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Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data

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ABSTRACT

To learn more about the movement patterns of bigeye tuna (*Thunnus obesus*), we deployed archival tags on 87 fish ranging in fork length from 50 to 154 cm. Thirteen fish were recaptured, from which 11 archival tags were returned, representing in aggregate 943 days-at-liberty. We successfully retrieved data from 10 tags, representing 474 days in aggregate. The largest fish recaptured was 44.5 kg [131 cm fork length (FL)] and the smallest 2.8 kg (52 cm). The deepest descent recorded was 817 m, the coldest temperature visited 4.7°C, and minimum oxygen level reached ~1 mL L^{-1}. Fish spent little time at depths where water temperatures were below 7°C and oxygen levels less than ~2 mL L^{-1}. Five fish were recaptured near the offshore weather buoy where they were tagged. Based on vertical movement patterns, it appeared that all stayed immediately associated with the buoy for up to 34 days. During this time they remained primarily in the uniform temperature surface layer (i.e. above 100 m). In contrast, fish not associated with a floating object showed the W-shaped vertical movement patterns during the day characteristic of bigeye tuna (i.e. descending to ~300–500 m and then returning regularly to the surface layer). Four fish were tagged and subsequently recaptured near Cross Seamount up to 76 days later. These fish exhibited vertical movement patterns similar to, but less regular than, those of fish not associated with any structure. Bigeye tuna appear to follow the diel vertical movements of the deep sound scattering layer (SSL) organisms and thus to exploit them effectively as a prey resource. Average night-time depth was correlated with lunar illumination, a behaviour which mimics movements of the SSL.

Key words: depth, mixed layer, oxygen, residence time, temperature, thermocline, vertical distribution

INTRODUCTION

Because tunas are so highly mobile, robust population assessments depend on a thorough understanding of both short- and long-term movement patterns (Brill and Lutcavage, 2001). Traditionally, these data have been obtained either by analysis of catch statistics, conventional tag and release studies, or direct observation of individuals carrying ultrasonic (usually depth sensitive) transmitters. Although all three methods can be effective, each has limitations. Analysis of catch statistics to determine movement patterns requires high spatiotemporal contrast in the data and, as important, the ability to differentiate changes in abundance from changes in specific fishing gear vulnerability (Brill, 1994; Fréon and Misund, 1999). Tag and release studies provide fish positions at release and recapture, but offer no data on daily movements. Ultrasonic telemetry can provide detailed data on vertical and horizontal movements, but the length of observation (usually no longer than 60 h) is limited by ship time, crew fatigue, or battery life of the transmitter (e.g. Holland *et al.*, 1990; Brill *et al.*, 1999; Dagorn *et al.*, 2000a). In contrast, recent advances in electronic data storage technology have made it possible to construct devices that allow the long-term recording (months to years) of vertical and horizontal movements of marine fishes (Arnold and Dewar,

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2001). The so-called 'archival tags' record data on ambient light levels (from which daily geolocations can be calculated), swimming depth, and temperature (external and internal) and have been used to chronicle horizontal and vertical movement patterns, residence times, feeding bouts, and possible spawning areas (Gunn and Block, 2001).

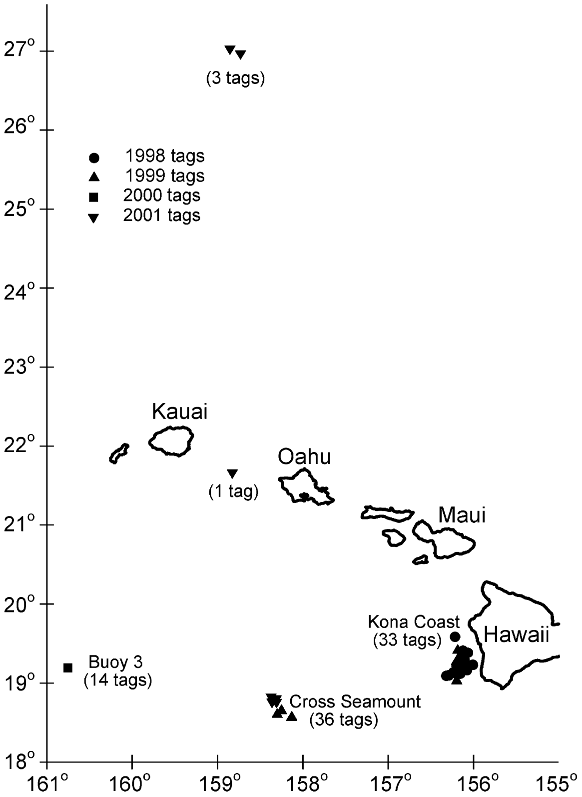
The harvest of adult bigeye tuna by commercial longline vessels has increased steadily since the 1970s, and stocks have been considered fully exploited since the early 1990s (Ward *et al.*, 1996). Moreover, purse-seine fleets in the eastern Pacific altered their fishing strategies in the mid-1990s to avoid capturing dolphins and began targeting skipjack, juvenile yellowfin and bigeye tunas aggregated under floating objects (Hampton *et al.*, 1998). The continually increasing harvest of juvenile bigeye tuna in the Pacific is now deemed cause for the implementation of precautionary management strategies. In Hawaii, the landings of longline-caught bigeye have risen steadily since 1975 (Boggs and Ito, 1993). This, plus a growing handline/troll fishery targeting juvenile bigeye tuna at Cross Seamount (*c.* 18°40′N, 158°17′W) and around NOAA weather buoys, has raised concerns about possible deleterious fisheries interactions and the status of the local resource (Sibert *et al.*, 2000). There is some evidence to suggest that local Hawaiian fisheries could not deplete far-ranging tuna species and that bigeye tuna form a single, highly mobile, Pacific-wide stock exploited predominantly on the high seas beyond the Hawaii fishery (He and Boggs, 1996). However, recent genetic studies could neither confirm nor refute the null hypothesis of panmixia in Pacific bigeye tuna (Chow *et al.*, 2000). Nevertheless, as has been shown for yellowfin tuna in the eastern Atlantic (Maury *et al.*, 2001), if local fishing effort is intense and if fish are not as highly mobile as presumed, then local overfishing is possible. We therefore initiated a study to examine temporal and spatial movement patterns of bigeye tuna near the main Hawaiian Islands to provide the data for improving population assessments and predicting fisheries interactions. The project specifically complements recent conventional tagging studies of bigeye and yellowfin tunas undertaken in the same area (Itano and Holland, 2000).

Our objectives were to quantify the horizontal and vertical movement patterns of bigeye tuna, and specifically when and how the offshore weather buoys and seamounts affect behaviours. This is especially important for resource assessment issues if behaviours around seamounts and buoys make bigeye tuna either more or less vulnerable to specific fishing methods. Acoustic tracking studies have shown that bigeye tuna display W-shaped vertical movement patterns during the day when not associated with floating objects – deep descents followed by upward excursions into the uniform-temperature surface layer to warm muscles and/or to repay oxygen debts (Holland *et al.*, 1990, 1992; Brill, 1994). At night, however, bigeye tuna generally restrict their vertical movements to the surface layer. In contrast, when associated with floating objects, bigeye tuna remain in the surface layer both day and night (Holland *et al.*, 1990). We wanted to determine if these behaviours persisted for extended periods and whether bigeye tuna in other environments displayed the same patterns. Our strategy was therefore to place archival tags into fish captured near buoys, seamounts, and the Island of Hawaii. Secondly, we wanted to examine movements in the context of fish size and proposed physiological limitations on tuna movements and distribution, as well as to explore possible seasonal or lunar correlations which are unavailable with short-term acoustic tracking studies. Finally, we anticipated that our data would provide needed input for fisheries exploitation models where indices of abundance (i.e. catch-per-unit-effort or CPUE) can be improved when information on depth distributions, oceanographic conditions, and specific gear vulnerability are incorporated (Bigelow *et al.*, 2002).

METHODS AND MATERIALS

Operations were conducted from the NOAA ship *Townsend Cromwell* in areas centred on the western (leeward) coast of the Island of Hawaii (*c.* 19°N, 156°W), at NOAA weather buoy 51003 (*c.* 19°11′N, 160°44′W, henceforth referred to as 'Buoy 3'), and over Cross Seamount (*c.* 18°40′N, 158°17′W) (Fig. 1). These were chosen because of the high fishing pressure by the Hawaii-based troll/handline fleet, and the high rates of return for conventionally (i.e. plastic dart) tagged bigeye and yellowfin tunas (Itano and Holland, 2000). Buoy 3 is owned and maintained by the National Data Buoy Center and is a 6-m NOMAD buoy anchored in water 4943 m deep. Cross Seamount rises to within 350 m of the ocean surface from a sea floor of about 4400 m at a slope gradient of about 15°. The summit (∼8 km diameter, ∼5.5 km^2 surface area) is flat, except for a cluster of 20–30 m high basalt dikes near the eastern edge (Noble and Mullineaux, 1989). Oceanographic conditions were monitored with conductivity-temperature-depth (CTD) casts (Sea-Bird Electronics Inc., Bellevue, WA, USA). The CTD stations were conducted immediately adjacent to and at stations

Figure 1. Sites where archival tags were deployed on bigeye tuna (*Thunnus obesus*) near the main Hawaiian Islands.



18.5 km (10 nmi) away from Buoy 3. At Cross Seamount, CTD stations were positioned on the seamount summit and at stations along a transect immediately moving onto and off the seamount with spatial sampling resolution of about 3.7 km (2 nmi). All casts were made to about 500 m with a SeaBird SBE 9/11 + CTD system additionally equipped with a SeaBird SBE-13 dissolved oxygen sensor (Sea-Bird Electronics Inc., Bellevue, WA, USA) containing a Beckman polarographic element for profiling *in situ* dissolved oxygen concentration. Downcast CTD data were processed, binned (2-m depth bins), and variables (e.g. salinity, density) derived using the SeaBird SEASOFT© software package (Sea-Bird Electronics Inc.) vs 4.244 subroutines.

Adult bigeye tuna were captured using conventional swordfish longline sets (i.e. night-time deployment with five hooks between floats and green chemical light sticks attached above the baited hooks). Temperature-depth recorders (TDRs) (Wildlife Computers, Redmond, WA, USA) attached to the longline indicated hook depths were generally less than 100 m. Shallow fishing was necessary to reduce incidents of barotrauma. Fish were brought aboard using a nylon mesh sling suspended within a rigid frame (approximately 2 m × 1 m) and laid on a moistened foam rubber mattress. A wet chamois cloth was placed over the eyes to calm the fish while the hook was removed and fork length measured. Smaller fish were caught using handlines and rod and reel. They were netted at the surface, lifted onboard, and placed on a padded V-shape surgery table.

From April 1998 to April 2001, we implanted archival tags into 87 bigeye tuna ranging in size from 50 to 154 cm fork length. Thirty-nine of the tags were made by Northwest Marine Technologies (NMT, Shaw Island, WA, USA) and 48 by Wildlife Computers (WC, Redmond, WA, USA, Model MK7) (Table 1). The former consisted of cylindrical stainless steel tube (1.6 cm diameter by 10 cm long, weighing 52 g in air) with a 20-cm-long Teflon light/external temperature sensor stalk protruding from one end. The latter were roughly rectangular (8.5 cm long by 2 cm wide by 1 cm high, weighing 30 g in air) with one end tapered to a point. The light/external temperature sensor stalk protruded from the top of the tag body, about 2.5 cm from the non-tapered edge. The stalk rises vertically for about 5 cm and then bends at a 90° angle and continues for another 25 cm. The tag is designed for implantation into the peritoneal cavity.

The NMT tags were placed intramuscularly through a 1–1.5 cm incision approximately 2 cm lateral to the origin of the first dorsal fin. The tag bodies were generally orientated posteriorly at a 45° angle to the dorsal body surface. For WC tags, a 1–1.5 cm horizontal incision was made about 1.5–2 cm off the midline and anterior to the vent by about 2–3 cm. The body wall was penetrated until membranes of peritoneum were observed. The membranes were then torn by a gloved finger, and a space in the visceral cavity (where the tag would be inserted) carefully wedged out to help ensure that no damage occurred to internal organs. In both cases, the tags were liberally bathed in Betadine solution (a 10% solution of povidone-iodine) immediately before insertion. The incisions were closed with one or two sutures (no. 4 braided silk) and sealed with *n*-butyl cyanoacrylate ester tissue adhesive (Vetbond, Animal Care Products, 3M, St Paul, MN, USA). The entire implantation procedure generally took less then 2 min. Fish were also tagged with conventional plastic dart tags (Hallprint) placed between the pterygiophores adjacent to the insertion of the second dorsal fin.

The NMT tags were programmed to take internal temperature, external temperature, light intensity and pressure (depth) every 8.5 min. At this acquisition rate, pristine data could have been recorded for about

Table 1. Details of archival tags implanted into bigeye tuna (*Thunnus obesus*) near the main Hawaiian Islands.

Date	Location	Latitude	Longitude	Capture method	Tag type*	Tag placement†	Mean fork length ± SD (cm)
April 1998	Kona Coast	19°08′N	156°17′W	Longline	24 NMT	2 IP 22 IM	81 ± 7 116 ± 14
January 1999	Kona Coast	19°15′N	156°12′W	Longline	9 NMT	IM	106 ± 10
	Cross Seamount	18°39′N	158°15′W	Longline	2 NMT	IM	117 ± 1
	Cross Seamount	18°39′N	158°15′W	Handline, rod and reel	14 WC 1 NMT	IP IM	60 ± 5 65
November 1999	Cross Seamount	18°42′N	158°17′W	Rod and reel	3 NMT 10 WC	IP IP	55 ± 5 69 ± 9
April 2000	Sea Buoy 3	19°11′N	160°44′W	Rod and reel	14 WC	IP	68 ± 5
March 2001	Sea Buoy 3	21°40′N	158°59′W	Longline	1 WC	IP	154
April 2001	Sea Buoy 3	26°58′–27°2′N	158°43–51′W	Longline	3 WC	IP	99 ± 22
April 2001	Cross Seamount	18°45–49′N	158°19–22′W	Longline	6 WC	IP	85 ± 16

*NMT: Northwest Marine Technologies: WC: Wildlife Computers (Model MK7).

†IP: interperitoneal; IM: intramuscular (adjacent to anterior edge of the first dorsal fin).

326 days (256 Kbyte battery-backed RAM). Data acquired from each of the four sensors were stored as eight-bit binary integers (i.e. with possible values between 0 and 255). Temperature had a resolution of 0.2°C, and depth had a resolution of 1 m to a depth of 126 m and a 3-m resolution beyond.

Although NMT tags were designed to automatically estimate geolocations from times of sunrise, sunset, and local noon by a proprietary algorithm, the tags proved to be unable to record ambient light at depths visited by adult bigeye tuna during daytime. For the one adult fish recaptured with a fully functional NMT tag, we used the fish's crepuscular diving to estimate times of sunrise, sunset, and local noon. [From these, longitude and latitude can be determined using standard astronomical formulae (Duffet-Smith, 1988).] We assumed civil twilight to be indicated by the fish crossing a threshold depth (TD) separating night-time from daytime behaviour. Qualifying transition intervals (ascents or descents) were defined as those ending at data points on one side of the TD where no more than 30% (i.e. two out of seven) of observations over the preceding hour, and no less than 70% (i.e. five out of seven) of observations in the ensuing hour were on the other side of the TD. One of several successive qualifying transitional data points was chosen to indicate the time of civil twilight according to the following rules. Dawn civil twilight was indicated by the first qualified descent below TD unless this descent was not continued over the next two data acquisition intervals. This process was repeated until a qualified descent was determined. Evening civil twilight was indicated by the first qualified ascent above the TD depth. Twilight times were estimated as the interpolated time of crossing the TD depth.

The WC tags were set to sample data on each of the four channels (depth, light, internal and external temperature) every 60 s. Data could be collected at this rate for 353 days before filling memory (2 Mbyte of non-volatile EEPROM memory). Temperature had a resolution of 0.05°C, depth had a resolution of 0.5 m. Light-level data were downloaded from the WC tags, and geographical positions estimated using the dusk and dawn symmetry method (Hill and Braun, 2001; Musyl *et al*., 2001).

The time-at-depth and time-at-temperature data were aggregated into 10 m and 1°C bins, respectively, based on the above analyses. These data were subsequently expressed as a fraction of the total time of observation for each fish, and the fractional data bins averaged across all fish within each category.

As we were interested in the vertical movement patterns and temperature preferences of different-sized bigeye tuna, we used Kolmogorov–Smirnov tests to compare distributions of ambient temperature and depth data to that of a normal distribution. We also used two-sample Kolmogorov–Smirnov tests to compare temperature and depth distributions within and among tags. To look for patterns in the data, the

Table 2. Mark and recapture details for bigeye tuna (*Thunnus obesus*) implanted with archival tags near the main Hawaiian Islands. For temperature and depth data, mean ± SD and range in parentheses are given (n.a. = data not available)

	Fish 509	Fish 241	Fish 625	Fish 509-2	Fish 224	Fish 298	Fish 301	Fish 388	Fish 390	Fish 392
Deployment details										
Date	4/9/98	1/21/99	11/19/99	11/20/99	11/20/99	4/16/00	4/16/00	4/16/00	4/16/00	4/16/00
Latitude	19°07′N	18°42′N	18°42′N	18°42′N	18°42′N	19°11′N	19°11′N	19°11′N	19°11′N	19°11′N
Longitude	156°13′W	158°18′W	158°18′W	158°18′W	158°18′W	160°44′W	160°44′W	160°44′W	160°44′W	160°44′W
Location	Kona Coast	Cross Seamount	Cross Seamount	Cross Seamount	Cross Seamount	Buoy 3†	Buoy 3	Buoy 3	Buoy 3	Buoy 3
Recapture details										
Date	8/2/98	10/2/99	1/9/00	12/6/99	11/29/99	5/9/00	5/17/00	5/17/00	5/5/00	5/20/00
Latitude	19°23′N	n.a.	n.a.	n.a.	n.a.	n.a.	n.a	n.a.	n.a.	n.a.
Longitude	155°59′W	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Location	Kona Coast	Cross Seamount	Cross Seamount	Cross Seamount	Cross Seamount	Buoy 3	Buoy 3	Buoy 3	Buoy 3	Buoy 3
Fork length (cm)	131	79	71	84	86	65	62	52	60	61
Weight (kg)	44.5	10.3	n.a.	6.9	13.6	n.a.	5	2.8	4.2	n.a.
Days at liberty	84	272‡	51	16	9	23	31	31	19	34
Temperature and depth summary										
Daytime internal temperature (°C)	21 ± 2 (15–27)	21 ± 4 (12–27)	22 ± 3 (13–27)	22 ± 4 (13–27)	22 ± 3 (12–27)	25 ± 0.3 (19–25)	25 ± 1.5 (13–27)	24 ± 2 (13–26)	25 ± 1 (16–26)	25 ± 1 (12–26)
Daytime external temperature (°C)	13 ± 6 (5–26)	18 ± 6 (6–25)	18 ± 6 (7–26)	n.a.§	n.a.§	24 ± 0.5 (15–25)	24 ± 2 (6–26)	24 ± 3 (8–29)	24 ± 2 (6–28)	24 ± 2 (6–26)
Daytime internal–external temperature(°C)	9 ± 5 (0–18)	3 ± 3 (0–19)	5 ± 4 (0–18)	n.a.§	n.a.§	0.6 ± 0.5 (0–9)	1 ± 1 (0–16)	1 ± 1 (0–15)	1 ± 2 (0–19)	0.5 ± 1 (0–14)
Daytime depth (m)	307 ± 130 (0–735)	191 ± 128 (0–657)	217 ± 120 (5–545)	179 ± 115 (0–765)	202 ± 107 (12–497)	56 ± 39 (0–425)	71 ± 60 (0–598)	70 ± 61 (0–401)	71 ± 54 (0–457)	64 ± 56 (0–585)
Correlation with lunar illumination (r)¶	0.25*	0.14	0.52***	0.48	0.06	0.38	0.52**	0.21	0.48*	0.36*
Night-time internal temperature (°C)	25 ± 1 (21–27)	25 ± 1 (15–27)	25 ± 1 (15–27)	26 ± 1 (16–27)	25 ± 2 (12–27)	25 ± 0.2 (22–26)	26 ± 0.6 (17–27)	25 ± 0.5 (18–26)	25 ± 0.5 (18–26)	25 ± 0.6 (13–26)

Night-time external temperature (°C)	24 ± 0.9 (13–27)	24 ± 1 (5–25)	24 ± 2 (7–26)	n.a.§	n.a.§	25 ± 0.3 (15–25)	25 ± 0.5 (13–25)	24 ± 0.5 (13–25)	25 ± 0.6 (14–25)	25 ± 0.6 (8–26)
Night-time internal–external temperature (°C)	0.7 ± 0.6 (0–10)	1 ± 1 (0–20)	1 ± 2 (0–18)	n.a.§	n.a§	0.5 ± 0.3 (0–9)	0.9 ± 0.5 (0–11)	0.9 ± 0.3 (0–9.8)	0.7 ± 0.4 (0–8)	0.5 ± 1 (0–14)
Night-time depth (m)	40 ± 33 (0–267)	50 ± 47 (0–817)	79 ± 63 (3–585)	59 ± 50 (0–363)	87 ± 67 (0–513)	42 ± 23 (0–273)	51 ± 27 (2–290)	50 ± 28 (4–281)	54 ± 27 (1–281)	50 ± 31 (0–441)
Correlation with lunar illumination (*r*)¶	0.74***	0.30**	0.24	0.12	0.47	0.31	0.34	0.48**	0.25	0.45**

† Anotherbigeye tuna (Fish 309) tagged at Buoy 3 on April 16, 2000 was recaptured (FL = 81 cm) near Cross Seamount 373 days after release, but only the first 21 days of light intensity data were available.

‡Because of tag malfunction, data from only the first 76 days at liberty were recovered.

§External thermistor failure.

¶Correlation coefficient (*r*) between depth and lunar illumination where $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

greatest vertical distance between cumulative distribution functions (D_{N}) among tags (from two-sample Kolmogorov–Smirnov tests) were formatted into an input matrix for UPGMA (unweighted pair-group method using arithmetic averages) clustering (Sneath and Sokal, 1973). We used one-way Kruskal–Wallis ANOVAs to compare median differences among all tags, and Mann–Whitney *W*-tests to compare differences in medians between two tags (Zar, 1996). Spectral analyses were used to examine for periodicity and patterns in the time series of diving behaviour. All statistical tests were performed at the $P = 0.05$ level of significance.

RESULTS

Between April 1998 and July 2001, commercial fishermen recaptured 13 tagged bigeye tuna, a 15% recapture rate. Eleven archival tags were returned, representing in aggregate 943 days-at-liberty (Table 2). From these, we successfully retrieved data from 10 tags yielding data from 474 days in aggregate. The average days-at-liberty for fish from which archival tags were returned was 86, and the average number of days from which we retrieved data was 36. Accumulation of biofilm on light sensor stalks was minimal, even for fish at liberty for over 1 year. Accumulation of biofilm on archival tags held on a mooring line for approximately 1 year in the central north Pacific did not affect the efficacy of geolocation algorithms (Musyl *et al.*, 2001).

We were able to retrieve tags directly from two individuals (Fish 388 and 390) at liberty for 31 and 19 days, respectively. In these two individuals, we found the tags to be completely walled-off from the peritoneal cavity and to be surrounded on the body surface with substantial areas of inflamed and necrotic tissue. These observations may indicate a possible route of tag loss through the ventral body wall as has been described in other fish species (Marty and Summerfelt, 1988). During necropsy of Fish 309, which had been at liberty for 1 year, we likewise found the tag body completely sealed off from the peritoneal cavity. But in this instance there were no indications that the tag would have been shed any time soon, as the amount of necrotic tissue around the exit point of the light sensor stalk was minimal.

Vertical movement patterns

Sibert *et al.* (2003) provide descriptions of the horizontal movements of the tagged fish. We therefore focus primarily on vertical movement patterns and the ambient temperature and oxygen conditions experienced. In brief, our results indicate some clear

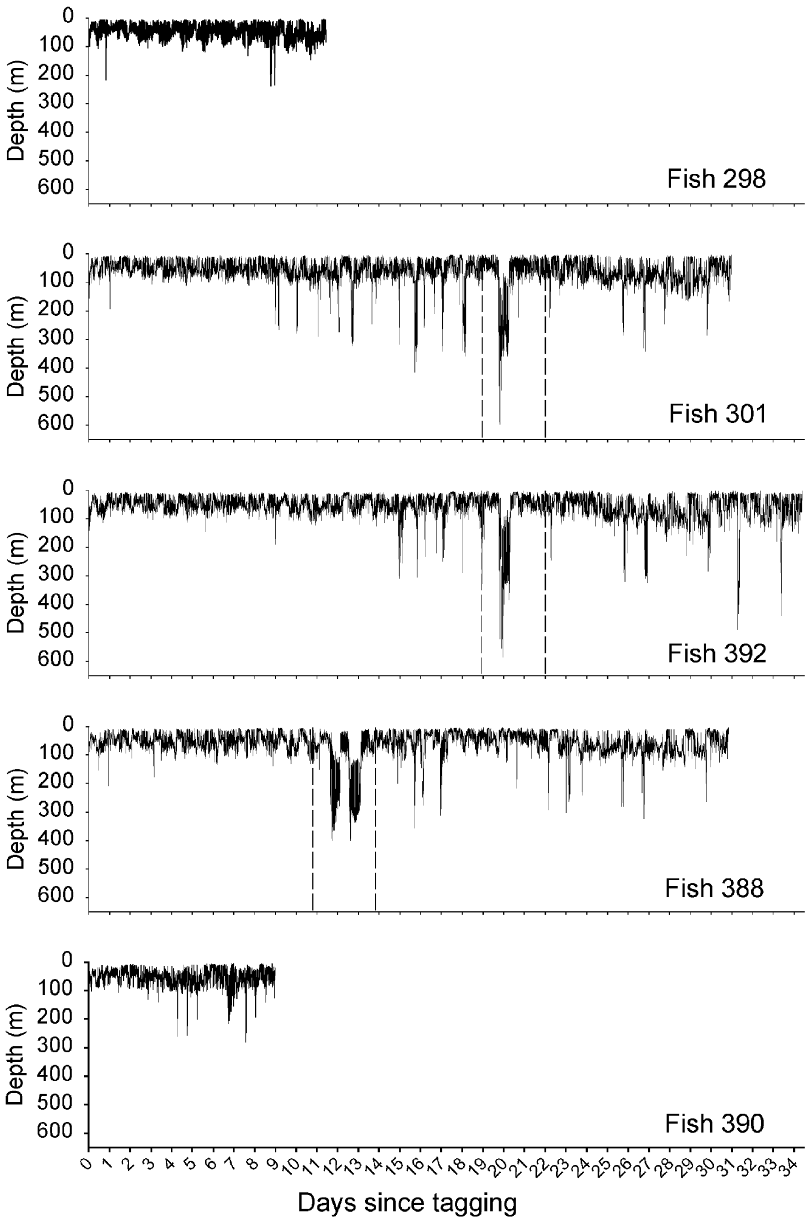


Figure 2. Depth records from bigeye tuna (Fish 298, 301, 392, 388, and 390) released and recaptured near Buoy 3. All fish were tagged April 16, 2000 (Day 0). Vertical dashed lines show the portion of depth record expanded in subsequent figure.

patterns, but also a high degree of variability across all fish.

All five fish released and recaptured at Buoy 3 spent the majority of their time in the upper, uniform temperature surface layer and several showed remarkably synchronous vertical movements (Fig. 2). This apparent school fidelity is especially noticeable in Fishes 301 and 392, where the occasional deep forays occurred at the same time in both individuals. It also appears that the fish did not stray far from their release sites immediately adjacent to the buoy, as all geolocation estimates (Sibert *et al.*, 2003) were within the range of errors in tags attached to a mooring line (Musyl *et al.*, 2001). Moreover, on only rare occasions did Fishes 301, 388, and 392 appear to move far enough away from the buoy that their vertical movement patterns reflected those of bigeye tuna not associated with floating objects (Holland *et al.*, 1990; Dagorn *et al.*, 2000a). In other words, out of the 96 days of observation, on only 3 days (Fig. 3) did the depth records reflect the W-shaped pattern (i.e. where the fish descend below 400 m during the daytime and make regular forays into the warm surface layer) characteristic of bigeye tuna not associated with floating objects.

Fish 509 was released and recaptured off the western coast of the Island of Hawaii (Table 2). The fish appears to have remained within the immediate vicinity of the island and did not at anytime appear to

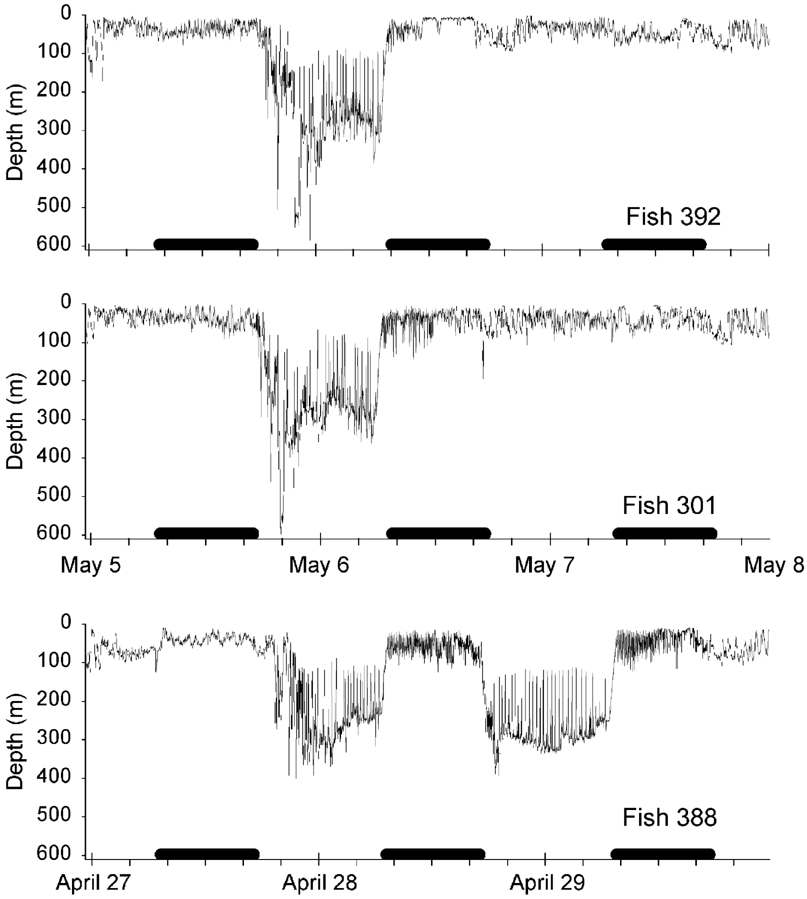


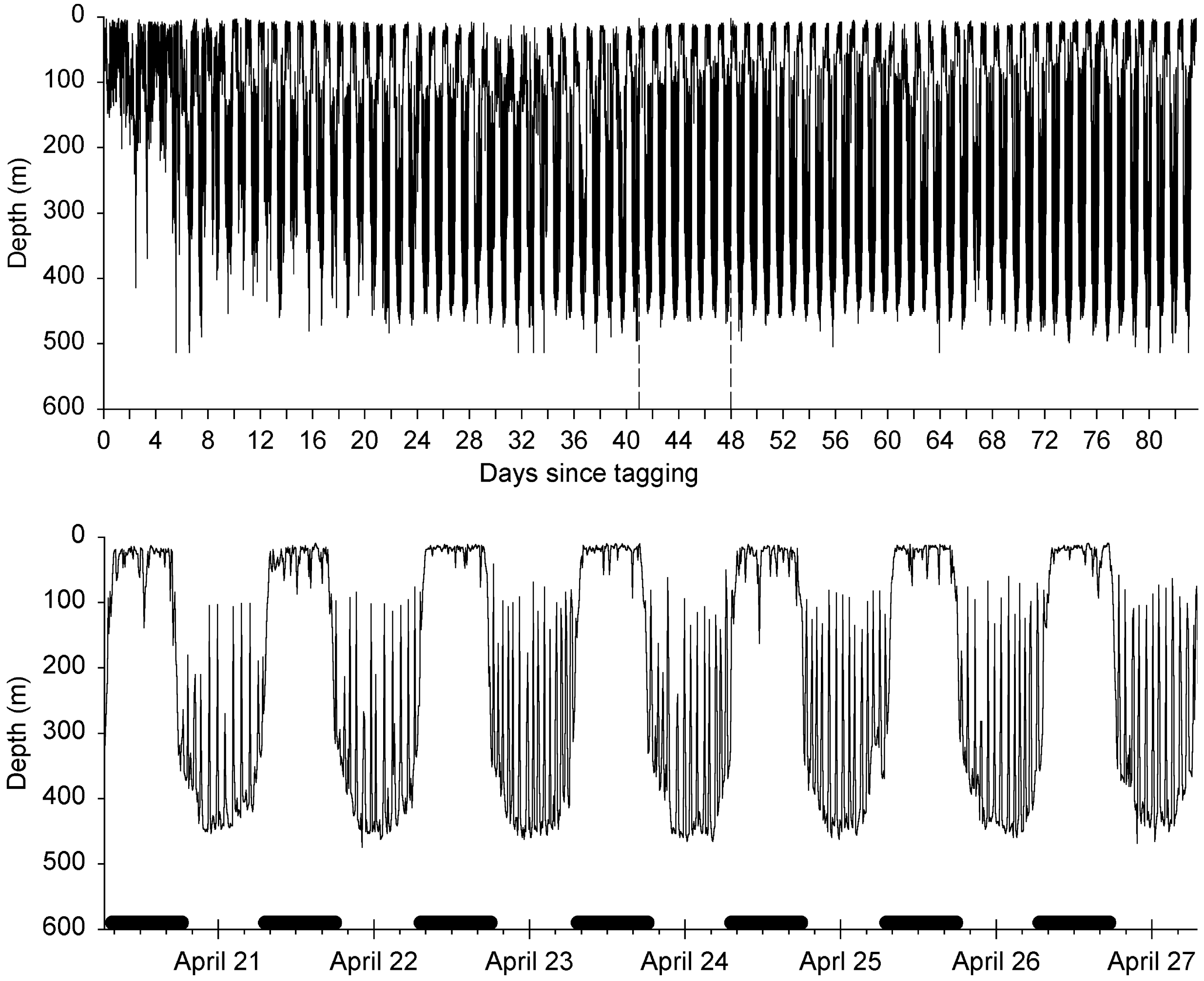
Figure 3. Depth record of Fish 392, 301 and 388 when they apparently moved far enough away from Buoy 3 to resume the characteristic W-shaped vertical movement patterns of bigeye tuna during the daytime. Dates show 12:00 (noon) and minor tick marks are at 4-h intervals. The dark horizontal bars indicate night-time.

become associated with Buoy 3 or Cross Seamount, as its vertical movement patterns contrasts sharply with those of buoy-associated or seamount-associated fish. Except for about the first 7 days following release, the fish displayed the remarkably consistent rhythm in day–night vertical movements characteristic of bigeye tuna. The fish descended at dawn to depths generally below 450 m, made regular upward excursions into the warm surface layer at approximately hourly intervals, then ascended into the surface layer at dusk and remained there until the following dawn (Fig. 4).

Fish 625 was released at Cross Seamount in November 1999 and recaptured in the same area 51 days later. It appeared to remain in association with the seamount for the entire time at liberty (Sibert *et al.*, 2002). Vertical movement patterns were reminiscent of those of Fish 509, in that the fish generally constrained its vertical movements to the surface layer at night and descended to approximately 400 m at dawn (Fig. 5). However, there were also clear differences. The vertical movements of Fish 625 during the night were more extensive (Table 2), the day–night transitions were not as clear, and the regular upward excursions during the day were not as regular.

Fish 241 was also tagged at Cross Seamount (but approximately 10 months prior to Fish 625) and recaptured in the same area. Although this fish was at liberty 272 days, we were able only to recover data from the first 76 days. In contrast to Fish 625, Fish 241 did not remain associated with the seamount. From the vertical movement patterns, the fish appears to have departed the seamount a few days after release and become associated with a floating object for approximately 10 days (Fig. 6). From the geolocation data, the floating object could have been NOAA weather-data buoy 51002 (Buoy 2; *c.* 17°11′N, 157°49′W), although we have no way to confirm this (Sibert *et al.*, 2003). The fish then moved east and resumed a vertical movement pattern characteristic of bigeye tuna in open water. However, as shown in the lower panel of Fig. 6, the fish displayed sudden transitions in vertical movement patterns, possibly indicating that it may have become reassociated with

Figure 4. Depth record of Fish 509. The upper panel shows the entire record covering 84 days at liberty, while the lower panel covers a 6-day period during which the fish showed the characteristic W-shaped daytime vertical movement patterns and the dawn and dusk transitions. The vertical dashed lines in the upper panel show the portion of the depth record expanded in the lower panel. Dates show 12:00 (noon) and minor tick marks are at 4-h intervals. The dark horizontal bars indicate night-time.

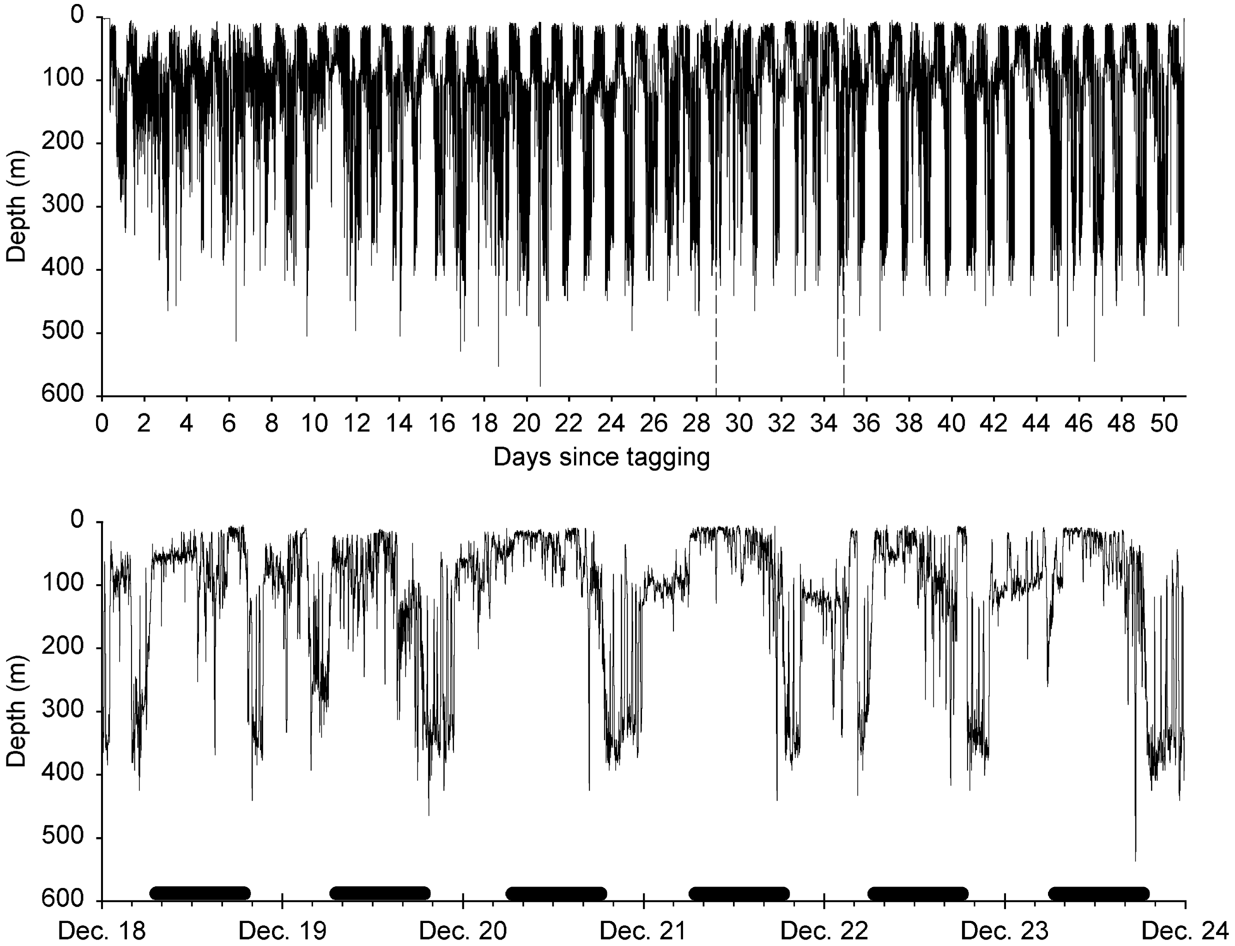


specific geographical features, perhaps with one of the seamounts located to the south-east of the Island of Hawaii. As the stored data record was incomplete, it was not possible to determine when the fish returned to Cross Seamount prior to its recapture.

Fish 509-2 was at liberty for approximately 17 days, exhibiting vertical movements similar to those of the other fish associated with Cross Seamount. Another bigeye tuna tagged at Buoy 3 (Fish 309) in April 2000 was recaptured at Cross Seamount 373 days after release. Due to tag failure we could retrieve only the first 21 days of light intensity readings, but the data indicated that the fish was associated with Buoy 3 at least over this 3-week period (Sibert *et al.*, 2003).

Of the three fish at liberty long enough to have experienced several lunar cycles (Fishes 509, 241, and 625), Fish 509 exhibited the clearest correlation between average night-time depth and lunar illumination ($r = 0.74$, $P < 0.001$, Table 2). The fish occupied mean deeper night-time depths during the full moon and shallower depths during the new moon (Fig. 7). Fish 241 also showed a significant, but weaker, correlation of mean night-time depth with lunar phase probably because its vertical behaviours were modified by its presumed occasional association with seamounts and Buoy 2. Surprisingly, Fish 509 and Fish 625 also showed a significant correlation of mean daytime depths with lunar illumination (Table 2). Spectral

Figure 5. Depth record of Fish 625. The fish was originally captured near Cross Seamount. The upper panel shows the entire record covering 51 days at liberty, while the lower panel covers a 6-day period at which time this fish appears to have moved off the seamount. The vertical dashed lines in the upper panel show the portion of the depth record expanded in the lower panel. Dates show 12:00 (noon) and minor tick marks are at 4-h intervals. The dark horizontal bars indicate night-time.



analyses on depth data showed dominant peaks around 24 h and secondary peaks around 12 h for all fish.

Despite our low sample size, the trend of deeper daytime depth distribution appeared to be associated with fish size. We found strong correlation between fish size (and/or maturity) and average daytime depth ($r = 0.88$). We calculated the power (i.e. probability of correctly rejecting the null hypothesis when it is false) of the this test (H_0: $\rho = 0$) to be 0.96. In other words, to reject this test 99% of the time with $r \geq 0.88$ at the 0.05 level of significance, a sample size of at least 13 samples would be required (Zar, 1996). Because of the congruence between depth and temperature, the inverse trend was also seen when average daytime temperature was substituted for depth ($r = -0.90$). In contrast, average night-time depth was not significantly correlated ($r = 0.06$) with fish size.

Depth distributions in relation to ambient temperature and oxygen conditions

Ambient temperature and depth distributions (night, day, and combined), tested for conformity to the normal distribution using the Kolmogorov–Smirnov *D*-test for Goodness of Fit, were all clearly non-normal. We therefore subjected the data to separate Kruskal–Wallis one-way ANOVAs to test for differences between medians, and all comparisons were significantly different. We found virtually identical results among fish for day and night temperature and depth distributions when we subjected the data to heterogeneity chi-square analyses using the G-test for Goodness of Fit (Zar, 1996). Using Kolmogorov–Smirnov two sample tests, we found day and night ambient temperature and depth distributions were

Figure 6. Depth record Fish 241 captured near Cross Seamount. The upper panel shows the entire record covering 76 days at liberty, while the lower panel covers a 6-day period. The vertical dashed lines in the upper panel show the portion of the depth record expanded in the lower panel. Dates show 12:00 (noon) and minor tick marks are at 4-h intervals. The dark horizontal bars indicate night-time.

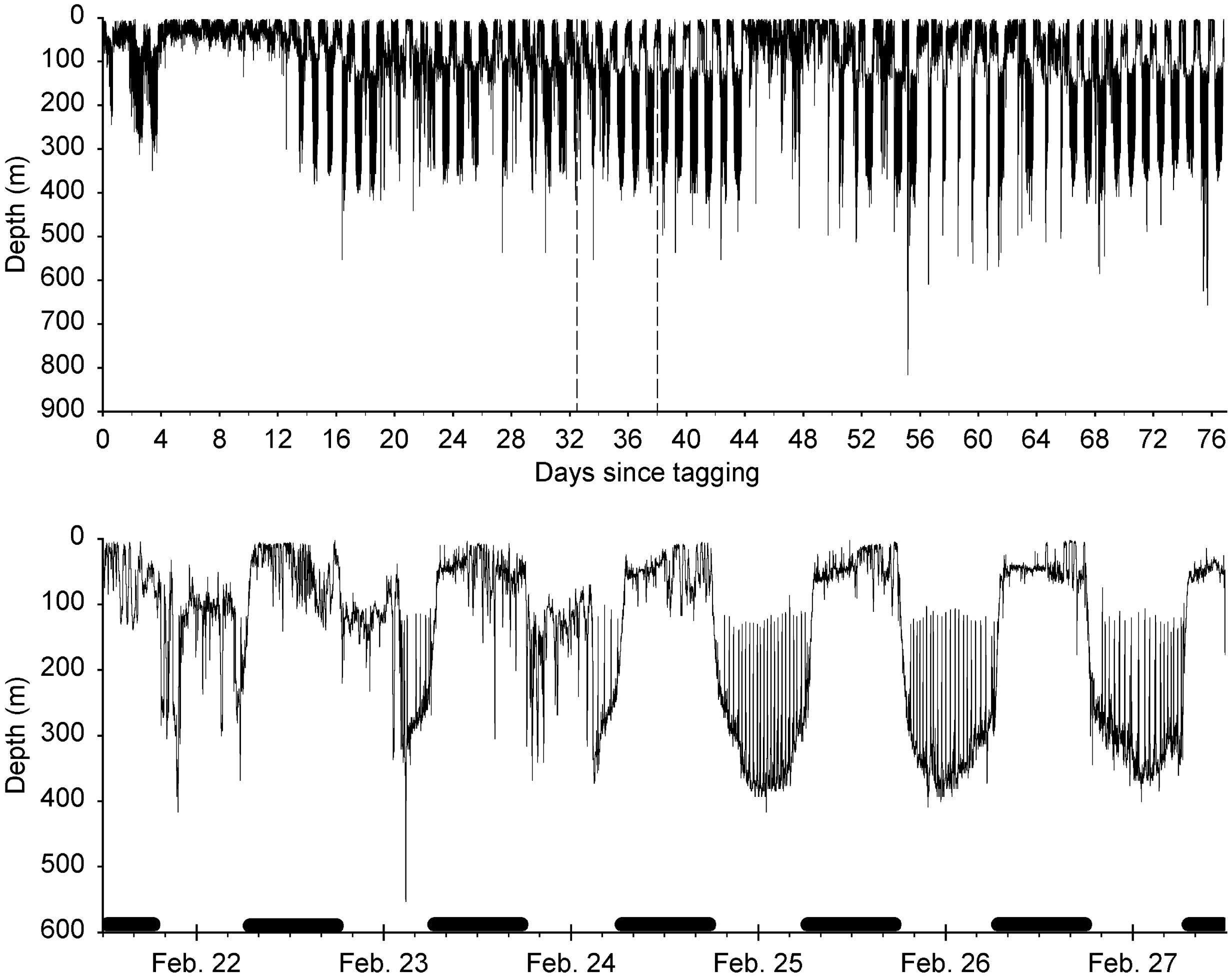
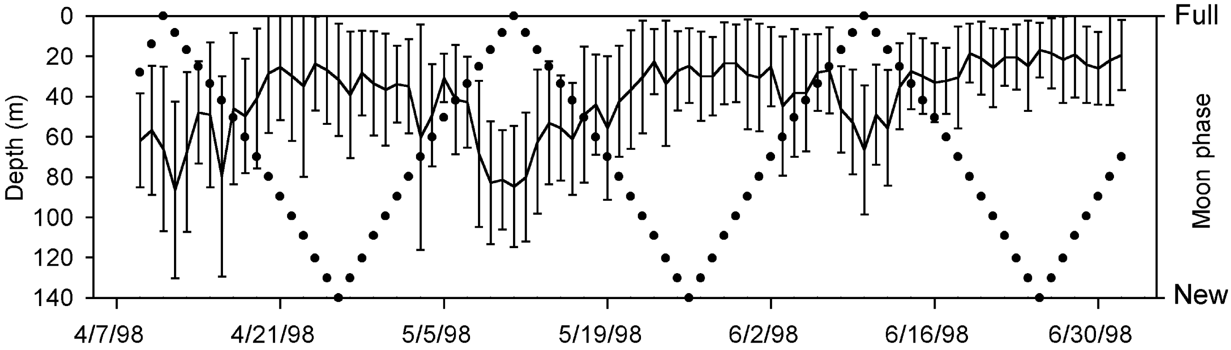


Figure 7. Lunar illumination (dots) and average (±SD) night-time depth of Fish 509.



significantly different for each fish. Similarly, all of the Kolmogorov–Smirnov two-sample tests comparing daytime external temperature distributions between fish were significant, as were the depth distributions. Likewise, separate tests comparing night-time external temperature and depth distributions between fish (73 possible combined comparisons) were all significantly different. Moreover, separate Mann–Whitney W-tests comparing medians within each archival tag for night and day ambient temperature and depth differences were all significantly different at $P < 0.05$. In brief, we found clear variability among individual fish, as well as clear night and day differences within each fish.

To explore temperature and depth patterns, we took the results from two sample Kolmogorov–Smirnov tests and computed dissimilarity matrices for temperature and depth distributions, both day and night, using the maximum vertical distance between cumulative distribution functions (D_N) between samples and subjected the input matrices to UPGMA clustering (Sneath and Sokal, 1973). For cumulative distribution functions between samples (D_N) using daytime depth and temperature data, the resultant clustering dendrograms were similar in topology to one another and clearly grouped the fish by location of release and body size (Fig. 8). For example, the daytime depth distributions of fish released and recaptured at Buoy 3 (Fish 298, 301, 388, 390, 392, mean FL = 59.9 ± 4.9 cm) formed the tightest and most distinct cluster. The next most distinct cluster was formed by the fish released at Cross Seamount (Fish 224, 241, 509-2, and 625, mean FL = 80.0 ± 6.9 cm). The adult fish caught and released near the Kona Coast (Fish 509, FL ~ 131 cm) was clearly distinct from both groups, but aligned more closely with the fish caught and released at Cross Seamount.

UPGMA clustering on the cumulative distribution functions between samples (D_N) using night-time depth and temperature data, however, indicated some mismatches to the above scenario (Fig. 8). In other words, night-time depth and external temperature distributions were not related to areas of capture and release, nor fish size. It should be pointed out that the observed clustering patterns were the consequence of the data and not attributable to the merits of a particular algorithm because other algorithms (e.g. nearest neighbour) produced similar results.

Figure 9 shows depth data arranged by bins grouped based on tagging location. The appropriateness of such grouping is supported by the UPGMA cluster analyses based on daytime depth (Fig. 8). As found previously (Holland *et al*., 1990; Dagorn *et al*., 2000a), there were marked day/night differences. Bigeye tuna not associated with Buoy 3 clearly spent more time at greater depths during the day.

Figure 8. UPGMA (unweighted pair-group method using arithmetic average) clustering using the Kolmogorov–Smirnov D_N dissimilarity distance matrix among samples constructed from depth and external temperature data. Fishes associated with Buoy 3 are shown by underlining.

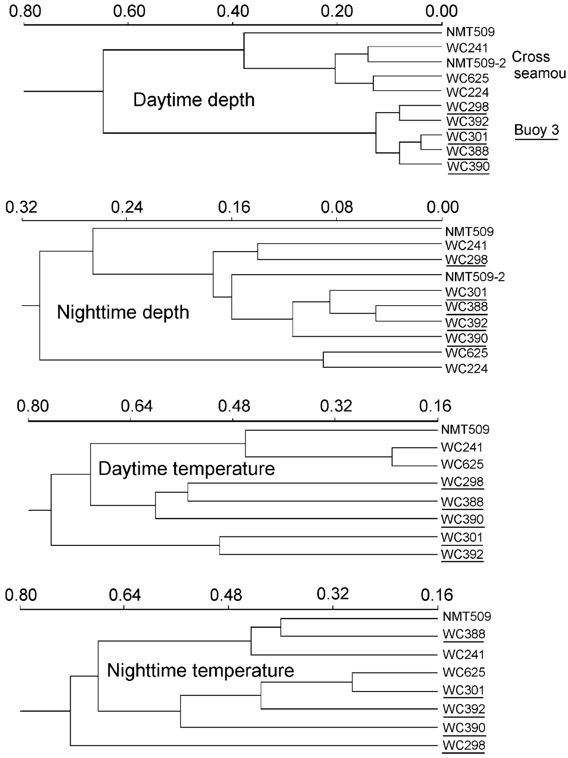


Figure 10 presents the time-at-temperature histograms with the fish grouped as in Fig. 9. The coldest temperatures occupied for significant periods of during the day by Fish 509 was 7°C, and by the four fish associated with Cross Seamount it was 10°C. Both groups made occasional descents into ~5–6°C water.

We have no direct measures of time spent at various ambient oxygen levels, as there was no way to collect data exactly coincident in space and time with the tagged fish. However, times at various ambient oxygen levels can be estimated because of the relative consistency of depth-oxygen profiles taken in the vicinity of Cross Seamount, off the western coast of the Island of Hawaii, and immediately adjacent to Buoy 3. Representative traces showing changes in ambient oxygen levels with depth have been added to Fig. 9. As fish associated with Buoy 3 remained in the surface layer, they experienced no significant changes in ambient

Figure 9. Histograms showing percentage time (±SE) spent at various depths. Fish have been grouped according to the clustering shown in Figure 8. The panel labelled 'Cross Seamount' shows data from Fish 241, 625, 509-2, 224, and the panel labelled 'Buoy 3' data from Fish 298, 301, 388, 390, 392. Lines represent changes in ambient oxygen levels (±SD). The changes in oxygen levels with depth were taken from CTD casts conducted during tagging operations.

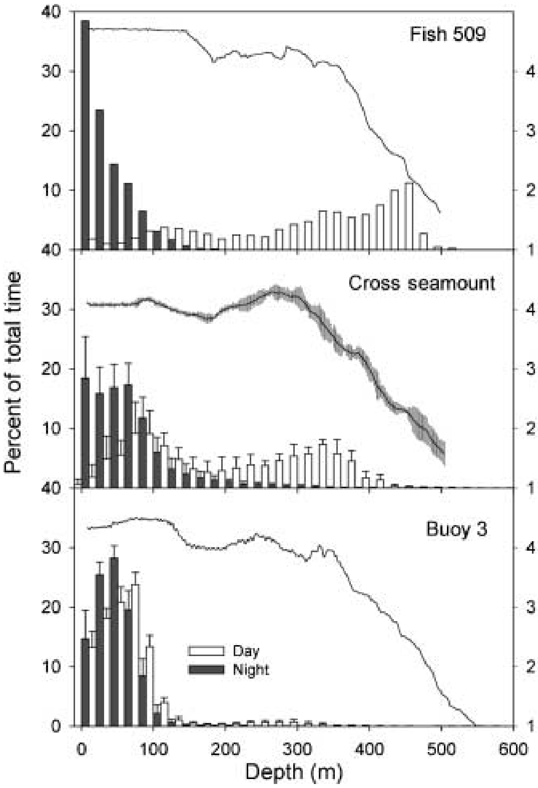
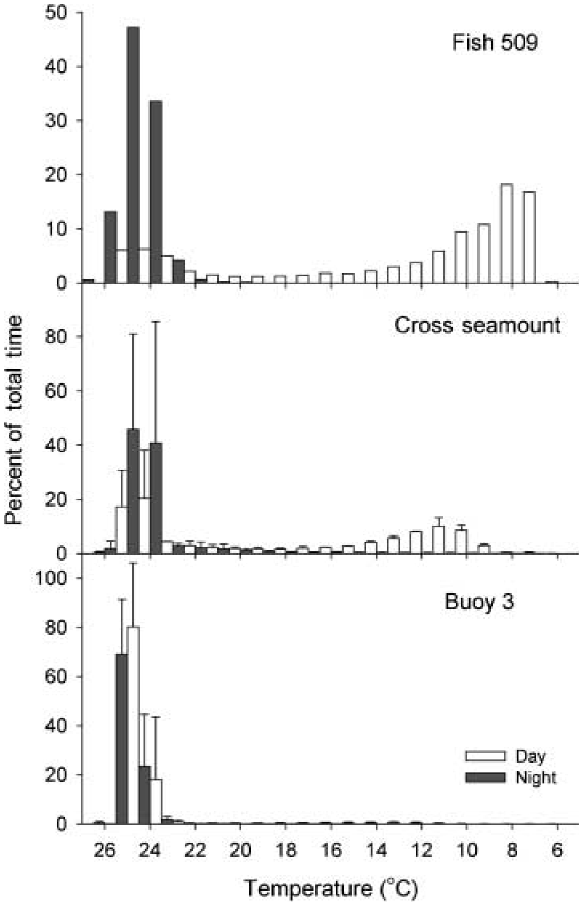


Figure 10. Histograms showing percentage time (±SE) spent at various temperatures. Fish have been grouped according to the clustering shown in Figure 9. The panel labelled 'Cross Seamount' shows data from Fishes 241, 625, 509-2, 224 and the panel labelled 'Buoy 3' data from Fishes 298, 301, 388, 390, 392.



oxygen during their vertical movements. The maximum depths of bigeye tuna associated with Cross Seamount appeared to be limited by reductions of ambient oxygen down to ~3.5 mL L^{-1}, although this was probably more reflective of depth of the summit of the seamount (350 m). In contrast, Fish 509 demonstrated the remarkable tolerance of bigeye tuna to low ambient oxygen.

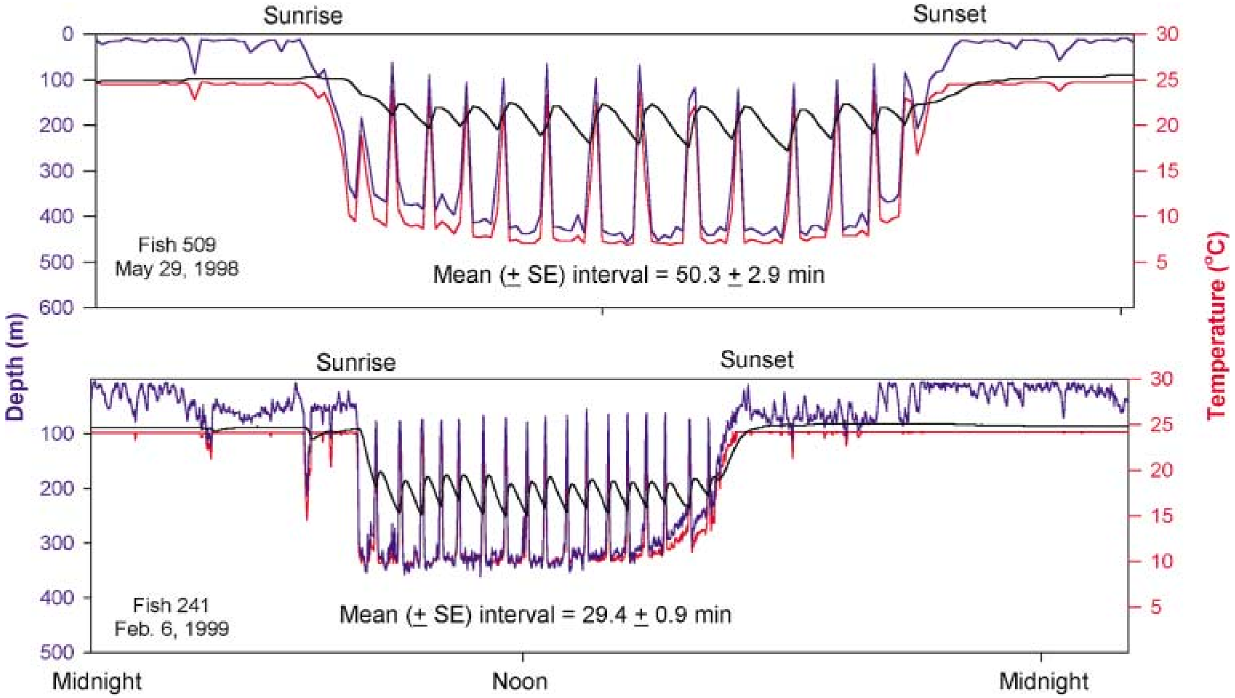
Vertical movements and thermoregulation

The largest bigeye tuna recapture in our study (Fish 509, 131 cm FL, 44 kg) showed a characteristic W-shaped vertical movement pattern during the day (Fig. 4). The fish would descend below the thermocline and then return to the mixed layer, ostensibly to warm muscles, at ~50-min intervals (Fig. 11, upper). On the other hand, the upward excursions of the smaller tunas (e.g. Fish 241, 79 cm FL, 10.3 kg) was roughly double the frequency of Fish 509 (Fig. 11, lower).

DISCUSSION

Our surgical techniques of implanting archival tags into bigeye tuna apparently did not produce any higher tagging mortalities than expected with conventional plastic dart tags. The rate of recapture for bigeye tuna implanted with archival tags (15%) was comparable with that of similarly sized bigeye tuna in the same area implanted with simple dart tags (14.4%, D. Itano, Hawaii Tuna Tagging Program, pers. comm.). The fish cutter who discovered the NMT tag in Fish 509 stated during an interview that the surgical site was clear and smooth. Fishermen

Figure 11. Twenty hour record of depth, body temperature, and water temperature for Fish 509 and 241.



finding the NMT tag in Fish 509-2 also offered that the tag was encapsulated with surrounding fibrous tissues with no apparent ulcerations or lesions. These results confirm the suitability of intramuscular implantation of archival tags first reported by Brill *et al.* (1997). We have had no fish recaptured with just a plastic dart tag and no archival tag, so we have no direct confirmation that archival tags can be shed. However, based on our observations during the necropsy of recaptured bigeye tuna, we feel that the physical extrusion of the device from the body cavity remains a possibility.

Vertical movement patterns

We found the regular vertical movement patterns of bigeye tuna carrying archival tags to be roughly similar to those reported by Holland *et al.* (1990) and Dagorn *et al.* (2000a) for fish carrying ultrasonic transmitters. This periodicity has similarly been observed in Pacific bluefin tuna (*Thunnus thynnus orientalis*; Kitagawa *et al.*, 2000) and yellowtail (*Seriola quinqueradiata*; Kasai *et al.*, 2000) indicating diel vertical patterns punctuated by day-night transitions. The maximum depth and minimum temperatures reached by bigeye tuna carrying archival tags did differ from those of fish carrying acoustic transmitters. The former clearly displayed a significantly greater vertical range often exceeding 500 m depth (Fig. 9). We did not find, however, any indication that tunas have a lengthy period of abnormal behaviour following capture and tagging as has been reported for salmon (Walker *et al.*, 2000).

Several investigators (e.g. Dagorn *et al.*, 2000b; Marcinek *et al.*, 2001) have concluded that tunas' movements coincide with those of prey organisms such as squid, euphausiids, and mesopelagic fish (i.e. the organisms comprising the sound scattering layer, SSL) which undertake extensive diurnal vertical migrations (Longhurst, 1976; Marchal and Lebourges, 1996; Yatsu *et al.*, 1999). Bigeye tuna also consume these species (Miyabe and Bayliff, 1998). Josse *et al.* (1998) recorded the movements of a bigeye tuna in French Polynesia carrying a depth-sensitive ultrasonic transmitter while simultaneously using an echosounder to follow the movements of the SSL. They found that excursions of bigeye tuna mirrored the daily vertical movements of the SSL. Carey (1990), using similar technologies, found the same thing occurring in swordfish (*Xiphias gladius*). Fish 509 whose mean nighttime average depths that were clearly correlated with lunar illumination (Fig. 7), may well have been following vertically migrating organisms near the surface and altering its behaviour according to prey responses to lunar illumination. In other words, the fish was mirroring the movements of nocturnally migrating organisms of the SSL which were, in turn, attempting to occupy an isolume (Widder and Frank, 2001).

The vertical movements of fish associated with Buoy 3 were strikingly different in that they generally remained in the surface layer, as has been previously observed in bigeye tuna carrying ultrasonic transmitters associated with moored FADs similar to Buoy 3 (Holland *et al.*, 1990; Dagorn *et al.*, 2000a). From these studies, it appears this change in behaviour is effected only when the fish are within about 0.5 nmi of the floating object. Once further away, bigeye tuna resume a W-shaped vertical movement pattern during the daytime (Holland *et al.*, 1990). Based on the observed vertical movements, we conclude that the fish remained essentially associated with Buoy 3 until recaptured (average ± SE time-at-liberty: 28 ± 6 days). This residence time is much longer than that reported by Klimley and Holloway (1999) for yellowfin tuna tagged adjacent to a buoy near the main Hawaiian Islands. However, as shown in Fig. 2, juvenile bigeye tuna also show months-long school fidelity first reported with juvenile yellowfin tuna by Klimley and Holloway (1999).

It remains an open question whether tunas can remain closely associated with an anchored floating object for this period of time without outstripping the available resources, even if food resources were continuously advected past. Brock (1985) noted that yellowfin tuna stayed around anchored buoys for about 2–3 weeks, but could do so only by a significant shift in diet. A possible explanation for the ability of bigeye tuna to remain near Buoy 3 may be the abundance of the local anchovy (*Encrasicholina punctifer*). Bigeye tuna consume this species (Hida, 1973); fishermen who recaptured tagged fish from Buoy 3 reported bigeye tuna feeding on massive schools of anchovy. However, Ménard *et al.* (2000) reported finding 'numerous empty stomachs' in yellowfin tuna caught near buoys in the eastern Atlantic and suggested that tunas may utilize floating objects as a 'refuge or meeting point' (Dagorn and Fréon, 1999), rather than an enhanced feeding opportunity.

Based on estimated geolocations and vertical movement patterns, we conclude that all but one fish released at Cross Seamout (Fish 241) remained associated with the seamount for an average (± SE) residence time of 25 ± 12 days. Holland *et al.* (1999) found similar results from a study conducted on Cross Seamount where 835 bigeye tuna were marked with plastic dart tags. In that study, bigeye tuna were found to have an average residence time of about 32 days. Cross Seamount clearly acts as a natural aggregation point.

Bigeye tuna associated with Cross Seamount exhibited vertical movement patterns that were generally similar, but not identical, to those of Fish 509. Although the fish associated with Cross Seamount also displayed characteristic W-shaped vertical movement patterns, their vertical movements did not extend as deep and were much more variable. It is possible that these patterns may have been tempered if tagged bigeye were associated near the edges of the seamount where fishermen routinely target them with handlines. Yellowfin tuna tagged and released at Cross Seamount had an average residence time of only 15 days and Holland *et al.* (1999) concluded that bigeye tuna could sustain longer residence times at the seamount because they have the ability to exploit the resources of more of the water column (i.e. bigeye tuna have greater vertical mobility then yellowfin tuna). Our observations support this argument, although we have no depth records of yellowfin tuna associated with Cross Seamount.

Based on length/age relationships for bigeye tuna in the Pacific (Kume and Joseph, 1966), it appears that Fish 509 was probably at least 3–4-year-old while fish tagged and released at Buoy 3 were probably around 1 year old (mean FL of 60 ± 5 cm). Fish associated with Cross Seamount (mean FL of 80 ± 7 cm) were probably 1–2 years old. We conclude that the observed differences in behaviour patterns have more to do with the fish being associated with Buoy 3 and Cross Seamount, than differences in maturity. However, the possible correlation between fish size and/or maturity and vertical movement patterns warrant further investigation.

Environmental limits on vertical movements

The water column near the main Hawaiian Islands is generally characterized by a wind-mixed surface layer of uniform properties (temperature, salinity, nutrients). Surface layer depth typically varies from nearly 120 m in winter to less than 30 m in summer. Below the surface layer, there is a fairly rapid decrease in temperature from about 25°C to 5°C at about 600 m. Dissolved oxygen levels remain at (or slightly above) saturation within the photic zone (~200–300 m), then decrease almost linearly with depth to less than $1.0\ \mathrm{mL\ L^{-1}}$ below ~600–700 m depth (Juvick and Juvick, 1998). It is within this environment that the bigeye tuna carrying archival tags were operating.

Tunas have evolved unique physiological and morphological adaptations (such as vascular countercurrent heat exchangers) that, combined with behavioural strategies, allow them to maintain their body temperature for longer periods below the themocline and thus to exploit food resources more effectively than other fishes (Stevens and Neill, 1978). Two basic schools of thought, not necessarily mutually exclusive, have been promulgated to explain the factors controlling the vertical movement behaviours of tunas. One is physiological (Brill *et al.*, 1999) and the other is biotic (Dagorn *et al.*, 2000b; Marcinek *et al.*, 2001). Our data clearly confirm that bigeye tuna exploit deeper and colder habitats, at least on a transient basis, than other tunas (Sund *et al.*, 1981). We hypothesize that this strategy would allow tuna to exploit the organisms of the SSL as food. However, after spending time in conditions where ambient temperatures are considerably less than body temperature, bigeye tuna must return to the warm surface layer to increase muscle temperature (Fig. 11). So vertical movements traversing up and down through the thermocline during the day are based on physiological constraints. This type of vertical movement pattern is, however, also an excellent method for exploiting the organisms of the SSL as a resource, and it is possible that tunas' vertical movements mirror those of their prey to the extent allowed by each species' physiological abilities (Josse *et al.*, 1998). Furthermore, different species of tuna may also be limited in vertical movement patterns based on visual acuity and their ability to see in dim light (Somiya *et al.*, 2000).

Bigeye tuna are also tolerant of low ambient oxygen (hypoxia) and routinely inhabit water with an oxygen content of <2 mL L^{-1} Hanamoto (1987). In contrast, a reduction of oxygen content to only 3.5 mL L^{-1} limits the depth distribution of skipjack and yellowfin tunas (Barkley *et al.*, 1978; Cayré and Marsac, 1993; Brill, 1994). In laboratory studies, the onset of cardiorespiratory adjustments seen during acute hypoxia occurs at lower ambient oxygen levels in bigeye tuna than in skipjack or yellowfin tunas (Bushnell *et al.*, 1990). Although bigeye tuna can clearly tolerate lower ambient oxygen conditions than other tuna species, their tolerance does not appear to be quite as extensive as postulated (down to 1 mL L^{-1}) by Hanamoto (1987). As expected, bigeye tuna have blood with a higher oxygen affinity than do skipjack or yellowfin tunas (Lowe *et al.*, 2000). However, to maintain elevated metabolic rates characteristic of tunas (Brill, 1996) requires that bigeye tuna blood also have an unusual characteristic where oxygen affinity is reduced as the blood is warmed during its passage through the vascular counter-current heat exchangers (Lowe *et al.*, 2000). This, in turn, requires maintenance of elevated muscle temperatures and may explain bigeye unas' regular upward excursions into the warm surface layer. For bigeye tuna, maintenance of warm muscles may well be more then advantageous, it may be obligatory.

As yet unexplained is how bigeye tuna can maintain cardiac function in the face of 17°C temperature reductions (from 25 to 8°C) occurring over minutes during their regular vertical movements. Such temperature changes do not seem to be tolerated by yellowfin or skipjack tunas (R.W. Brill, K. Cousin, T. Lowe, unpublished data), as they cannot maintain cardiac output in the face of more then 10°C acute reductions in temperature (from 25 to 15°C). The effect of temperature on cardiac function has been suggested to be the factor limiting vertical movements in several tuna and billfish species (Brill *et al.*, 1999), although this idea still lacks direct experimental confirmation.

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