L. Dagorn · P. Bach · E. Josse

Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry

Abstract The horizontal and vertical movements of large bigeye tuna (*Thunnus obesus* Lowe, 1839; 25 to 50 kg) captured in the south Pacific Ocean (French Polynesia) were determined using pressure-sensitive ultrasonic transmitters. Bigeye tuna swam within the first 100 m below the surface during the night-time and at depths between 400 and 500 m during the daytime. The fish exhibited clear relationships with the sound scattering layer (SSL). They followed its vertical movements at dawn and dusk, and were probably foraging on the organisms of the SSL. Bigeye tuna did, however, make regular rapid upward vertical excursions into the warm surface layer, most probably in order to regulate body temperature and, perhaps, to compensate for an accumulated oxygen debt (i.e. to metabolize lactate). The characteristics of these dives differ from those reported from previous studies on smaller bigeye tuna (~12 kg) near the main Hawaiian Islands. During the daytime, the large fish in French Polynesia made upward excursions approximately only every 2.5 h, whereas smaller fish in Hawaiian waters made upward excursions approximately every hour. Our data are the first observations on the role of body size in the vertical behavior of bigeye tuna.

L. Dagorn (⊠) · P. Bach
Centre Institut de Recherche pour le
Développement (IRD) Montpellier,
Laboratoire HEA,
BP 5045, F-34032 Montpellier Cédex 1,
France

Fax: 0033 (0) 4 67 41 94 30
e-mail: dagorn@ird.fr

E. Josse
Centre IRD de Brest, BP 70,
F-29280 Plouzane Cédex, France

Introduction

Bigeye tuna (*Thunnus obesus* Lowe, 1839) occur throughout the tropical ocean, and are a highly valuable commercial species. Most bigeye tuna landed are captured by subsurface (longline) fishing gear, and are mainly large individuals of >20 kg, although smaller individuals are also caught near the surface by purse seine. The dynamics and causal mechanisms of the vertical movements of large bigeye tuna are not known, yet this information is critical for accurate population assessments based on catch-per-unit-effort data and effective fisheries management and resource conservation.

Bigeye tuna have evolved a unique anatomy and physiology that allows an unparalleled behavioral repertoire: they have the ability to hunt both in surface waters and in the cooler depths below the upper mixed layer (Holland et al. 1992; Holland and Sibert 1994). During tracking studies in which both swimming depth and body temperature were recorded, Holland et al. (1992) demonstrated that bigeye tuna have the capacity for short-latency physiological thermoregulation. This ability, coupled with behavioral thermoregulation expressed as brief vertical excursions, allows bigeye tuna to forage in deep colder waters and still maintain the advantages of high muscle temperatures derived from their tropical lineage. Organisms of the sound-scattering layer, which migrate to depths below 400 m during daytime in French Polynesia, could be exploited as prey by tuna species able to forage at these depths.

Based on depth-of-capture with longline fishing gear, Hanamoto (1987) and Boggs (1992) reported depth distributions of bigeye tuna to be 250 to 400 m and 200 to 400 m, respectively. Hanamoto (1986), however, also suggested that the vertical distribution of bigeye tuna ranges between the surface and 600 m. Sonic tracking of individual fish provides a complementary way of estimating the depth range of pelagic species. Prior to our study, tracks of seven juvenile bigeye tuna (all near the main Hawaiian Islands) were reported (Holland et al.

1990a, 1992; Holland and Sibert 1994). The depth distribution indicated by their experiments was slightly shallower than that indicated by longline depth-of-capture studies. This disparity, however, may be due to the attraction of their tracked bigeye tuna to FADs (fish aggregating devices) or to size-related differences, since all the individuals tracked weighed < 12 kg. Longline-caught bigeye tuna are usually larger (>20 kg), and longline fishing gear is generally deployed in the open ocean, far away from any FAD.

Prior to our study, no information was available on the short-term vertical and horizontal movements of large bigeye tuna (>20 kg) in the open ocean. During our study, we tracked four fish (estimated mass between 25 and 50 kg) carrying ultrasonic depth-sensitive transmitters in waters of the French Polynesian economic exclusive zone (EEZ). Herein, we elucidate the role of body size in the frequency or time-course of the daytime upward excursions of bigeye tuna by comparing our data to data obtained from smaller individuals tracked near the Hawaiian Islands. Our study constitutes the first records of bigeye tuna movements complemented with simultaneous records of their biological environment obtained with an echo-sounder. The study was finalized as part of the ECOTAP project (a study of tuna behavior using acoustic and longline fishing experiments in the economic zone of French Polynesia), the aim of which is to study the distribution and the behavior of bigeye tuna, yellowfin tuna (*Thunnus albacares* Bonnaterre, 1788), and albacore tuna (*T. alalunga* Bonnaterre, 1788), species exploited by longline fishing operations in French Polynesia.

Materials and methods

Ultrasonic tracking was conducted using the IRD 28 m R.V. "Alis". Vemco (Shad Bay, Nova Scotia, Canada) acoustic transmitters and receiving equipment were used. The transmitters (Model V16P: 50 kHz, 500 psi, or Model V22P: 50 kHz, 1000 psi) were equipped with pressure sensors, and therefore telemetered information on fish depth. We deployed a Vemco V41 four-hydrophone array on a V-fin towed depressor. The signals from the individual hydrophones were received aboard by a Vemco four-channel VR28 ultrasonic receiver. Vemco software ("TRACK") was running on an attached computer, and depth data were stored at 1 s intervals on disk. The computer was also connected to a global positioning system (GPS), and recorded geographical co-ordinates of the tracking vessel every 5 s.

Two different techniques were employed to capture large *Thunnus obesus*. (1) Polynesian fishing vessels using standard commercial monofilament longlines caught the fish, and the R.V. "Alis" was used only for tracking; fishermen set the gear early in the morning and retrieved it in the night of the same day; no data are available on time and depth of capture. (2) the R.V. "Alis" set standard, monofilament, longline fishing gear with 200 hooks, which was retrieved after a relative short soak time (4 to 5 h); when a fish suitable for tracking was caught, the branchline was cut from the mainline and a radio-transmitter buoy was attached with a 100 m-long tether; the vessel then completed retrieval of the remaining fishing gear before returning to the fish attached to the radio-buoy; fish were tethered for < 2 h and were, therefore, hooked for a maximum of 6 to 7 h before an ultrasonic transmitter was attached. Boggs (1992) has reported that 85% of bigeye tuna that remained

for > 6 to 7 h on longline hooks were recovered alive, indicating good survival abilities. Even though our technique (capture by longline fishing gear followed by tethering to a buoy) is probably stressful, the relatively short maximum amount of time each fish remained hooked ensured worthwhile results.

Because of the large size of the fish used in this study, no attempt was made to bring the fish aboard for attaching the transmitter. Rather, the fish were brought alongside the ship, and the ultrasonic transmitter was attached while the fish remained in the water. A stainless steel arrowhead, wired to the transmitter, was placed in the fish's anterior dorsal musculature by means of a tagging pole, as described for marlin by Holland et al. (1990b) and Brill et al. (1993).

While following the fish carrying ultrasonic transmitters, we collected simultaneous acoustic data with a scientific echo-sounder (Model EK500, Simrad, Horten, Norway) connected to a hull-mounted, split-beam transducer (Model ES38B, Simrad, frequency 38 kHz, beam angle 6.9°, rated to 500 m) using a medium pulse-length (1.0 ms). Acoustic data and vessel position were simultaneously logged on a second computer running appropriate software (Program EP500, Simrad).

Just before a fishing or a tracking operation, water temperature, dissolved oxygen, salinity and light intensity were measured at 1 m intervals between the surface and 700 m depth by a multiparameter conductivity–temperature–depth (CTD) probe (Model Seacat SBE19, Sea-Bird Electronics, Inc., Bellevue, Washington, USA).

Results

Horizontal movements

Currently-available, ultrasonic-telemetry receiving-equipment provides accurate direction, but only rough estimates of the distance between the transmitter (fish) and the receiver. As a result, the movements of the tracking boat reflect only in a very general way the minute-to-minute movements of *Thunnus obesus* in our study. Over a sufficiently long period (e.g. a few hours), however, the movements of the tracking vessel can provide estimates of the path length (the actual distance covered) and the diffusion distance (the distance between the start and end points of the tracks) of the fish. In turn, these data can be used to quantify horizontal movement patterns. We therefore calculated path length and diffusion distance for the total duration of each track, and also for the daytime and for the night-time separately (for Bigeye No. 1 dawn was at 05:00 hrs, whereas it was at 06:00 hrs for the other three fish; dusk was 18:00 hrs for all tracks). Fig. 1 and Table 1 show the locations of the different tracking operations and the characteristics of each track (including path length and diffusion distance), respectively. Fig. 2 shows the horizontal movements of the four fish.

Bigeye No. 1 (estimated body mass 25 kg) was caught by a commercial longline fishing-vessel off Tetiaroa atoll (an atoll of the Winward Islands of the Society Islands archipelago), and was tagged and released at 01:00 hrs. The fish stayed in the area of release during the first hour, and then contact was lost between 02:00 and 04:00 hrs. From 04:00 hrs to the end of the track at 14:00 hrs, the fish proceeded northeast (Fig. 2a).

Bigeye No. 2 (estimated body mass 30 kg) was caught by a commercial longline fishing-vessel in the western
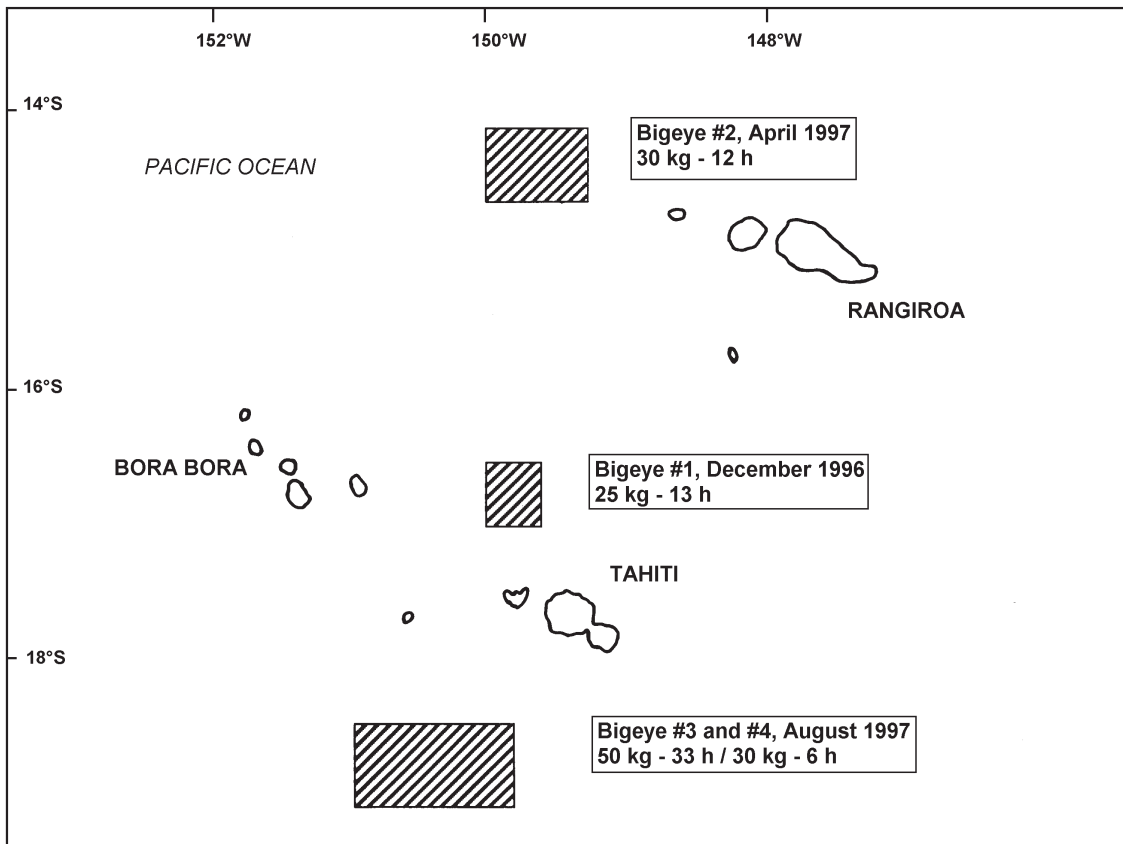
Fig. 1 Locations of tracking operations on bigeye tuna *Thunnus obesus* in French Polynesia. Body mass and duration of tracking are given for each fish

part of the Tuamotu Islands archipelago. The fish was tagged and released at 21:00 hrs. It moved west/north-west during the night, passing close to the fishing vessel that had originally caught it at 02:50 hrs. At 08:00 hrs, the fish changed direction, moving north/northeast, apparently towards a seamount ≃9.7 km distant. After 12 h tracking, the fish was lost at 09:10 hrs, at which time it was still swimming towards the seamount which was still 6.5 km away (Fig. 2b).

Bigeye No. 3 (estimated body mass 50 kg) was caught by the tracking vessel south of Tahiti (Society Islands archipelago). It was tagged at 15:00 hrs and tracked for 33.5 h. Contact was lost at 00:30 hrs on the third day because of problems with the hydrophones. Immediately after release, the fish moved northeast (Fig. 2c). During the first night (18:00 to 06:00 hrs), however, its movements were erratic, with no constant direction. During the daytime (06:00 to 18:00 hrs), this fish again followed a direct northeast course, as on the first afternoon after release. During the second night, from 18:00 hrs until the last contact, the fish displayed more erratic movements, similar to those exhibited during the first night.

Bigeye No. 4 (estimated body mass 30 kg) was caught in the same area as Bigeye No. 3, and was tagged at

Table 1 *Thunnus obesus*. Track dates and estimated fish weight, path length, ground speed and diffusion distance for four bigeye tuna equipped with ultrasonic depth-sensitive transmitters. Diffusion distance is distance between start and end points

Track dates	Path length (km)	Ground speed (ms^{-1})	Diffusion distance (km)
Fish 1 (25 kg)			
18 Dec 1996			
total (11 h)[a]	40.3	1.0	8.1
day (9 h)	36.6	1.1	8.5
Fish 2 (30 kg)			
20–21 Apr 1997			
total (12 h)	63.4	1.5	29.8
day (3 h)	24.7	2.3	11.5
night (9 h)	38.7	1.2	19.8
Fish 3 (50 kg)			
1–3 Aug 1997			
total (33.5 h)	106.6	0.9	59.2
2nd day (12 h)	43.5	1.0	35.9
1st night (12 h)	37.8	0.9	15.2
2nd night (6.5 h)	20.5	0.9	2.0
Fish 4 (30 kg)			
5 Aug 1997			
total (6 h)	25.5	1.2	5.4
night (5 h)	21.4	1.2	3.9

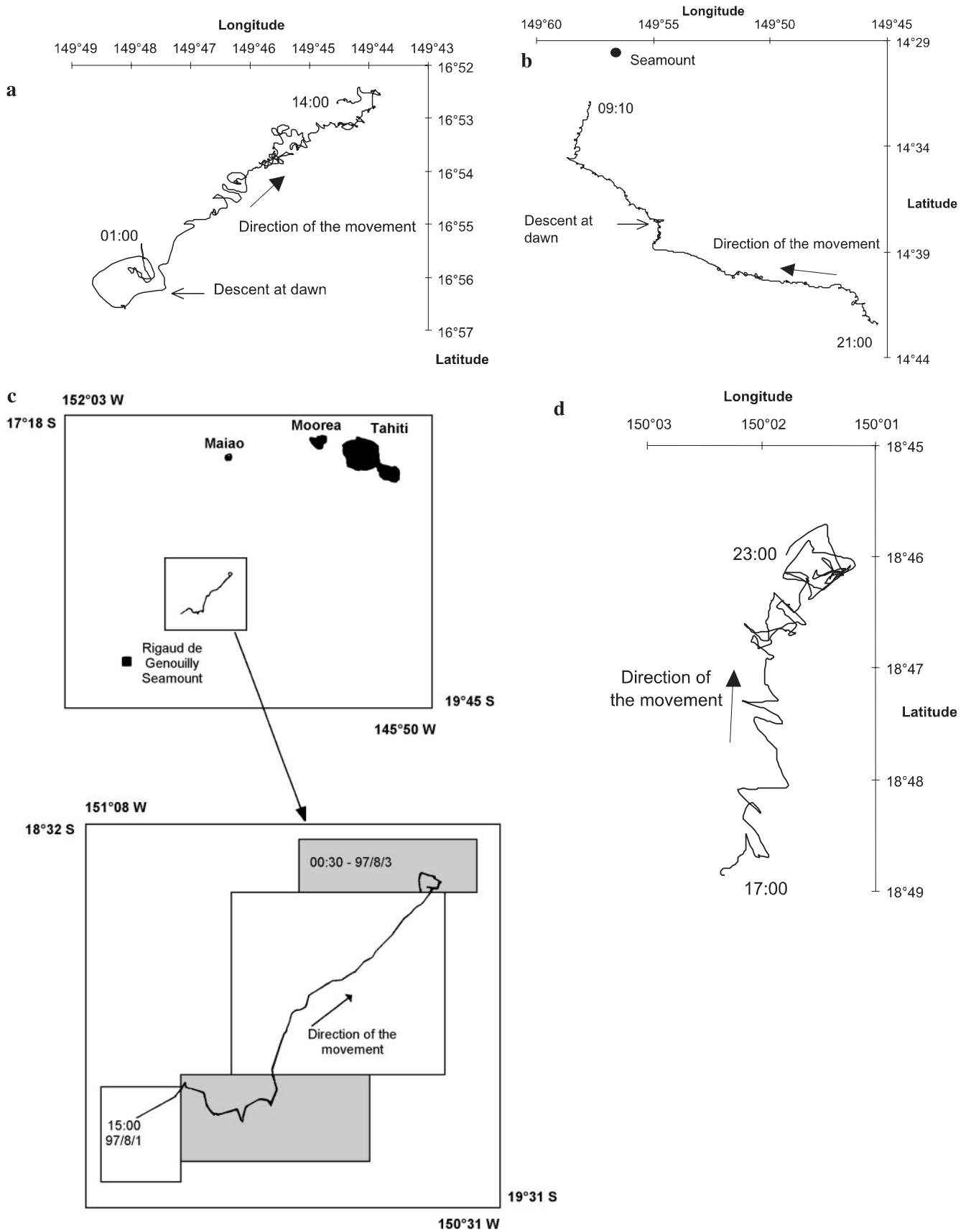[a] Only 11 effective hours of tracking, since contact was lost for 2 h during the night

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a

Longitude

149°49 149°48 149°47 149°46 149°45 149°44 149°43

16°52

16°53

14:00

16°54

Direction of the movement

01:00

16°55

16°56

Descent at dawn

16°57

Latitude

b

Longitude

149°60 149°55 149°50 149°45

14°29

Seamount

09:10

14°34

Latitude

Descent at
dawn

14°39

Direction of the movement

21:00

14°44

c

152°03 W

17°18 S

Maiao

Moorea Tahiti

Rigaud de
Genouilly
Seamount

19°45 S

145°50 W

151°08 W

18°32 S

00:30 - 97/8/3

Direction of the
movement

15:00
97/8/1

19°31 S

150°31 W

d

Longitude

150°03 150°02 150°01

18°45

23:00

18°46

Direction of
the movement

18°47

Latitude

18°48

17:00

18°49

◄

Fig. 2 *Thunnus obesus*. Horizontal movements of the four bigeye tuna tracked in this study. **a**, **b**, **c**, **d** Bigeye Nos. 1, 2, 3, 4, respectively. Time (hrs) of start and end of each track is shown

17:00 hrs. It proceeded north during the whole of its 6 h track (Fig. 2d).

Vertical movements

Fig. 3 shows the vertical movements of the four fish, and Fig. 4 oceanographic conditions at the time of these movements.

Bigeye No. 1

Because this fish was caught by a commercial fishing vessel, no information is available on time and depth of capture. Previous observations with time–depth recorders (TDRs), however, showed that the deeper hooks were probably 250 and 500 m deep. During the night immediately following its release, the fish remained principally above 140 m (Fig. 3a). At dawn (∼05:00 hrs), it left the mixed layer and swam slowly down to 350 m. The simultaneous mapping of its vertical movements and the echo-sounding records clearly shows that the fish was
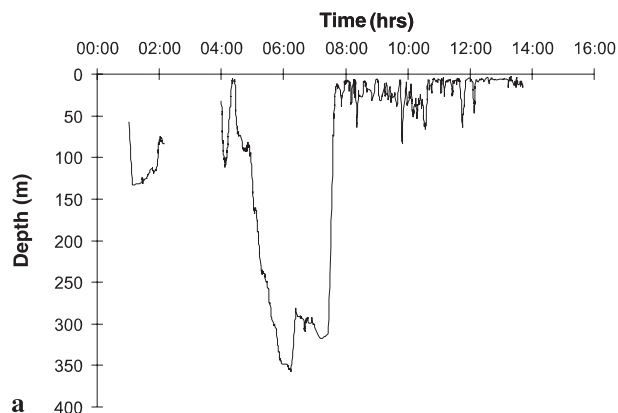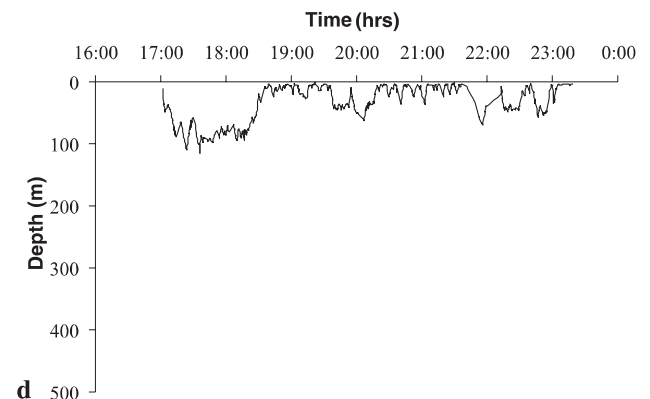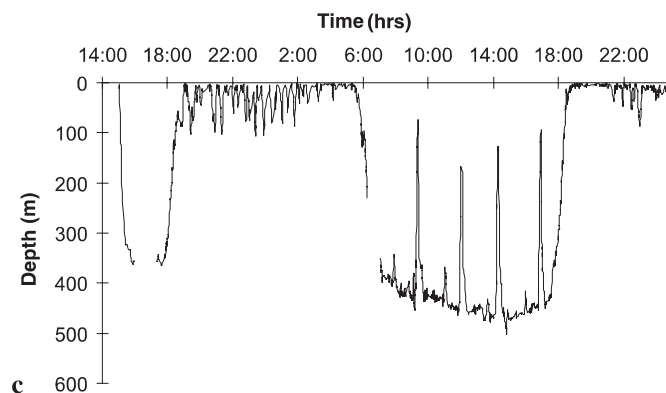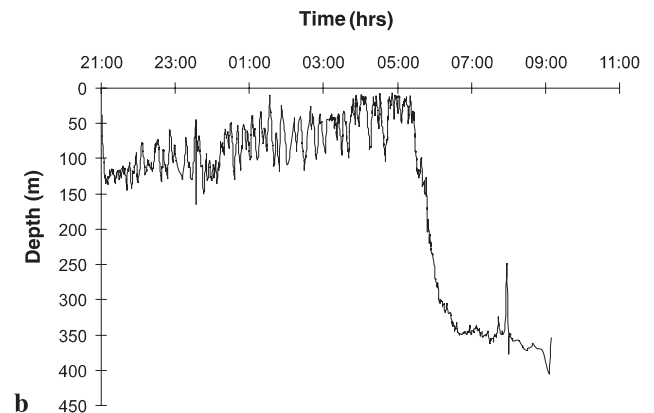
following the downward movement of the SSL at first light. It stopped descending at 350 m (water temperature = 15 °C), whereas the SSL continued downward to 550 m (see Fig. 5). The fish remained between 300 and 350 m for about 2 h, and then swam upwards to the surface layer, where it remained until contact was lost around 14:00 hrs.

Bigeye No. 2

This fish was also caught by a commercial fishing vessel, and again no information is available on time and depth of capture, although the deeper hooks were probably 250 and 500 m deep. During the night, the fish stayed in depths shallower than 150 m (Fig. 3b). As with Bigeye No. 1, at first light this fish also descended simultaneously with the SSL, and also stopped descending at 350 m (water temperature = 13.5 °C). It remained between 350 and 400 m, with one rapid 100 m ascent to 250 m at 08:00 hrs, before descending again to 400 m. Contact was lost at 09:10 hrs, when the fish was under the boat at a depth of ∼400 m, and the transmitter could no longer be heard. Contact could not be taken up again later.

Bigeye No. 3

The hook that captured this fish was not equipped with a hook-timer, and it was therefore not possible to determine the exact depth of capture. However, data from
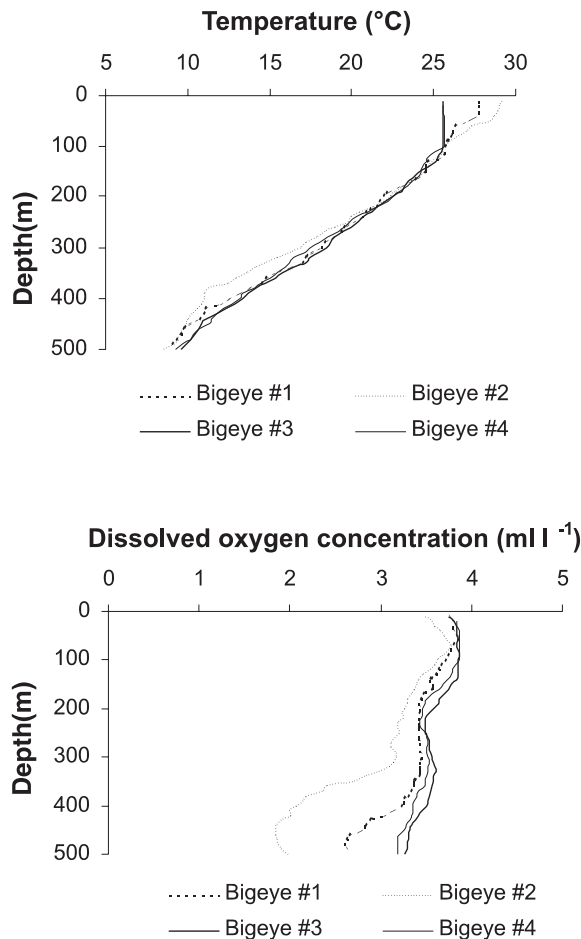
Fig. 3 *Thunnus obesus*. Vertical movements of the four bigeye tuna tracked in this study. **a**, **b**, **c**, **d** Bigeye Nos. 1, 2, 3, 4, respectively

Temperature (°C)

Dissolved oxygen concentration (ml l⁻¹)

Fig. 4 *Thunnus obesus*. Temperature and oxygen profiles along each track

TDRs and other bigeye tuna caught on hooks with hook-timers in the same set of longlines show capture depths between 400 and 450 m. The fish was followed for 33.5 h. After release, it remained for only 1 min in the first 10 m, then descended to 320 m within the following 10 min. Contact was lost at 16:02 hrs, between 350 and 360 m. The fish appeared to slow its descent in waters with a positive vertical oxygen concentration gradient (between 210 and 330 m, this latter depth being the secondary maximum oxygen concentration below the upper mixed layer with a temperature of 17 °C). When relocated again at 17:19 hrs, the fish was exactly at the same depth (between 350 and 360 m), and remained at this depth until dusk (17:50 hrs). It then ascended to the surface, which it reached at 19:00 hrs (Fig. 3c).

During the first night, Bigeye No. 3 exhibited frequent and rapid vertical movements. It descended to a maximum of 110 m, immediately above the maximum depth of the SSL (125 m: Fig. 5). Its range of vertical excursions had lessened by the end of the night. At 05:30 hrs, the fish began to descend, reaching 100 m at 05:55 hrs. It remained briefly (10 min) between 100 and

120 m, and then continued downwards, finally reaching 390 m at 07:10 hrs. Thereafter, the fish remained between 400 and 500 m and made only four vertical excursions (to depths between 75 and 165 m) until its last ascent at 17:35 hrs. Details of these four large upward movements are given in Table 2 and mean values with standard deviations in Table 3. Bigeye No. 3 also exhibited smaller vertical movements between two large upward excursions, one of those small vertical movements being always larger than the other small ones. Table 4 shows the range of the smaller vertical movements, and their temporal relationship to the nearest large upward excursion. Bigeye No. 3 reached its maximum depth (503 m) at 14:47 hrs (water temperature = 9.6 °C). At 18:50 hrs it reached the surface, and thereafter exhibited vertical movements between the surface and 85 m. Contact was definitively lost at 00:34 hrs while the fish was at 9 m depth.

Bigeye No. 4

The exact depth of capture is not known. However, based on the depths of capture of five other bigeye tuna caught on similar hook positions on the same longline, Bigeye No. 4 was most likely to have been caught at 430 to 480 m. After release, it stayed between 60 and 115 m for 80 min, and then rose to the surface around 18:30 hrs. The fish then remained between the surface and 60 m, making frequent, short up-and-down movements until the last contact at 23:15 hrs.

Oceanographic observations

Oceanographic observations were made prior to tagging and releasing each fish (Fig. 4). For Bigeyes 1 to 4, CTD casts were made 4 to 8 h prior to the start of the tracks. Bigeye No. 3 was followed for 33.5 h, and no other cast during the period of tracking was made to control for fluctuations in environmental conditions during the 33.5 h track. However, four casts made during the 5 d around the tracking period (before and after the tracking) showed that the physical environment remained stable, indicating that environmental conditions were likely to have been stable during the 33.5 h track.

Discussion

Horizontal movements

Horizontal movements of tropical tunas are known to be affected by well-defined physical structures such as FADs, outer reef drop-offs, or seamounts (Yuen 1970; Cayré and Chabanne 1986; Carey and Scharold 1990; Holland et al. 1990a; Cayré 1991; Marsac et al. 1996; Bach et al. 1998; Josse et al. 1998; Marsac and Cayré 1998). In our study on *Thunnus obesus*, except for Bigeye
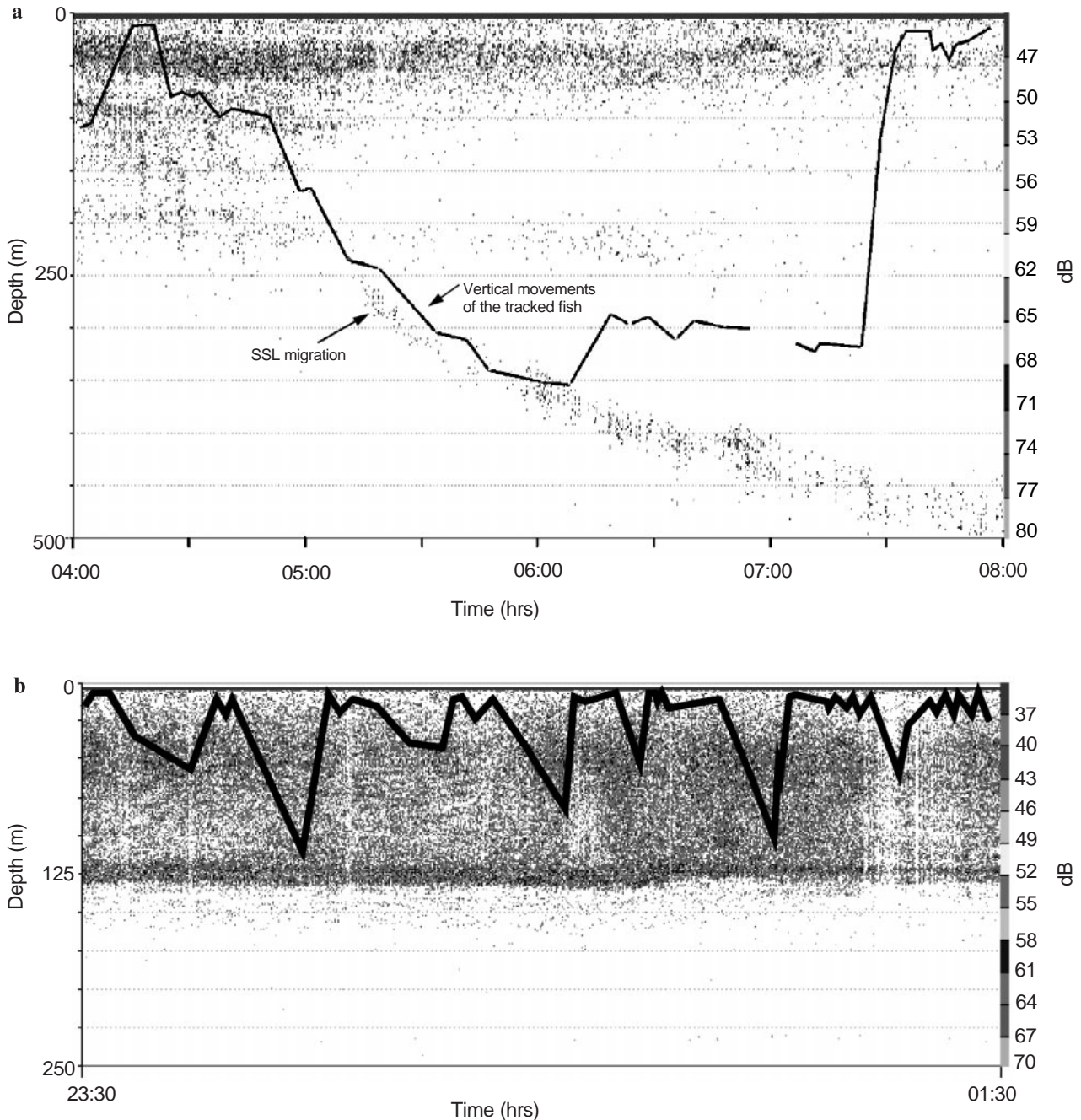
Fig. 5 *Thunnus obesus*. Vertical movements of fish and simultaneous acoustic observations of sound-scattering layer (*SSL*). **a** Bigeye No. 1 at dawn; **b** Bigeye No. 3 during night-time

No. 2, which suddenly changed its swimming direction while 9.7 km from a seamount, no fish swam close to any physical structures. From ultrasonic tagging studies on tunas around anchored FADs (Cayré and Chabanne 1986; Holland et al. 1990a; Cayré 1991) and from computer models of tuna behavior (Hilborn and Medley 1989; Kleiber and Hampton 1994), the radius of attraction of a FAD is estimated as 7 to 13 km. The distance at which Bigeye No. 2 changed its direction

toward the seamount lies within this range. Unfortunately, the fish was lost while swimming toward the seamount, and we do not know if it indeed reached the structure. The horizontal movements of the other fish cannot be related to any particular physical feature.

Bigeye No. 3 exhibited clear differences in horizontal movement patterns between day and night. Daytime movements were relatively straight (diffusion distance:path length $\simeq 1$), whereas night-time movements were more erratic (diffusion distance:path length = 0.4 the first night and 0.1 the second night). Unfortunately, we were able to track no other fish for more than 24 h. It is worth noting that similar differences in day–night

Table 2 *Thunnus obesus.* Time, depth, sea temperature and dissolved oxygen immediately prior to (*Peak begin*), at top of (*Peak top*), during decrease (*Peak drop*) and immediately after (*Peak end*) the four large peaks in vertical movements of Bigeye No. 3 during daytime. Oceanographic data were collected on preceding day in same area before tagging

Characteristics	Peak			
	1	2	3	4
Peak begin				
time (hrs)	09:14	11:54	14:08	16:45
depth (m)	400	435	460	440
T (°C)	13.4	11.5	10.6	11.1
oxygen (ml l^{-1})	3.51	3.35	3.31	3.34
Peak top				
time (hrs)	09:21	12:01	14:16	16:53
depth (m)	74	119	115	78
T (°C)	25.6	25.2	25.3	25.6
oxygen (ml l^{-1})	3.85	3.84	3.87	3.86
Peak drop				
time (hrs)	09:26	12:07	14:23	16:58
depth (m)	330	355	345	320
T (°C)	17.2	15.4	16.0	17.5
oxygen (ml l^{-1})	3.62	3.56	3.61	3.60
Peak end				
time (hrs)	09:33	12:18	14:36	17:10
depth (m)	378	455	465	450
T (°C)	14.3	10.8	10.5	10.9
oxygen (ml l^{-1})	3.55	3.32	3.29	3.33

Table 4 *Thunnus obesus.* Characteristics of small upward movements of Bigeye No. 3 in daytime, made between two large excursions into mixed layer. The fish did not reach mixed layer during these small upward movements

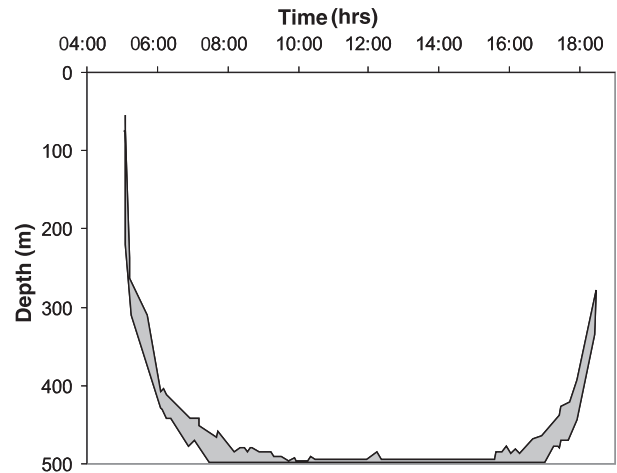| Small Peak No.	Vertical range (m)	Time to next large peak (h: min)	Time from last large peak (h: min)
1	58	1: 28	1: 39
2	72	1: 01	1: 37
3	32	38	1: 41
4	48	56	

Fig. 6 *Thunnus obesus.* Depth pattern of sound-scattering layer during daytime, from acoustic observations made on day of tagging Bigeye No. 3 in same area

patterns of horizontal movements have been observed in a 55 cm skipjack tuna (*Katsuwonus pelamis*) and a 51 cm yellowfin tuna tracked in the open sea in the Atlantic Ocean (Josse, unpublished observations). These movement patterns are opposite to those observed in yellowfin tuna associated with FADs or reefs (Holland et al. 1990a; Cayré 1991). The different movement patterns could reflect responses to different prey environments: the open ocean versus a coastal area (Bach et al. 1998). More sonic tracking studies on tuna in the open ocean are needed to clarify this.

Swimming depths and the SSL

As reported by Holland et al. (1990a, 1992) for smaller (< 12 kg) bigeye tuna, all the large bigeye tuna we tracked occupied the upper mixed layer during the night, at depths similar to those occupied by organisms of the SSL, and followed the SSL during its shifts at dawn and dusk. Carey (1990) and Nelson et al. (1997) observed

parallel behaviors in swordfish (*Xiphias gladius*) and megamouth shark (*Megachasma pelagios*), respectively, whose ascents and descents during crepuscular periods coincided with isolume changes in light intensity. Organisms of the SSL cue to light levels, and predators may use the same cues to keep contact with this prey community.

Fig. 6 shows a depth profile (one day before the experiment) of the SSL recorded by the echo-sounder in the area where Bigeyes 3 and 4 were tracked. Both the progressive and slow stabilization of the depth of the SSL in the morning and its progressive ascent in the afternoon match the vertical patterns and mean depth of Bigeye No. 3. The movements of the SSL also correspond to the vertical movements of Bigeye No. 2 in the early morning. We therefore surmise that Bigeye No. 3

Table 3 *Thunnus obesus.* Mean duration, mean differences in depth, sea temperature and dissolved oxygen (±SD) of the four large peaks in vertical movements of Bigeye No. 3

Parameter	Ascent	Descent	
		First half	Second half
Duration (min)	7.5 (±0.6)	5.7 (±1.0)	16.5 (±3.3)
Changes in:			
depth (m)	337.2 (±20.4)	241 (±11.1)	340.5 (±28.5)
sea temperature (°C)	13.8 (±1.1)	8.9 (±0.8)	13.8 (±1.7)
oxygen (ml l^{-1})	0.48 (±0.08)	0.26 (±0.02)	0.48 (±0.11)

was foraging in the top of the SSL during the daytime, as were Bigeyes 1 and 2 in the early morning. Moreover, stomach-content analyses of bigeye caught between 400 and 500 m in the same week and area as Bigeyes 3 and 4 support our conjecture. These fish were found to have eaten cephalopods (*Japetella diaphana*) and fish species (*Argyropelecus aculeata*, *Myctophum selenops*, *Scopelarchus analis*, *Diaphus mollis*) known to inhabit the SSL (F.-X. Bard, Institut de Recherche pour le Développement, personal communication). Based on all these observations, we conclude that bigeye tuna are able to reach depths that enable them to forage on organisms of the SSL during the daytime.

As described by Westerberg (1984) and Carey and Scharold (1990), food-searching behavior by olfaction in open water is more effective when it comprises a combination of horizontal and vertical movements, rather than horizontal movements alone. Therefore, the small up-and-down movements exhibited by bigeye during the night-time in the surface layer could constitute a searching or feeding behavior inside the SSL. If the reason for such behavior during the night in the upper surface layer is searching, then similar vertical-movement patterns would be expected when the fish occupy greater depths during the daytime. In fact, between two excursions into the warmer surface layer during the daytime, Bigeye No. 3 exhibited small up-and-down movements, although of a smaller amplitude than those exhibited during the night. The extent of such small vertical movements could depend on the distribution of prey (different thickness and density of the SSL during the day and night), day–night differences in the efficacy of searching behaviors, or physiological constraints in deep waters.

The shallow swimming depths of Bigeye No. 1 after its descent at dawn were striking. Block et al. (1992) and Brill et al. (1993) observed very shallow swimming depths during the daytime for one Indo-Pacific blue marlin (*Makaira mazara*) and one striped marlin (*Tetrapturus audax*), respectively. This behavior was considered indicative of badly injured fish, as both subsequently died and sank. Injury could explain the shallow swimming depths of Bigeye No. 1 during the daytime. Its ascent could, however, reflect a different foraging strategy (i.e. exploiting organisms in the surface water), a different stomach fullness (e.g. satiety after foraging success in the SSL), or a particular stimulus. For example, some *Thunnus albacares* exhibited similar shallow swimming depths when they became associated with the tracking vessel during some experiments in French Polynesia (Dagorn, Josse, Bach, unpublished observations). The lack of information on the stomach fullness of fishes prevents us from drawing a clear conclusion.

Swimming depths and oceanographic conditions

Bigeye No. 3 spent most of the daytime at 400 to 500 m (10 to 13 °C), with four vertical excursions into the upper mixed layer (Bigeye No. 4 was not tracked during daytime hours). The smaller (< 12 kg) bigeye tuna tracked by Holland et al. (1990a) remained in 14 to 17 °C water during the daytime. They exhibited regular upward excursions, similar to those shown by Bigeye No. 3 in the present study, although the excursions were more frequent. For instance, a 74.5 cm fork-length bigeye tuna (Fish BE8205: Holland et al. 1990a) exhibited 13 large upward excursions during the daytime, whereas the large bigeye tuna we tracked exhibited only four. The movements of BE8205 (Holland et al. 1990a) had a peak-to-peak interval of 57.7 min ($\pm$7.0 min SD), whereas the peak-to-peak interval of our Bigeye No. 3 was 150.7 min ($\pm$13.6 min SD). Holland et al. (1992) have shown that brief upward excursions into the warmer mixed layer enable bigeye tuna to increase their body temperature rapidly. Body mass, however, clearly affects the rates of muscle temperature change following an abrupt change in ambient temperature (Neill and Stevens 1974; Neill et al. 1976; Brill et al. 1994). The change in muscle temperature is slower in larger fish, which may explain why the larger fish we tracked ascended less often than the smaller bigeye tuna followed by Holland et al. (1992).

The daytime ascents of Bigeye No. 3 lasted between 7 and 8 min, with the same vertical speed ($\simeq$0.75 m s^{-1}) during all daytime upward movements. The fish never rose above 74 m. In contrast, each of its descents can be separated into two phases. The first phase was abrupt and brief (between 5 and 7 min), with a mean vertical diving speed similar to that during the ascents. During the second phase (i.e. 7 min), the fish slowed until it reached the depth at which it began its previous ascent. A whole descent (first plus second phases) lasted 16.5 min ($\pm$3.3 min SD). The ambient temperature difference experienced by Bigeye No. 3 during its vertical movements was high (13.8 °C $\pm$ 1.1 C° during ascents). During the 100 m rapid vertical excursion of Bigeye No. 2 at 8:00 hrs, the change in ambient temperature was less (6.2 C°).

Besides temperature, oxygen concentration appears to have played an important role in the ascents of Bigeye No. 3 and in the shorter excursion of Bigeye No. 2. Our data show that the oxygen gradient limited the maximum depth attained by Bigeyes 1 and 2 during their descents at dawn. In the absence of such an oxygen gradient, Bigeye No. 3 did not exhibit the same limits, and dove deeper at dawn than Bigeyes 1 and 2. The change in oxygen concentration (0.52 ml l^{-1}) experienced by Bigeye No. 2 during its 100 m ascent was similar to the mean change experienced by Bigeye No. 3 during its rapid upward movements (0.48 ml l^{-1} $\pm$ 0.08) (Table 3). Bigeye No. 3 ended its ascents at depths corresponding to the oxygen concentration maximum.

The point at which Bigeye No. 3 changed its descent pattern (i.e. the point of separation of the first and second phases of each descent) always corresponded to the depth at which a secondary oxygen concentration maximum occurred. It always remained in water with dis-

solved oxygen concentrations >3.25 ml l^{-1} (~4.55 mg l^{-1}), concentrations well above those reported to affect bigeye tuna cardiac output (1.9 to 2.6 mg l^{-1}, i.e. ~1.3 to 1.8 ml l^{-1}) and heart rate (2.7 to 3.5 mg l^{-1}, i.e. ~1.9 to 2.5 ml l^{-1}) (Bushnell et al. 1990). In the early morning, Bigeye No. 2 spent almost 3 h at depths where oxygen concentrations were between 2.0 and 2.5 ml l^{-1}. These concentrations are still above those reported to affect cardiac output, but correspond to the concentrations that might affect heart rate. Bigeye No. 2's 100 m upward excursion, as well as the upward movements of Bigeye No. 3, might also have permitted recovery from an accumulated oxygen debt (i.e. metabolized lactate).

During the daytime, Bigeye No. 3 always made one small upward movement between two large ones. These smaller movements may have corresponded to a foraging strategy, as previously suggested for the smaller movements inside the SSL (see preceding subsection "Swimming depths and the SSL"), but may also have been recovery movements, as there appears to be a positive correlation between the magnitude of the upward movements and the time between them. The time between a large upward excursion and a consecutive small upward excursion appeared to be constant, while the time between the last small upward and the next large upward excursion appeared to depend on the vertical range of the preceding small upward movement (Table 4). However, using electronic time–depth recorders on Antarctic fur seals (*Arctocephalus gazella*), Boyd et al. (1994) found a positive correlation between mean dive duration and mean time interval spent on the surface. Considering the small and large upward excursions of Bigeye No. 3, and the possible relationship between the vertical range of these upward excursions and the time before the next upward excursion, the pattern could be the same for bigeye tuna. Nothing is known about how temperature may influence low ambient-oxygen tolerance in tunas (Brill 1994), but our data suggest that bigeye tuna may make upward excursions to increase muscle temperature and to recover from oxygen debt. How these two factors interact is not known; specifically designed experiments are clearly needed to elucidate the relationships between temperature and oxygen levels and the vertical movements of tunas. Cayré and Marsac (1993) have studied the influence of the vertical oxygen gradient on the vertical movements of yellowfin tuna in the Indian Ocean, but no such studies have been carried out for bigeye tuna.

The regular upward excursions of bigeye tuna to increase muscle temperatures or repay an oxygen debt are, therefore, roughly analogous to the way in which marine mammals return to the surface to breath (Brill 1994). In other words, bigeye tuna are "obliged" to swim upwards in order to increase body temperature or to recover metabolically in more oxygenated waters. Regular and large upward excursions have also been observed during the daytime in other pelagic predatory species such as blue sharks (*Prionace glauca*) (Carey and Scharold 1990) and mako sharks (*Isurus oxyrinchus*) (Carey et al. 1981).

Carey and Scharold proposed that these movements represent behavioral thermoregulation, or a hunting tactic in blue sharks. The differences in the range, frequency, and duration of vertical movements in bigeye tuna could reflect different reasons for making such movements (e.g. thermoregulation, oxygen-debt recovery, foraging, travelling). Additional experiments are clearly needed to understand and eventually predict the vertical behavior of large bigeye tuna under different biological and oceanographic conditions.

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