Diving patterns and performance of Pacific bluefin tuna (*Thunnus thynnus orientalis*) as recorded by archival tags

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Archival tagged immature Pacific bluefin tuna were released off Tsushima Island in the East China Sea. Time-series data on swimming depth, ambient temperature, internal body temperature, and light intensity were recorded every 128 s to evaluate: 1) their vertical swimming patterns to depths below the thermocline and 2) the development of their diving performance with growth. In summer, the tuna spent most of their time at the surface, but occasionally dove to depths below the thermocline during the daytime, and at dawn and dusk. In addition, bluefin dove at increasing descent rates and surfaced more slowly when they made excursions to deeper depths. Larger-sized bluefin dove to much deeper depths than smaller individuals, suggesting that the diving performance of bluefin is related to their body size and larger size enables them to expand their vertical movement range.

Key words: Pacific bluefin tuna, archival tag, diving behavior, diving performance, descent/ascent rate, swimbladder

INTRODUCTION

Pacific bluefin tuna, *Thunnus thynnus orientalis*, are highly migratory predators, due in part to their speed and power, a result of their large size, high body temperature, and streamlined body shape. Immature bluefin are mainly distributed in the seas around Japan. The East China Sea (Fig. 1, ECS) is a wintering habitat for the immature bluefin, and from this area they often migrate to the western North Pacific (WPO) or to the Sea of Japan (SOJ) in late spring-summer. Some of them also migrate across the Pacific to the Gulf of Alaska-California coast (Clemens and Flitter 1969, Bayliff 1994). After spending 2 to 6 yr in the eastern North Pacific, bluefin return to the WPO to spawn (Bayliff 1980). However, due to the magnitude of the high-speed movements of bluefin, direct observation and recording of high-speed swimming is difficult to achieve.

Recently micro data loggers (archival tags) have been developed and applied to a few free ranging tunas (e.g. Gunn et al. 1994, 2001; Block et al. 1998a, 1998b; Kitagawa et al. 2000, 2001, 2002a, 2002b; Inagake et al. 2001, Itoh et al. 2003a, 2003b). Since these recoverable data loggers enable us to record time-series data for longer durations and with higher resolutions, the behavior, physiology and ecology of fish have gradually been clarified. In the present study, we analyzed comprehensive data on vertical distribution and movement of Pacific bluefin obtained from archival tags. Our main aims are to examine their vertical swimming patterns to deeper depths below the thermocline and the development of their diving performance with growth. The results of an analysis of diurnal and seasonal changes in the swimming depth of some bluefin tuna and their thermocon-servation mechanism under low ambient temperatures have been published (Kitagawa et al. 2000, 2001, 2002a, 2003b).

MATERIALS AND METHODS

The archival tag (Northwest Marine Technology, Inc. WA, U.S.) records external and internal temperatures, swimming depth, and ambient light levels at intervals of 128 seconds (675 data per day) for 80 days at maximum. Fish locations are roughly estimated every day from the time of sunrise and sunset as detected by the light sensor. Detailed specifications of the archival tag were described in Anonymous (1994) and Block et al. (1998b).

We captured 166 immature tuna with fork lengths of 47 to 63 cm, ≤ 1 yr old (Yukinawa and Yabuta, 1967) by trolling off Tsushima Island, placed archival tags in the peritoneal cavity, and released them in three different batches: in Dec. 1995, Nov.1996, and Nov. 1997. Of these, data from thirteen individuals (5 in 1995, 5 in 1996, and 3 in 1997) recovered by fisheries were analysed. Eight were recovered in the ECS and four were recovered by fisheries in the WPO within 6 months to 4 years, and the last one was recovered in the SOJ. Detailed information on the methods of tag implantation has been described by Kitagawa et al. (2000).

Time-series data for 1995 were recorded for the initial 40 d after the tags were turned on, and for an additional 40 d before the data was recovered In 1996 and 1997 on the other hand, data were recorded for 20 d after switching the tags on, and then for a further 60 d before data recovery. Therefore, when the tags were recovered, more than 80 d of data was recorded in 2 time-slots: an initial 20 to 40 d after the release, and a final period of 40 to 60 d before recovery.
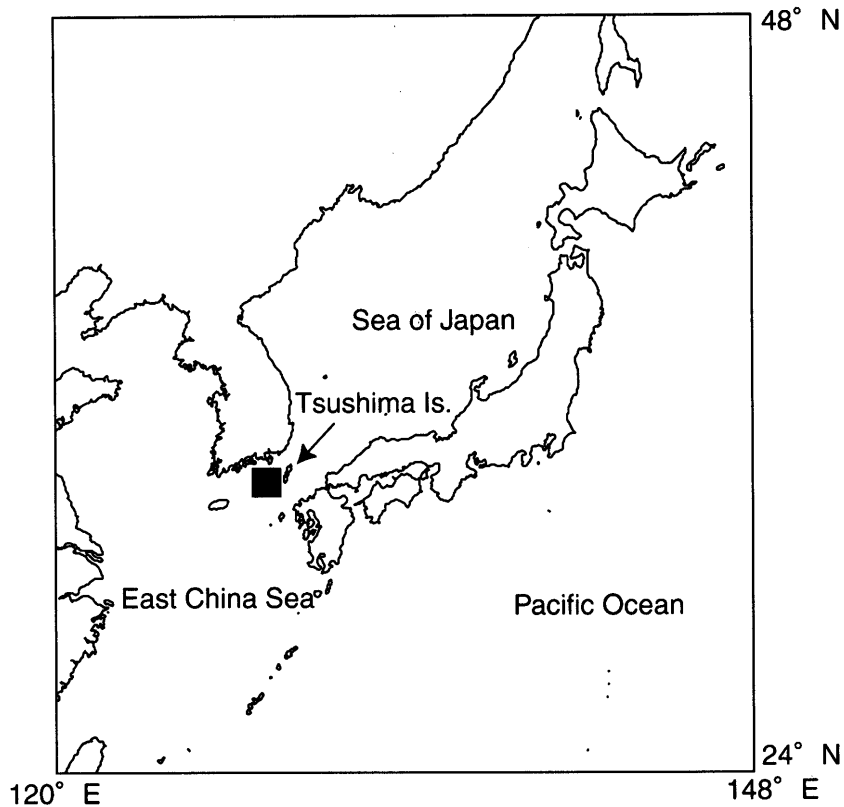
Fig. 1.   Site of release (■) of Pacific bluefin tuna marked with and archival tag.

Table 1.   Date of release, body size, swimming duration and recovery site for the individuals used for this study. ECS, WPO and SOJ indicate the East China Sea, the western North Pacific, and the Sea of Japan, respectively. FL indicates fork length.

Bluefin No.	Date of release	FL at release (cm)	Swimming duration (d)	Recovery site	Analysed data duration	FL at recovery (cm)
177	Dec. 14, 1995	52.0	201	ECS	May. 24, 1996–Jun. 30, 1996	56.0
194	Dec. 14, 1995	49.0	1285	WPO	May .19, 1999–Jun. 20, 1999	139.4
199	Dec. 11, 1995	54.0	1285	WPO	May. 29, 1999–Jul. 3, 1999	144.3
209	Dec. 11, 1995	53.0	180	WPO	May. 16, 1996–Jun. 6, 1996	64.2
226	Dec. 10, 1995	50.0	1302	WPO	May. 14, 1999–Jun. 15, 1999	142.2
232	Nov. 29, 1996	60.0	211	ECS	May. 24, 1997–Jun. 26, 1997	83.5
256	Nov. 29, 1996	54.0	209	ECS	May. 2, 1997–Jun. 24, 1997	60.0
282	Nov. 29, 1996	50.0	169	ECS	Mar. 21, 1997–May. 15, 1997	56.0
321	Nov. 29, 1996	53.0	209	ECS	May 2, 1997–Jun. 24, 1997	66.5
328	Nov. 29, 1996	50.0	209	ECS	May 1, 1997–Jun. 24, 1997	63.5
516	Nov. 24, 1997	49.0	209	ECS	Apr. 30, 1998–Jun. 19, 1998	62.5
687	Nov. 23, 1997	46.0	210	ECS	Apr. 30, 1998–Jun. 19, 1998	57.8
688	Nov. 21, 1997	47.0	360	ECS	Sep. 20, 1998–Nov. 14, 1998	81.3
698	Nov. 19, 1997	63.0	205	SOJ	Apr. 25, 1998–Jun. 10, 1998	76.0

In the present study, we analyzed the swimming depth and ambient water temperature data recorded in the second period to discuss the diving patterns and performance of tuna in summer (Mar. to Nov., Table 1). Light level data were mainly used for discriminating daytime from nighttime. For analyzing daily activity patterns, days were divided into 4 phases: nighttime, dawn (from 30 min. before sunrise to 30 min. after sunrise), daytime, and dusk (from 30 min. before sunset to 30 min. after sunset).

For the dive analysis of blufin tuna, a dive was defined as the period when the tuna remained submerged below the surface (≤ 10 m) (Fig. 2). Dive depth is defined as the maxi-

mum depth recorded in a dive, and only the dives deeper than 50 m were analyzed. In addition, because data were recorded every 128 s, descent/ascent rates were calculated by the difference between a dive depth and the next recorded depth, and the highest value of each dive was defined as a descent/ascents rate of the dive.

RESULTS

Time-series data of swimming depth and ambient temperature from 12:00 on 15 June, 1997 to 12:00 on 17 June, 1997 obtained from Bluefin 232 (BF 232) is shown in Fig. 3. This data was similar to those for other individuals with
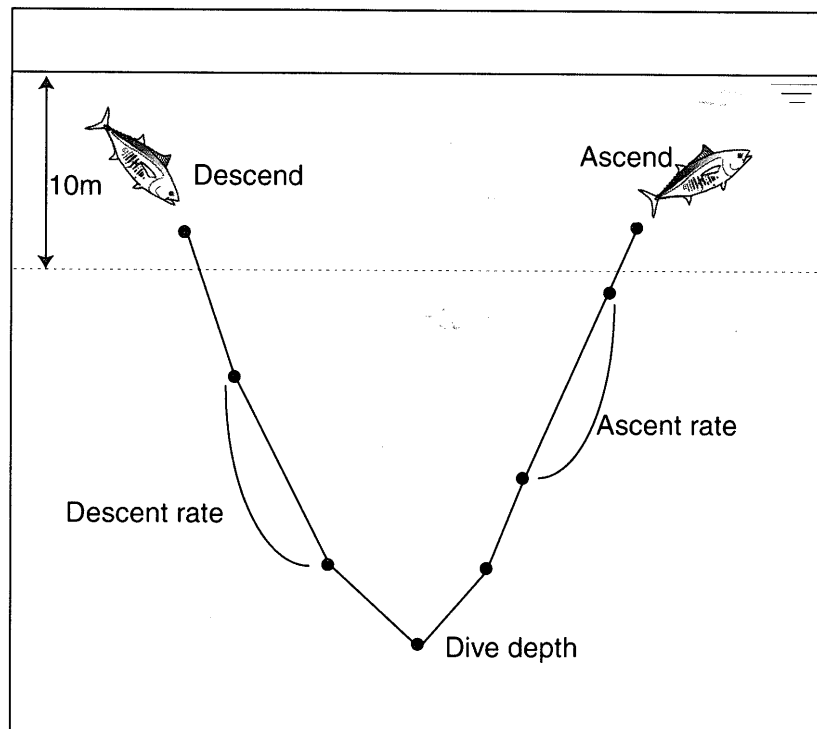
Fig. 2.   Dive profile of bluefin tuna described in the present study.
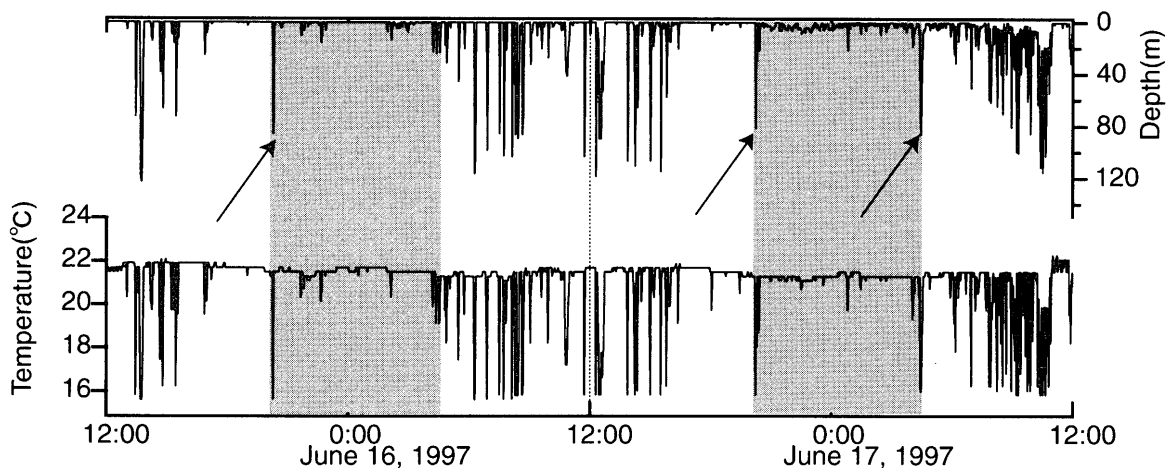

Fig. 3.   Time-series data from 12:00 on 15 June, 1997 to 12:00 on 17 June, 1997 for depth (top) and ambient water temperature (bottom) obtained from Bluefin 232. Shaded areas indicate nighttime.

similar body size. BF 232 spent most of the time at the surface both day (68.2% of total time in June) and night (94.5% of total time of June), and made occasional dives to depths through the seasonal thermocline during the day with a maximum diving depth of about 120 m. The diving resulted in a marked change in ambient temperature because of the existence of a seasonal thermocline below the surface mixed layer. Further, BF 232 also showed distinctive vertical migration at dawn and dusk as indicated by arrows in Fig 3. According to Itoh et al. (2003b) who analyzed the same archival tag data, at dawn these dives consist of slow and constant descents for 40 min followed by a rapid ascent, and while at dusk these dives exhibit a slow, constant ascent followed by a rapid descent.

As for relationships between descent/ascent rate and dive depth for all individuals, positive correlations were observed in all cases. (Table 2. Spearman rank correlation

coefficient, $p<0.0001$). This indicates that it is necessary for bluefin to gain speed in order to dive to deeper depths when there is little difference in diving angles on between ascent and descent. There is little difference between descent and ascent rates for most individuals during time of dawn, daytime, and nighttime. At dusk, however, descent rates are significantly higher than ascent rates for all individuals except for BF 177 and 194 (Wilcoxon test, $p<0.05$, Table 3.).

Figure 4 shows the relationship between descent or ascent rate and dive depth for BF 199 whose body size at recovery was much larger than that of BF 232. BF 199 also showed increased descent and ascent rates on diving to deeper depths (Spearman rank correlation coefficient (a) 0.874 and (b) 0.780, $p<0.0001$). In addition, when bluefin dove to depths more than 200 m, their descent rates increase (Fig. 6(a)) although their ascent rates became almost

Table 2. Spearman rank correlation analysis for the relationships between descent/ascent rate and dive depth.

Bluefin No.	Spearman rank correlation coefficient (Descent)	Probability	Spearman rank correlation coefficient (Ascent)	Probability
177	0.768	$p<0.0001$	0.707	$p<0.0001$
194	0.820	$p<0.0001$	0.777	$p<0.0001$
199	0.874	$p<0.0001$	0.780	$p<0.0001$
209	0.694	$p<0.0001$	0.751	$p<0.0001$
226	0.899	$p<0.0001$	0.797	$p<0.0001$
232	0.779	$p<0.0001$	0.766	$p<0.0001$
256	0.749	$p<0.0001$	0.737	$p<0.0001$
282	0.638	$p<0.0001$	0.659	$p<0.0001$
321	0.734	$p<0.0001$	0.740	$p<0.0001$
328	0.675	$p<0.0001$	0.682	$p<0.0001$
516	0.741	$p<0.0001$	0.709	$p<0.0001$
687	0.735	$p<0.0001$	0.700	$p<0.0001$
688	0.767	$p<0.0001$	0.735	$p<0.0001$
698	0.763	$p<0.0001$	0.735	$p<0.0001$

Table 3. Average descent and ascent rate (ms^{-1}) during dawn, daytime, dusk and nighttime. The Wilcoxon test was used for statistical significance if difference between the descent and ascent rate. Asterisks indicate significant differences $(p<0.05)$.

Bluefin No.	Dawn			Daytime			Dusk			Nighttime		
	Descent rate (ms^{-1})	Ascent rate (ms^{-1})	Sample size	Descent rate (ms^{-1})	Ascent rate (ms^{-1})	Sample size	Descent rate (ms^{-1})	Ascent rate (ms^{-1})	Sample size	Descent rate (ms^{-1})	Ascent rate (ms^{-1})	Sample size
177	0.61	0.54	9	0.55	0.54	313	0.60	0.51	7	0.41	0.41	1
194	1.21	0.78	8	0.8*	0.65	196	0.83	0.46	5	0.56	0.54	69
199	0.68	0.62	19	0.61	0.62	164	1.73*	0.65	19	0.65	0.53	50
209	0.97*	0.62	13	0.52	0.52	64	1.26*	0.55	13	0.54*	0.62	73
226	1.00	0.63	27	0.72	0.67	108	1.79*	0.67	41	0.54*	0.45	49
232	0.56	0.55	23	0.56	0.55	373	0.60*	0.50	13	0.52	0.52	23
256	0.50	0.51	41	0.55	0.56	723	0.65*	0.47	41	0.52	0.53	31
282	0.45	0.51*	66	0.55	0.58*	683	0.62*	0.48	66	0.49	0.53*	335
321	0.46	0.58*	31	0.56	0.56	695	0.66*	0.45	18	0.54	0.55	69
328	0.46	0.51*	39	0.54	0.56*	716	0.60*	0.40	44	0.46	0.47	62
516	0.55	0.57	28	0.52	0.51	541	0.64*	0.45	40	0.46	0.52	60
687	0.52	0.53	29	0.51	0.52	658	0.69*	0.48	32	0.52	0.55	39
688	0.50	0.52	57	0.58	0.60	281	0.74*	0.50	23	0.56	0.64*	113
698	0.50	0.52	29	0.61	0.60	365	0.62*	0.38	25	0.50	0.56*	93
Total	0.56	0.55	30	0.56	0.56	420	0.84	0.49	28	0.52	0.55	76

constant (Fig. 6(b)). Furthermore, at dusk with its average descent rate was 1.73 ms^{-1}, and much higher than those in ascent (Table 3). These results were similar to those for the other two (BF194 and 226) with similar body size.

The maximum dive depth of bluefin was correlated to body size (fork length, FL) at recovery of the bluefin (Fig.5 Spearman rank correlation coefficient 0.584 n=14, p< 0.05). However, no significant correlation was found between fork length and the highest descent rate in FL s^{-1} (Fig. 6).

DISCUSSION

In our previous studies, we determined diurnal and seasonal changes in the swimming depth of bluefin tuna and examined the effect of ambient temperature on their vertical distribution and migration (Kitagawa et al. 2000),

and investigated their thermoconservation mechanisms during dives to cooler waters below the thermocline in Kitagawa et al. (2001). As a result, in winter the bluefin swam within the surface mixed layer at shallower depths during nighttime than during daytime and swimming depth displayed diel periodicity. In summer, with the development of a sharper thermocline, the bluefin spent most of their time at the surface, suggesting that bluefin avoid rapid temperature change at the thermocline. During summer, however, the fish occasionally dove through the thermocline for short periods (~640 sec) during the day, maintaining body temperature. This result also indicates that since bluefin maintain body temperature for only short periods of time, they avoid rapid temperature change at the thermocline through behavioral thermoregulation. In addition, Kitagawa et al. (2002) and Kitagawa et al. (2001) reported
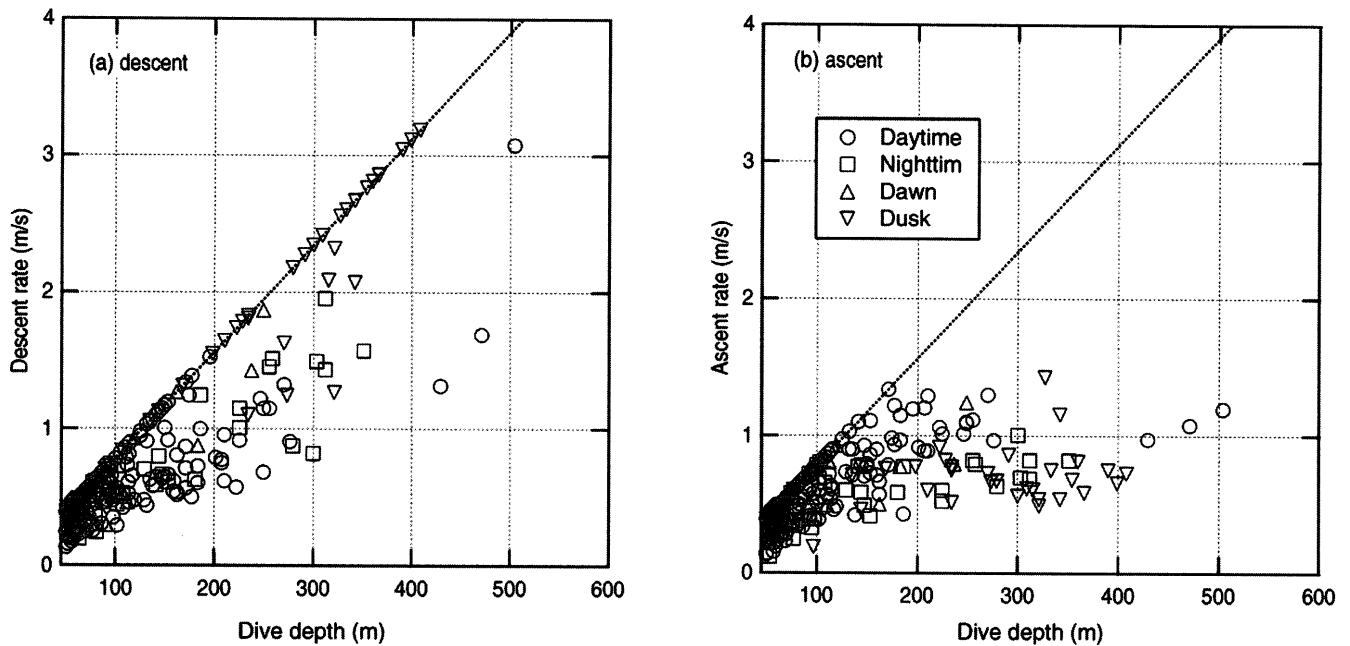
Fig. 4. Relationships between dive depth and (a) descent rate for BF 199, and (b) ascent rate for BF 199. There are no values higher than 1/128×dive depth in Fig. 5(a) or (b) since depth since the depth was recorded every 128 sec.
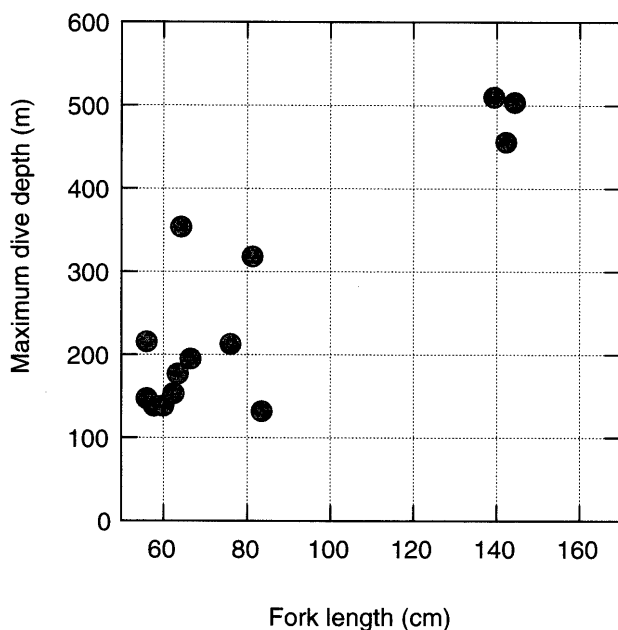

Fig. 5. Relationship between fork length (FL) and maximum descent rate. Both horizontal and vertical axes in logarithm scale. Solid lines indicate a maximum descent rate equal to 1–5 FLs^{-1}.
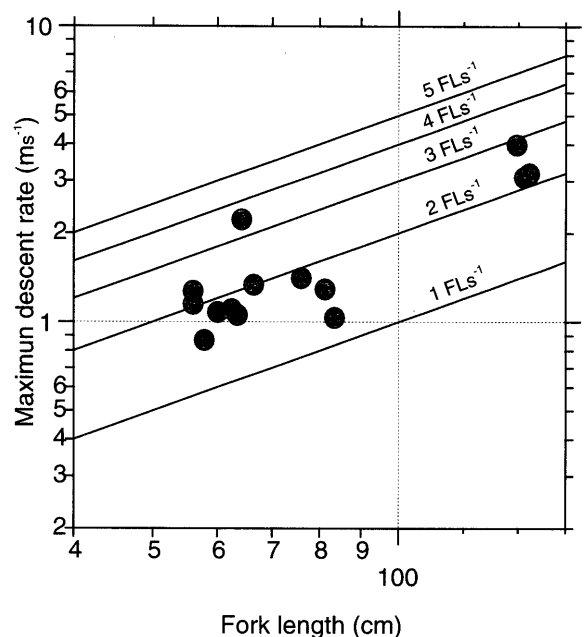

Fig. 6. Relationship between fork length (FL) and maximum dive depth.

that this diving behavior is probably related to feeding at a time of depletion of food in the surface, since the diving frequency was quite high in the daytime, and this species is known as a visual predator.

Bluefin food items and their swimming depths reported are shown in Table 4. Bluefin tuna (20–65 cm in length) consume anchovies in the south of Japan (Yokota et al. 1963). Although anchovy is generally a pelagic fish, in spring and summer their swimming depth often extended to slightly deeper depths in the daytime with the greatest swimming depth at 125 min spring and 70 min summer (Nozu 1966). Furthermore, demersal lightfish, *Maurolicus*

Muelleri, were found in the bluefin stomach (Dragovich 1969). This is the most dominant micronekton in the ECS, and is distributed to depths of up to 150 min the daytime (Ohshimo 1998). Other pelagic species such as sardine, common squid and round herring are often distributed to deeper depths, and this supports the hypotheses that the diving behavior may be related to feeding on prey concentrated at deeper depths (Kitagawa et al. 2000).

However, we would like to emphasize that the purpose of the dives at dawn and dusk is probably not for feeding, mainly because of the automatic and mechanical nature of these twice-daily diving patterns. Further, Masuma et al. (2001) also suggests bluefin experience visual disorienta-

Table 4. Food items for Pacific bluefin tuna. Surface indicates depths less than 30 m.

	Food item	Swimming layer in the daytime	Literature sited
Pelagic	Anchovy (*Engraulis japonica*)	Surface to 125 m	Nozu (1966)
	Sardine (*Sardinops melanostictus*)	Surface to 110 m	Aoki and Murayama (1993), Yokota (1957)
	Japanese common squid (*Todarodes pacificus*)	30–70 m to 150–200 m	Hamabe (1964), Suzuki et al. (1974)
	Round herring (*Etrumeus teres*)	Below the layer of anchovy or sardine	Kishida (1986)
Mesopelagic	Light fish (*Maurolicus muelleri*)	Surface to 150 m	Ohshimo (1998)

tion at these times due to the incompatibility of the retina to adapt to the change in ambient light intensity, and so these dives might be related to a behavioral compensation to avoid the visual disorientation in the rapid change in the ambient light.

As dive depths for bluefin deepen, descent rates increase (Fig. 4). In addition, mean maximum dive depths for the larger bluefin are significantly deeper than those for other smaller bluefin (Fig. 5). On the other hand, there is no significant correlation between body size and maximum descent rate in FLs^{-1} (Fig. 6). These facts suggest only that as body size increases, so does diving performance and they develop tolerance to water pressure at deeper depths. Another explanation is that it may be related the lower body density of larger compared to smaller bluefin. Itazawa (1973) suggested that among species with swimbladders such as in the genus *Thunnus*, swimbladder growth results in lower body density and higher buoyancy with growth due to a faster increasing swimbladder volume compared to that of body weight. Therefore, larger bluefin possibly have to dive at higher descent rates in order to overcome their higher buoyancy compared to smaller bluefin. In any rate, bluefin diving performance is related to their large body size and this makes it possible to expand their vertical movement ranges into much deeper depths.

On the other hand, when bluefin ascended from deeper depths to the surface, their ascent rates were significantly lower than their descent rates especially at dusk (Fig. 4). This indicates that when bluefin dive to deeper depths, they descend quickly and return to the surface more slowly. This is probably related to buoyancy control. In many fish the swimbladder duct degenerates, leaving no connection between the swimbladder and the outside. These fish (including *Thunnus*) are called physoclist fish (Shimidt-Nielsen 1990), and the gases in the swimbladder must originate in the blood and be secreted into the swimbladder at a pressure equal to the depth at which the fish live. Assuming that bluefins maintain neutral buoyancy at the surface where they spend most of their time and that they do not control the volume of the swimbladder, at deeper depths the fish will be much heavier than the surrounding water since the swimbladder is compressed by water pressure of deeper depths. Therefore, they would need much more time to ascend in order to lift their now heavier body.

On the other hand, if the fish actively secretes gas into the swimbladder to maintain the neutral buoyancy at deeper depths, when the fish rises above the level of neutral buoyancy, pressure is reduced, the swimbladder expands, and fish gains increased lift. If the ascent rate is not careful-

ly controlled, the swimbladder will expand too rapidly, resulting in the death of the fish, so this may also explain the slow ascent rates of large bluefin.

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