

Vertical and horizontal movements of striped marlin (*Tetrapturus audax*) near the Hawaiian Islands, determined by ultrasonic telemetry, with simultaneous measurement of oceanic currents

R. W. Brill¹, D. B. Holts², R. K. C. Chang¹, S. Sullivan¹, H. Dewar³, F. G. Carey⁴

¹ Honolulu Laboratory, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, Hawaii 96822-2396, USA

² La Jolla Laboratory, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, La Jolla, California 92038, USA

³ Physiological Research Laboratory, Scripps Institution of Oceanography, University of California at San Diego, La Jolla, California 92093, USA

⁴ Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, USA

Received: 7 May 1993 / Accepted: 22 June 1993

Abstract. We measured the vertical and horizontal movements of striped marlin (*Tetrapturus audax*) off the leeward coast of the Island of Hawaii between 20 November and 18 December 1992 while simultaneously gathering data on water temperature and oceanic currents. Fish movements were monitored by ultrasonic depth-sensitive transmitters, depth-temperature profiles by an expendable bathythermograph system, and oceanic current patterns by an acoustic Doppler current profiler. Like Indo-Pacific blue marlin (*Makaira mazara*), striped marlin near Hawaii spend > 85% of their time in the mixed layer (i.e., above 90 m depth). The maximum depth for striped marlin appears to be limited by water temperatures 8°C colder than the mixed layer, rather than by an absolute lower temperature. We also found that the horizontal displacements of some striped marlin can be strongly influenced by currents.

Introduction

Striped marlin (*Tetrapturus audax*) are widely distributed in the Pacific and Indian Oceans, but are absent from the Atlantic Ocean (Ueyanagi and Wares 1974, Squire and Suzuki 1990). Like other members of the Istiophoridae, striped marlin are large pelagic predators which make extensive movements. They are not, however, considered as highly migratory as bluefin tuna (*Thunnus thynnus*) or albacore (*T. alalunga*), which undertake rapid and regular transoceanic migrations (Squire and Suzuki 1990). Also, like other members of the Istiophoridae, striped marlin are apparently adapted for attaining and rapidly recovering from extraordinary peak levels of activity, rather than for sustaining high cruising speeds (Johnston and Salmonski 1984, Daxboeck and Davie 1986, Wells and Davie 1986, Wells et al. 1986, Davie 1990). Recently, direct measurements of swimming speeds of Indo-Pacific

blue marlin (*Makaira mazara*¹) confirmed that this species spends the majority of its time moving at relatively slow, and presumably aerobically sustainable, speeds (Block et al. 1992a).

Data are available on the short-term vertical and horizontal movements of striped marlin near the California coast. Holts and Bedford (1990) tracked 11 striped marlin and found that these fish spend most of their time in the mixed layer (19 to 20°C) and only occasionally descend into water where the temperature is < 12°C. Five of the eight marlin followed for 20 to 48 h moved predominantly in one direction at an average ground speed of 1.18 knots (0.607 m s⁻¹). The other three fish remained in the vicinity where they had been initially captured and released.

Prior to our study, no information was available on the short-term vertical and horizontal movements of striped marlin near the Hawaiian Islands, an environment quite different from the waters off California (McGary 1955, Seckel 1955, Lynn et al. 1982, Holland et al. 1990a, b, Holts and Bedford 1990). Comparison of the vertical movements and depth distributions of striped marlin near California and Hawaii can reveal factors limiting vertical distribution of this species. Data on vertical movements is additionally useful for resource conservation and fisheries' management. For example, knowledge of the depth distributions of billfishes can enable commercial longline fleets to alter their gear (i.e., adjust hook depths) to minimize the catch of particular species.

Our study also provides the first description of the movements of pelagic fish with simultaneously gathered data on the speed and direction of oceanic currents obtained directly using an acoustic Doppler current profiling system. Previous studies using ultrasonic telemetry to

¹ The common and scientific names for the billfishes used herein follow Nakamura (1985), whereby Atlantic and Indo-Pacific blue marlin are recognized as separate species: *Makaira nigricans* and *M. mazara*, respectively.

determine tuna and billfish activities (e.g. Yuen 1970, Laurs et al. 1977, Carey and Robinson 1981, Holland et al. 1990 a, b, Holts and Bedford 1990) reported rates of movement which were actually speed over ground (i.e., speed was calculated from positional data) rather than true swimming speed (i.e., speed through the water). Also, without data on oceanic currents, no conclusions could be drawn as to the effects of currents on horizontal displacements. Block et al. (1992 a) partially circumvented these problems by employing telemetry transmitters capable of directly measuring the swimming speed of Indo-Pacific blue marlin, but they lacked a quantitative measurement of currents. Carey and Scharold (1990) directly telemetered swimming speeds of blue sharks (*Prionace glauca*) with current speed and direction estimated from the drift of fishing gear and satellite sea-surface temperature images. These investigators found that both the speed and direction of blue shark movements can be strongly influenced by currents.

Materials and methods

Two research vessels were employed during our study, the 11 m "Kaahale'ale" and the 53 m National Oceanic and Atmospheric Administration (NOAA) ship "Townsend Cromwell". The hydrophone mounting system aboard the "Kaahale'ale" has been described previously (Brill et al. 1984, Holland et al. 1985). The system aboard the "Townsend Cromwell" was a four-hydrophone array (VEMCO, Halifax, Nova Scotia, Canada) mounted beneath a modified fiberglass depressor wing (V-FIN, Environmental Devices Corporation, Marion, Massachusetts, USA). During tracking operations, the depressor wing was towed amidships ≈ 5 m beneath the surface. Hydrophones were selected individually by a four-position switch mounted near the receiver.

Tetrapturus audax were captured by standard commercial monofilament longline gear between 20 November and 18 December 1992. Fishing operations were conducted off the western coast of the Island of Hawaii ($156^{\circ}00' - 157^{\circ}00' W$; $19^{\circ}15' - 20^{\circ}15' N$) because the high volcanoes provide a lee of up to ≈ 10 nautical miles (18.5 km), from the strong northeasterly trade winds. About 120 baited hooks, attached to ≈ 3 to 6 nautical miles (6 to 11 km) of longline, were deployed from the "Townsend Cromwell", soaked for 4 to 8 h, and then retrieved. Individual fish were identified to species and body weights estimated independently by two experienced observers (R. W. Brill and D. B. Holts). Striped marlin that appeared healthy were brought alongside the ship and an ultrasonic depth-sensitive transmitter (VEMCO, Halifax, Nova Scotia, Canada, Model VP-3) was attached to the anterior dorsal musculature using a standard tagging pole. The transmitter attachment system employed the stainless arrowhead design used previously by Holland et al. (1990 a). Immediately after attachment of the transmitter, the fish was released by cutting the leader as close as practical to the fish. No attempt was made to retrieve the hook. Individuals were initially followed by the "Kaahale'ale" until the remainder of the longline gear had been retrieved (usually 1 to 2 h). The "Townsend Cromwell" would then join the other vessel and the fish were tracked in tandem.

The transmitters encoded depth information by varying pulse interval. The output from the transmitters was received aboard both vessels by VEMCO VR-60 ultrasonic receivers. The audio output from the receiver aboard the "Kaahale'ale" was recorded by a standard audio-tape deck. Aboard the "Townsend Cromwell", a frequency counter and IBM PC were used to measure and convert every other pulse interval to depth, and to store the data digitally. The audiotapes recorded aboard the "Kaahale'ale" were later digitized by the computer system aboard the "Townsend Cromwell".

Positional information was obtained aboard both vessels using global positioning system (GPS) satellite receivers. Aboard the "Townsend Cromwell", positional information was also obtained using a satellite navigation system (SATNAV) receiver, LORAN-C receiver, and radar fixes from the nearest point of land. The ships' positions were assumed to be the same as that of the fish and were recorded approximately every 15 min. Oceanic current data (absolute directions and speeds) were collected by an RD Instruments (San Diego, California) acoustic Doppler current profiler (ADCP) aboard the "Townsend Cromwell". Depth-temperature profiles were collected by a Sippican Ocean Systems (Marion, Massachusetts) expendable bathythermograph (XBT) recorder aboard the "Townsend Cromwell". XBT probes were launched approximately every 6 h during a track.

Aggregate depth and temperature distributions were calculated based on 10 m and $1^{\circ}C$ bins, respectively (Holland et al. 1990 a, b). These data were expressed as a fraction of the total track time for each fish, and the bins were averaged across all fish. Aggregate temperature distributions also were calculated, where by temperatures are expressed relative to the mixed-layer temperature.

Results

Estimated body weights, calculated fork lengths, and the duration of the tracks of *Tetrapturus audax* are given in Table 1. Fish 4 apparently died after 4 h, although it had appeared healthy upon release. Its rate of descent (≈ 10 m min^{-1}) was clearly that of a dead or dying fish, and was far slower than that of a shed transmitter (≈ 30 m min^{-1} , Holland et al. 1990 b). All data from Fish 4 have been omitted. No other marlin succumbed nor shed its transmitter whilst being tracked. All fish, except Fish 6, were followed until they were lost in deteriorating sea conditions: the fish were at the surface and the choppy seas and large swells significantly reduced the range over which the transmitter could be heard. Fish 6 had to be abandoned after 51 h because of lack of ship time.

Vertical movements and temperature

Vertical movements of the marlin and the simultaneously gathered depth-temperature data are shown in Fig. 1. It is apparent from this figure that striped marlin in Hawaiian waters spend the majority of their time either in, or immediately below, the mixed layer. The fish do make brief excursions into water as cold as $18^{\circ}C$, but no signifi-

Table 1. *Tetrapturus audax*. Estimated body weight, calculated fork length, and duration and dates of tracks for six striped marlin equipped with ultrasonic transmitters. Fork lengths were calculated from estimated body weights using weight-length regression equation given in Skillman and Yong (1974)

Fish No.	Estimated wt (kg)	Fork length (cm)	Duration of track (h)	Date of track
1	37	210	14	22–23 Nov.
2	45	220	22	24–25 Nov.
3	37	210	23	3–4 Dec.
4	57	230	4	7 Dec.
5	50	230	41	9–11 Dec.
6	45	220	51	16–18 Dec.

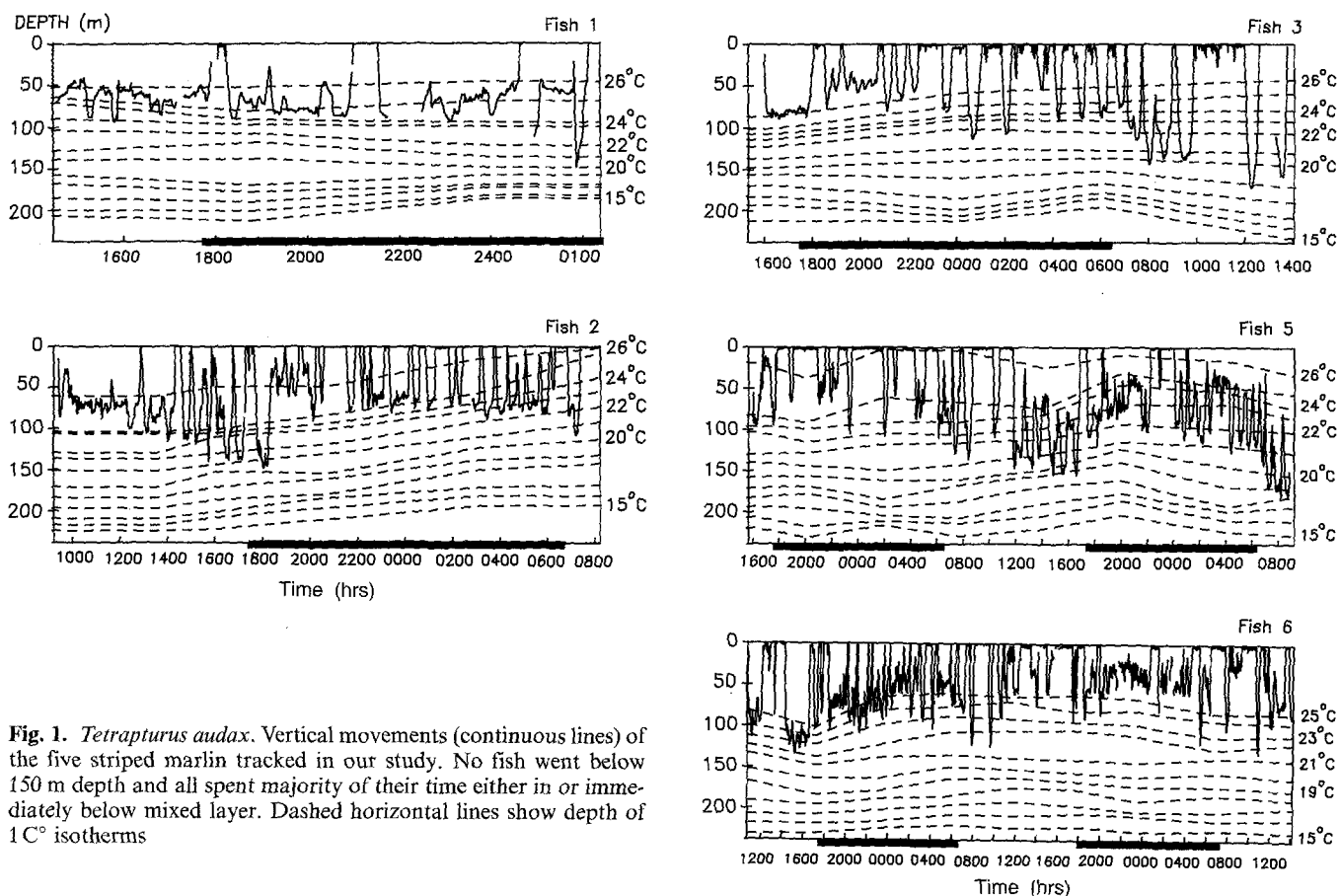


Fig. 1. *Tetrapturus audax*. Vertical movements (continuous lines) of the five striped marlin tracked in our study. No fish went below 150 m depth and all spent majority of their time either in or immediately below mixed layer. Dashed horizontal lines show depth of 1°C isotherms

ificant amount of time is spent at this temperature. Fig. 1 also shows that there are no obvious day–night differences in depth distribution, as seen in tunas (Holland et al. 1990 b).

Fig. 2 summarizes time at depth and time at temperature for all fish. The striped marlin in our study spent almost 30% of their time at depths shallower than 10 m (Fig. 2a). The second peak in the time at depth distribution (51 to 90 m, Fig. 2a) reflects the approximate depth of the bottom of the mixed layer. Fig. 2b shows the time spent at various absolute temperatures and Fig. 2c the time spent at temperatures relative to the mixed-layer temperature. Both (b) and (c) reveal that striped marlin spend >85% of their time either within, or immediately below, the mixed layer.

Horizontal movements

Fish 1

Fish 1 was captured \cong 8 nautical miles (15 km) northwest of Keahole Point (Fig. 3) and was released at 11.07 hrs. Because of equipment failure, neither depth nor positional data (except the point of capture) were obtained until 13.00 hrs. The GPS satellite was not transmitting during the majority of the track, so oceanic current information was not obtained. (The ADCP requires real-time data on ship position and speed provided by the

GPS receiver). Also, accurate positional information was unobtainable between 18.00 and 22.00 hrs because the GPS satellite was not transmitting and the data from the other navigational systems were unreliable.

Fish 1 moved north, both day and night (Fig. 3), until contact was lost at \cong 01.00 hrs in rough water near the edge of the Alenuihaha Channel. The fish had an average ground speed of 2.0 knots (1.0 m s^{-1}).

The Alenuihaha Channel is noted for its difficult sea conditions, because the trade winds are funneled between the islands of Hawaii and Maui (the island immediately to the north). Because Fish 1 moved rapidly north into the channel, all subsequent fishing efforts were moved \cong 20 to 25 nautical miles (37 to 46 km) south.

Fish 2

Fish 2 was released at 09.26 hrs at a point \cong 12 nautical miles (22 km) southwest of Keahole Point. It moved south for about 20 min, then turned and headed north for the remainder of the track (Fig. 3). Contact was lost at around 07.30 hrs the following morning in rough sea conditions [\cong 1 to 2 m swells and 20 to 25 knot (10 to 13 m s^{-1}) wind]. The marlin was briefly relocated at 09.05 hrs and then immediately lost again. The fish's course paralleled that of Fish 1 for the entire track. Oceanic current data were not obtained because the GPS satellite was again transmitting only intermittently.

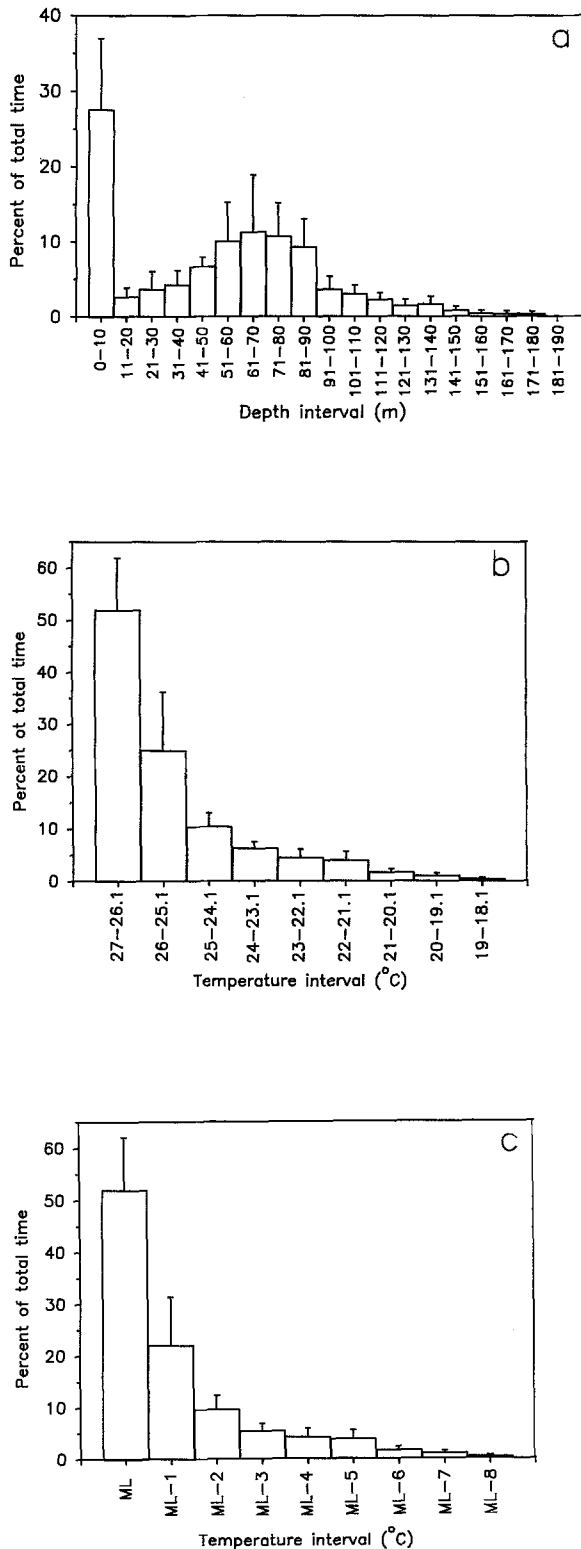


Fig. 2. *Tetrapturus audax*. Vertical distributions of striped marlin in Hawaiian waters expressed as percent time (mean \pm standard error of mean) spent at a specific depth (a), at a specific temperature (b), and at temperatures relative to mixed-layer (ML) temperature (c). In (c), ML-1 represents water temperature 1°C below mixed-layer temperature, ML-2 water temperature 2°C below mixed-layer temperature, etc. Data confirm that striped marlin spend most of their time in or immediately below mixed layer (i.e., the warmest water available). Maximum depths reached by striped marlin appear to be limited by temperatures that are 8°C below (ML-8) mixed-layer temperature

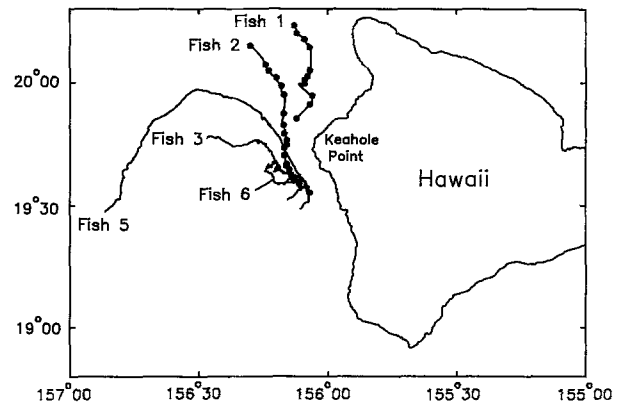


Fig. 3. *Tetrapturus audax*. Island of Hawaii and movements of five striped marlin. Distance scale for fish movements in this and subsequent figures is represented by longitude (1 min of longitude = 1 nautical mile = 1.852 km), with circles indicating hourly positions. Hourly positions have been omitted from tracks of Fish 3, 5, and 6 for legibility

Fish 3

Fish 3 was released at 15.59 hrs in approximately the same area as Fish 2 (Fig. 3). It proceeded north for 2 h, then turned to a more northwesterly heading until first light the following morning (07.00 hrs), when it changed to an almost due westerly course (Fig. 4a). Most (but not all) of the horizontal movements of Fish 3 appear to be due to the prevailing currents (cf. Fig. 4a and b). After \sim 18.00 hrs (2 h after release), the fish seemed to attempt to maintain a westerly heading but was pushed onto a northwesterly course by the current. The fish's speed over ground at this time was 1.8 knots (0.93 m s^{-1}). When the fish reached an area where the currents were more westerly (at \approx 07.00 hrs), its speed over ground increased to 3.9 knots (2.0 m s^{-1}), presumably because the fish's intended heading and the current were almost parallel.

Fish 5

Fish 5 was released at 16.00 hrs in approximately the same area as Fish 2 and 3 (Fig. 3). This marlin moved northwest for the first night, then gradually turned west and then southwest over the next day. It finally assumed an almost due-south heading during the second night and next morning (Fig. 5a). Average speed over ground for the first 37 h of the track from (16.00 to 07.00 hrs, Fig. 5a) was 2.0 knots (1.0 m s^{-1}). The overall displacement of this fish appears to have been caused by currents, since its course parallels the direction of the currents until approximately dawn (07.00 hrs) on the second day (Fig. 5b). The fish may have been attempting to maintain a due westerly course after dawn on the second day, but was pushed to a southwesterly course by the strong (4.2 knots, 2.2 m s^{-1}) southerly current.

Fish 6

Fish 6 was released (at 10.42 hrs in roughly the same place as Fish 3 and 5 (Fig. 3). For the first 24 h, the

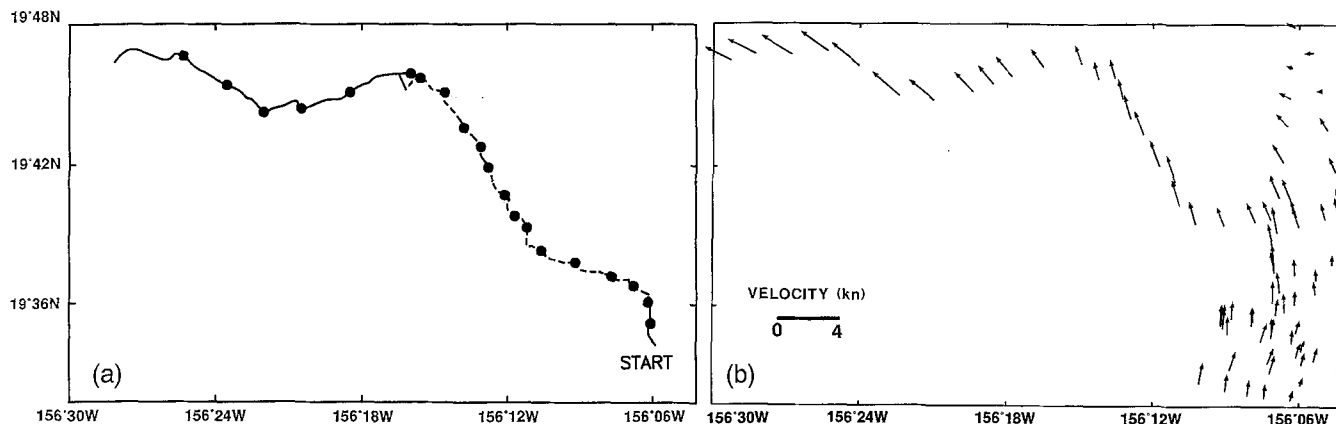


Fig. 4. *Tetrapturus audax*. Horizontal movements of Fish 3 (a) and simultaneously gathered oceanic current data (b). Current data are for 20 to 40 m depth, i.e., shallowest depth range from which reliable data can be obtained by acoustic Doppler current profiler. For

current speed, 4 knot scale-line = 2.06 m s^{-1} . Here and in Figs. 5 and 6, continuous portion of trace indicates daylight movements and dashed portion nighttime movements

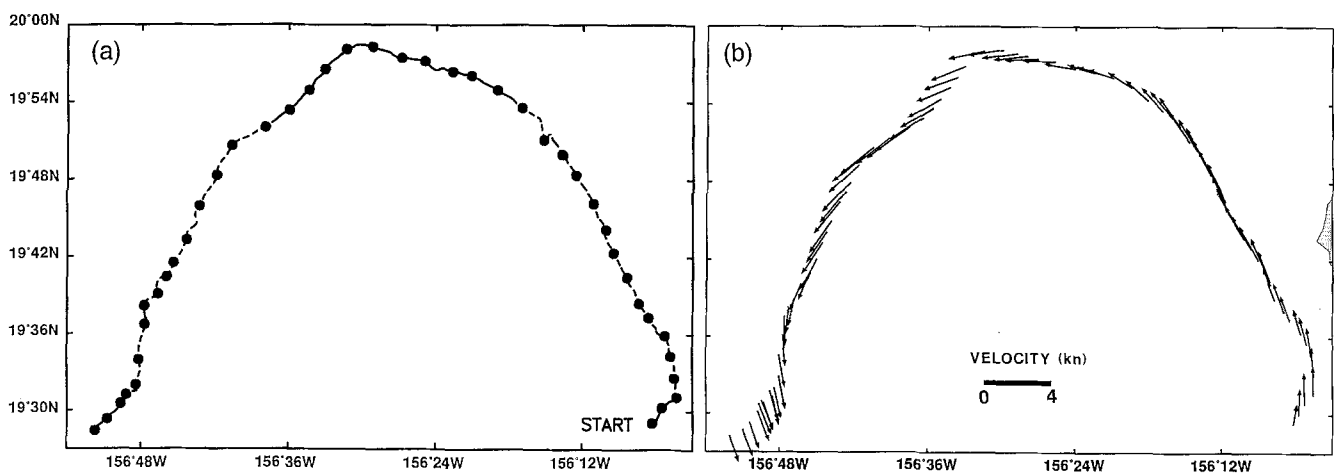


Fig. 5. *Tetrapturus audax*. Horizontal movements of Fish 5 (a) and simultaneously gathered current data (b). Fish's movements appeared to be strongly influenced by current direction for most (37 h)

of track. During last 5 h (07.00 to 11.00 hrs), fish appeared to attempt to hold a westerly course, but was pushed to southwest by a strong (4.2 knots, 2.2 m s^{-1}) southerly current

“Kaahele’ale” followed the marlin while the “Townsend Cromwell” mapped the local current field. The fish moved in a looping pattern (Fig. 6a), so that it remained in the same area rather than moving off as the other marlin had done. Unlike the other fish, the movements of Fish 6 appear to be almost totally uninfluenced by the northerly-directed current (Fig. 6b). Its speed over ground, however, was strongly influenced by the current. When moving nearly parallel with the current (from the start of the track until ≈ 14.30 hrs), ground speed was about 2.1 knots (1.1 m s^{-1}). When clearly moving against the current (from ≈ 14.30 to 18.00 hrs), its ground speed was considerably slower (0.7 knots, 0.36 m s^{-1}).

Discussion

The depth preferences of the *Tetrapturus audax* in our study are similar, but not identical, to those of striped marlin tracked off California by Holts and Bedford

(1990). During both studies, the fish spent a significant amount of time in the upper 10 m. Three of the eight fish tracked by Holts and Bedford did not descend below 40 m, and the deepest dive was 93 m. The deepest descent observed during our study was ≈ 170 m, and our fish spent $\approx 40\%$ of their time between 51 and 90 m. Our results are consistent with those of Boggs (1992), who found the catch rates of striped marlin near the Hawaiian Islands to be highest for longline hook fishing between 40 and 120 m.

It seems likely that the depth distribution of striped marlin is strongly influenced by water temperature rather than by an absolute depth preference. Comparison of our data with those of Holts and Bedford (1990), reveals that striped marlin do not have an absolute temperature preference. The fish we followed spent $\approx 80\%$ of their time between 25.1 and 27°C , and never ventured in water colder than 18°C . In contrast, because of the lower mixed-layer temperature, the striped marlin tracked off California spent the majority of their time between 20

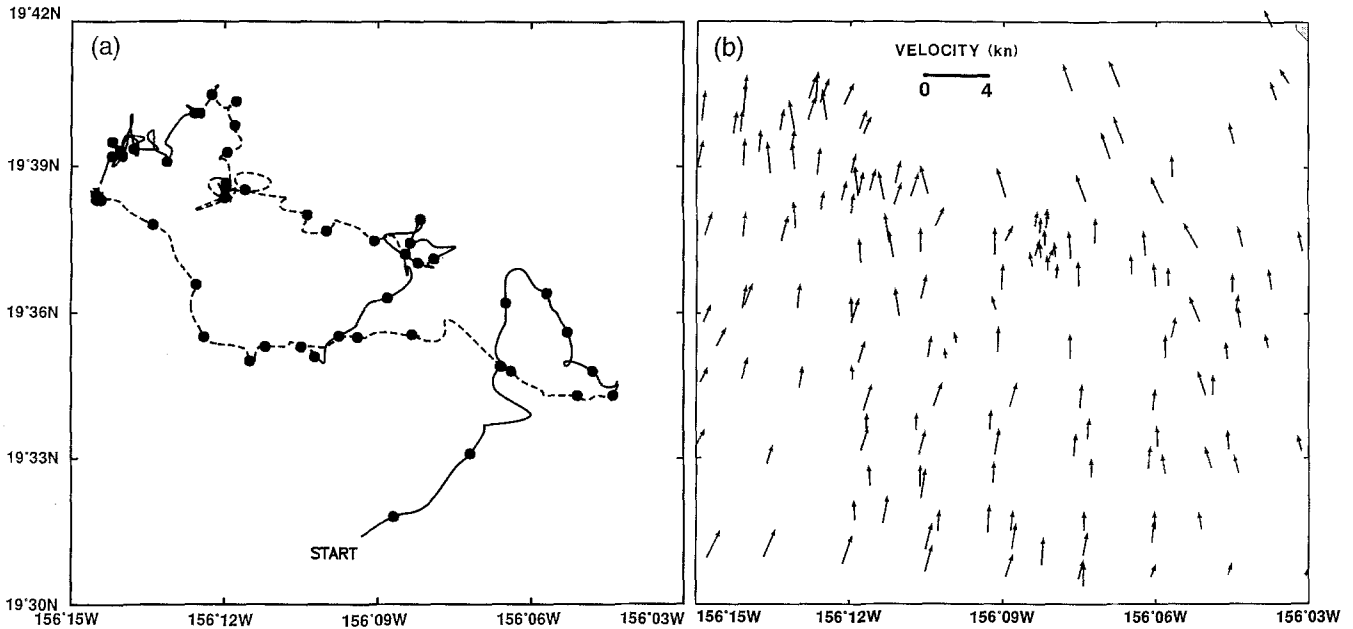


Fig. 6. *Tetrapturus audax*. Horizontal movements of Fish 6 (a) and simultaneously gathered current data (b). Unlike other striped marlin tracked during our study, and despite a relatively strong

(≈ 2.5 knots, 1.3 m s^{-1}) northerly current, fish remained in relatively small area by moving in looping pattern

and 21°C , and regularly penetrated into waters of 14°C , or even 12°C . When temperature is expressed relative to the mixed layer (Fig. 2c), however, the distributions appears to be the same for both groups. Striped marlin near the Hawaiian Islands and near California both spent the vast majority of their time either in the mixed layer or in water no colder than 2°C below that of the mixed layer. No fish in either study descended into waters that were more than 8°C colder than the temperature of the mixed layer. This similarity in behavior occurred in spite of the fact that the fish tracked by Holts and Bedford were somewhat larger (50 to 80 kg) than the fish tracked in our study (37 to 57 kg). In brief, striped marlin appear to spend the majority of their time at the highest water temperature available, and water temperature more than 8°C below mixed layer temperature forms the floor of the striped marlin habitat. It is the change in water temperature (relative to mixed-layer temperature), rather than absolute temperature, that limits striped marlin vertical movements.

The horizontal displacements of striped marlin off California (Holts and Bedford 1990) and those near the Hawaiian Islands also appear strikingly similar. In both studies, most fish moved in relatively straight lines or slowly curving arcs. Similar horizontal displacements have been observed in Indo-Pacific blue marlin in Hawaiian waters (Yuen et al. 1974, Holland et al. 1990a, Block et al. 1992a). Although oceanic current data were not collected simultaneously in these studies, the paths of Indo-Pacific blue marlin appear to follow the probable cyclonic and anticyclonic eddy patterns (Robinson and Lobel 1985, Lobel and Robinson 1986) which occur on the leeward side of the Island of Hawaii where the fish were tracked.

Relatively straight-line movement is not universal, however. Of the eight striped marlin tracked for 20 h or more by Holts and Bedford (1990), three followed looping courses that kept them in the areas where they were originally caught. Of the five fish tracked in our study, four left the areas where they were caught, and one did not. Because of the overall similarity of the vertical movements in all striped marlin tracked to date, the differences in horizontal movement patterns are probably not due to differences in the extent of injuries acquired during capture. Indeed, Fish 4, the individual that died 4 h after capture, spent the entire time within a few meters of the surface. This appears to be a behavior pattern indicative of badly injured fish. An almost identical situation was observed by Block et al. (1992a). In their study, the one Indo-Pacific blue marlin that was confirmed to have been killed by a shark also spent the entire tracking period (15 h) immediately below the surface, and never ventured deeper than ≈ 30 m.

The relatively straight-line movement patterns of striped and Indo-Pacific blue marlin contrast sharply with those of skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna, and bigeye tuna tracked near the Hawaiian Islands (Yuen 1970, Holland et al. 1990b). The tunas showed a strong 24 h rhythm in their behaviors. They repeatedly returned to the same areas at the same time for several days, and often returned via different routes. It appears unlikely, therefore, that tuna movements are significantly affected by currents. The reasons for the dramatic differences in the behaviors of tunas and marlins remain unexplained and should be investigated, particularly because tunas are major prey items (in terms of weight) of Indo-Pacific blue and striped marlin (Baker 1966, Brock 1984).

Because our data clearly show that striped marlin movements can be strongly influenced by oceanic currents, we suspect that in studies showing relatively straight-line movements of Indo-Pacific blue and striped marlin (Holland et al. 1990a, Holts and Bedford 1990, Block et al. 1992a, b), some fraction of the overall horizontal displacements of the tracked fish were due to currents. Similar influences of currents on the movements of blue sharks have been observed by Carey and Scharold (1990). Comparisons of "swimming speeds" between studies that do not telemeter this parameter directly are, therefore, problematic. Note, however, that ground speeds ($\cong 1$ to 2 knots) of Indo-Pacific blue and striped marlin are remarkably similar whether observed by acoustic telemetry (Holland et al. 1990b, Holts and Bedford 1990, Block et al. 1992b, and present study) or by release and recapture of tagged individuals (Squire 1987). The similarity of these data may reflect either common oceanic current velocities (Lobel and Robinson 1986), common swimming speeds or, most likely, a combination of the two.

Because of the imprecision of estimating geographical position and distances from the tracking vessel to the fish, a zig-zag pattern of fish movement is not really detectable. If fish movement is indeed highly irregular, ground speeds calculated from the tracking vessel's position may underestimate sustainable swimming speeds. In the one study that directly telemetered swimming speeds of Indo-Pacific blue marlin (Block et al. 1992b), the fish swam slower than 2 knots (1.0 m s^{-1}) for 93% of the time. Bursts of high speeds, up to 3.6 knots (1.8 m s^{-1}), lasted <1 min. When not in currents, ground speeds of blue sharks approximated measured swimming speeds, indicating that both Indo-Pacific blue marlin and blue sharks do not dart about (Carey and Scharold 1990, Carey unpublished observations) It seems likely that the same is true for striped marlin.

Acknowledgements. The authors wish to sincerely thank the officers and crew of the "Townsend Cromwell" for providing valuable help and expertise, and for teaching us the importance of respecting local traditions and ancient Hawaiian ceremonies. The editorial assistance of L. C. Williams is also gratefully acknowledged.

References

- Baker, A. N. (1966). Food of marlins from New Zealand waters. *Copeia* 1966: 818–822
- Block, B. A., Booth, D. T., Carey, F. G. (1992a). Depth and temperature of the blue marlin, *Makaira nigricans*, observed by acoustic telemetry. *Mar. Biol.* 114: 175–183
- Block, B. A., Booth, D. T., Carey, F. G. (1992b). Direct measurement of swimming speeds and depth of blue marlin. *J. exp. Biol.* 166: 267–284
- Boggs, C. H. (1992). Depth, capture time, and hooked longevity of longline-caught pelagic fish: timing the bites of fish with chips. *Fish. Bull. U.S.* 90: 642–658
- Brill, R. W., Holland, K. N., Ferguson, J. S. (1984). Use of ultrasonic telemetry to determine the short-term movements and residence times of tunas around fish aggregating devices. In: Proceedings of the Pacific Congress on Marine Technology, PACON 84: Marine Technology Society, Hawaii Section, Honolulu, p. MRM1/1-MRM1/7
- Brock, R. W. (1984). A contribution to the trophic biology of the blue marlin (*Makaira nigricans* Lacepède, 1802) in Hawaii. *Pacif. Sci.* 38: 141–149
- Carey, F. G., Robinson, B. H. (1981). Daily patterns of activities of the swordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fish. Bull. U.S.* 79: 227–292
- Carey, F. G., Scharold, J. V. (1990). Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar. Biol.* 106: 329–342
- Davie, P. S. (1990). Pacific marlins, anatomy and physiology. Massey University Printery, Massey, New Zealand
- Daxboeck, C., Davie, P. S. (1986). Physiological investigations of marlin. In: Nilsson, S., Holmgren, S. (eds.) *Fish physiology: recent advances*. Croom Helm, Ltd., London, p. 50–70
- Holland, K., Brill, R. W., Chang, R. K. C. (1990a). Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. *Fish. Bull. U.S.* 88: 397–402
- Holland, K. N., Brill, R. W., Chang, R. K. C. (1990b). Horizontal and vertical movement of yellowfin and bigeye tuna associated with fish aggregating devices. *Fish. Bull. U.S.* 88: 493–507
- Holland, K., Brill, R., Ferguson, S., Chang, R., Yost, R. (1985). A small vessel technique for tracking pelagic fish. *Mar. Fish. Rev.* 47(4): 26–32
- Holts, D., Bedford, D. (1990). Activity patterns of striped marlin in the southern California bight. In: Stroud, R. S. (ed.) *Planning the future of billfishes*. National Coalition for Marine Conservation, Inc., Savannah, Georgia, p. 81–93
- Johnston, I. A., Salmonski, J. (1984). Power output and force-velocity relationships of red and white muscle fibers from the Pacific blue marlin (*Makaira nigricans*). *J. exp. Biol.* 111: 171–177
- Laurs, M. E., Yuen, H. S. H., Johnson, J. H. (1977). Small-scale movements of albacore, *Thunnus alalunga*, in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. *Fish. Bull. U.S.* 75: 347–355
- Lobel, P. S., Robinson, A. R. (1986). Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters. *Deep-Sea Res.* 33: 483–500
- Lynn, R. J., Bliss, K. A., Eber, L. E. (1982). Vertical and horizontal distributions of seasonal mean temperature, salinity, sigma-T, stability, dynamic height, oxygen, and oxygen saturation in the California current, 1950–1978. In: Fleming, A. (ed.) *CALCOFI Atlas No. 30*. Marine Life Research Program, Scripps Institution of Oceanography, La Jolla, California, p. 513
- McGary, J. W. (1955). Mid-Pacific oceanography, Part VI – Hawaiian offshore waters, December 1949–November 1951. *Spec. scient. Rep. U.S. Fish Wildl. Serv. (Fish.)* 152: 1–138
- Nakamura, I. (1985). *FAO species catalogue*. Vol. 5. Billfishes of the world. An annotated and illustrated catalogue of marlins, sailfishes, spearfishes and swordfishes known to date. *F.A.O. Fish. Synopsis* 125(5): 1–65
- Robinson, A. R., Lobel, P. S. (1985). Impact of ocean eddies on coastal currents. In: Madaard, L., Pujale, R., Gaynor, V. (eds.) *HOE: The Hawaiian ocean experiment*. Proceedings of the Hawaiian Winter Workshop. Hawaii Institute of Geophysics Honolulu, p. 325–334 (Spec. Publ. Hawaii Inst. Geophys.)
- Seckel, G. R. (1955). Mid-Pacific oceanography, Part VII. Hawaiian offshore waters, September 1952–August 1953. *Spec. scient. Rep. U.S. Fish Wildl. Serv. (Fish.)* 164: 1–250
- Skillman, R. A., Yong, M. A. (1974). Length–weight relationships for six species of billfishes in the Central Pacific Ocean. *NOAA natn. mar. Fish. Serv. tech. Rep. U.S. Dep. Commerce SSRF-675*: 126–137
- Squire, J. L. (1987). Striped marlin migration patterns and rates in the Northeast Pacific Ocean as determined by a cooperative tagging program: its relation to resource management. *Mar. Fish. Rev.* 49(2): 26–43
- Squire, J. L., Suzuki, A. (1990). Migratory trends of striped marlin (*Tetrapturus audax*) in the Pacific Ocean. In: Stroud, R. H. (ed.) *Planning the future of billfishes*, National Coalition for Marine Conservation, Inc., Savannah, Georgia, p. 76–80
- Ueyanagi, S., Wares, P. G. (1974). Synopsis of biological data on striped marlin, *Tetrapturus audax* (Philippi, 1887). *NOAA natn.*

- mar. Fish. Serv. tech. Rep. U.S. Dep. Commerce SSRF-675: 132–159
- Wells, R. M. G, Davie, P. S. (1986). Physiological stress responses in big gamefish after capture: observations on plasma chemistry and blood factors. *Comp. Physiol. Biochem.* 81A: 643–646
- Wells, R. M. G., McIntyre, R. H., Morgan, A. K., Davie, P. S. (1986). Physiological stress responses in big gamefish after capture: observations on plasma chemistry and blood factors. *Comp. Biochem. Physiol.* 84A: 565–571
- Yuen, H. S. H. (1970). Behavior of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic telemetry. *J. Fish. Res. Bd Can.* 27: 2071–2079
- Yuen, H. S. H., Dizon, A. E., Uchiyama, J. H. (1974). Notes on the tracking of the Pacific blue marlin, *Makaira nigricans*. NOAA natn. mar. Fish. Serv. tech. Rep. U.S. Dep. Commerce SSRF-675: 265–268

Communicated by M. G. Hadfield, Honolulu