Depth and Muscle Temperature of Pacific Bluefin Tuna Examined with Acoustic and Pop-up Satellite Tags

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Abstract

Six Pacific bluefin tuna were tracked with ultrasonic telemetry and two with pop-up satellite archival tags (PSATs) in the eastern Pacific Ocean from 1997 to 1999. Both pressure and temperature ultrasonic transmitters were used to examine the behavior of the 2 - 4 year-old bluefin tuna. The bluefin spent over 80% of their time in the top 40 meters of the water column and made occasional dives into deeper, cooler water. The mean slow-oxidative muscle temperatures of three fish instrumented with pressure and temperature transmitters were 22.0 - 26.1°C in water temperatures that averaged 15.7 - 17.5°C. The thermal excesses in slow oxidative muscle averaged 6.2 - 8.6°C. Variation in the temperature of the slow oxidative muscle in the bluefin was not correlated with water temperature or swimming speeds. For comparison with the acoustic tracking we examined the depth and ambient temperature of two Pacific bluefin tagged with pop-off satellite archival tags for 24 and 52 days. The PSAT data sets show similar depth and temperature distributions of the bluefin tuna to the acoustic data set. Swimming speeds calculated from horizontal distances with the acoustic data indicate the fish mean speeds were 1.1 - 1.4 fork lengths/s (FLs^{-1}). Pacific bluefin spent the majority of their time in the top parts of the water column in the eastern Pacific Ocean in a pattern similar to that observed for yellowfin tuna, despite the greater ability of Pacific bluefin tuna to maintain body temperature above ambient temperature.

Introduction

Bluefin tuna are members of the family Scombridae that comprises the mackerels, bonitos, and tunas (Collette and Nauen 1983). The bluefin tuna group includes ~~the southern bluefin (Thunnus maccoyii),~~ the Atlantic bluefin (T. thynnus), and the Pacific bluefin (T. orientalis) (Gibbs and Collette 1966; Collette 1999). While acoustic telemetry has yielded important insights into the biology of the Atlantic and southern bluefin (Carey and Teal 1969; Carey and Lawson 1973; Davis 1994; Block et al. 1998b; Lutcavage et al. 1999), little is known about the physiological ecology of Pacific bluefin tuna, particularly in the eastern Pacific Ocean. This species ranges throughout the Pacific Ocean and spawns only in the western Pacific. During their first year of life many of these fish migrate to the eastern Pacific, where they remain for 2 - 6 years before returning to the western Pacific to spawn (Sund et al. 1981; Bayliff 1994). Recently, a single bluefin tuna recovery of a western archivally tagged Pacific bluefin revealed an extensive period of residency along the western North American coastline (Tsuji et al. 1999). Our knowledge of the movement patterns, temperature preferences, thermal biology, and habitat use of bluefin in the eastern Pacific are limited to this one archival tag return.

Tunas are distinct from other teleosts in possessing well-developed counter-current heat exchangers that allow them to conserve heat in their slow-oxidative axial muscle (Carey and Teal 1966; Carey et al. 1971). Blood supplying the axial slow-oxidative muscle passes through the lateral counter-heat exchangers in all tuna species. As a result, the temperature of slow-oxidative muscle can be maintained warmer than ambient temperature. In some species of tunas, including albacore (T.

alalunga), bigeye (T. obesus), and three species of bluefin there are additional heat exchangers in the cranial cavity and viscera (Carey et al. 1984). The presence of these additional counter-current heat exchangers in the eyes, brain, and viscera and more extensive lateral heat exchangers supplying the slow-twitch muscle of bluefin, albacore and bigeye tuna have led to the greater ability of these species to maintain elevated temperatures in their bodies compared to other tuna species (Gibbs and Collette 1966; Carey and Teal 1969). The increased ability of these tunas to conserve metabolic heat is correlated with the occupation of a greater thermal range than tunas with less well-developed heat-conserving mechanisms. Fisheries data and electronic tagging studies indicate that yellowfin (T. albacares), blackfin (T. atlanticus), longtail (T. tongol), and skipjack (Katsuwonus pelamis) tunas reside in tropical waters and spend the majority of their time above the thermocline (Sund et al. 1981; Carey and Olson 1982; Block et al. 1993; Brill et al. 1999). Bluefin, albacore, and bigeye occupy cooler waters over a wider range of latitudes or spend more time at greater depths in tropical waters (Carey and Lawson 1973; Laurs et al. 1977; Holland et al. 1990; Block et al. 1998a; Lutcavage et al. 2000). Catch records indicate that Pacific bluefin tuna occupy waters with sea surface temperatures between 17 - 23°C, while in the eastern Pacific (Bell 1963). Several studies using ultrasonic telemetry and archival tagging have demonstrated that Atlantic bluefin tuna can occupy water as cold as 3°C and can maintain body temperatures as much as 21°C above ambient in their slow-twitch muscle (Carey and Teal 1966; Carey and Teal 1969; Carey and Lawson 1973; Block et al. 2001) and 15°C above ambient in their viscera (Carey et al. 1984; Block et al. 1998a; Lutcavage et al. 1999). No studies have examined the thermal biology of the axial musculature and only one study has examined the thermal biology of the viscera (Tsuji et al. 1999) of Pacific bluefin tuna.

In this study, ultrasonic telemetry was used to examine the movement and thermal biology of Pacific bluefin tuna in the eastern Pacific Ocean. The results with acoustic tags are compared to similar data obtained from pop-up satellite archival tags that tracked the movements of two fish for longer periods of time in the same region. Because we measured oceanographic variables throughout the water column at regular intervals while tracking, and three of the fish were equipped with pressure and temperature transmitters, we were able to examine the temperature of the slow-oxidative muscle of these three fish with respect to their depth movements and ambient temperature.

Materials and Methods

Six Pacific bluefin tuna were monitored with ultrasonic telemetry using a combination of pressure and temperature transmitters (Table 1). The fish were tracked during October of 1997 and July of 1998 in the eastern Pacific Ocean from the *R/V Point Sur* (47 m). The strait fork length of the fish ranged from 81 to 119 cm. In 1997 the fish had been held in commercial pens several km south of Bahía Todos Santos off the coast of Baja California for 2 months where they were fed 6 times per week prior to their release. The fish were caught from the pen with hook and line and brought aboard a wetted vinyl mat placed on a floating platform. Ultrasonic transmitters (Vemco Ltd., Armdale, Nova Scotia) containing either a pressure transducer (V22 extra power), used to monitor depth of the fish, or a temperature sensor with an external thermistor (V16), used to monitor slow-oxidative muscle temperature, were attached to the fish as described below. Two fish, 9701 and 9703, were instrumented with a 34 kHz transmitter equipped with a pressure transducer and the other, 9702, carried a 50 kHz transmitter equipped with an external thermistor inserted into the slow-oxidative muscle. Bluefin 9701 was tracked in two segments. During the second segment, bluefin 9702 was tracked on a 50 kHz transmitter while the track of 9701 was resumed on its 34 kHz transmitter.

The fish tracked in 1998 were caught by the F/V Shogun (22 m) on hook and line using jig poles. The fish were briefly held (2 - 48h) aboard the vessel in flooded holds or in the ocean beside the vessel in an oceanic pen (8-m diameter, 4-m depth). Holding fish made possible the release of multiple fish at once and ensured a reliable supply of bluefin for tracking. For tracks 9801 and 9802, fish were removed from the holds in water-filled slings and outfitted with transmitters. For these two tracks, multiple fish were released simultaneously. Only bluefin 9803, which was released from the oceanic pen, was released alone. In 1998, all the fish carried both a pressure (34 kHz V22 extra power) and temperature transmitter (50 kHz V16). In five out of six tracks in 1997 and 1998, the fish with the transmitter was released with several other fish to allow the fish to school.

Ultrasonic transmitters and attachment

The 34 kHz pressure transmitters (Vemco V22-5XSEP) used were 120 mm long with a diameter of 22 mm, and weighed 40 grams in water (Vemco Ltd.).

Pressure was converted to depth using calibrations for each transmitter supplied by the manufacturer. The pressure transmitters were accurate to ± 1.0 m. The temperature transmitters (Vemco V16T-4L) were 80 mm long with a diameter of 16 mm and weighed 12 g in water. The anterior and posterior ends of each tag were equipped with a medical grade nylon Billfish Foundation type darthead connected to the tag with 22-kg monofilament, which was coated with shrink-wrap to reduce the possibility of the monofilament cutting through the skin. These dart heads were inserted into the dorsal musculature at the anterior and posterior margins of the second dorsal fin. Proper placement of the thermistor in the slow-twitch muscle was determined prior to the experiments through dissection of bluefin tuna of similar size. Using a modified piece of stainless steel tubing (3 mm internal diameter) the thermistor was inserted into the slow-oxidative muscle at 50% fork length starting at a point 3 - 4 cm from the dorsal midline. The needle was inserted 10 - 15 cm into the body perpendicular to the anterior-posterior axis and parallel to the dorsal-ventral axis. The thermistor was held in place with a thin plastic hook secured to the tip and sutured at the point of entry into the muscle with Ethicon PDS II absorbable suture.

Tracking system

Individual bluefin were released from the <u>F/V Shogun</u> or the floating platform in the pen and tracked from the <u>R/V Point Sur</u> using a towed-array hydrophone system described in Block et al. (1997). Tracking of the fish and the recording of depth data were accomplished using a Vemco VR-28 receiver tuned to the 34 kHz transmitter attached to a laptop computer. A Vemco VR41 hydrophone was used to receive the signal. Depth and temperature data were collected on a laptop computer connected to a multichannel Vemco VR-60 receiver. The software coupled to the VR-60 monitored 34 kHz for the pressure transmitter for 10 s then switched to monitor 50kHz for the temperature transmitter for 30s. Laptop computers associated with both receiver systems were running Vemco tracking software. The software running with the VR-28 displayed both the direction and relative distance of the fish from the vessel (Block et al. 1997). The signal strengths from the 34 and 50 kHz transmitters were calibrated by attaching them to buoys and moving away and toward them at ship speeds of 1 - 2 knots. Calibrations indicated that the useful range was approximately 0.8-0.9 NM and 0.6-0.7 NM for the 34 and 50 kHz transmitters, respectively. During tracking operation distances of 0.3 NM or more from the fish were routine.

The research vessel was equipped with a Seabird CTD (conductivity, temperature, depth) array that allowed simultaneous monitoring of the temperature and oxygen content of the water throughout the tracks at 2 to 4 hour intervals (the CTD was deployed while the tracking continued at a reduced speed). Expendable bathythermographs (XBT) (Sippican T-4) also were employed to measure the temperature profile of the water column when it was not practical to deploy the CTD unit while underway. Data from both the CTD and XBT systems were recorded by an onboard computer. Sea surface temperature was also monitored continuously by the ship's SAIL system. An acoustic doppler current profiler allowed continuous monitoring of current direction and speed under the vessel throughout the track. A 28 kHz echosounder was used to mark the scattering layer at various points in the track.

Data analysis

Data were acquired for both depth and temperature at 1 - 2 Hz. Raw data obtained during the track were filtered to eliminate spurious depth readings, by calculating a rate of change in depth for each inter-sample interval and eliminating depth readings for which the rate of change was greater than 6 ms^{-1}. To condense the data, filtered depth data were averaged in groups of 4, yielding a depth reading on average every 6 s. The same type of filtering was applied to the temperature data. Temperature samples that differed from the previous sample by more than 0.2°Cs^{-1} were deleted. After filtering, temperature data from each inter-depth interval on the VR-60 were averaged. This procedure resulted in the averaging of temperature data in groups of approximately 10, yielding a temperature reading on average every 22 s.

Water temperature and oxygen content profiles for plots of depth versus time were constructed by connecting the depths at which the temperature and oxygen content changed 1°C or 1 mgO$_2$L^{-1}, respectively, between each CTD or XBT (temperature only) cast. Ambient temperatures were assigned to each depth measurement of the fish by assuming a linear change in water temperature with depth between each CTD or XBT.

Pop-up satellite archival tag deployments

Two Pacific bluefin tuna were caught on rod and reel with 27-kg line and barbless circle hooks on July 15 1999. They were pulled onto a wet vinyl-covered mat located on the swimstep of the F/V Shogun. The eyes were covered with a soft rag soaked in Polyaqua artificial fish slime (Kordon division of Novalek, Inc, Hayward, CA) and the curved length of the fish was measured. The pop-up satellite archival tags were attached to the tuna using a machined titanium applicator dart (fish 99-048) or a "bluefin-type" molded NMFS nylon dart (fish 99-043). The dart was inserted to a depth of 7.5 cm (fish 99-048) and 8.9 cm (fish 99-043) at the base of the second dorsal fin (see Block et al. 1998a for further information on the tags and tagging procedure). The fish were released by sliding them off the mat into the water. Time spent out of the water was less than one minute. The pop-up satellite archival tags (Wildlife Computers of Redmond, WA) were programmed to surface after 24 days for fish 99-048 and 52 days for fish 99-043 (Table 1). The tags were second generation PSATs that were programmed to sample pressure and ambient temperature every minute, and binned the collected data into histograms that were transmitted to the ARGOS satellite after the tag released from the fish. The tags also recorded depth and temperature profiles, which provided information on the movement of the fish in relation to the thermocline.

Swimming speeds

Swimming speed was calculated by two methods. The first used the ship's position determined by GPS at 5-minute intervals to approximate the horizontal displacement of the fish. The second method incorporated both the horizontal displacement as described above and the total vertical movements during the same 5-minute interval. The vertical distance traveled by the fish was calculated by summing over 5-minute intervals the absolute value of depth changes between each data point after filtering and averaging. The distance traveled by the fish in 5-minutes was taken to be the hypotenuse of the right triangle formed by the horizontal and vertical distance vectors.

Results

A total of six Pacific bluefin tuna ranging in length from 81 to 119 cm were acoustically tracked in 1997 and 1998 (Tables 1 and 2). Three individuals carried both temperature and pressure transmitters (9801, 9802, 9803), two carried pressure transmitters only (9701 and 9703) and one carried only a temperature transmitter (9702). Fish 9701 was tracked in two segments, the second of which was done simultaneously with fish 9702 (Table 2). The five tracks, involving six individuals, provide 255.5 hours (10.6 days) of data on Pacific bluefin behavior and 141.5 hours of data on thermal physiology. In addition the depth and water temperature distributions are presented for two bluefin tuna (127 cm and 143 cm) that carried pop-up satellite archival tags for 24 and 52 days, respectively.

Horizontal movements

The bluefin tracked in 1998 were wild fish caught offshore. Bluefin tuna 9801 was released with 2 other bluefin on the warm side of a temperature front in a sea surface temperature (SST) of 18.7°C. Upon release it slowly moved east-southeast toward the edge of the front. Fish 9801 spent a large portion of the track near the cooler edge of the front.

Bluefin 9802 was caught and released in 18°C water with 3 albacore. All 4 fish had been caught in the same school. Upon release, bluefin 9802 swam west into cooler water, 17°C SST, before turning southeast and moving into warmer water where the SST was at or near 19°C for the remainder of the track.

Bluefin 9803 was released in warm water (SST = 19.5°C), moved in a westerly direction (Figure 1A) and crossed into cooler water during the first several hours of the track. From approximately 2200 on July 20 to 0200 on July 21, tuna 9803 appeared to cross back and forth over a 0.5°C temperature break as indicated by the SST measured by the ship's SAIL system. At about 0900 on July 21 the fish made a relatively abrupt change of direction and began a general southerly heading, which it maintained to the end of the track.

In contrast to the open ocean experiments which were conducted offshore in the Southern California Bight, all bluefin in 1997 were released close to the Mexican coast (south of Bahía Todos Santos) from a pen. The fish tracked in 1997 remained in shallow, warm water (SST 20 - 22°C) within 15 NM of the coast for the majority of the tracks (Figure 1B). The first fish, 9701, was released on October 3 1997 and tracked for 47 hours before the track was terminated after it entered an area of Bahía Todos Santos, due to the risk of entangling the tow-body with commercial longline gear. This fish was encountered again on October 5 near the commercial pen. Because tuna 9701 was carrying a 34 kHz transmitter capable of lasting 7 - 9 days, we resumed our track of tuna 9701 while initiating a simultaneous second track of another bluefin tuna, 9702, that had been tagged with a 50 kHz temperature transmitter. This second bluefin was released with 6 yellowfin tuna from the pen.

From the acoustic tracks, it was clear the two bluefin tuna remained together for the next 11 hours, enabling us to record depth information for fish 9701, while recording muscle temperature of tuna 9702. Contact with 9702 was lost after both fish moved offshore. Tuna 9701 was followed until 0530 on October 6 1997 at which point the track was terminated. The third fish tracked in 1997, tuna 9703, remained near the coast for nearly the entire 15 hour track. The track of 9703 was terminated at 0812 on October 7 due to deteriorating weather conditions.

Vertical movements and water temperature

After release, bluefin 9801 made a brief dive to 50 m then remained above the 18°C isotherm at 30 m for the next 6 hours, with the exception of a 10-minute dive to 60 m into 14°C water at 2030 (Figure 2A). During the remainder of the track, it spent the majority of its time moving between the surface and 60 m, showing a preference for the mixed layer. Particularly striking are the periods during the afternoons, when it stayed within 10 m of the surface. Despite the clear preference for the mixed layer, on several occasions this bluefin spent extended periods at depth in cooler water. During these periods the fish was often associated with a dense scattering layer or schools of potential prey items detected on the echosounder (indicated by arrows in Figure 2). Because the echosounder was not on continuously, we don't know if tuna were associated with schools of forage fish or in the presence of the scattering layer during other periods where similar behavior was observed. Bluefin 9801 also made many deep short-duration dives into cool water (11 - 15°C) and regular dives at sunrise and sunset.

After release, bluefin 9802 immediately dove to 55 m, encountering water temperatures of 15 - 16°C for 25 minutes. For the remainder of the track it showed a preference for depths less than 40m (Figure 2B), similar to the behavior observed for tuna 9801. The pattern of deep diving was also similar between 9801 and 9802. Tuna 9802 made several brief deep dives to cold water, one to waters less than 11°C, and also made regular dives at sunrise and sunset on all 3 days of the track. In addition to the characteristic diving behavior, tuna 9802 also spent extended periods near the surface during the afternoon of July 19.

Bluefin 9803 was released alone and spent the majority of the 48 hour track alternating between the surface and 60 m. Like the other two tuna in 1998, upon release it dove to 55 m. Whereas 9801 and 9802 returned to the surface shortly after release, tuna 9803 spent most of the first 80 minutes of the track below 40 m. This fish displayed a larger amplitude oscillatory diving pattern than either tuna 9801 or 9802 and as a consequence spent a significant amount of time below 50 m in 14 - 16 °C water. Like bluefin 9801 and 9802, bluefin 9803 also made deep dives to cold water and regular sunrise and sunset dives.

The two fish tracked with pressure transmitters in 1997 spent the majority of their time above 20 m in warm surface water (Figure 3). Bluefin 9701 exhibited shallow oscillatory diving behavior, showing a strong preference for the mixed layer. It spent extended periods in surface waters during two afternoons, October 3 and 5 (Figure 3A). Like the fish tracked in 1998, the time in the upper layers of the water column for bluefin 9701 was interrupted by brief deep dives into cold water (less than 10°C) and extended dives to more moderate depths.

Bluefin 9703 showed a strong preference for the mixed layer (Figure 3B). This fish displayed shallow oscillatory behavior throughout the 15-hour track. During the last 9 hours of the track, the fish expanded its depth range as the 22°C isotherm moved deeper in the water column. Unlike the other four bluefin that carried pressure transmitters, bluefin 9703 spent the entire track above 45 m.

Oxygen content

The three fish tracked in 1998 spent the majority of their time in water above 8 mgO_2L^{-1}. During 1998 the oxygen content of the water mass was 8 mgO_2L^{-1} down to 80 m or deeper for the majority of the tracking time (Fig. 5) and was clearly not limiting the vertical movements of the fish. In 1997 the water occupied by the two fish carrying pressure transmitters was typically between 7 - 9 mgO_2L^{-1} (Figure 5). Only during the second segment of track 9701, when the fish moved offshore into deeper water did the fish regularly experience water where the oxygen content dropped to below 6 mgO_2L^{-1}.

Depth distribution

The frequency distribution of depths for Pacific bluefin tracked during both years indicate that the fish spent the majority of their time in the top 20 m of the water column (Figure 6). Fish tracked in 1998 exhibited a broader depth distribution, but spent approximately 50% of their time in the top 20 m of the water column (Figure 6A). The tuna tracked in 1997 were shallower, above 20 m more than 70% of the time (Figure 6B). The day-night depth distributions were significantly different for data from 1997 and 1998 according to the Kolmogorov-Smirnov test for different distributions, using data pooled by year (maximum unsigned difference for 1997 $D = 0.0696 > D_{.05} = 0.0157$ and $D = 0.1069 > D_{.05} = 0.0083$ for 1998). Although the data indicate that the nighttime depth distribution for the fish tracked in 1998 is deeper than that during the day, the differences between day and night depth distributions do not demonstrate an obvious pattern for the fish tracked in 1997.

Water temperature distribution

The acoustic tracking data indicate that the Pacific bluefin tuna spent the majority of their time in the warmest parts of the water column. Tuna 9801 spent over 65% of its time in 18 - 19°C water (Figure 7A). In contrast, tunas 9802 and 9803 displayed a broader temperature distribution, spending the majority of their time between 15 - 18°C. There was also substantial individual variation in temperature distributions between 9701 and 9703 (Figure 7C). Tuna 9701 had a broad temperature distribution, spending the majority of the track in 19 - 22°C water, whereas 9703 was in 22°C water for more than 80% of the track. When the distribution of ambient temperature in relation to the SST is examined the temperature distributions of the fish are much more similar (Figure 7B and D).

Four out of five fish tracked with pressure transmitters showed a tendency to occupy the warmest water available, resulting in right-skewed histograms (Figures 8B and D). These four fish spent more than 70% of their time in water temperature within 2°C of SST. Bluefin 9803, which exhibited a broad temperature distribution, spent most of its time in waters 2 - 5°C below SST.

Slow oxidative muscle temperature

For the three fish tracked in 1998, mean thermal excess in the muscle was calculated from the mean water temperature and slow-oxidative muscle temperature every five minutes (Table 3). Both bluefin 9801 and 9802 exhibited an average 8°C thermal excess, whereas the thermal excess of tuna 9803 was 6°C. Mean slow-oxidative muscle temperature of bluefin 9702 was 26.9 °C. Thermal excess is unknown for this fish because it was carrying only a temperature transmitter and therefore ambient temperatures are not known.

There was no significant correlation between muscle temperature and water temperature nor between thermal excess and water temperature (data not shown) for the fish tracked in 1998. Muscle temperature of bluefin 9801 was 28°C at the beginning of the track and gradually decreased over the next 3 hours to 23.5°C (Figure 8A). On several occasions during the track, elevations of muscle temperature occurred. Near sunset on July 11, muscle temperature began to rise gradually until it peaked at 29°C during a dive into cold water (Figure 8A arrow 1). The temperature then dropped 2°C in about an hour at 0100 on July 12 (Figure 8A arrow 2). This corresponded to a period when the fish made repeated dives into 15-16°C water to depths associated with the scattering layer (Figure 2A). Muscle temperature fluctuated between 25 and 28°C for most of the remaining time until the temperature signal was lost due to the loss of the battery power in the transmitter.

The muscle temperature of fish 9802 was 29.4°C immediately after release. This quickly dropped to 24.5°C in the first 40 minutes of the track (Figure 8B). Muscle temperature continued to decrease gradually for several hours to 22.7°C, then began a gradual increase in the evening of July 18. The muscle temperature continued to increase until the temperature signal was lost upon losing the fish for an hour.

Immediately after release the muscle temperature of tuna 9803 was 27.6°C (Figure 8C). The temperature of the muscle initially increased to 28.1°C, followed by a decline to 24°C over the next 2 hours, before dropping to 21 - 23°C for the remainder of the track.

Swimming speeds

Mean swimming speeds for all bluefin tuna tracked were 1.09 - 1.38 ms^{-1} (1.02 - 1.34 FLs^{-1}) using speed over ground (horizontal distance only) and 1.2 - 1.6 ms^{-1} (1.24 - 1.50 FLs^{-1}) using both horizontal and vertical distances. Combining the vertical and horizontal distances added an average of 13% (range 6 - 29%) to the swimming speeds of five bluefin calculated using only distance over ground (Table 4). Maximum speeds averaged over 5-minute intervals are in every case 2 - 2.5 times the mean speeds (Table 4). The direction of the fish's movement was independent of current direction and there was no correlation between current and fish swimming speed (data not shown).

Pop-up Satellite Archival Tag Data

The pop-up tags from fish 99-048 and 99-043 released at 23°32.76 N, 118°00.96 W and 31°55.14 N, 119°1.68 W, respectively. The fish were tagged in the same vicinity as the acoustic tagging experiments the year before and bluefin 99-043 pop–up endpoint overlapped the acoustic tracking region. Fish 99-048 had moved south of the study region in comparison to 1997 and 1998 acoustic-tracked fish (Figure 1). The tags at the surface transmitted depth and temperature histogram data (Figure 9), as well as depth/temperature profile and data for 10.1 and 10.3 days, respectively. Both fish showed a preference for shallow water: 99-048 spent 94% of it's time in the top 10 m and 99-043 spent 73% of it's time in the top 20 m. The thermocline for both tracks as determined from the daily depth/temperature profiles was in the vicinity of 25-50m. Bluefin 99-048 made infrequent dives to 50-100m and one dive to 350-450 meters. Bluefin 99-043 had a broader depth distribution and made more frequent dives to 100m depths and dove to 450-550 meters. The fish spent only 1 – 3 min. at the deepest depths. These dives are much deeper than any dives observed for the acoustically tracked fish. Temperature preferences were also similar for the two pop-up tagged fish, with 99-048 spending 99% of it's time in 17.5-22.5°C whereas fish 99-043 spent 95% of it's time in 17.0-21.0°C.

Discussion

This study uses two types of electronic tagging technology to examine the vertical distributions and ambient and muscle temperatures experienced by Pacific bluefin tuna. Analysis of our data in the context of earlier tracking studies on the behavior, vertical profiles, and muscle and visceral temperatures of several species of tunas (Carey and Teal 1969; Laurs et al. 1977; Carey and Olson 1982; Carey et al. 1984; Holland et al. 1990; Holland et al. 1992; Block et al. 1997; Brill et al. 1999) yields insight into how the physiological ecology of tunas differs between species. This study is unique in that 5 out of 6 of the bluefin tracked in 1997 and 1998 were released with other fish. Tuna are known to aggregate in multi-species schools in the wild (Sund et al. 1981; Carey and Olson 1982). We, therefore, attempted to approximate more natural conditions during the tracks by releasing several fish simultaneously.

Depth distributions

The depth distributions of bluefin tuna tracked during this study are characterized by short oscillatory dives near the surface. This diving pattern was interrupted by several distinct behaviors. The longest such interruptions were during the afternoons, when many of the fish spent several hours within 5 m of the surface. Despite the tendency to remain in the top 20 m, the fish tracked in 1998 also spent prolonged periods at various depths. It is likely that these were foraging dives, as they were often associated with the presence of the scattering layer or schools of forage fish.

In addition to the foraging dives, the bluefin made regular sunrise and sunset dives characterized by relatively deep dives followed by an immediate return to the surface shortly before sunrise and just after sunset. While apparent in both 1997 and 1998, this behavior was much more regular during the tracks in 1998 (Figures 3 and 4). At least one of these dives was to a depth associated with the scattering layer, which rises at sunset and sinks at sunrise. The bluefin may be following the vertical migrations of the scattering layer during these dives. Sunrise and sunset dives were observed for yellowfin tuna tracked by Block et al. (1997) in the eastern Pacific Ocean.

Josse et al. (1998) demonstrated that some of the vertical migrations of yellowfin and bigeye tuna are closely correlated with the position of the scattering layer. If the movement of the scattering layer is driving the diving behavior of yellowfin and bluefin tuna during the crepuscular periods, it remains unclear why they return to the surface immediately after the dive. It may be that the fish is orienting itself to a light source and that this behavior somehow plays a role in navigation by the fish or it may be simply returning to the warmer surface waters.

The distributions of ambient temperature relative to sea surface temperature support the conclusion that the bluefin in this region and of this size class (2 - 4 years of age) are spending the majority of their time in the warm mixed-layer. The acoustic data set was corroborated by the similar depth and temperature distributions of the two pop-up satellite archival tagged Pacific bluefin tuna (Figure 9). The only difference in the pop-up satellite data set was that occasional dives to significantly deeper depths than recorded by acoustic tags were observed. Together both electronic tagging data sets indicate a tendency to remain in waters above the thermocline. Only bluefin 9803 spent significant time in water more than 2°C below the temperature of the mixed layer. The distributions of the temperature differences between SST and the those experienced by the fish are similar to distributions observed for yellowfin tuna near Hawaii (Holland et al. 1990; Brill et al. 1999) and Southern California (Block et al. 1997), blue marlin (*Makaira nigricans*) (Block et al. 1992b), and striped marlin (*Tetrapturus audax*) (Brill et al. 1993).

The similarities between the relative temperature distributions of yellowfin tuna and Pacific bluefin in the eastern Pacific are in contrast to the behavior of yellowfin and bigeye tracked near the Hawaiian Islands (Holland et al. 1990; Brill et al. 1999). A major difference between these studies is water temperature and depth of the thermocline. In the eastern Pacific Ocean off of southern California where this study and that of Block et al. (1997) took place, the surface water temperatures ranged from 16 - 22°C and the mixed layer typically extended to only 20 m below the surface. In the waters off Hawaii, the mixed layer commonly extends to more than 50 m below the surface, and SST can reach 26°C. Therefore, although bluefin and yellowfin tuna tracked near Southern California appear to spend more time close to the surface than do yellowfin off Hawaii, the position of the fish in the water column relative to the mixed layer is similar in the two regions of the ocean. Southern bluefin tuna near Australia also showed a preference for depths above the thermocline, although these tracks were limited to shallow water with a vertical temperature gradient of only a few degrees (Davis 1994). Examination of the depth movements of Atlantic bluefin tuna with both acoustic and archival tags indicates a strong preference for the top 20m (Block et al. 1998b; Lutcavage et al. 2000; Block et al. 2001).

Slow-twitch muscle temperature

The bluefin tracked in 1998 maintained mean thermal excesses of 6.2 - 8.6°C in their axial musculature and maximum slow-twitch muscle temperature recorded was 29.4°C in bluefin 9801. These values are in agreement with thermal excesses reported for slow-twitch muscle of much larger Atlantic bluefin tuna in waters of similar temperature (Carey and Teal 1969; Carey and Lawson 1973). The muscle temperatures reported in this study show fewer fluctuations than peritoneal temperatures reported from archival tag returns from Atlantic and Pacific bluefin (Block et al. 1998b; Tsuji et al. 1999). Elevated muscle temperatures in tuna skeletal muscle are likely to result in increased power output of the muscle, as demonstrated in vitro by Altringham and Block (1997). Increased power output of the aerobic muscle would be advantageous to the bluefin while traveling between patches of prey or when making long migrations (Bayliff 1994), as it would allow the tuna to sustain higher swimming speeds.

The muscle temperature of bluefin 9801 was the most variable of all the fish and had a minimum of 23°C and a maximum of 29.4°C, which corresponded to thermal excesses of 5.7°C and 11.6°C, respectively. Variation in slow-oxidative muscle temperature was also observed among individuals, with mean body temperatures ranging from 22.0 - 26.1°C. Differences in muscle temperature among individuals, however, could be the result of variation in the placement of the thermistor in the muscle. The high initial temperatures observed immediately after release of all three bluefin are most likely due to the stress of capture and the limited ability of the fish to cool while out of the water during tag attachment. Similar elevations in muscle temperatures were observed in blue marlin and swordfish (Xiphias gladius) after release (Carey and Robison 1981; Block et al. 1992b).

The variation of muscle temperature in the three bluefin tuna was independent of ambient temperature. There were several instances where changes in body temperature were associated with diving. These changes, however, were both positively and negatively correlated with changes in ambient temperature. Activity levels were not the cause of the observed variation in body temperature, as no correlation was observed between slow-oxidative muscle temperature and swimming speed for any of the fish. Carey and Lawson (1973) observed active thermoregulation in Atlantic bluefin tuna. There is also extensive evidence of control of the efficiency of heat exchange from bigeye, albacore, and yellowfin tunas across a range of water temperature (Graham and Dickson 1981; Holland et al. 1992; Dewar et al. 1994). A similar ability in the Pacific bluefin may explain the fluctuations in body temperature that appear to be independent of both activity and water temperature.

Niche utilization

Bluefin tuna have a larger oceanographic range and occupy a wider range of SSTs than do tunas with less robust heat-conserving mechanisms (Sund et al. 1981). However, the greater ability of Pacific bluefin to conserve metabolic heat does not appear to have led to an expansion of their vertical distribution in the eastern Pacific. The Pacific bluefin tuna in this study spent the majority of their time in waters less than 2°C below SST, a pattern that has been observed for species with less ability to maintain elevated body temperatures such as yellowfin tuna, blue marlin and striped marlin. Some other physical variable, such as oxygen content of the water, may limit the vertical movements of Pacific bluefin. However, the bluefin in the present study spent the majority of their time in water with greater than 7 mgO_2L^{-1} and did not appear to be limited by the oxygen content of the water they encountered. Even the lowest oxygen content encountered by a fish during this study, 4.4 mgO_2L^{-1} during track 9803, is well above the hypoxia tolerances measured for other tuna species (Bushnell and Brill 1992; Korsemeyer et al. 1996).

Brill et al. (1993; 1999) suggested that the vertical distributions of several species of scombroids are limited by the effect of temperature on cardiac function. Physiological studies confirm significant temperature sensitivities in cardiac performance of yellowfin tuna. Korsemeyer et al. (1997) reports a Q_{10} of 2.37 for heart rate of yellowfin tuna between 18 and 25°C. In vitro studies of yellowfin ventricular tissue (Freund 1999) showed a decrease in maximum contraction frequency from 3 to 2 Hz associated with a decrease in temperature from 25 to 20°C. This reduction in heart rate with decreasing temperature would result in a significant reduction in cardiac output at cooler temperatures. Unfortunately, there have been no studies on the effect of temperature on cardiac function in bluefin tuna. If reduced cardiac output following acute reductions in temperature does indeed prove to be the limiting factor to the vertical mobility of many scombroids, it will be interesting to elucidate the biochemical and physiological adaptations that allow movement between water masses that differ by more than 15°C over periods of days to weeks in Atlantic bluefin (Block et al. 1998a; Lutcavage et al. 1999).

An alternative explanation for the limited vertical distribution of Pacific bluefin in this region of the eastern Pacific Ocean is that of prey abundance. The shallow depths occupied by the Pacific bluefin during this study may have more to do with the location of prey, and the physiological limitations of the prey, than physiological limitations of the bluefin. Pacific bluefin tracked in the eastern Pacific in more northerly locations frequent waters as cool as 14°C at the surface indicative of this species ability to range into cooler waters (Farwell et al. 2001). The tracks in this study occurred at approximately 31° N, where fish constitute a significant part of the diet of Pacific bluefin (Scott and Flintner 1972). In this region, northern anchovies (Engraulis mordax) are an important prey item of bluefin tuna (Pinkas et al. 1971). Evidence from acoustic surveys as well as fisheries data and the type of gear used in the anchovy fishery in the eastern Pacific indicates that E. mordax is primarily found above the thermocline (Wood and Strachan 1970; Holliday and Larsen 1979). The depth distribution of E. mordax may have been a major factor in keeping the bluefin in this study in the top 20 m of the water column. To test hypotheses on the factors determining the vertical distribution of bluefin tuna in the eastern Pacific, it will be necessary to track the tuna while simultaneously monitoring both prey abundance and distribution, and more complex physiological parameters pertaining to the tracked fish.

Swimming speeds

Mean swimming speeds for Pacific bluefin tuna in this study were calculated using two different methods. The first method, used previously in acoustic tracking studies, calculates speed from the ship's GPS readings every five minutes, yielding estimates of 1.09 - 1.38 ms^{-1}. This method underestimates the speed of the fish under all conditions, because only horizontal displacement is measured and averaged over small-scale movements. The second method uses the same horizontal displacement, but also incorporates the vertical distance traveled for each 5-minute period. This method results in swimming speeds between 1.20 - 1.57 ms^{-1}. All acoustic tracking studies of tunas have demonstrated a continuous oscillatory diving pattern, which suggests that vertical movements are a significant part of tuna locomotory behavior. This is confirmed by our finding that adding a vertical component to the estimation of speed adds 6-29 % to the speed estimated by horizontal displacement alone (Table 4). We suggest that the addition of the vertical component to calculations of swimming speed represents a better estimate of true swimming speed than using horizontal displacement (i. e. ship's position) alone.

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FIGURE LEGENDS

Figure 1. Horizontal movements of acoustically tracked bluefin tuna. A) Bluefin tuna tracked in 1998. Track ID numbers are given at the start of each track for 1998. B) Bluefin tuna tracked in 1997. Track ID numbers are given at the end of each track for 1997. The large bay is Bahía Todos Santos. The pen site indicated is the start site of all the tracks. Track "9701 cont." is the path taken by fish 9701 after the track was resumed 24 hours after terminating the track in Bahía Todos Santos. Fish 9702 was tracked simultaneously with 9701 cont. The arrow indicates the site where the temperature signal from tuna 9702 was lost as the two fish separated.

Figure 2. Vertical movements of bluefin tuna tracked in 1998. Depth and water temperature isotherms are plotted against time for three bluefin tracked in 1998. Light lines represent water temperature isotherms, labeled on the right sides of the plots. Black bars across the top of the plots represent nighttime. Times when fish positions are associated with the potential prey as identified by the echosounder are indicated by arrows. A) 9801, B) 9802, C) 9803

Figure 3. Vertical movements of bluefin tuna tracked in 1997. Depth and water temperature isotherms are plotted as in figure 2. A) 9701, B) 9703.

Figure 4. Vertical movements of bluefin tuna tracked in 1998 in relation to oxygen content of the water. A) 9801, B) 9802, C) 9803.

Figure 5. Vertical movements of bluefin tuna tracked in 1997 in relation to oxygen content of the water. A) 9701, B) 9702.

Figure 6. Depth distribution for bluefin tuna. Data for all tracks in A) 1998 and B) 1997 were divided into night and day activity based on time of first light and sunset from tracking notes. Mean frequencies (± S.E.) of time spent in each depth interval were calculated for each track. The intervals are labeled such that the 0 m depth interval includes depths from 0 - 9.99 m, the 10 m interval includes 10.0 - 19.99 m

Figure 7. Water temperature preferences for bluefin tuna. The distributions of the water temperatures occupied by the fish (T_w) for bluefin tracked in 1998 and 1997 are presented in (A) and (C), respectively. The intervals are labeled such that the 10°C interval includes temperatures from 10.0 - 19.9°C. Distributions of T_w in relation to the sea-surface temperature (SST) are presented for bluefin tuna tracked in 1998 (B) and 1997 (C). The 1°C bin indicates the frequency in which the fish occupied water 1°C cooler than SST.

Figure 8. Slow-oxidative muscle temperatures and ambient temperatures for the bluefin tuna tracked in 1998. Body temperature (T_b) and water temperatures (T_w) were averaged for each 5-minute interval of the tracks. Black bars indicate nighttime activity. Arrows indicate events where T_b changes are associated with diving events, as explained in the text.

Figure 9. Frequency distributions of depth and water temperature from PSAT data. Mean frequency time (± S.E.) spent at different depths (A and C) and temperatures (B and D) for 2 Pacific bluefin, 99-048 (A and B) and 99-043 (C and D). Black bars = 00:00 - 08:00 hrs PST, white bars = 08:00 – 16:00 hrs PST, gray bars = 16:00 – 24:00 hrs PST.

Table 1. Fish identification. Curved length was converted to fork length by multiplying by 0.955 and rounded to the nearest cm. Fish weight is estimated using the weight-length regression for Pacific bluefin tuna from Bayliff (1991). Tracks of tunas 9701 and 9702 overlapped on October 5. The sizes of bluefin 99-048 and 99-043 are the size at release.

Tuna ID	Dates	Transmitter description	Fork length (cm)	Fish weight (kg)	Duration (hours)
9701	Oct. 2-6 1997	Depth	119	34.4	63.5
9702	Oct. 5 1997	Muscle Temperature	95	18.3	9.0
9703	Oct. 6-7 1997	Depth	117	32.8	16.0
9801	July 10-14 1998	Depth	86	13.9	89.0
		Muscle Temperature			68.0
9802	July 18-20 1998	Depth	98	20.0	40.5
		Muscle Temperature			18.0
9803	July 20-22 1998	Depth	81	11.8	46.5
		Muscle Temperature			46.5
99-048	July 15-Aug. 8 1999	PSAT	127	41.3	24 days
99-043	July 15-Sept. 5 1999	PSAT	143	57.6	52 days

Table 2. Times and locations of the beginning and end of each track. The start time for the two pop-up fish is the time of tagging and the end time is the point at which the tag released from the fish and transmitted to the satellite.

Tuna ID	**Start time**	**Start Location**		**End time**	**End location**	
		Latitude	**Longitude**		**Latitude**	**Longitude**
9701	10:29 Oct. 2 1997	31°42.014 N	116°42.014 W	05:33 Oct. 6 1997	31°52.166 N	116°48.912 W
9702	13:43 Oct. 5 1997	31°42.482 N	116°42.014 W	22:41 5 Oct. 1997	31°45.622 N	116°57.615 W
9703	16:56 Oct. 6 1997	31°42.122 N	116°42.049 W	08:56 Oct. 7 1997	31°27.475 N	116°53.347 W
9801	19:15 July 10 1998	30°33.521 N	118°08.160 W	12:37 July 14 1998	30°08.476 N	118°23.390 W
9802	15:39 July 18 1998	31°22.265 N	118°16.146 W	08:22 July 20 1998	30°57.438 N	118°11.935 W
9803	16:50 July 20 1998	31°45.772 N	117°50.787 W	15:31 July 22 1998	31°17.474 N	118°22.274 W
99-048	July 15 1999	29°59 N	116°44 W	Aug 8 1999	23°32 N	118°01 W
99-043	July 15 1999	29°59 N	116°43 W	Sept 5 1999	31°55 N	119°02 W

Table 3. Mean water temperature, body temperature, and mean thermal excess. Means values were calculated from water and body temperatures averaged every five minutes. Thermal excesses were calculated at each time point by subtracting water temperature from body temperature. Data are presented as means ± S.D. for each track.

Tuna ID	Water Temperature (°C)	Body Temperature (°C)	Thermal Excess (°C)
9801	17.51 ± 0.74	26.11 ± 1.28	8.60 ± 1.50
9803	15.69 ± 0.63	23.82 ± 0.90	8.14 ± 1.16
9804	15.77 ± 1.00	22.01 ± 0.74	6.24 ± 1.04
9702	NA	26.0 ± 1.0	NA

Table 4. Mean speeds for bluefin tuna. Speeds were calculated as explained in the text. The maximum speed presented is the maximum calculated speed over a five-minute interval. Means ± S.D.

Tuna ID		Horizontal Distance			Horizontal + Vertical		
		mean	median	max	mean	median	max
9801	m/s	1.14 ± 0.64	1.10	3.42	1.28 ± 0.54	1.20	3.43
	FL/s	1.32 ± 0.70	1.28	3.98	1.50 ± 0.63	1.40	3.99
9802	m/s	1.25 ± 0.47	1.20	3.22	1.36 ± 0.43	1.30	3.26
	FL/s	1.27 ± 0.48	1.22	3.27	1.38 ± 0.44	1.32	3.31
9803	m/s	1.09 ± 0.41	1.10	3.05	1.20 ± 0.37	1.20	3.05
	FL/s	1.34 ± 0.51	1.36	3.75	1.47 ± 0.46	1.48	3.76
9701	m/s	1.22 ± 0.59	1.20	3.02	1.57 ± 0.52	1.50	3.08
	FL/s	1.02 ± 0.50	1.01	2.53	1.32 ± 0.44	1.26	2.58
9703	m/s	1.38 ± 0.46	1.30	3.55	1.46 ± 0.47	1.40	3.55
	FL/s	1.17 ± 0.40	1.11	3.02	1.24 ± 0.40	1.19	3.02

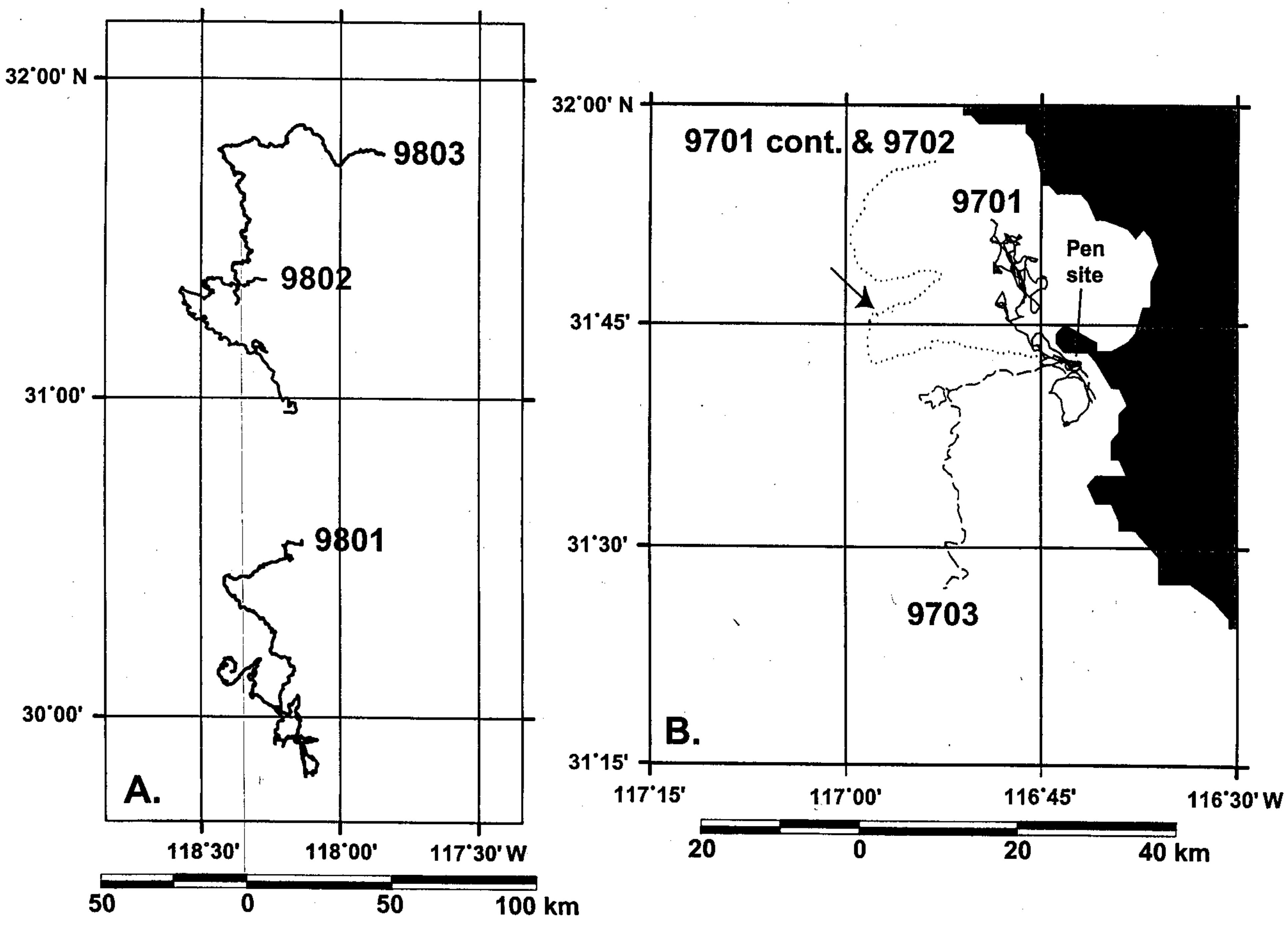
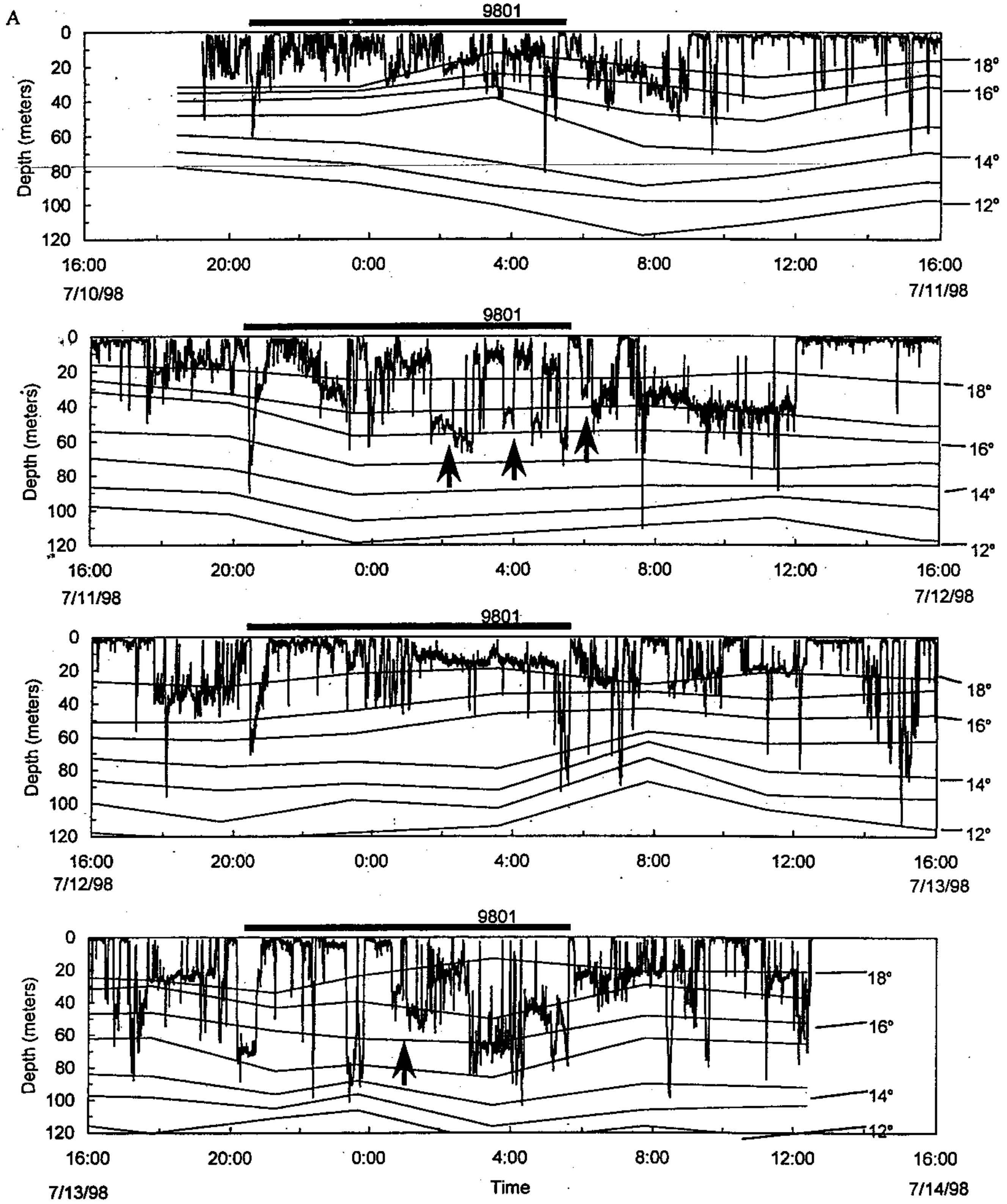

A.
32°00' N
31°00'
30°00'
118°30'
118°00'
117°30' W
9803
9802
9801
50
0
50
100 km
B.
32°00' N
31°45'
31°30'
31°15'
117°15'
117°00'
116°45'
116°30' W
9701 cont. & 9702
9701
9703
Pen site
20
0
20
40 km

Fig 2


A
9801
0
20
40
60
80
100
120
Depth (meters)
18°
16°
14°
12°
16:00
20:00
0:00
4:00
8:00
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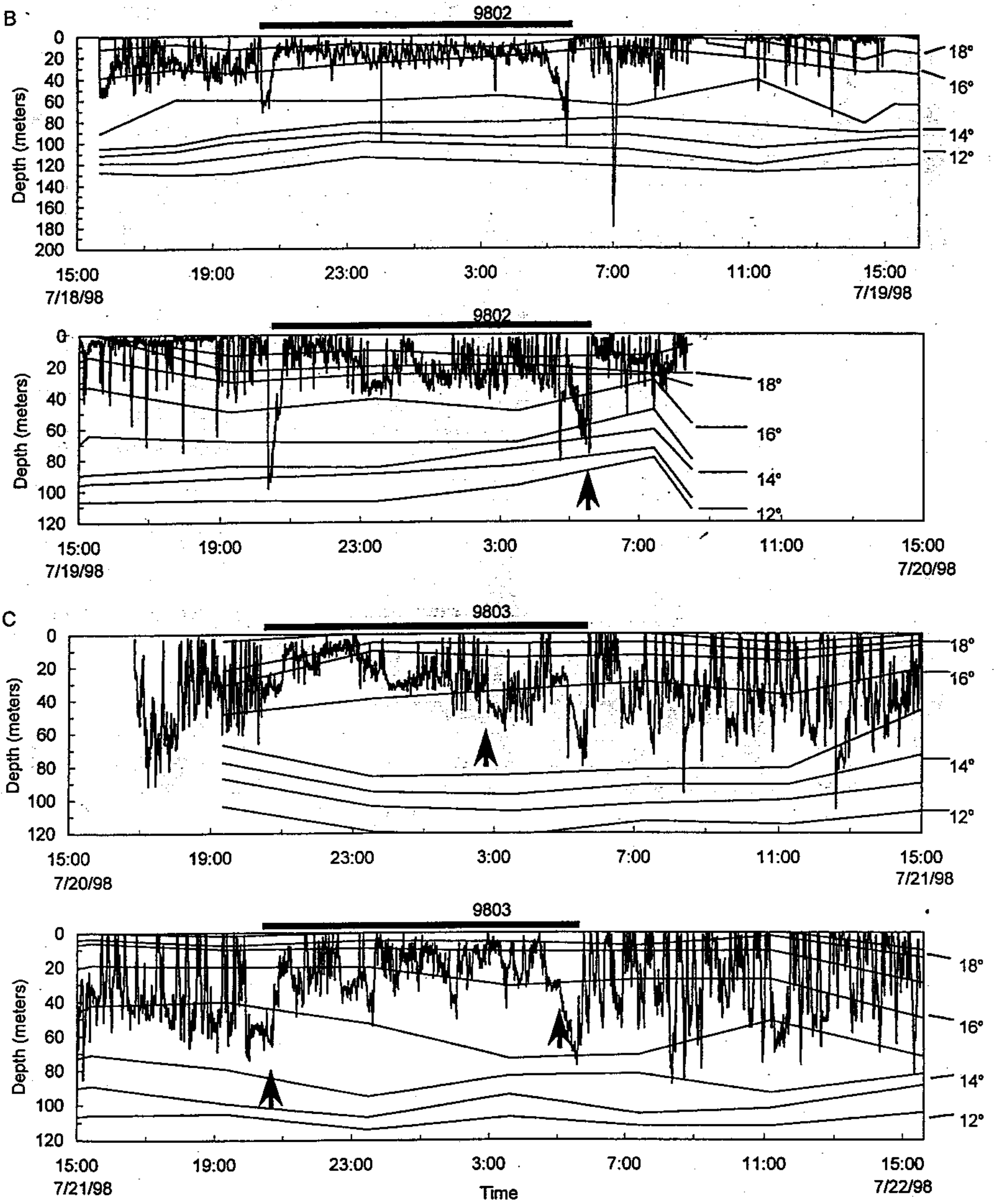
16:00
7/10/98
7/11/98
7/12/98
7/13/98
7/14/98
Time

Fig. 2cont


B
9802
Depth (meters)
0
20
40
60
80
100
120
140
160
180
200
18°
16°
14°
12°
15:00
7/18/98
19:00
23:00
3:00
7:00
11:00
15:00
7/19/98
9802
Depth (meters)
0
20
40
60
80
100
120
18°
16°
14°
12°
15:00
7/19/98
19:00
23:00
3:00
7:00
11:00
15:00
7/20/98
C
9803
Depth (meters)
0
20
40
60
80
100
120
18°
16°
14°
12°
15:00
7/20/98
19:00
23:00
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11:00
15:00
7/21/98
9803
Depth (meters)
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100
120
18°
16°
14°
12°
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19:00
23:00
3:00
7:00
11:00
15:00
7/22/98
Time

Fig. 3

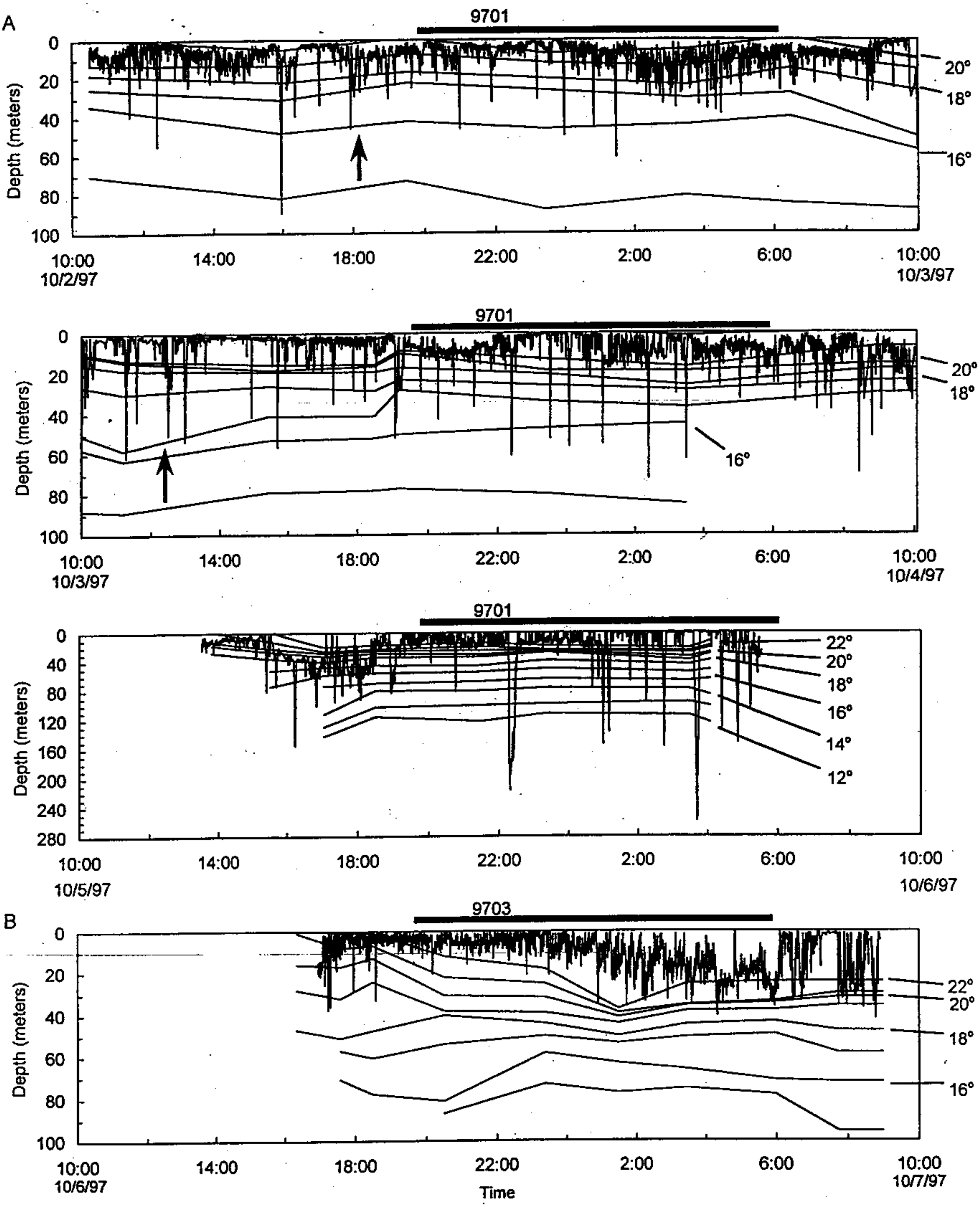

A
9701
0
20
40
60
80
100
Depth (meters)
20°
18°
16°
10:00
10/2/97
14:00
18:00
22:00
2:00
6:00
10:00
10/3/97
9701
0
20
40
60
80
100
Depth (meters)
20°
18°
16°
10:00
10/3/97
14:00
18:00
22:00
2:00
6:00
10:00
10/4/97
9701
0
40
80
120
160
200
240
280
Depth (meters)
22°
20°
18°
16°
14°
12°
10:00
10/5/97
14:00
18:00
22:00
2:00
6:00
10:00
10/6/97
B
9703
0
20
40
60
80
100
Depth (meters)
22°
20°
18°
16°
10:00
10/6/97
14:00
18:00
22:00
2:00
6:00
10:00
10/7/97
Time

Fig 4

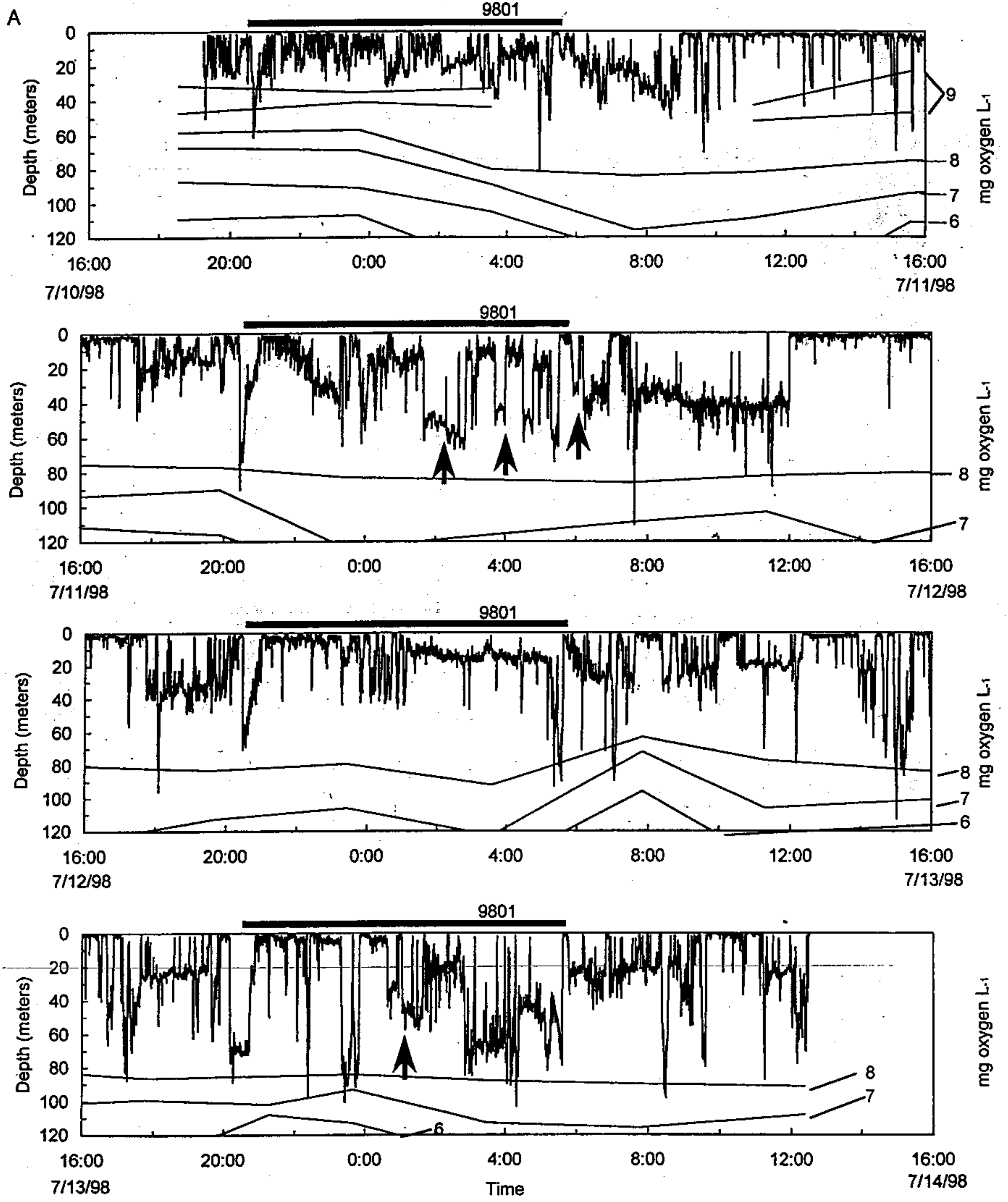

A
9801
Depth (meters)
mg oxygen L-1
0
20
40
60
80
100
120
9
8
7
6
16:00
7/10/98
20:00
0:00
4:00
8:00
12:00
16:00
7/11/98
9801
16:00
7/11/98
16:00
7/12/98
9801
16:00
7/12/98
16:00
7/13/98
9801
16:00
7/13/98
16:00
7/14/98
Time

Fig 4. cont

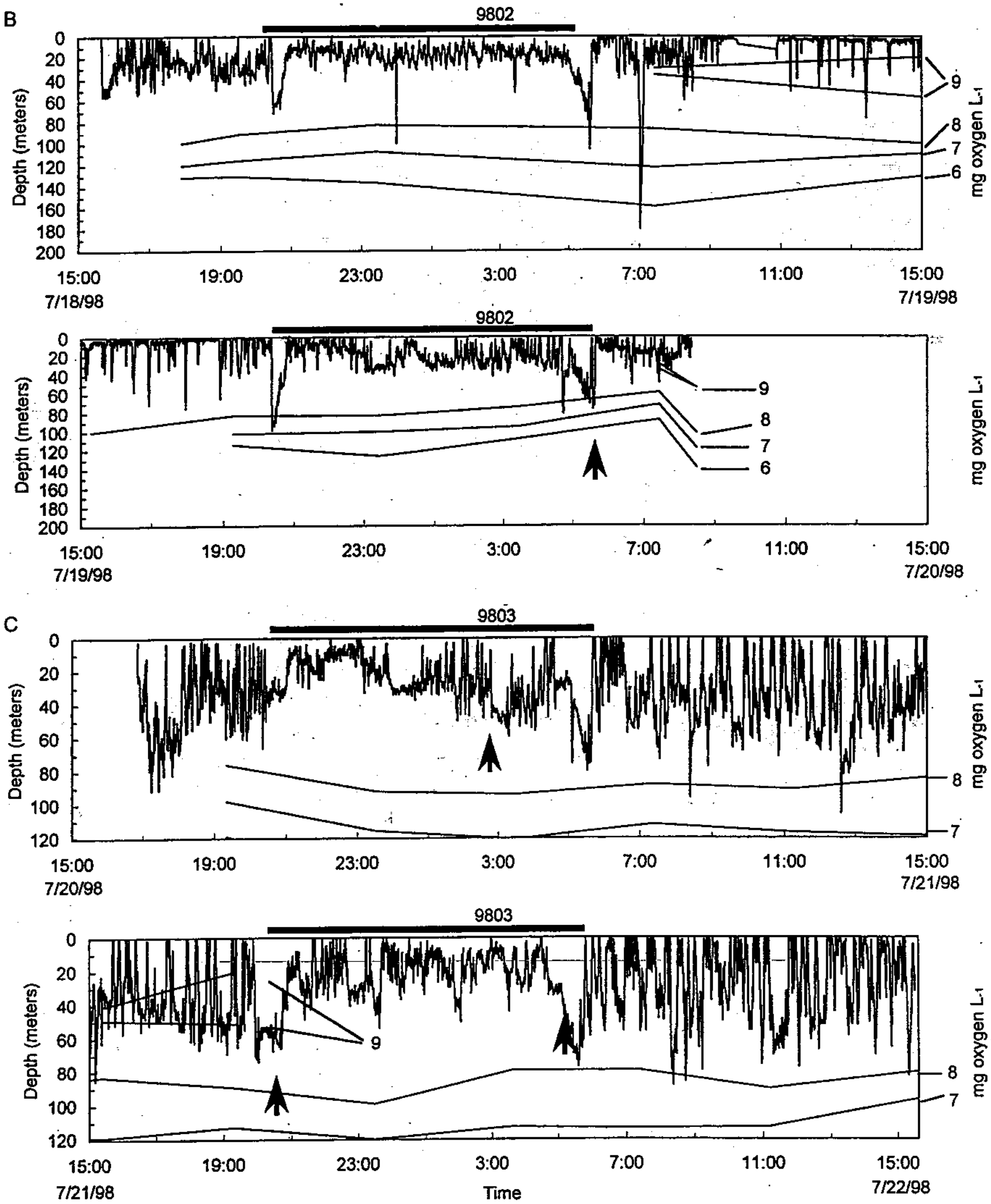

B
9802
Depth (meters)
0
20
40
60
80
100
120
140
160
180
200
15:00
7/18/98
19:00
23:00
3:00
7:00
11:00
15:00
7/19/98
9
8
7
6
mg oxygen L-1
9802
15:00
7/19/98
19:00
23:00
3:00
7:00
11:00
15:00
7/20/98
C
9803
15:00
7/20/98
15:00
7/21/98
9803
15:00
7/21/98
15:00
7/22/98
Time

Fig 5

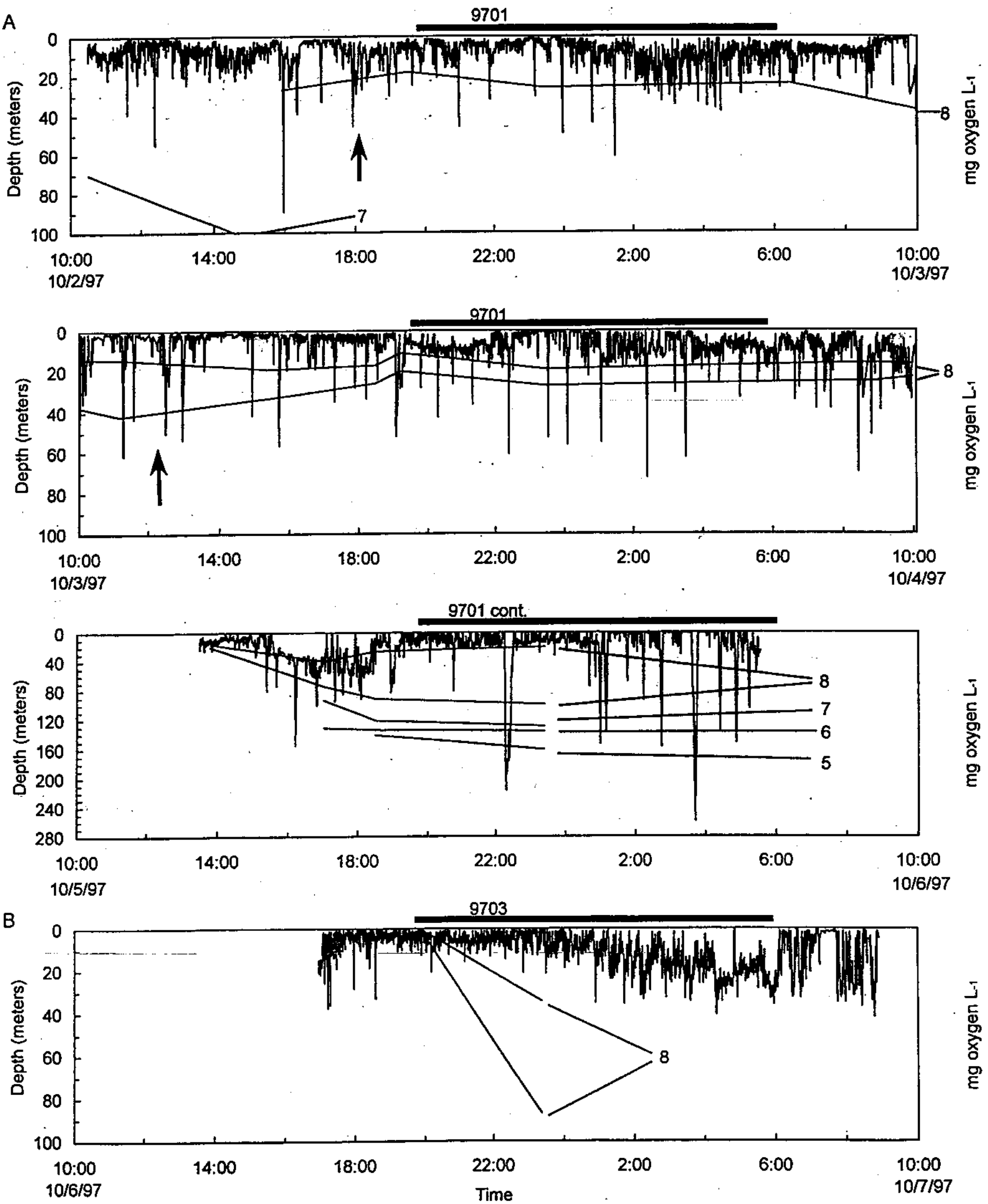

A
9701
Depth (meters)
mg oxygen L-1
8
7
10:00 10/2/97
14:00
18:00
22:00
2:00
6:00
10:00 10/3/97
9701
8
10:00 10/3/97
10:00 10/4/97
9701 cont.
8
7
6
5
10:00 10/5/97
10:00 10/6/97
B
9703
8
10:00 10/6/97
10:00 10/7/97
Time
0
20
40
60
80
100
120
160
200
240
280

Fig 6

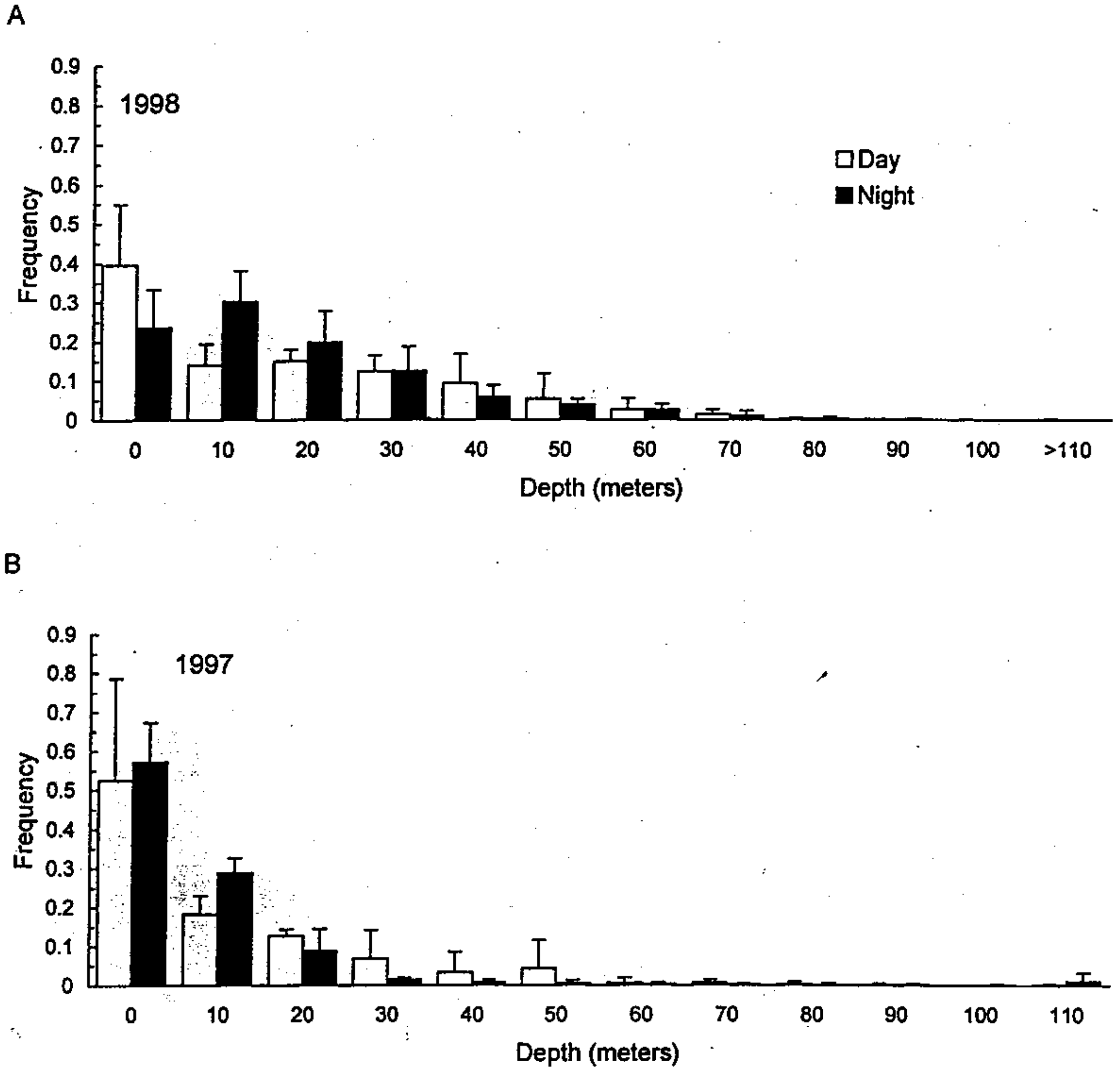

A
1998
Day
Night
Frequency
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
10
20
30
40
50
60
70
80
90
100
>110
Depth (meters)
B
1997
Frequency
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
10
20
30
40
50
60
70
80
90
100
110
Depth (meters)

Fig. 7.

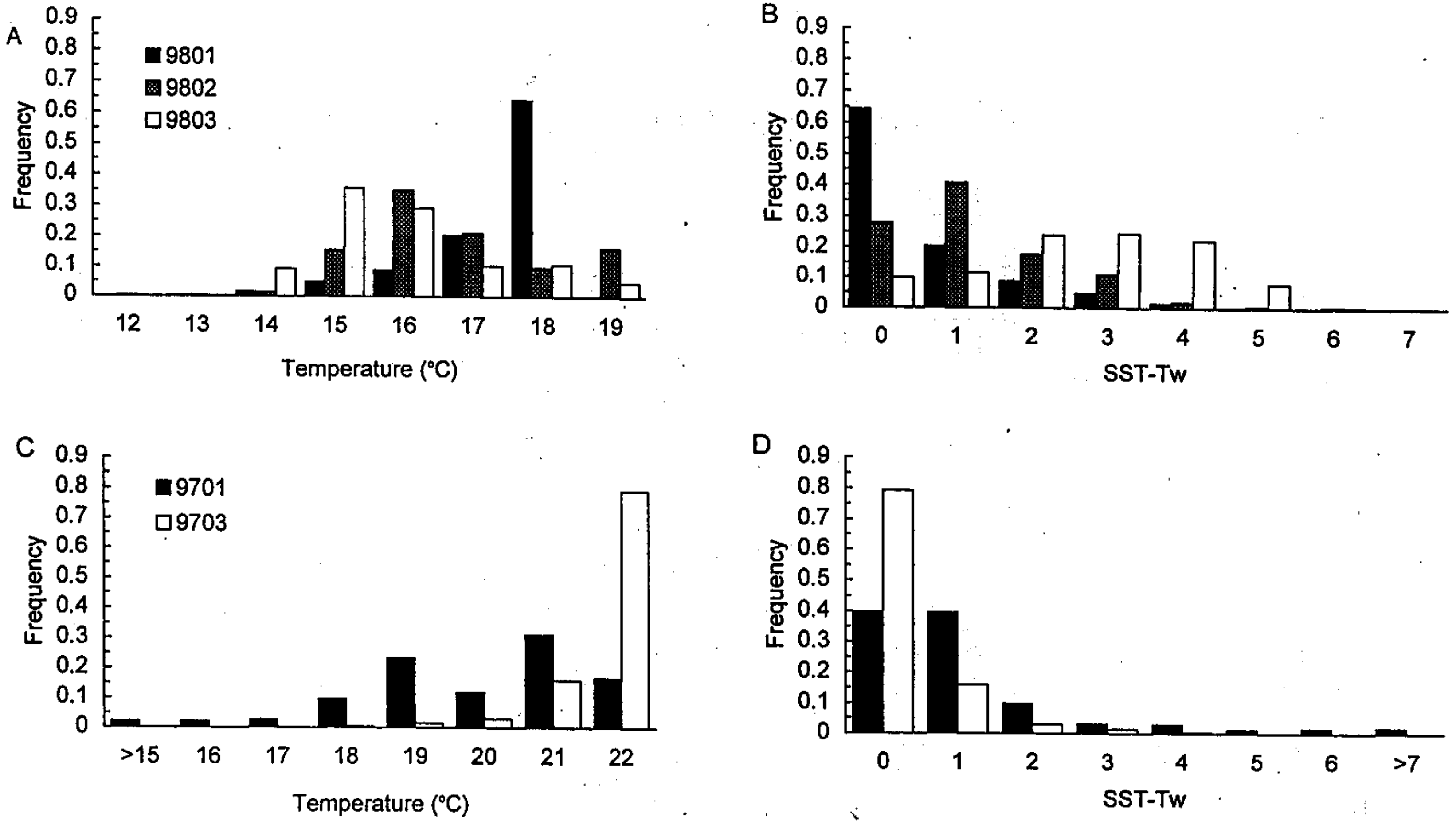

A
B
C
D
Frequency
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
■ 9801
▨ 9802
□ 9803
12
13
14
15
16
17
18
19
Temperature (°C)
0
1
2
3
4
5
6
7
SST-Tw
■ 9701
□ 9703
>15
16
17
18
19
20
21
22
>7

Fig. 8

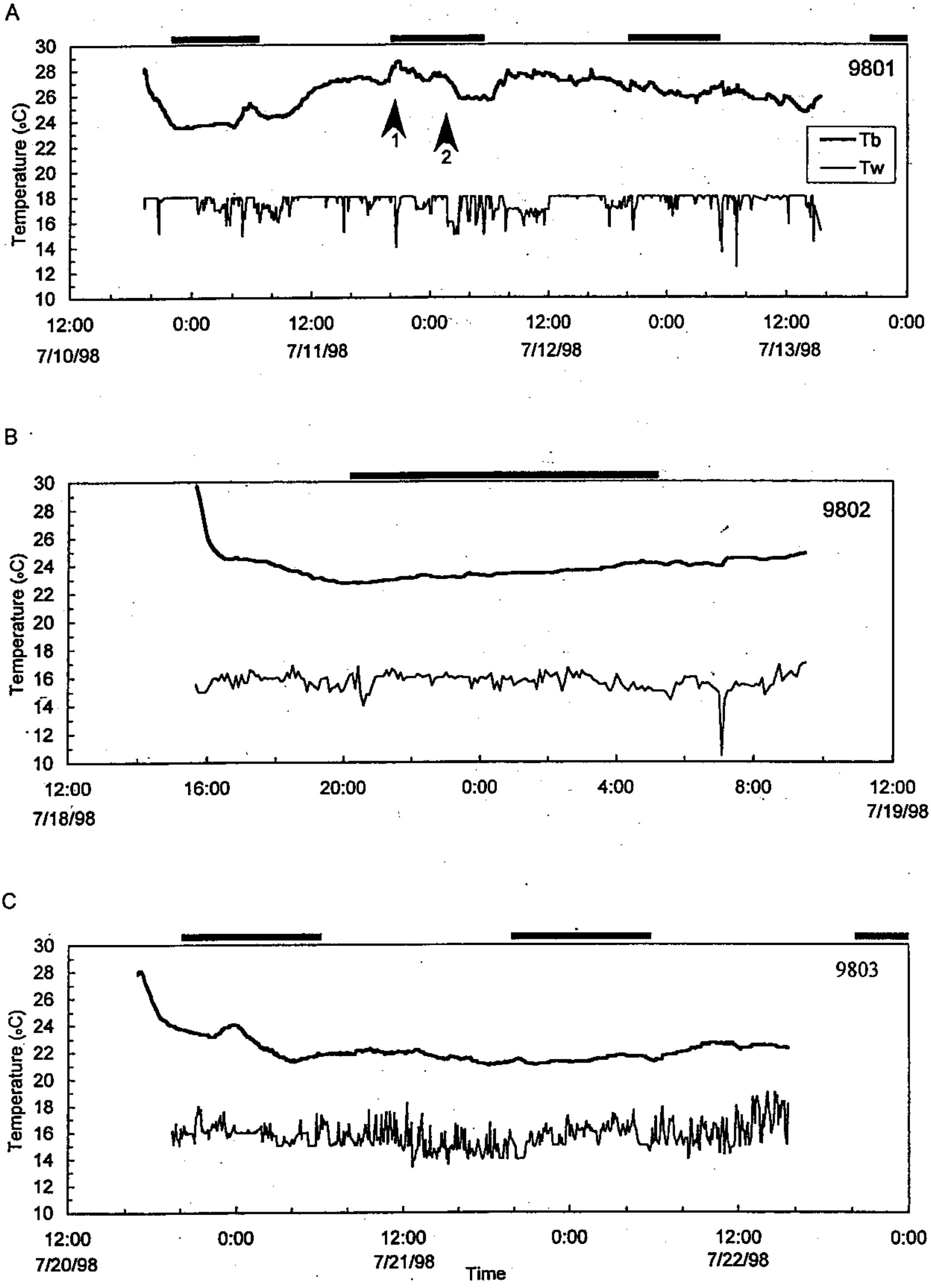
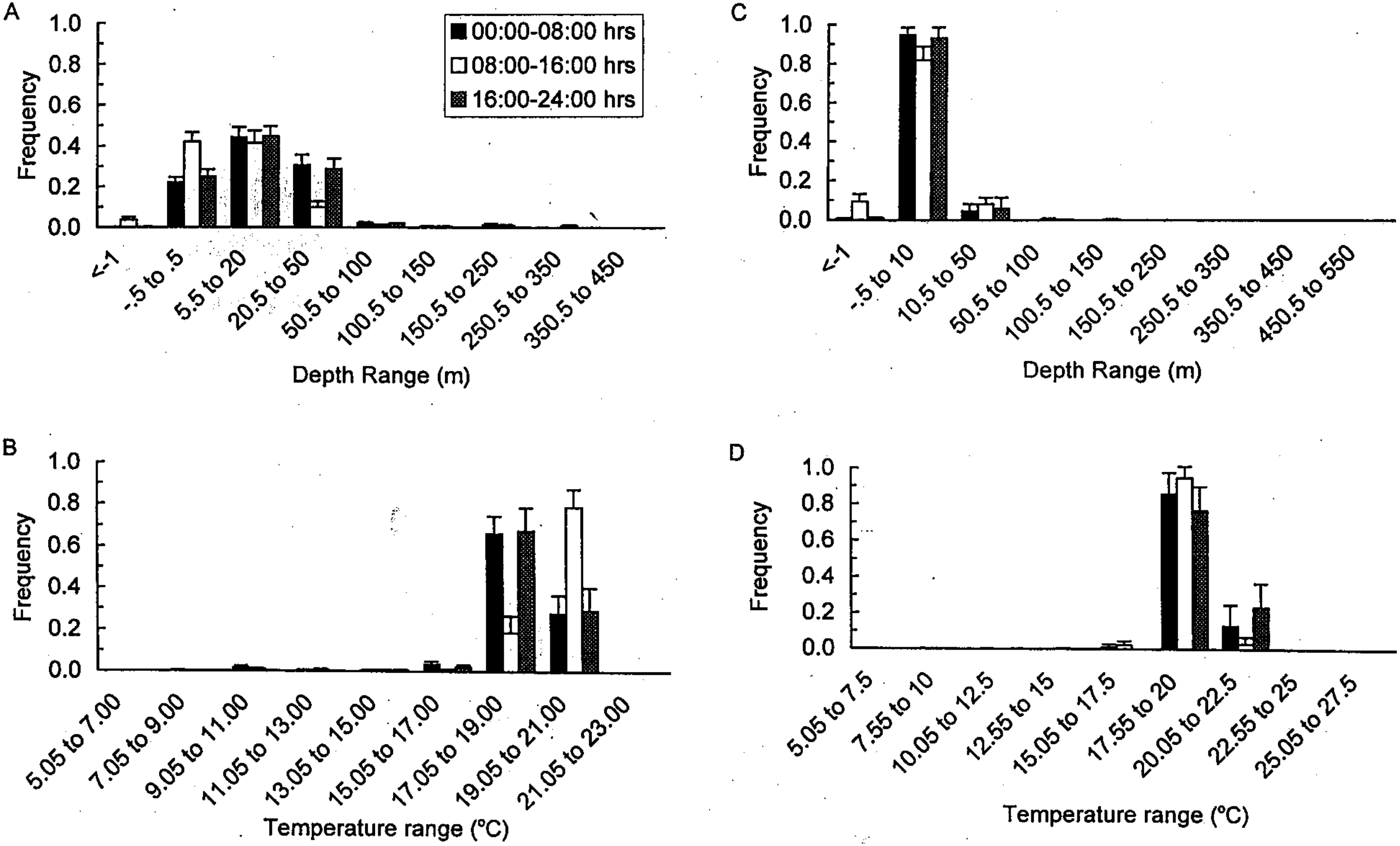

A
30
28
26
24
22
20
18
16
14
12
10
Temperature (oC)
9801
1
2
Tb
Tw
12:00
7/10/98
0:00
12:00
7/11/98
0:00
12:00
7/12/98
0:00
12:00
7/13/98
0:00
B
30
28
26
24
22
20
18
16
14
12
10
Temperature (oC)
9802
12:00
7/18/98
16:00
20:00
0:00
4:00
8:00
12:00
7/19/98
C
30
28
26
24
22
20
18
16
14
12
10
Temperature (oC)
9803
12:00
7/20/98
0:00
12:00
7/21/98
0:00
12:00
7/22/98
0:00
Time

Fig. 9


A
Frequency
1.0
0.8
0.6
0.4
0.2
0.0
■ 00:00-08:00 hrs
□ 08:00-16:00 hrs
▨ 16:00-24:00 hrs
<-1
-.5 to .5
5.5 to 20
20.5 to 50
50.5 to 100
100.5 to 150
150.5 to 250
250.5 to 350
350.5 to 450
Depth Range (m)
C
Frequency
1.0
0.8
0.6
0.4
0.2
0.0
<-1
-.5 to 10
10.5 to 50
50.5 to 100
100.5 to 150
150.5 to 250
250.5 to 350
350.5 to 450
450.5 to 550
Depth Range (m)
B
Frequency
1.0
0.8
0.6
0.4
0.2
0.0
5.05 to 7.00
7.05 to 9.00
9.05 to 11.00
11.05 to 13.00
13.05 to 15.00
15.05 to 17.00
17.05 to 19.00
19.05 to 21.00
21.05 to 23.00
Temperature range (°C)
D
Frequency
1.0
0.8
0.6
0.4
0.2
0.0
5.05 to 7.5
7.55 to 10
10.05 to 12.5
12.55 to 15
15.05 to 17.5
17.55 to 20
20.05 to 22.5
22.55 to 25
25.05 to 27.5
Temperature range (°C)