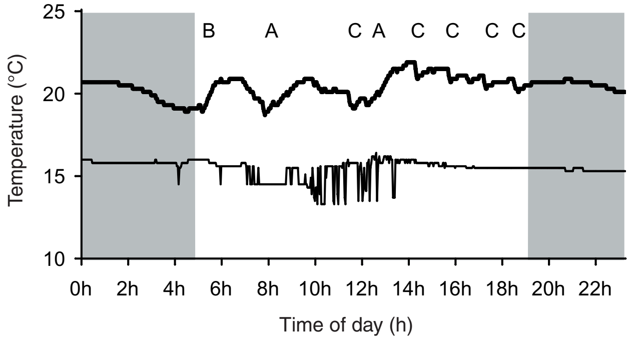


Figure 7

An example of visceral temperature change in a wild young Pacific bluefin tuna recorded by an archival tag. Visceral temperature (thick line) and water temperature (thin line) are shown. Shadows indicate nighttime. Data are from a fish in the Sea of Japan on 2 May 1996. A, B, and C indicate the types of visceral temperature changes described on page 540.

---

[2] Yonemori, T. 1982. Swimming behavior of tunas by the use of sonic tags—a study particularly of swimming depth. Far Seas Fish. Res.Lab. Newsletter 44:1–5. Pelagic Fish Resource Division, 5-7-1 Shimizu-Orido, Shizuoka, Shizuoka, 424-8633, Japan. [In Japanese.]

Robison, 1981); blue marlin, *Makaira nigricans* (Holland et al., 1990a); mako shark, *Isurus oxyrinchus*; and blue shark, *Prionace glauca* (Carey and Scharold, 1990). However some reports did not note any difference in swimming depth between day and night, such as that of Block et al. (1997) for yellowfin tuna, Cayré (1991) for skipjack tuna, and Brill et al. (1993) for striped marlin, *Tetrapturus audax*. The swimming depth of young bluefin tuna recorded by the archival tags in the present study was deeper during the day for 70% of recorded days. This finding agrees with the speculation made by Carey and Olson (1982) that a deeper swimming depth in the daytime is a common feature for large pelagic fish.

Vertical swimming behavior at dawn and dusk

A characteristic vertical movement pattern was found in young Pacific bluefin tuna. They dived gradually and constantly for about 40 minutes and then rapidly ascended to the sea surface at dawn. Inverse behavior were observed at dusk. The same behavior was reported in larger size Pacific bluefin tuna in the eastern Pacific Ocean and in yellowfin tuna (Block et al., 1997; Marcinek et al., 2001). The percentage of days when this behavior was observed varied according to the season and area. This variation was commonly observed in individuals as well as in the group as a whole.

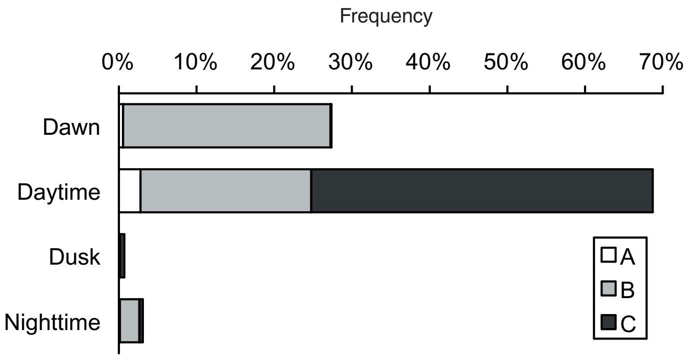


Figure 8

Frequency of feeding events of young Pacific bluefin tuna by period within a day. Only data taken more than 60 days after release were used. A, B, and C indicate the types of temperature changes of viscera described on page 540.

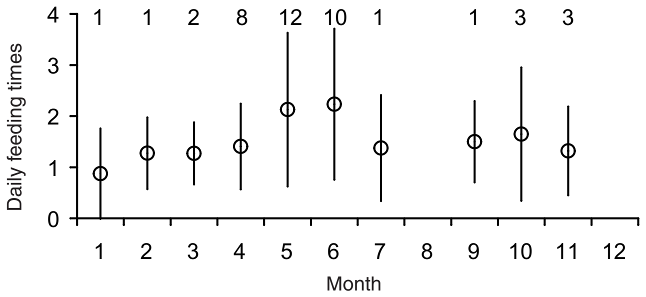


Figure 9

Average frequency of feeding events by month for young Pacific bluefin tuna. Only data taken more than 60 days after release were used. The number above each point indicates the number of individuals contributing to the average. Bars show standard deviations.

Two potential reasons for this behavior were considered. The first one was avoidance of a specific range of light intensities. The times of onset and end of the behavior are apparently related to the time of sunrise and sunset. Assuming that young Pacific bluefin tuna dislike a specific light intensity range, we describe their vertical movements at dawn and at dusk as follows. About 80 minutes before sunrise when the light intensity at the sea surface reaches a specific value near the lower boundary of the avoided range, fish begin descending into water with lower light intensity. About 40 minutes before sunrise when the light intensity in deep water reaches that avoided range, the fish rapidly ascend almost to sea surface, and as the light brightens further, gradually expand into their normal distribution pattern while staying within the range of water depths where light intensities exceed the avoided low-intensity range. A possible reason for avoiding a specific intensity range might be an increased risk of predation at intensities where tuna see less well than some predator that hunts visually.

The other potential reason for the characteristic vertical movements is feeding. It is well known that some small animals show diurnal vertical migration, i.e. they descend gradually as the light level increases toward dawn and rise again at dusk. Young Pacific bluefin tuna following these species to feed on them would show similar behavior. However, young Pacific bluefin tuna were observed to feed only at dawn, not at dusk, although the characteristic vertical behavior was observed at both dawn and dusk. In addition, rapid ascents and descents at a specific time with respect to sunrise and sunset could not be explained by the vertical migration behavior of bait species. Therefore, feeding seems not to be a primary cause of the vertical migration in young Pacific bluefin tuna.

Generally speaking, fishermen consider dawn and dusk to be good times for catching Pacific bluefin tuna. The archival tag records showed that young Pacific bluefin tuna did not usually feed at dusk, although tag records showed that fish aggregated very close to the sea surface after their rapid ascent at dawn and before their rapid descent at dusk. Judging from this behavior, good fishing seemed to be caused by a concentration of fish near the sea surface rather than by the feeding activities. Moreover, the low light level at these times would make it difficult for fish to distinguish between artificial bait with a hook and live prey.

Preferred water temperature

Water temperature is thought to be one of the most important environmental factors controlling the distribution of young Pacific bluefin tuna (Sund et al., 1981; Koido and Mizuno, 1989; Ogawa and Ishida, 1989). Kitagawa et al. (2000) attached importance to the gradient of water temperature; however Uda (1957) emphasized the absolute value of temperature, although his study was presumably for large-size fish. Data from the archival tags indicated that young Pacific bluefin tuna seemed to prefer to remain in water of 14–20°C. When there was no accessible water within this temperature range, the fish tended to stay in water of a temperature as close as possible to this range. In addition, archival tags showed that the vertical distribution of young Pacific bluefin tuna was restricted by the thermocline, even when the temperature below the thermocline was in the tuna's preferred temperature range (14–20°C). These observations support the importance of water temperature as shown in previous studies and suggest that both the absolute value and the gradient of water temperature are important as environmental factors controlling the distribution of young Pacific bluefin tuna.

Feeding

Visceral temperature of pen-held Pacific bluefin tuna with archival tags changed in a specific way during feeding. Stomach temperature changes have also been observed in pen-held giant bluefin tuna in the Atlantic and in pen-held southern bluefin tuna (Carey et al., 1984; Gunn et al., 2001). The cycle of visceral temperature change for young Pacific bluefin tuna was completed in 21 hours (shorter than that observed in previous studies of 1.5 to 2 days) probably due to the smaller size of the fish. Similar visceral temperature changes were also noted in the records of archival tags recovered from wild fish, ranging from a distinct pattern the same as that observed in pen-held fish (type A) to less distinct ones such as type B or type C, which were observed more frequently. All of these changes could be distinguished quite easily from gradual decreases of visceral temperature when fish dived into cold water. Therefore, we assumed that these three types of temperature changes were caused by feeding. Temperature changes of type A could be expected if fish consumed a large amount of food at one time as they do when fed in a pen. However, wild fish may seldom have an opportunity for such large meals, and the apparently more frequent small meals would be expected to cause the less dramatic visceral temperature changes of types B or C.

In the present study, a visceral temperature change was taken to indicate feeding only when that change could not be explained by a change in water temperature. Also, when the water temperature changed very frequently, it was difficult to decide whether water temperature could account for a feeding event and it was not counted as such. Finally it is possible that feeding might not cause a recognizable change in visceral temperature. As a result of these three factors the feeding frequency estimated in our study might have been underestimated.

Frequencies of feeding events did not change much over the year, although there was a slightly higher frequency in early summer. Growth in length of young Pacific bluefin tuna is known to become slow in winter (Yukinawa and Yabuta, 1967; Bayliff, 1993). Because fish weight at a length was constant throughout the year for wild young Pacific bluefin tuna (Itoh, 2001), food consumption in winter appears not to be used for increasing weight at a length. We did not reach a conclusion on this question and further investigation of seasonal change in food items and of the physiology of tuna is needed.

Acknowledgments

We thank the staff of Marino Forum 21 and the Kagoshima Fisheries Experimental Station for their cooperation in the pe-held fish experiment. We also thank troll fishermen, staff in the Kamiagata Fisheries Cooperative Association, the Tsushima Fisheries Extension Service, and the Nagasaki Fisheries Experimental Station for their cooperation with the experiment on wild fish. We greatly acknowledge fishermen, consumers, and staff at the Inter-American Tropical Tuna Commission for their kindness in returning recovered archival tags bearing the information necessary for our study. We especially thank J. Gunn at CSIRO for giving us valuable information about implanting the archival tag in fish. We are also grateful to the staff of Northwest Marine Technology Inc. and Tanaka Sanjiro Co., Ltd., for providing us with tags. We would like to thank P. Ekstrom of Northwest Marine Technology Inc. for his critical review and help with the English text. We thank our staff in Japan NUS Co., Ltd., the Suidosya Co., Ltd., and the National Research Institute of Far Seas Fisheries, and also T. Kitagawa in the Ocean Research Institute of the University of Tokyo, for their efforts in regard to implantation of the tags in fish. We gratefully acknowledge S. Kume of Japan NUS Co., Ltd., N. Baba of Fishery Research Agency, Z. Suzuki, and Y. Uozumi of National Research Institute of Far Seas Fisheries for their critical review.

Literature cited

Bayliff, W. H.
1993. Growth and age composition of northern bluefin tuna, *Thunnus thynnus*, caught in the eastern Pacific Ocean, as estimated from length-frequency data, with comments on trans-pacific migrations. Bull. IATTC 20:503–540.

Block, B. A., H. Dewar, E. V. Freund, C. Farwell, and E. D. Prince.
1998a. A new satellite technology for tracking the movements of Atlantic bluefin tuna. Proc. Natl. Acad. Sci. USA 95:9384–9389.

Block, B. A., H. Dewar, T. Williams, E. D. Prince, C. Farwell, and D. Fudge.
1998b. Archival tagging of Atlantic bluefin tuna (*Thunnus thynnus thynnus*). Mar. Tech. Soc. J. 32: 37–46.

Block, B. A., J. E. Keen, B. Castillo, H. Dewar, E. V. Freund, D. J. Marcinek, R. W. Brill, and C. Farwell.
1997. Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. Mar. Biol. 130:119–132.

Brill, R. W., D. B. Holts, R. K. C. Chang, S. Sullivan, H. Dewar, and F. G. Carey.
1993. Vertical and horizontal movements of striped marlin (*Tetrapturus audax*) near the Hawaiian Islands, determined by ultrasonic telemetry, with simultaneous measurement of oceanic currents. Mar. Biol. 117:567–574.

Carey, F. G., J. W. Kanwisher, and E. D. Stevens.
1984. Bluefin tuna warm their viscera during digestion. J. Exp. Biol. 109:1–20.

Carey, F. G., and K. D. Lawson.
1973. Temperature regulation in free-swimming bluefin tuna. Comp. Biochem. Physiol. 44A:375–392.

Carey, F. G., and R. J. Olson
1982. Sonic tracking experiments with tunas. ICCAT Collective Volume of Scientific Papers XVII. 2:458–466.

Carey, F. G., and B. H. Robison
1981. Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. Fish. Bull. 79: 277–292.

Carey, F. G., and J. V. Scharold
1990. Movements of blue sharks (*Prionace glauca*) in depth and course. Mar. Biol. 106:329–342.

Cayré, P.
1991. Behavior of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) around fish aggregating devices (FADs) in the Comoros Islands as determined by ultrasonic tagging. Aquat. Living. Resour. 4:1–12.

Cayré, P. and F. Marsac.
1993. Modeling the yellowfin tuna (*Thunnus albacares*) vertical distribution using sonic tagging results and local environmental parameters. Aquat. Living Resours. 6:1–14.

Dizon, A. E., R. W. Brill, and H. S. H. Yuen.
1978. Correlations between environment, physiology, and activity and the effects on thermoregulation in skipjack tuna. *In* The pysiological ecology of tunas (G. D. Sharp and A. E. Dizon, eds.), p. 233–259. Academic Press, New York, NY.

Gunn, J., and B. Block.
2001. Advances in acoustic, archival, and satellite tagging of tunas. *In* Tuna: physiology, ecology, and evolution (B. A. Block and E. D. Stevens, eds.), p. 167–224. Academic Press, San Diego, CA.

Gunn, J., J. Hartog, and K. Rough.
2001. The relationship between food intake and visceral warming in southern bluefin tuna (*Thunnus maccoyii*). Can we predict from archival tag data how much a tuna has eaten? *In* Electronic tagging and tracking in marine fisheries (J. R. Sibert and J. L. Nielsen, eds.), p. 109–130. Kluwer Academic Publisher, Netherlands.

Holland, K. N., R. W. Brill, and R. K. C. Chang.
1990a. Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. Fish. Bull. 88:397–402.
1990b. Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. Fish. Bull. 88:493–507.

Itoh, T.
2001. Estimation of total catch in weight and catch-at-age in number of bluefin tuna *Thunnus orientalis* in the whole Pacific Ocean. Bull. Nat. Res. Inst. Far Seas Fish. 38: 83–111. [In Japanese.]

Itoh, T., S. Tsuji, and A. Nitta.
2003. Migration patterns of young Pacific bluefin tuna (*Thunnus orientalis*) determined with archival tags. Fish. Bull. 101: 514–534.

Kitagawa, T., H. Nakata, S. Kimura, T. Itoh, S. Tsuji, and A. Nitta.
2000. Effect of ambient temperature on the vertical distribution and movement of Pacific bluefin tuna *Thunnus thynnus orientalis*. Mar. Ecol. Prog. Ser. 206:251–260.

Koido, T., and K. Mizuno.
1989. Fluctuation of catch for bluefin tuna (*Thunnus thynnus*) by trap nets in Sanriku coast with reference to hydrographic condition. Bull. Jpn. Soc. Fish. Oceanogr. 53: 138–152. [In Japanese.]

Laurs, R. M., H. S. H. Yuen, and J. H. Johnson
1977. Small-scale movements of albacore, *Thunnus alalunga*, in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. Fish. Bull. 75: 347–355.

Marcinek, D. J., S. B. Blackwell, H. Dewar, E. V. Freund, C. Farwell, D. Dau, A. C. Seitz and B. A. Block.
2001. Depth and muscle temperature of Pacific bluefin tuna examined with acoustic and pop-up satellite archival tags. Mar. Biol. 138:869–885.

Ogawa, Y., and T. Ishida.
1989. Hydrographic conditions governing fluctuations in the catch of *Thunnus thynnus* by set-nets along the Sanriku coast. Bull. Tohoku Reg. Fish. Res. Lab. 51:23–39. [In Japanese.]

Sund, P. N., M. Blackburn and F. Williams.
1981. Tunas and their environment in the Pacific Ocean: a review. Oceanogr. Mar. Biol. 19:443–512.

Uda, M.
1957. A consideration of the long years trend of the fisheries fluctuation in relation to sea condition. Bull. Jap. Soc. Sci. Fish. 23:368–372

Yabe, H., N. Anraku, and T. Mori.
1953. Scombroid youngs found in the coastal seas of Aburatu, Kyusyu, in summer. Contribution of Nankai Reg. Fish. Res. Lab. 1:1–10. [In Japanese.]

Yuen, H. S. H.
1970. Behavior of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic devices. J. Fish. Res. Board Canada 27:2071–2079.

Yukinawa, M., and Y. Yabuta.
1967. Age and growth of bluefin tuna, *Thunnus thynnus* (Linnaeus), in the north Pacific Ocean. Rep. Nankai Reg. Fish. Res. Lab. 25:1–18. [In Japanese.]