PRICKLY SHARK, *Echinorhinus cookei,* MOVEMENT AND HABITAT USE IN THE MONTEREY CANYON

A thesis submitted to the faculty of
San Francisco State University
In partial fulfillment of
The requirements for
The degree

Master of Science
In
Marine Science

by

Cyndi Lyn Dawson

San Francisco, California

May, 2007

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2007

Between March and August 2005, fifteen subadult prickly sharks (*Echinorhinus cookei*), from 170 – 270 cm TL were tagged with acoustic tags in the Monterey Canyon. The movements and activity patterns of 10 female and 5 males were examined using manual tracking and acoustic monitoring techniques. One female and 2 male sharks were tracked manually for 51.8, 61.0, and 62.8 h. Occurrence of those sharks and one other female was recorded for 101.2 – 123.6 d. An array of non-overlapping receivers extending 3.5 km offshore recorded the occurrence of five females and 3 male sharks for 400 – 561 d. Also, 3 female sharks were tagged with archival transmitters. All tagged sharks demonstrated a pronounced diel movement pattern, moving offshore to discrete areas during day and moving inshore along the axis of the canyon and actively swimming off the bottom at night. Subadult prickly sharks tagged in this study were present in the upper reaches of the Monterey Canyon during all four seasons.

ACKNOWLEDGEMENTS

This study was made possible, in part by funding provided by the Monterey Bay Aquarium, Dr. Jose Castro, Pacific Shark Research Center, PADI Aware Foundation, Packard Foundation Scholarship, American Academy of Underwater Sciences Scholarship, John H. Martin Scholarship and the Earl H. and Ethel M. Myers Oceanographic and Marine Biological Trust. Additional funding to support travel to conferences to present results was received from the Western Groundfish Conference Student Travel Award and the American Institute of Fishery Research Biologists Research Assistance Award Program. This study was conducted in accordance with and under the approval of the SFSU Committee for the Protection of Human and Animal Subjects Protocol #A5-008. I would like to thank Dr. Richard Starr for his enthusiasm for the study of prickly sharks and for trusting me with this project including a lot of expensive acoustic tracking gear. I would also like to thank my other committee members for their help in bringing this research to fruition; Dr. Ralph Larson for his editing and helpful comments, Dr. James Harvey for his editing help and outstanding teaching in all courses I was lucky enough to have him as an instructor at MLML, and Dr. Gregor Cailliet, for your invaluable guidance at every turn and infectious enthusiasm for all aspects of being scientist. You always were there when things got rough in the field with a helpful suggestion or kind word of encouragement and I sincerely appreciate it. I hold enormous gratitude to the too many to name here members of the 2005 Prickly Shark Tag Team without their enthusiastic help I would not have been able to complete this study. I would like to especially thank Donna Kline who was out on almost every fishing adventure throughout this study and without her expert assistance and on-going encouragement this study certainly wouldn't have been completed. With much appreciation I also would like to acknowledge John Douglas, Scott Hansen, and Diana Steller, for their friendship and active and on-going support of this study. Dr. Kenneth Coale for his support of this project and passionate leadership of MLML. My father, Roy Dawson, for fostering in me an appreciation for the natural environment and an inquisitive nature. I also want to thank the rest of my family Sue Dawson (mom), Nick Dawson (Brother), and Carmen Bettencourt (Grandmother) for their unwavering love and support. Erin Twomey for too many things to name, I dedicate this work to you and thank you for all your love and support through all the ups and downs of the past few years of graduate school craziness.

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Introduction

Higher trophic-level predators play a central role in structuring many ecosystems and communities (Cowen 1983, Shears & Babcock 2002, Carr et al. 2002, Bascompte et al. 2005, Reisewitz et al. 2006). Until recently, it has been difficult to understand the life history of large mobile predators such as sharks because there were few techniques for studying large sharks *in situ* (Kohler & Turner 2001). Historically, capture records and tag and recapture studies were the only techniques available to gather data on the habitat use and movement of a species. Traditional techniques such as these provide incomplete knowledge of habitat use and the movement of species, which are fundamental for understanding a species life history and ecology (Andrew & Mapstone 1987, Zeller 1997).

Since the 1960s, there have been several observations of the prickly shark, *Echinorhinus cookei,* at head of the Monterey Canyon, near Moss Landing, CA. Recorded occurrences come from gill nets deployed off the former Sandholt pier by researchers from Moss Landing Marine Laboratories (MLML) and from rod and reel catches by local recreational fisherman. Prickly sharks also have occasionally washed up on shore, and one large female (300 cm TL) was removed from intake pipes in Elkhorn Slough in 1995. These records provided evidence that prickly sharks, which are purported to be both rare and to live in deep water, may venture regularly into waters less than 80 m depth at the head of the Monterey Canyon.

Acoustic telemetry techniques have been used for the last 30 years for studying large mobile animals *in situ*. More recently, the technology has advanced to a level where highly detailed information on short-term movements, and information on long-term seasonal activity patterns of large mobile marine animals, can be attained (Holland et al. 2001). Acoustic telemetry has been used successfully on several species of marine fishes to gain these types of data (Zeller 1997, Arnold & Dewar 2000, Starr et al. 2002, Lowe et al. 2003, Cartamil et al. 2003, Starr et al. 2004, Cartamil & Lowe 2004,Topping et al. 2005, Humston et al. 2005, Meyer & Holland 2005, Jadot et al. 2006). Modern acoustic telemetry techniques can be used to collect detailed information about the spatial and temporal distribution of a species which can provide insights into habitat use, reproduction, feeding, physiology, and home range, which can help determine the role of a species in structuring communities (Sims et al. 2001).

Although sharks were some of the first marine species to carry acoustic tags due to their larger size, little is known about the activity patterns for the majority of elasmobranch species (Voegeli et al. 2001). Early work using telemetry systems was completed by Standora & Nelson (1976) on the angel shark, *Squatina californica*, and Scariotta & Nelson (1977) on the blue shark, *Prionace glauca*. These researchers used early telemetry systems to study rate of movement, activity patterns, ambient temperatures, and depth preferences. Both species of sharks were basically nocturnal, with peaks in activity during night and crepuscular periods. Although early systems did allow researchers to gather detailed information on activity patterns, they were expensive and required intensive manual tracking to collect data.

Acoustic telemetry systems became more widely available in the 1980s. This decreased the price of telemetry, but manual tracking was still required to retrieve data, which greatly limited the number of animals that could be followed during a study. Carey et al. (1982) published results for one white shark, *Carcharodon carcharias*, and Yano & Tanaka (1986) published results for one specimen of the deep-water needle dogfish, *Centrophorus acus.* In some cases, the limitations on sample size were overcome by conducting studies on species that showed site fidelity in confined bays or estuaries where it was easier to locate and track animals. Gruber et al. (1988) followed 9 juvenile lemon sharks, *Negaprion brevirostris*, using manual tracking techniques in Bimini lagoon and reported lemon shark activity space from 9 - 93 km^2.

Advances in acoustic telemetry technology rapidly occurred during the late 1980s and early 1990s, further reducing the price of equipment and the size of transmitters. Smaller equipment allowed for the development of new ways to deploy transmitters and track tagged animals. Holland et al. (1993) fed transmitters to Hammerhead pups (*Sphyra lewini*) off Oahu, Hawaii, and tracked the sharks from small boats. They reported that hammerhead pups exhibited diel movement patterns that were hypothesized to be related to the sharks seeking refugia from predators.

One of the biggest changes in acoustic telemetry techniques was the creation of automated data receivers during the late 1980s. This allowed researchers to collect data for longer durations on more tagged animals (Heupel et al 2004). Although the first of these receivers appeared commercially in 1985, their use in research on sharks was not common until the late 1990s (Voegeli et al. 2001). The reduction in transmitter sizes and availability of automated receivers have allowed these techniques to be used effectively to study the habitat use patterns of small reef-associated sharks that exhibit site fidelity (Economakis & Lobel 1998; *Carcharhinus amblyrhynchos*, Sundstrom & Gruber 1998; *Negaprion brevirostris*, Simpredorfer et al. 2002; *C. limbatus*, Chapman et al. 2005; *Ginglymostoma cirratum* and *C. perezi.*). The increase in battery life and transmitter signal strength has allowed more precise and longer duration studies on larger pelagic and benthic sharks (Carey & Scharold 1990; *Pronace glauca*, Heithus et al. 2002; *Galeocerdo cuvier*, Stokesbury et al. 2005; *Somniosus microcephalus*, Lowe et al. 2006; *Galeocerdo cuvier* and *C. galapagensis*). For species that exhibit some degree of site fidelity, the combination of acoustic monitoring and manual tracking provides both detailed short-term and long-term data that can accurately characterize the activity space of a species.

In recent years, archival tags have been developed which collect data at programmed time intervals and then store averaged values to memory. Through two-way communication with a specialized receiver, these tags can provide continuously collected data without using resource-intensive manual tracking. The combination of manual tracking, acoustic monitoring, and archival monitoring is the most effective way to investigate the habitat use patterns and movements of species that exhibit site fidelity.

The prickly shark is a poorly known predatory shark that commonly occurs at the head of the Monterey Canyon (Varoujean 1972, Anderson et al. 1979, Crane & Heine 1992). Based on a limited number of catch records, the distribution of prickly sharks is currently reported as pan-Pacific, in temperate and tropical waters (Pietschmann 1930, Taniuchi & Yanagisawa 1983, Crow et al. 1996, Barry & Maher 2000, Brito 2004, Long & McCosker[1]). Prickly sharks are generally characterized in the literature as deep-water sharks that are uncommon or rare, occuring from 100 to 650 m depth. However, these characterizations could be artifacts of infrequent capture, unavailable local reports, misidentification, and limited commercial value (Hubbs & Clark 1945, Collyer 1953, Aguirre et al. 2002). Capture records indicate a depth range from 11 to 650 m, and perhaps to depths

[1] Long DJ (dlong@calacademy.org), McCosker JD In prep. Tropical Eastern Pacific Records of the Prickly Shark, *Echinorhinus cookei* Pietschmann, 1928 (Chondrichthyes: Echinorhinidae).

as great as 1,000 m (Compagno 1984, Kobayashi 1986, Melendez & Menses 1986).

Morphometric and biological information reported for the prickly shark come almost exclusively from individuals caught as bycatch from research cruises and a small number from fisheries bycatch (Garrick 1960, Garrick & Moreland 1968, Anderson et al. 1979, Kobayashi 1986, Crow et al. 1996, Aguirre et al. 2002). Prickly shark length at sexual maturity is 290 cm TL for females and 240 cm TL for males (Compagno 1984, Ebert 2003). There are no published reports about mating or courtship behavior. Females exhibit aplacental viviparity and are highly fecund (Collyer 1953, Crow et al. 1996). Ikehara (1961) reported a 304.8 cm female specimen pregnant with 114 pups. Length at birth is 21 to 61 cm TL (Ikehara 1961, Compagno 1984, Crow et al. 1996, Aguirre et al. 2002). Based on stomach content analyses of 25 individuals, the prickly shark's diet consists of a variety of small unidentified teleosts, small sharks, egg cases of other sharks and rays, octopus, squid, chimera, and meso-pelagic fishes (Pietschmann 1930, Collyer 1953, Garrick 1960, Garrick & Moreland 1968, Varoujean 1972, Crow et al. 1996).

Several underwater observations and catches of prickly sharks were made at the head of the Monterey Canyon in water depths less than 80 m. These records are in contrast with the generally accepted depth range of prickly sharks and leads to questions about the depths predominately used by this species.

Crane and Heine (1992) found large (> 30 sharks) aggregations of prickly sharks during monthly scuba surveys conducted between June 1990 and September 1991. Since 1990 and before the beginning of my research, 36 prickly sharks have been tagged in the Monterey Canyon with conventional external tags (N. Crane & J. O'Sullivan[2]). According to past researcher's recollection, 5 to 9 individuals were re-sighted or recaptured at the head of the canyon, including one shark that was documented to have been at liberty for 6 years (N. Crane & J. O'Sullivan[2], Felton[3]). These recaptures indicated that prickly sharks likely had a long-term or at least a periodic presence at the head of the canyon. The occurrence of prickly sharks in highly accessible nearshore waters presented a unique opportunity to study the movements and habitat use of a large elasmobranch predator.

In 1999, researchers from Moss Landing Marine Laboratories (MLML) and the Monterey Bay Aquarium (MBA) conducted a pilot study to develop capture and tagging procedures for prickly sharks. The study area was located at the head of the Monterey Canyon (121° 47' 28.04" W; 36° 48' 4.66" N), adjacent to Moss Landing, California (Figure 1). In July of 1999, 8 sharks were tagged externally with acoustic transmitters; four of the transmitters contained depth sensors (Felton[3]). Tagged sharks were successfully tracked during the three-month battery

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[2] N. Crane, ncrane@mpc.edu, Monterey Peninsula College, 980 Fremont St., Monterey, CA 93940
J. O'Sullivan,JOSullivan@mbayaq.org, Monterey Bay Aquarium, 886 Cannery Row, Monterey, CA 93940

[3] J. Felton, jfelton@mlml.calstate.edu, Moss Landing Marine Laboratories, 8272 Moss Landing Rd. Moss Landing, CA 95039

life of each transmitter. Tagged sharks spent approximately week-long periods at the head of the canyon. During that time, they migrated vertically daily, moving from approximately 100 m depth during the day to as shallow as 3 m depth at night. Several individuals moved from the head of the canyon offshore as far as 9 km and to depths of at least 375 m, remaining there for about a week before returning to the head of the canyon. Lengths of time at particular depths, and duration and length of horizontal movements along the axis of the canyon, were variable among tagged individuals. However, all tagged sharks displayed a consistent pattern of movement, moving from deeper water during daylight hours to shallower water at night, regardless of whether the shark was at the head of the canyon or further offshore.

The goal of my research was to characterize the movements and habitat use of prickly sharks in the Monterey Canyon during a one year study period. Based on the pilot study, I was particularly interested in verifying the diel pattern that was observed. I also wanted to determine if the use of the upper reaches of the canyon varied seasonally or between males and females. My objectives were to tag 15 prickly sharks with internally placed acoustic transmitters and employ both manual and active tracking techniques to collect data on shark movements.

I hypothesized that both male and female prickly sharks would be present at the head of the canyon year-round. There was some evidence from previous studies that supported prickly sharks exhibiting behavioral thermoregulation and utilizing the warmer shallower water at the head of the canyon during large portions of their diel movement cycle. I wanted to determine if the head of the canyon (< 80 m) was utilized by the tagged prickly sharks during a large portion of time each day and how the head of the canyon related both temporally and spatially to other habitats the tagged prickly shark used.

Methods

Study Site

The Monterey Canyon is a large submarine canyon located in the middle of Monterey Bay, adjacent to Moss Landing, California (Figure 1). The Monterey Canyon is 470 km long, 12 km at its widest point, and has a maximum rim-to-floor relief of 1700 m. The head of the canyon is located approximately 200 m due west of Moss Landing, CA (36° 48' 3.85" N; 121° 47' 22.66").

The upper reaches of the Monterey Canyon, and more specifically the head of the canyon, undergo fluctuations in oceanographic parameters and physical structure on both short- and long-term time scales (Greene et al. 1989, Breaker & Broenkow 1994, Okey 1999, Carter & Gregg 2002, Greene et al. 2002, Smith et al. 2005). The study site experiences seasonal upwelling, which is characterized by strong northwesterly winds and colder average water temperatures than during the non-upwelling seasons. The strongest upwelling generally occurs during the spring. For this study, I defined the head of the canyon as waters less than 80 m deep, located just offshore of Moss Landing near the axis of the canyon.

Fishing and Tagging

I captured prickly sharks by deploying baited set lines in the axis of the canyon-head during flood tides during the day and night. On each fishing trip, I deployed five drop lines at the head of the Monterey Canyon in 30, 40, 50, 55, and 65 m of water depth (Figure 2). Each dropline consisted of a weight, line, hooks, and a surface float. Each line contained two 16/oo barbed circle-hooks baited with salmon. Each hook was attached to 1 m of 0.16 cm (1/16") wire leader covered with a plastic sleeve. Each leader was attached to a swiveled long-line clip attached to 0.32 cm (1/8") braided fishing line, with 250 kg breaking strength, at 1 m and 6 m above a 5 kg lead weight. After the line was deployed, a surface buoy was attached to each line. The bottom 5 m of line was covered by vinyl tubing to prevent hooked sharks from wrapping in the line and injuring themselves. At the end of a 45 - 50 min set, each line was retrieved, the bait was checked, and the line re-deployed. If a surface buoy had sustained movement before the end of a set, that line was checked immediately.

All set lines were retrieved by hand from depth. When a shark was on the line, the hand retrieval was slowed to allow time for tagging preparations. It took approximately 2 – 3 min to bring a shark to the surface. As a shark was landed, we placed a 2 m - long nylon stretcher along the side of the boat. When the shark was at the surface, the leader was unclipped from the down line and clipped into a shorter line which was used to maneuver the shark into the open stretcher. After the shark was in the stretcher, the sides of the stretcher were brought together and secured to the side of the boat. The hook was left in the shark's mouth and the leader was secured to the side of the boat. The shark's head was kept submerged in the water throughout the surgical procedure. It took a vessel operator and five tagging team members to complete this operation successfully.

I surgically implanted two types of Vemco V16 transmitters into prickly sharks. I used coded and continuous Vemco V16 transmitters that were 16 x 92 mm long and weighed 16 g in water. V16 coded tags transmitted a unique coded tag identification string during each pulse transmission on a frequency of 69 kHz. The coded transmitters emitted pulse trains randomly with a delay of 45 to 105 s between each transmission. The random delay between transmissions made it possible to have multiple tags transmitting on the same frequency in the same area, by ensuring minimal acoustic collisions between transmitters, minimizing the loss of data. The estimated battery life for the coded transmitters was either, 439 d or 1,442 d. The second type of V16 transmitter I implanted was a V16 continuous transmitter; which transmitted pulses on unique operating frequencies (54, 63, 75, 78 kHz). The unique identifying pulse train was emitted every 1500 ms with a fixed 5 sec delay between transmissions. Having a unique frequency allowed multiple tags transmitting almost continuously to be in the same area at the same time. The estimated battery life for the continuous transmitters was 95 d.

I also implanted Vemco Communicating History Acoustic Transponder (CHAT) archival tags that were 32 x 150 mm long and weighed 75 g in water. CHAT tags stored countinous data within the transmitter's memory and, through two-way communication with a specialized receiver, transmitted the data stored in memory. The data were downloaded in incremental bins when the tag was in range of the CHAT receiver, which freed up memory in the CHAT tag. The CHAT tags were programmed to record average depth and the temperature of a tagged individual's body cavity every 10 min. Those values were averaged hourly and stored to the CHAT tag memory. The estimated battery life of the CHAT tags was 365 d.

I implanted transmitters by using a sterile # 22 surgical scalpel to make a small incision of approximately 2 cm in length, just larger than the 1.8 cm diameter of the Vemco V16 transmitters, in the shark's ventral surface, anterior to the pelvic fins and just axial to the ventral mid-line. The surgical incisions for the Vemco CHAT archival tags were approximately 4 cm long, which was just larger than the 3.2 cm diameter of the tags. I then gently pushed the transmitters through the incision with a slight rotating motion. I sutured the incision closed using a 0.95 cm (3/8") circle reverse-cutting-edge suture needle and attached surgical monofilament line. All surgical instruments and transmitters were bathed in an antiseptic iodine solution before surgery on a shark.

After surgery was completed, the shark was gently rolled over onto its ventral surface. I placed an external dart tag just in front of the first dorsal fin in the dorsal musculature and retrieved a small sample of skin (0.25 cm^2) for future stable isotope and DNA analyses. Total body length, and the internal and external length of the claspers were recorded for each shark. After all data were collected, the tagging vessel was put into gear and water was run over the shark's gills. When the shark began to exhibit spontaneous tail movements, the hook was cut out of the shark's mouth using bolt cutters and the shark was released in the approximate location of capture.

Manual Tracking

I used a Vemco VR60 receiver, with a V10 hydrophone to track manually 3 sharks for non-consecutive 6 - hour blocks (0000 - 0600 h, 0600 - 1200 h, 1200 - 1800 h, 1800 - 0000 h) from a surface vessel. I tracked each shark at least once in each block of time to ensure that a representative sample of activity patterns was recorded at all times of day. I deployed the hydrophone over the side of the tracking vessel and listened on each of the three frequencies transmitted from the Vemco V16 continuous transmitters. I listened to each frequency for 2 min during the initial 8 min search phase. If no animals were detected, the vessel moved to another location and the initial listening phase was repeated. Once a shark was detected, I continuously tracked that shark for the rest of the 6 h tracking block or for as long as was possible given weather conditions. Towards the end of the battery life of the continuous transmitters, tracking blocks were reapportioned to concentrate on crepuscular periods (0200 – 0800 h, 1600 – 2200 h).

The ArcNav extension (Hatcher 1997) for ESRI® Arcview 3.2 software was used to record GPS positions of the tracking vessel in real time as sharks were tracked. A positive geographic "fix" for a shark was recorded when the hydrophone was slowly spun 360° and there was no noticeable degradation in signal strength from a transmitter. "Fixes" were annotated directly into the electronic tracking file during active tracking at least every 10 min using a laptop computer. The range for the VR60 receiver and V10 hydrophone was approximately 100 to 200 m, based on range testing conducted during the 1999 pilot study. All geographic fixes of the vessel were assumed to be within 200 m of the actual location of the tagged shark.

I calculated the mean rate of movement (ROM) for sharks that were tracked manually by taking the distance between two successive points ("fixes") within a tracking block and dividing it by the elapsed time between the two points. I then averaged those values among sharks. I also calculated the mean ROM for each shark during each diel activity period (Dawn = 0600 – 0800 h, Day = 0800 – 1730 h, Dusk = 1730 – 1930 h, Night = 1930 – 0600 h).

The Animal Movement Analyst Extension (AMAE) (Hooge & Eichenlaub 2000a) was used to analyze positional "fixes". Home range estimates were determined for each shark I manually tracked using the AMAE to calculate a kernel utilization distribution (KUD) (Worton 1987, 1989). A KUD is a graphical depiction of the likelihood of being found within a discrete area during a particular time period. I calculated KUDs at the 90, 75, and 50% probability levels. These probability levels were chosen because they most accurately reflected the actual area used by the sharks.

An animal must exhibit site fidelity for a home range to exist (Spencer et al. 1990). I conducted a site fidelity test using the AMAE on all positional "fixes" for each shark that I manually tracked. This function conducts a modified Monte Carlo random walk test. Site fidelity exists if the animal's real locations are neither significantly dispersed nor significantly linear (Spencer et al 1990). This is a robust and powerful test that is used to discern changes in behavior between site fidelity, and random or directed explorations (Hooge et al. 2000b).

I used the function that calculated the KUDs in AMAE to calculate a serial autocorrelation value as described in Swihart & Slade (1985), because probabilistic home range techniques can be sensitive to serial autocorrelation. The risk of autocorrelation increases when sample size increases or the core area used by an animal changes frequently (non-stationary home range). The number of positional fixes for this study was relatively low (< 400 $animal^{-1}$) and the home ranges were stationary. When these conditions are present, using the kernel or polygon methods for estimating home range are relatively unaffected by using moderately autocorrelated data (Swihart & Slade 1997). Also, the corrections for autocorrelation may lead to more bias than the autocorrelation itself (Hooge et al.

2000b). Home range estimates were calculated using uncorrected data and using the least-squares cross validation (LCSV) as the smoothing factor which is considered the most robust technique (Seaman & Powell 1996).

I conducted a bootstrap analysis and plotted calculated home range size as a function of the number of geographic "fixes" to determine if enough geographic "fixes" were obtained to calculate a robust estimate of home range (Zeller 1997, Seaman et al. 1999). This function in the AMAE calculates home range estimates using the Minimum Convex Polygon (MCP) method. The MCP method is sensitive to sample size effects and is greatly affected by outliers (Worton 1987). The MCP bootstrap analysis provides an inflated estimate of the sample size needed to calculate a robust home range estimate using the less sample size sensitive KUD. The bootstrap analysis was included to address the issue of adequate sample size for the calculation of MCPs which can be used to compare with other movement studies; as MCPs have traditionally been the most widely used estimate of home range. All sharks were determined to have an adequate sample size to calculate a robust home range estimate using MCP and KUD techniques.

I conducted spatial analysis using the Hawth's Analysis Tools (HAT) extension for ESRI® ArcGIS (Beyer 2004) to determine the importance of the head of the canyon to prickly sharks. I created a polygon that encompassed the head of the canyon, which included the area within the axis of the canyon and the surrounding area out to 80 m depth (2.45 km^2). The HAT extension calculated the number of positional "fixes" encompassed within the boundaries of the polygon, therefore in the head of the canyon area. I calculated the proportion of those fixes within each diel activity period to assess which times of day the head of the canyon was used most often.

Acoustic Monitoring

I conducted range testing of the transmitters and VR2 receivers before deploying the transmitters and beginning acoustic monitoring of tagged sharks. For range testing, I activated 4 V16 coded transmitters and used zip ties to secure each tag into a net bag. I separated each bag by approximately 10 m and secured the net bags to a weighted downline. I used a small vessel to temporarily moor a VR2 receiver in 50 m of water at the head of the canyon. I then navigated to selected GPS locations that were at 100 m intervals away from the moored VR2 receiver. At each station, I deployed the downline with attached transmitters from the vessel and left it on station for 10 min. I retrieved the downline and repeated the 10 min listening period at each successive station moving offshore up to 1 km away from the moored receiver. I retrieved and downloaded the data from the VR2 and determined that range that the transmitters could be detected by the VR2 receiver was 500 m.

I deployed 3 VR2 receivers in the axis of the canyon to monitor tag transmissions in the upper reaches of the Monterey Canyon (Figure 3). Receiver1 was deployed approximately 200 m from shore at the head of the canyon on a mooring with a surface float in 30 m depth (Figure 3). The rigging for the receiver array from bottom to top consisted of a cement pier support (18 kg), 1 m of 5 cm diameter galvanized chain, 5 m of 1.5 cm (½") nylon line, a VR2 receiver, 5 m of 1.5 cm (½") nylon line, a hard plastic float (5 kg lift), and 1.5 cm (½") nylon line to a surface buoy. Links in the array rigging were made using galvanized and stainless steel shackles 1.6 cm in diameter. The depth of the water encompassed by the receiving range of Receiver 1 extended to approximately 80 m of depth within the axis of the canyon.

Two VR2 receivers were deployed offshore in the axis of the canyon using Benthos Model 875 acoustic releases. Receivers 2 and 3 were moored at approximately 1.5 and 3.5 km offshore of Receiver 1 in the axis of the canyon at 80 m and 130 m water depth. The rigging for a sub-surface mooring was similar to the receiver at the head of the canyon except for the addition of a 5 m length of line, an acoustic release, and the absence of the line to the surface. All VR2 receivers were retrieved and downloaded approximately every 85 d throughout the study period. A Benthos DS-8750 Acoustic Deck Set was used to retrieve the two offshore receivers. To retrieve the receivers, I maneuvered a surface vessel to the GPS location of the drop site and transmitted the release signal from the deck set to the acoustic release at least three times. After the last signal was sent to the acoustic release I scanned the surface for the buoy for at least 15 min before concluding that the array was not going to surface. When the buoy was spotted I maneuvered the surface vessel near to the buoy array and used a boat hook to retrieve it.

A VR20 receiver and a CHAT receiver also were deployed at the head of the canyon using the same rigging described above (Figure 3). The VR20 and CHAT receivers had a greater receiving range than the VR2 receivers. Depending on physical properties of the water column, the range for the VR20 and CHAT receiver was as great as 1 km, which was determined by the depth data collected during this study. The VR20 receiver recorded the depth and transmitter number when a tagged shark was in range of the receiver. The CHAT receiver recorded tag transmissions, which included hourly average depth, average body cavity temperature, and tag number. These receivers were retrieved approximately every 29 d, which corresponded to the battery life of the receivers. The average range of the VR20 and CHAT receiver was not tested.

Due the numerous factors that can affect the transmission of sound through water and lead to invalid or spurious readings, I required at least two detections within a 1 d period to indicate a valid detection of a tagged shark at a receiver. I calculated total number of detections and proportion of time spent at each VR2 receiver to identify areas within the receiving array that were heavily used by tagged prickly sharks. Monthly graphs also were created using VR2 data from Receiver 1 to define temporal patterns of use at head of the canyon.

I calculated a depth anomaly for each shark using data collected by the VR20 receiver to determine if there were similar diel activity patterns among the four sharks. The depth anomaly was calculated by taking the hourly mean depth of a tagged shark and then subtracting that value from the overall average depth of that shark. The depth anomalies were averaged among the four sharks to standardize the depth usage patterns on a single axis and make them easily comparable among sharks. The average hourly depth was calculated for all CHAT data collected to define diel depth patterns. The time periods for daylight and nighttime used in the analysis were slightly different between the VR20 and CHAT data. These times were based on average sunrise and sunset during the time of year when the data were collected.

Temperature Logging

Receiver 1 and Receiver 3 were equipped with Alpha Mach iBCod temperature loggers (Figure 3). The temperature logger recorded the ambient water temperature every hour. As mentioned above, the VR2 receivers were retrieved approximately every 85 d, which corresponded to the storage capacity of the temperature logger. Temperature data were collected at Receiver 1 and Receiver 3 starting on 3 September 2005 after all animals had been tagged.

Receiver 3 collected a continuous record of hourly temperature at 85 m depth in the axis of the canyon between 3 September 2005 and 12 September 2006, with the exception of 16 days in July when unavailability of personnel prevented switching out the logger when the memory was full. Receiver 1 had a temperature record from 5 July – 22 February 2005 and 20 April – 24 May 2006. These data were used to characterize the oceanographic seasons within the vicinity of the study area to determine if there was a difference in habitat use patterns at the head of the canyon among oceanographic seasons. Initial inspection of the temperature data did not detect a clear difference in the temperature record collected during this study or from regional buoy data that could delineate more than two oceanographic seasons; upwelling from 17 April 2006 to 11 July 2006 and non-upwelling 9 September 2005 to 16 April 2006 and 12 July 2006 to 13 September 2006.

Results

Fishing, Tagging, Tracking, and Monitoring

Fishing and Tagging

Twenty-six prickly sharks and 6 spiny dogfish (*Squalus acanthias*) were caught between February and August 2005, during 26 fishing trips, over 13 days and 13 nights (Table 1). The average length of all fishing trips was 3.1 h ± 0.1 SE and the average length of each fishing set was 51 min ± 0.5 SE. Fishing occurred during day between February and April 2005, and average catch-per-unit-effort (CPUE) for prickly sharks was low at 0.06 sharks h^{-1} ± 0.24 SE. Initial data collected from sharks tagged during that period indicated that tagged individuals were at the head of the canyon more consistently during night. Fishing operations were switched to night between May and August 2005, and average CPUE increased more then ten fold to 0.71 sharks h^{-1} ± 0.21 SE. The greatest monthly CPUE occurred in August (1.07 sharks h^{-1}, Table 1). Sharks resisted capture more actively while being retrieved from depth and during the tagging procedures at night than during day. Males did not occur in the catch until June, and females dominated the catch until late July when the sex ratio became more evenly distributed. Not all sharks hooked and reported here were landed successfully, which prevented sex determination on some sharks.

Between February and August 2005, 10 female and 5 male prickly sharks, from 170 to 270 cm TL, were tagged internally with acoustic transmitters (Table 2). Average handling time (defined as the period of time from when the shark reached the surface to recovery and release after implantation surgery) was16 min ± 1 SE for sharks carrying the smaller diameter Vemco V16 transmitters (16 mm) and 21 min ± 2 SE for those carrying the larger diameter Vemco CHAT archival transmitters (32 mm). The average number of sutures used to close the incisions was 2.3 ± 0.1 SE for the V16 transmitters and 3.7 ± 0.3 SE for the CHAT archival tags. All sharks survived surgery and swam away in apparent good condition. All tagged sharks were heard by acoustic receivers at least 1 month after surgery and most were heard throughout the study period, thus providing evidence of 100% survival rate for prickly sharks tagged in this study (Table 2).

Manual Tracking

One female and 2 males (Tag no. 10, 11, 12) were tracked manually for 61.0, 62.8, and 51.8 h in the time blocks described earlier (Table 3). The mean time for all sharks tracked was 58.5 h ± 3.4 SE. Sharks were tracked 8 – 20 h $block^{-1}$, and the mean number of hours tracked per block was 8.8 ± 0.7 SE – 18.5 h ± 1.5 SE. I tracked sharks for the least amount of time in the afternoon block (1200 – 1800 h) due to foul weather and windy conditions often present during this time period. An additional 6 h of tracking data were collected in each crepuscular tracking block (1600 – 2200 h, 0200 – 0800 h) for the female (Tag no. 10) and one male (Tag no. 12) shark. One of the male sharks (Tag no. 11) could not be located during the crepuscular tracking blocks.

Acoustic Monitoring

VR20 Receiver

The same three sharks that were tracked manually (Tag no. 10, 11, 12) and a 250 cm TL female (Tag no. 9) were monitored using a VR20 receiver that was moored at the head of the canyon in 30 m depth (Figure 3). The receiver was deployed from 14 May until the batteries expired on 11 June 2005. The unavailability of personnel prevented retrieval of the receiver until 11 July 2005, at which time it was retrieved, downloaded, and re-deployed. Batteries were successfully replaced in the receiver at least every 29 d until 11 December 2005 when the receiver was retrieved and not redeployed. The VR20 receiver was deployed for a total of 181 d. The first continuous transmitter was deployed on 13 May 2005 and the last recorded detection was 23 August 2005, which likely corresponded to the expiration of the transmitter battery projected by the manufacture to be 21 August 2005. The other transmitters were all deployed on 10 August 2005. Although the receiver was deployed for an extended period of time, the transmitters were only monitored for the duration of their battery, which was projected by the manufacture to be 100 d. The transmitters were monitored between 102 – 123 d. The total number of detections for all transmitters was 184,671.

CHAT Receiver

Three female sharks (Tag no. 13, 14, 15) were tagged internally with Vemco VX32TP Communicating History Acoustic Transponder (CHAT) tags (Figure 3). A CHAT receiver was deployed at the head of the canyon in 30 m depth for 99 d (29 August - 6 December 2005). One successful download of 8.9 d was obtained for the 198 cm TL female (Tag no. 15). The first data were recorded in the memory of the CHAT tag beginning immediately after tagging at 22:48 on 9 August 2005. The data collected during the first hour after the shark was tagged was discarded to discount any possible tagging stress and therefore 214 h of data were collected from 10 August 00:29 to 18 August 2005 22:29. The CHAT receiver recorded no other transmitted data.

VR2 Receiver Array

Eight sharks (Tag no. 1 - 8) were monitored between 343 - 504 d using an array of 3 Vemco VR2 receivers (Figure 3). The total number of detections for all transmitters and among all receivers was 853,535. Three receivers were lost during the study period, which prevented monitoring in some areas during certain periods (Table 4). When all three receivers within the array were deployed, the 8 sharks tagged with coded transmitters were within the array between 14 and 30% of the total time they were monitored, which was an estimate calculated based of the total transmissions detected divided by the estimated total possible transmissions during the time monitored. Because the receiving array did not have overlapping receiving ranges, this estimate should not be interpreted to indicate that the sharks were not in the upper reaches of the canyon when they were out of the receiving range of the array of receivers.

Activity Patterns

Habitat Use and Diel Movement

Throughout the study period prickly sharks often used the upper reaches of the canyon and particularly the head of the canyon (< 80 m depth). While within the range of the array, signals from tagged sharks were recorded 61% of the time at Receiver 1 (Figure 4.) For the two periods of time when all 3 VR2 receivers were deployed in the axis of the canyon, 10 October 2005 – 12 February 2006 and

15 June – 12 September 2006 (214 d), 572,188 detections were recorded for all sharks tagged with coded transmitters (Tag no. 1 – 8). The total detections for all tagged sharks at each receiver during the time periods described above, were 349,850 detections at Receiver 1, 180,747 detections at Receiver 2, and 41,591 detections at Receiver 3. The receivers were numbered successively moving from onshore to offshore.

Monitoring data from the three receivers in the VR2 monitoring array indicated a diel pattern of movement for all 8 tagged sharks. Receiver 1 at the head of the canyon recorded the greatest proportion of total detections, 66.3 %, during nighttime (1730 – 0600 h, Table 5). Receivers 2 and 3, which were moored offshore, recorded the greatest proportions (64.5%, 54.1%) of detections during the day (0600 – 1730 h). These data indicated that when sharks where in range of the monitoring array they most often used the head of the canyon during the night and were offshore during the day.

Monitoring data from the VR20 receiver also indicated a diel pattern of movement. The receiver also was moored in shallow water at the head of the canyon and the receiving range was greater than that of the VR2s receiving range. The receiving range for the VR20 extended at times greater than 1 km offshore of the receiver, into water 145 m deep. The daily receiving range of the VR20 was not tested but it likely averaged between 700 and 900 m based on the distance offshore required to obtain the depths recorded. The daily average depths for all four sharks were similar, at 53.3 and 45.2 m for the 2 females and 48.5 and 44.1 m for the 2 males. However, tag no. 9 was significantly different than the other sharks ($F = 1.723$; $df = 3,91$; $p = 0.17$). The average depth anomaly among the four sharks was + 12.1 m for daylight (0600 – 1900 h) and -14.0 m for nighttime hours (1900 – 0600 h). Sharks were shallower than their daily average depth during the day and deeper than their daily average depth during the night (Figure 5).

The single successful 8.9 d download of CHAT data from a 198 TL cm female (Tag no. 15) indicated a pronounced diel behavioral pattern (Figure 6). The average depth during the day (0530 – 2030 h) was 182.9 m ± 3.1 SE (Range 44.1 – 264.8 m) and the average for the night (2030 – 0530 h) was 46.4 m ± 2.4 SE (Range 3.7 – 103.0 m). The data indicated a consistent pattern of diel behavior, which included being at shallower depths during the night and the deepest depths during the day.

Data collected from manual tracking also indicated strong evidence to support the diel pattern observed during the acoustic monitoring. The proportions of the total number of individual positional fixes occurring within the boundaries of the head of the canyon were 54.4, 41.9, and 89.2 % (Tag no. 10, 11, 12, Table 6). During the nighttime tracking period 81.4, 78.0, and 79.9 % of the positional fixes were at the head of the canyon. During the day, 22.6, 5.0, and 95.0 % of the positional fixes were at the head of the canyon. Both male sharks (Tag no. 11, 12) used the head of the canyon most heavily during the night. During the day, males moved offshore to discrete areas in deeper water where there exhibited little movement whereas the female (Tag no. 10) moved offshore slightly and also exhibited little movement, remaining within the boundaries of the head of the canyon more often than the males.

Sharks exhibited three general patterns of habitat use: (1) inshore/offshore diel movement, (2) residency at the head of the canyon, and (3) absence from the head of the canyon (Figure 7). Beginning in August 2005, males and females exhibited the inshore/offshore diel movement pattern. This pattern was characterized by sharks being at the head of the canyon during the night and being absent during the day. Males exhibited a pronounced diel movement pattern whereas females generally used the head of the canyon (< 80 m depth) more consistently during August 2005.

During September 2005 all the females (Tag no. 1 - 4, 8) and 2 males (Tag no. 5, 7) exhibited sustained residency at the head of the canyon day and night for the duration of the month. Shark no. 7, a male, continued exhibiting the diel pattern described above during September 2005. In October 2005, the females continued to have an almost continuous presence at the head of the canyon, although the diel pattern was more evident as the month progressed. All 3 males exhibited the diel pattern during October 2005.

The period between November 2005 and February 2006 was characterized by almost daily use of the head of the canyon by all sharks. During this period all sharks exhibited a diel pattern, which was characterized by being in range of Receiver 1 at the head of the canyon during night and moving out of range of the receiver during day. Within the overall pattern, sharks would at times switch to sustained residency spending days at a time at the head of the canyon before switching back to the inshore/offshore diel pattern. For the entire study period, females were at the head of the canyon 64% of the time and males were present 36%. Due to the resolution of the VR2 data it is impossible to say if sharks exhibited the inshore/offshore diel pattern when they remained in range of the Receiver 1 at head of the canyon. However, the pilot study work in 1999 and the manual tracking I completed for this study indicated that some female sharks did exhibit the inshore/offshore diel pattern while remaining closer to shore than the males.

Receiver 1 at the head of the canyon was lost on 22 February 2006. A replacement receiver was deployed on 20 April 2006 for the duration of the study period. Sharks were detected at the head of the canyon 56.5 – 71.3% of the days that were monitored during the study period. All sharks were absent from the head of the canyon during May 2006 and showed sporadic use of the head of the canyon through June 2006 (Figure 8). All sharks returned to the head of the canyon in July 2006 and generally exhibited the inshore/offshore diel pattern until leaving the head of the canyon on either 25 or 26 July 2006. Signals from shark no. 5 were recorded at the head of the canyon briefly in the early morning hours on

16 August and 17 August 2006. A signal from shark no. 8 was heard once at the head of the canyon on 11 August 2006, which was likely a spurious reading. Signals were recorded at the head of the canyon from sharks no. 2 and 3 in the early morning hours briefly in September 2006. Other than these sporadic detections during August and September 2006, none of the tagged sharks were heard at the head of the canyon for the remainder of the study.

Although many sharks did not use the head of the canyon during the early fall of 2006, they were detected by the offshore receivers during this time. Sharks no. 2, 3, and 6 were heard at the offshore receivers during September 2006. Sharks no. 4, 5, 7 and 8 were heard at the offshore receivers until mid-August. Shark no. 1 was last heard in late July 2006 by the offshore receivers. This shark was not detected by any receivers after this point and appeared to have vacated the upper reaches of the canyon for the duration of the study period.

The data did indicate a difference in habitat use at the head of the canyon between males and females (Figure 9, Table 7). A seasonal difference in habitat use patterns for all sharks, both males and females, was detected among oceanographic seasons. Sharks were detected at the head of the canyon an average 17.9% of the days during the upwelling period, and 59.2% of the days during the non-upwelling time periods.

Kernel Utilization Distributions

Home range estimates for the 1 female and 2 male sharks (Tag no. 10, 11, 12) that were manually tracked for non-consecutive periods, and individual positional fixes were obtained (n = 332, 313, and 362). The activity spaces for the 1 female and 2 males were 0.20, 1.49, and 2.26 km^2 (Figure 10(a) – 12 (a)). All sharks spent the day (0800 – 1730 h) in discrete areas offshore and moved inshore and were actively swimming up in the water column at night (1930 – 0600 h). The female had a highly constrained diel pattern of movement, but overall followed the pattern of moving offshore to discrete areas during the day and moving onshore and actively swimming up in the water column at night (Figure 10(b)). The two males both moved further offshore than the female during the day and returned to the head of the canyon at night (Figures 11(b), 12(b)).

Rate of Movement

The mean rate of movement (ROM) for all 3 sharks that were tracked manually during a non-consecutive 24 h period was 10.0 m min^{-1} ± 0.3 SE. The difference in the actual position of the shark and the position of the tracking vessel on the surface when a shark was detected was not easily tested. It is likely that some ROM values may give a biased representation of the actual activity level of the shark during some time periods.

The mean ROM pooled for all sharks was not significantly different between day and night ($t(772) = -1.762$, $p > .05$). The mean ROM pooled for all sharks was greatest during dawn, 14.69 m min^{-1} ± 1.42 SE, followed by dusk 10.37 m min^{-1}± 0.97 SE. The mean ROM for each time period was similar among the 4 diel activity periods for the female shark (day = 0800 – 1730 h, dusk = 1730 – 1930 h, night = 1930 – 0600 h, dawn = 0600 – 0800 h, Table 8). The highest recorded ROM was at dawn for all 3 sharks (9.5 m min^{-1} ± 1.5 SE, 19.5 m min^{-1} ± 2.5 SE, 16.4 m min^{-1} ± 3.5 SE). All movements of tagged sharks during dawn were characterized by a directed offshore movement and during dusk by a directed onshore movement.

Discussion

Fishing & Tracking Techniques

The fishing gear was modified significantly from the pilot study. The addition of vinyl tubing on the bottom 5 m of the down line to protect a hooked shark and the addition of a second hook located 5 m above the bottom hook proved to be an effective combination that protected captured animals from injury and likely improved CPUE. The largest portion of the improvement in CPUE can be attributed to switching to night fishing operations. Future studies should use the modified gear and conduct fishing at night for prickly sharks.

Fishing operations took place in a highly confined area at the head of the canyon, encompassing only the first 0.30 km of the axis. This could have biased the size and/or sex ratio of prickly sharks caught. The size range of prickly sharks tagged was 170 – 270 cm TL. All these were likely subadult prickly sharks. Several dogfish less than 170 cm TL were captured, indicating that it was feasible for smaller sized animals to be captured. On 1 March 2005, I caught and brought to the surface a shark estimated to be 450 cm TL. There were also several other occasions were large sharks broke off the line at the surface. Both large and small animals were caught during the day and at night, which supports the hypothesis that the size of the individuals caught was likely not biased by the fishing gear or time of day fishing operations were conducted.

There was a shift in the sex ratio from being dominated exclusively by females in March – June 2005 to a more equal distribution among the sexes in July – August 2005. Fishing operations were conducted on 9 October 2006 to tag additional sharks with external tags, take additional DNA and stable isotope samples, and recapture previously tagged sharks. Although there were no successful recaptures, 3 male prickly sharks (172 – 181 cm TL) were captured and tagged with external tags. The sex-ratio of catches at the head of the canyon may have seasonal shifts. Future research needs to be conducted to determine if the sex-ratio of catches may shift from month-to month or seasonally.

The manual tracking techniques I used were effective, and I was able to consistently locate signals from tagged sharks. There were only two occasions when I was unable to locate the shark I was scheduled to track within the first 10 min of starting my survey. On both occasions, 11 November 2005 and 15 November 2005, I could not locate the shark no.11 (178 cm TL male). This shark was tagged 10 August 2005 and the transmitter's projected battery life was 100 d (expected to expire 21 November 2005).

The VR20 receiver at the head of the canyon stopped recording shark no. 11 at 02:53 h in the morning of 11 November 2005, and did not record the shark again until 13 November 2005. On 15 November 2005, the shark was recorded between 22:49 h and 23:21 h but was not recorded as being present during the first hour of the manual tracking period for that day (0200 – 0800 h). This shark continued to use the head of the canyon at night sporadically until 11 December 2005 when the receiver was retrieved and not redeployed. The inability to locate the shark while manually tracking appears to be reflective of the daily variability in use patterns of this shark and is likely not attributable to the battery failing early in this transmitter or the shark leaving the area for an extended amount of time.

Successfully deploying and retrieving sub-surface receivers in the axis of the canyon was difficult. The axis of the Monterey Canyon is a highly dynamic area that is subject to large turbidity currents that likely occur several times annually (Smith et al. 2005). In addition to turbidity currents, I observed evidence while diving of major slumps where large sections of the canyon's wall slid down into the axis of the canyon. During a dive to service a receiver at the head of the canyon on 19 April 2005, the bottom 7 m of the receiver mooring was completely covered by sediment. The walls surrounding the receiver had become vertical when previously they had sloped down to the axis at a 45 degree angle.

The combination of slumps and turbidity currents may have buried some of the receiver moorings, especially the offshore sub-surface moorings, which were lost and replaced several times throughout the study. If possible, future researchers should avoid deploying receivers directly in the axis of the canyon and use well-formed shelves or flat spots along the canyon walls. In some areas it also may be possible to deploy receivers on the flats just outside the canyon and still effectively gather acoustic data from within the walls of the canyon. The dynamic conditions at the head of the canyon required more weight than may be needed in other areas to secure receiver moorings to the substrate.

Habitat Use and Diel Pattern

The head of the canyon was an important area for the subadult prickly sharks tagged in this study. Generally, all sharks followed the pattern of being at the head of the canyon at night. As the sun began to rise, sharks exhibited a directed offshore movement within the axis of the canyon to discrete areas or refugia offshore. Tagged sharks remained in these discrete areas throughout the day and as the sun began to set they would meander inshore along the axis of the canyon. In general, this inshore/offshore diel pattern was consistent throughout the study period among male and female prickly sharks. These movements were not associated with either changes in water temperature or tide and are likely associated with light levels.

Diel movement patterns have been described for fishes including many elasmobranch species (Nelson & Johnson 1970, Standora and Nelson 1976, Bray and Hixon 1978, Nelson and Johnson 1980, Holland et al. 1993, Nelson et al. 1997, Zeller 1997, Matern et al. 2000, Sims 2001, Cartamil & Lowe 2004, Sims 2005a, Stokesbury et al. 2005, Jadot et al. 2006). Specifically, the pattern described by Sims (2005b) for the lesser spotted dogfish (*Scyliorinus canicula*) in a sea lough, seems to be an appropriate model for the prickly shark. Sims (2005b) describes a clearly different activity pattern between day and night, as well as between males and females. Male *S. canicula* generally had low activity during the day in deep water followed by more rapid movements into shallow areas at dusk and throughout the night. Male sharks returned to core areas in deeper water at dawn. Females exhibited the same pattern with the exception of their daytime resting areas were located in shallower and warmer areas.

Subadult prickly sharks tagged in this study exhibited the same general diel movement pattern as described in Sims (2005b). The mean ROM pooled for all prickly sharks reflected horizontal movements and was greatest during the crepuscular periods. These time periods were characterized by sharks making directed movements onshore at dusk and offshore at dawn. ROM was similar among day and night. The movements of the sharks at night were constrained to a very small area above and directly adjacent to the head of the canyon. Although the sharks were actively swimming up in the water column during the night, they were spatially constrained. This could explain the similarity in values between day ROM when the sharks were on the benthos in discrete areas exhibiting little movement and night ROM when the sharks were actively swimming in the middle of the water column.

Manual tracking completed at night was conducted from a research vessel that had a depth sounder. This allowed me to observe high resolution depth soundings during most tracking sessions. Images from the depth sounder indicated the presence of large schools of small fishes during all nighttime tracking sessions. These soundings were confirmed on several occasions by commercial fishing operations in the area landing anchovy (*Engraulis mordax*) and sardine (*Sardinops sagax*). Although no stomach samples were taken from sharks in this study, it is likely that shark movements in the middle of the water column at the head of the canyon at night were associated with feeding. Future studies should pursue stable isotope analysis coupled with detailed tracking to help determine if these movements are directly related to foraging (Cunjak et al. 2005).

Refuging and Sexual Segregation

Subadult prickly sharks remained in centralized areas during the non-active portion of their diel pattern. This behavioral pattern of a species remaining in a relatively small centralized discrete location within a species home range for a significant portion of a species diel cycle was first described by Hamilton & Watt (1970) and defined as refuging. Refuging has been documented for other elasmobranchs and is often associated with predation avoidance, avoidance of aggression from mature conspecifics, reduction of thermal stress, or energy conservation (McLaughlin & O'Gower 1971, Klimley 1984, Economakis & Lobel 1998, Holland et al. 1993, Sims 2005a). In the case of subadult prickly sharks it is difficult to determine which factor or combinations of factors are influencing this behavior. It is clear that subadult prickly sharks have a phase of their diel cycle in which they move little from a centralized location. Future studies are needed to further delineate the reason for this pattern, and to test proposed causal factors affecting the behavior in this population of subadult prickly sharks.

Sexual segregation has been described as a general characteristic of many shark populations (Springer 1967, Klimley 1987, Sims et al. 2001, Sims 2005b). The reason for this behavior is generally inferred to be associated with reproduction, but this has yet to be rigorously tested. Both male prickly sharks (Tag no. 11, 12) that were manually tracked moved to deeper and colder water during the day. This could be a way to slow their metabolism and conserve energy for the more active nighttime periods (Klimley 1984). The female, shark no. 10, displayed a much more highly constrained onshore/offshore diel movement pattern than the males. Shark no. 10 remained within the receiving range of Receiver 1 at the head of the canyon for the majority of the monitoring period during both day and night. Remaining in the warmer waters at the head of the canyon may increase the growth rate of female sharks (Economakis & Lobel 1998). Females with a larger body size will produce larger offspring that are likely superior competitors (Klimley 1987).

The VR20 monitoring data also indicated the same patterns observed in the active tracking of sharks no. 10 – 12. However, the additional female monitored, shark no. 9, had a pattern more similar to the males than the female, moving out of range of the Receiver 1 often during daylight hours. The transmitter for shark no. 9 was deployed much earlier in the study period (13 May 2005) than shark no. 10 – 12, which were tagged on 10 August 2006. The data that the onshore/offshore diel pattern of shark no. 9 changed, becoming more similar to the other female beginning in late July and continuing till 21 August 2005 when the battery likely expired. This may indicate a seasonal shift in habitat use patterns among females or may simply reflect individual variation.

The CHAT data collected for shark no. 15 (198 cm TL female) were collected during early August 2005, which overlapped with the sampling period for shark no. 10 – 12. The CHAT data reflected the more typical inshore/offshore diel pattern exhibited by the 2 males (Tag no. 11, 12). This may indicate that there is no difference in habitat use among male and female prickly sharks. There are several confounding factors, such as seasonal shifts in habitat use and ontogenic shifts in habitat use that could be masking a periodic difference in habitat use among males and females. Although the overall patterns of use are consistent, there is clearly individual variation among tagged sharks. This variation is coupled with a possible seasonal shift in activity patterns among male and female subadult prickly sharks. The CHAT data were collected in early August and this shark may not have made the seasonal shift yet or there simply may not be a clear separation in habitat usage during this period among males and females.

There are not enough data from this study to conclude that prickly sharks exhibit sexual segregation in habitat use. The number of sharks tracked using the highly detailed active tracking techniques was very low (n= 3) and the receiving range of the VR20 receiver was constrained to the head of the canyon. The data collected from the CHAT receiver were from the time period directly after the shark was tagged and the pattern observed may have been influenced by tagging stress. During the fall 2005, there was a difference in habitat use and activity patterns between the 2 male and 1 female prickly shark (Tag no. 10 - 12). However, the CHAT tag data collected from shark no. 15 brings into question the applicability of sexual segregation in this population of subadult prickly sharks.

Although it is not clear from this study if sexual segregation occurs in this population of subadult prickly sharks. The lack of movement from a discrete centralized location within the home range during the day indicates refuging behavior. Refuging behavior that leads to sexual segregation has been described in several species of elasmobranches (Springer 1967, Klimley 1987, Sims et al. 2001). To date, there have been few systematic, hypothesis-led investigations addressing causal factors of refuging behavior. Sims (2005b) suggests that sexual segregation could occur in elasmobranchs as a result of social factors such as aggression avoidance from conspecifics, sexual dimorphisim leading to different nutritional requirements (Klimley 1987), a higher level of predation risk avoidance by females, or differences in habitat selection influenced by water temperature. The social factor hypothesis predicts females segregate from males to avoid aggression. Sexual dimorphism when hypothesized to explain sexual segregation predicts that for species lacking sexual size dimorphism, segregation between the sexes should be limited or non-existent because nutritional requirements are similar. Predation risk when hypothesized to explain sexual segregation predicts that females will choose a habitat that is safe from predators and males seek habitats with high food availability (Ruckstuhl & Neuhaus 2000). Males and females occupying different thermal niches when hypothesized to explain sexual segregation predicts females will remain in warmer habitats to increase growth rates to reach maturity at a larger size than similarly aged males (Klimley 1987).

Assuming there is at least periodic sexual segregation, several hypotheses explaining refuging behavior do not seem applicable or require additional research to address their relationship to this population of subadult prickly sharks. It is clear from the data that during nighttime periods, male and female prickly sharks were in a very small area at the head of the canyon encompassed by the receiving ranges of the moored receivers (0.79 km^2). There were several occasions when the data recorded indicated that all 13 tagged prickly sharks that data were successfully collected from during this study were at the head of the canyon at the same time.

Because both male and female prickly sharks were at the head of the canyon together on a regular basis, aggression from conspecifics is not a factor influencing the behavioral patterns of this population of subadult prickly sharks. Prickly sharks may be sexually dimorphic, with females being larger than males. This sexual dimorphism hypothesis predicts female prickly sharks should reside in areas that have high prey availability, leading to higher growth rates (Klimley 1987, Sims 2005b). Further studies to determine if the prickly sharks are feeding at the head of the canyon and diet content analysis are needed to determine if differences in diet and energetic requirements can be detected among males and females. The predation risk for shark species similar in size to the prickly shark is assumed to be relatively low (Frisk et al. 2001, Heithaus 2004). However, other large sharks, such as sleeper (*Somniosus pacificus*), sixgill (*Hexanchus griseus*), and sevengill (*Notorynchus cepedianus*) sharks are capable of preying on prickly sharks, and are present in the upper reaches of the Monterey Canyon (Varoujean 1972). There could be a difference in predation risk between differing habitats within a prickly shark's home range. This would have to be tested in future studies to fully address whether the predation risk hypothesis is applicable.

There is some evidence from my work to support the concept of behavioral thermoregulation proposed by the thermal niche hypothesis. Data from manual tracking, as well as long-term acoustic monitoring, indicated a difference in use of the head of the canyon between males and females during certain portions of the year. As one would expect, the average temperatures at the head of the canyon in 30 m depth were greater than the average temperatures offshore in 85 m of depth on a shelf in the axis of the canyon. Subadult female prickly sharks may be remaining in the warmer waters at the head of the canyon to increase growth rates, allowing them to reach sexual maturity at a greater size than similarly aged males.

Prickly sharks are marine poikilotherms and their body temperature varies with the temperature of their surroundings. The rate of metabolic processes such as growth or digestion are linked to temperature; generally speaking, the greater the temperature the faster the processes (Carlson et al. 2004). In the nutrient-rich waters of the Monterey Bay, it is doubtful that food is a limiting resource for the prickly shark. Female prickly sharks may benefit by increasing their metabolic processes by moving into water masses with greater temperatures such as those found in the shallower waters at the head of the canyon

Behavioral thermoregulation for fish was defined by Neil (1979) as movement through a habitat in such a way as to maximize time spent at temperatures favorable to the joint conduct of life processes. Behavioral thermoregulation may allow female prickly sharks to create more surplus energy. Surplus energy can be defined as energy in excess of that required to maintain basic life processes, such as respiration and digestion (Bryan et al. 1990). Surplus energy can be devoted to processes such as somatic growth and reproduction. The maximum power principle first applied to fishes by Lotka (1922) and restated by Odum (1983) states that "biological systems prevail that develop designs that maximize the flow of useful energy." Future studies are needed to more discretely delineate the habitat use patterns of females and males over several seasons to provide insights into whether behavioral thermoregulation may be a factor influencing activity patterns. Improved archival tags as well as pop-off satellite archival tags may be appropriate for helping to address this question.

The presence of prickly sharks at the head of the Monterey Canyon provided a unique opportunity to study the movements and habitat use of a poorly known species. The close proximity of the study site to shore facilities made it easier to successfully conduct manual tracking and acoustic monitoring simultaneously. By using a combination of three types of acoustic transmitters, manual tracking, and acoustic monitoring techniques I was able to verify and more clearly delineate the diel movement patterns discovered during the pilot study. The head of the Monterey Canyon is an important habitat for subadult prickly shark. Males and females used the head of the canyon regularly during night for most of the study period. Males vacated the head of the canyon at dawn and remained offshore in refuge areas during the day, whereas females often stayed in shallower waters at the head of the canyon. Males and females returned to the head of the canyon at dusk and actively swam throughout the water column during night, possibly foraging on pelagic schooling fishes.

My research indicated that subadult prickly sharks inhabit the head of the canyon throughout most of the year. Interspersed throughout the sampling period, there were short periods of several days in which that sharks were absent from the head of the canyon before returning. The timing of these short absences was not consistent among sharks. There were two extended periods when most sharks were absent from the head of the canyon. During the spring and fall of 2006, signals from tagged sharks were very rarely recorded at the head of the canyon. Interpretation of these results is limited by the interruption of monitoring in spring 2006 when the receiver was lost and the end of the study period in fall 2006. Future studies should focus on these times of year.

It is clear from the receiver array data, that subadult prickly sharks do frequent the upper reaches of the Monterey Canyon throughout the year. However, during the one year duration of the study, sharks were at the head of the canyon rarely during the spring upwelling period. Although not all sharks were tagged during the spring upwelling period in 2005, the two sharks that were (Tag no. 1, 2) exhibited a consistent pattern of being absent from the head of the canyon during the spring in both 2005 and 2006. The upwelling period is characterized by colder average water temperatures at the head of the canyon. Sharks may vacate the head of the canyon at this time choosing to seek refugia in offshore areas of the canyon where conditions may be more favorable. Offshore waters at this time may have more stable temperature or food availability may be higher during this time. Future studies using stable isotope analysis are needed to help delineate the primary mode of feeding and content of prickly shark diet which may be useful in explaining the habitat use pattern observed in this research.

Subadult prickly sharks showed an inconsistent usage pattern at the head of the canyon in the fall of 2005 and the fall of 2006. Data collected in September 2005 indicated some of the greatest usage levels for males and females at the head of the canyon. Data in the fall 2006 indicated almost no use of the head of the canyon during August 2006 through the end of the study on 13 September 2006. Because the study ended 13 September 2006 it is difficult to speculate about what may be driving the differences between fall 2005 and fall 2006. One possibility is that these sharks may have switched to a different adult pattern of habitat use which is characterized by adult sharks not utilizing the head of the canyon as much as subadults do. However, this seems unlikely as the growth rate for prickly sharks is likely slow and the sizes of the tagged sharks (170 – 225 cm) are well below the estimated size at maturity (290 cm TL female, 240 cm TL male).

Changes in water temperature do not seem to explain the difference in habitat use between fall 2005 and fall 2006. The transition from spring upwelling to warmer water temperatures usually occurs sometime in late June to mid-July. Unfortunately, I did not have a temperature record from the inshore receiver during this time. The transition from upwelling to the non-upwelling season in 2006 did not appear to be particularly dramatic when compared with recent years, based on surface water temperatures from data collected at the Monterey buoy (36°45'11" N 122° 25'21"W).

The dramatic difference in behavior between fall 2005 and fall 2006 did not appear to be associated with the change in oceanographic conditions and could be attributed to any number of other factors such as a change in prey availability or a dramatic event such as a turbidity current. Future researchers should focus not only on long-term multi-season acoustic monitoring of prickly sharks, but also the collection of physical data at the head of the canyon. This will help to further describe the seasonal use of prickly sharks and will allow hypotheses to be tested that can address the causal factors that may be influencing the behavior of subadult prickly sharks in the upper reaches of the Monterey Canyon.

Subadult prickly sharks tagged in this study had a year-round presence in the upper reaches of the Monterey Canyon and exhibited a pronounced diel movement pattern that was associated with day and night periods. Tagged sharks exhibited the highest rates of horizontal movement during crepuscular periods. Although there was individual variability among sharks, when sharks were within range of the receiving array they were at the head of the canyon most often. The head of the canyon was the most important habitat within the study area and was used most often during the night which is likely associated with foraging behavior.

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TABLE 1. Summary of prickly shark catch-per-unit effort (sharks h^{-1}) and sex ratio at the head of the Monterey Canyon (< 80 m water depth) from February – August 2006. Not all sharks that were hooked were landed successfully; when this occurred, the sex was undetermined and is reported as unknown (UKN). Trips indicates the number of fishing trips undertaken that month and Time indicates whether the trip occurred during the day or night.

Month	CPUE	Hours	Trips	Sharks hooked	Time	Sex Ratio F:M:UNK
February	0.00	3.3	1	0	Day	0:0:0
March	0.18	22.3	7	4	Day	4:0:0
April	0.00	18.3	5	0	Day	0:0:0
May	0.94	7.4	4	7	Night	3:0:4
June	0.41	4.9	2	2	Night	0:1:1
July	0.42	14.4	5	6	Night	3:3:0
August	1.07	6.5	2	7	Night	3:3:1

TABLE 2. Acoustic tag type, date tag was deployed, projected end of battery life estimated by manufacturer, and the tracking type, sex, and total length (TL) of tagged sharks. Tracking type indicates the type of acoustic tracking or monitoring that was used for each tag. Monitoring was completed using moored receivers, manual tracking was completed with a hydrophone via a surface vessel, and archival monitoring was done using two-way communication via a specialized acoustic tag and moored receiver. Last detected indicates the date when that shark was last detected by acoustic monitoring. All tracking and monitoring activities were completed by 13 September 2006.

Shark	Vemco tag type	Battery life (d)	Date deployed	Tracking type	Sex	TL (cm)	End of battery life	Last detected	Days monitored
1	V16	1442	3/1/2005	Monitoring	F	217	2/10/2009	7/26/2006	504
2	V16	1442	3/12/2005	Monitoring	F	225	2/21/2009	9/7/2006	493
3	V16	1442	5/12/2005	Monitoring	F	190	4/23/2009	9/13/2006	432
4	V16	439	5/12/2005	Monitoring	F	184	7/25/2006	8/15/2006	432
5	V16	439	6/24/2005	Monitoring	M	176	9/6/2006	8/17/2006	389
6	V16	439	7/27/2005	Monitoring	M	170	10/9/2006	9/5/2006	356
7	V16	439	7/28/2005	Monitoring	M	200	10/10/2006	8/14/2006	355
8	V16	439	8/9/2005	Monitoring	F	175	10/22/2006	8/11/2006	343
9	V16	100	5/13/2005	Active & Monitoring	F	250	8/21/2005	8/23/2005	101
10	V16	100	8/10/2005	Active & Monitoring	F	220	11/18/2005	12/10/2005	123
11	V16	100	8/10/2005	Active & Monitoring	M	178	11/18/2005	12/11/2005	123
12	V16	100	8/10/2005	Active & Monitoring	M	184	11/18/2005	12/8/2005	123
13	CHAT	365	7/26/2005	Archival Monitoring	F	270	7/26/2006	Not detected	99
14	CHAT	365	7/27/2005	Archival Monitoring	F	225	7/27/2006	Not detected	99
15	CHAT	365	8/9/2005	Archival Monitoring	F	198	8/9/2006	8/19/2005	99

TABLE 3. Data summary for sharks tagged with continuous transmitters and manually tracked in the Monterey Canyon, between September and November 2005. Hours tracked are the total numbers of hours spent actively tracking each shark from a surface vessel. A tracking block was equal to a 6 h period. Initially tracking blocks were allocated throughout a 24 h period. Towards the end of the battery life of the continuous transmitters, tracking blocks were reapportioned to concentrate on crepuscular periods (Crepuscular). Tracking dates are reported as the first and last date an individual shark was detected from a surface vessel.

				Blocks (h)				
				24 h	Crepuscular		Dates Tracked (mm/dd/yy)	
Length (cm)	Sex	Date tagged	Hours Tracked (h)	(0:00/6:00/12:00/18:00)	1600-2200	0200-0800	Start	End
220	F	08/10/05	61.00	18/10/10/12	6	6	09/04/05	11/14/05
184	M	08/10/05	62.75	18/9/12/12	6	6	09/04/05	11/13/05
178	M	08/10/05	51.75	20/8/12/12	0	0	09/04/05	11/07/05

TABLE 4. Summary of the initial deployment date of VR2 receivers, the date each receiver was pulled from the study site, the number of times the receiver was retrieved and downloaded, the days not monitored during the study period when receiver was missing, and the total days monitored.

Receiver	Date deployed	Date pulled	Retrievals	Days not monitored (d)	Total days monitored (d)
1	3/1/2005	9/13/2006	12	57	504
2	3/9/2005	9/12/2006	5	249	303
3	3/9/2005	9/12/2006	9	0	553

TABLE 5. Proportion of total receptions at each receiver during each of the four diel activity periods (Day = 0800 - 1730 h, Dusk = 1730 – 1930 h, Night = 1930 – 0600 h, Dawn = 0600 – 0800 h). Total proportion of detections for all daylight (DAY = Day + Dawn) and nighttime (NIGHT = Night + Dusk) hours is also reported.

	Receiver		
	1	2	3
Dawn	7.7%	8.9%	6.5%
Day	26.0%	55.6%	47.6%
Total DAY	33.7%	64.5%	54.1%
Dusk	8.4%	8.2%	9.1%
Night	58.0%	27.4%	36.8%
Total NIGHT	66.3%	35.5%	45.9%

TABLE 6. Number and percentage of positional fixes obtained from manual tracking techniques that were located within the boundaries of the head of the Monterey Canyon (< 80 m) and total fixes recorded for each shark during manual tracking operations.

Tag no. 10	Fixes within Head of the Canyon	Total Fixes	Percentage at Head of the Canyon
NIGHT	123	154	79.9%
DAY	95	100	95.0%
DAWN	49	49	100.0%
DUSK	29	29	100.0%
TOTAL	296	332	89.2%
Tag no. 11			
NIGHT	103	132	78.0%
DAY	6	120	5.0%
DAWN	16	48	33.3%
DUSK	6	13	46.2%
TOTAL	131	313	41.9%
Tag no. 12			
NIGHT	140	172	81.4%
DAY	28	124	22.6%
DAWN	10	34	29.4%
DUSK	19	32	59.4%
TOTAL	197	362	54.4%

TABLE 7. Total detections at VR2 receivers by month. Fishing operations occurred between 1 March 2005 and 10 August 2005 and are denoted by vertically oriented text. All sharks were tagged by 10 August 2005 and horizontally oriented text indicated months where all sharks were tagged. Data collection for all receivers began in March 2005 and continued through September 2006. Data collected from Receiver 2 between March and May 2005 are shown in gray font italics as the receiver did not surface on 24 May 2005 and washed up on a beach north of the study site in early June 2005. Data collected during this period are difficult to interpret because the date the receiver came off the bottom is not known. Receiver 1 was missing between 2/22/2005 and 4/20/2005, Receiver 2 was missing between 6/6/2005 – 10/10/2005 and 2/12/2006 – 6/15/2006 data from these periods are indicated in gray font.

Shark #1 **217 cm F**

Rec	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	TOTAL
1	155	695	544	818	1258	4125	19729	15947	9925	4944	3074	3944	-	0	0	0	5459	0	0	70617
2		*2114*		-	-	-	-	1137	3601	2800	6069	2086	-	-	-	0	84	0	0	17891
3	582	862	664	7	0	0	0	0	6	56	231	696	1332	645	672	65	1885	0	0	7703
																		TOTAL		96211

TABLE 7. Continued

Shark #2 **225 cm F**

Rec	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	TOTAL
1	102	54	675	998	2254	13718	21949	18373	14432	6917	3294	7834	-	0	0	132	10571	0	60	101363
2		2574		-	-	-	-	749	1822	1924	4536	2348	-	-	-	481	206	0	0	14640
3	746	1617	567	0	0	0	0	0	0	15	267	23	616	631	556	1322	58	9	116	6543
																		TOTAL		122546

Shark #3 **190 cm F**

Rec	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	TOTAL
1	0	0	178	753	1288	2278	11375	10762	8737	5206	5920	7329	-	0	103	374	7289	0	50	61642
2		621		-	-	-	-	1440	2349	2722	6689	1648	-	-	-	20	122	1	0	15612
3	0	0	768	0	0	0	0	0	121	317	88	371	1578	114	141	193	37	37	0	3765
																		TOTAL		81019

TABLE 7. Continued.

Shark #4 **184 cm F**

Rec	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	TOTAL
1	0	0	1430	3688	5548	16409	24987	19239	18871	11175	6812	6696	-	0	79	418	10687	0	0	126039
2		710		-	-	-	-	1923	2580	1944	7299	1136	-	-	-	50	16	0	0	15658
3	0	0	666	1030	0	12	0	0	0	244	1055	1209	1065	219	244	838	2	61	0	5718
																		TOTAL		147415

Shark #8 **175 cm F**

Rec	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	TOTAL
1	0	0	0	0	0	3583	23068	12549	6480	6619	4200	1270	-	0	73	62	4516	1	0	62421
2	-	-	-	-	-	-	-	4869	12371	5398	11431	4739	-	-	-	81	6	2	0	38897
3	0	0	0	0	0	776	0	0	760	1463	2846	2716	4544	1602	2542	1030	132	62	0	18473
																		TOTAL		119791

TABLE 7. Continued.

Shark #5 **176 cm M**

Rec	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	TOTAL
1	0	0	0	72	3839	7093	20253	8208	7979	4813	1442	4166	-	0	25	214	5910	37	0	64051
2	-	-	-	-	-	-	-	7021	6831	9597	6798	3747	-	-	-	238	41	31	0	34304
3	0	0	0	354	1577	1668	0	0	706	1519	3620	3434	5031	1939	1498	738	456	397	0	22937
																		TOTAL		121292

Shark #6 **170 cm M**

Rec	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	TOTAL
1	0	0	0	0	20	1577	5566	9356	9788	9294	4111	6429	-	11	0	49	1030	0	0	47231
2	-	-	-	-	-	-	-	5941	6367	3952	6254	3123	-	-	-	64	406	1	0	26108
3	0	0	0	0	927	7836	114	0	617	1208	2614	1239	5137	2920	3825	1243	972	452	13	29117
																		TOTAL		102456

TABLE 7. Continued

Shark #7 **200 cm M**

Rec	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	TOTAL
1	0	0	0	0	30	2899	11550	5138	4047	3374	380	800	-	7	61	0	3167	0	0	31453
2	-	-	-	-	-	-	-	3493	6613	3948	7293	1951	-	-	-	195	163	0	0	23656
3	0	0	0	0	0	1439	0	0	1	390	929	1638	845	457	973	890	3	131	0	7696
																		TOTAL		62805

GRAND TOTAL OF ALL DETECTIONS 853535

TABLE 8. Mean rate of movement (ROM) for 2 males and 1 female tracked manually. The greatest ROMs were observed during the Dawn period and are underlined and shown in bold text.

		Day (0800-1730)	Dusk (1730-1930)	Night (1930-0600)	Dawn (0600-0800)
Shark ID #	Sex	Average ROM m min^{-1} ± SE/ Sample size (n)	Average ROM m min^{-1} ± SE/ Sample size (n)	Average ROM m min^{-1} ± SE/ Sample size (n)	Average ROM m min^{-1} ± SE/ Sample size (n)
10	F	6.43 ± 0.71 / 90	7.80 ± 0.96 / 33	9.40 ± 0.58 / 153	**9.47 ± 1.48 / 44**
11	M	9.34 ± 0.80 / 115	17.72 ± 2.80 /11	8.35 ± 0.58 /129	**19.51 ± 2.53 / 38**
12	M	11.21 ± 0.98 / 119	10.40 ± 1.62 / 32	10.10 ± 0.57 / 168	**16.38 ± 3.46 / 27**
All sharks	-	9.22 ± 0.51 / 324	10.37 ± 0.97 / 75	9.36 ± 0.33 / 451	**14.69 ± 1.42 / 110**
11 & 12	2 M	10.29 ± 0.64 / 234	9.65 ± 1.47 / 43	9.34 ± 0.42 / 297	**18.17 ± 2.06 / 66**

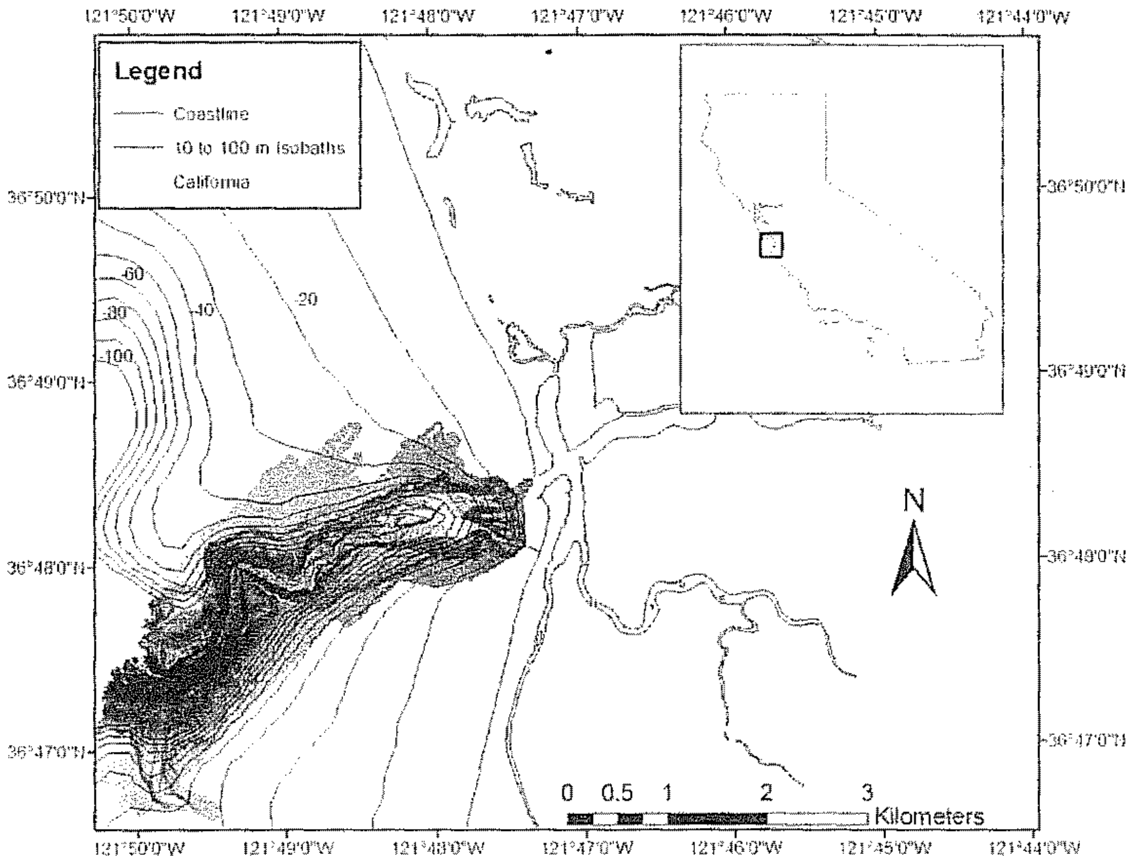


FIGURE 1. Study area with detail of the upper reaches of the Monterey Canyon, located adjacent to Moss Landing, CA. Depth is indicated by increasingly darker shading. Bathymetric data used in map were acquired, processed, archived, and distributed by the Sea Floor Mapping Lab of California State University Monterey Bay.

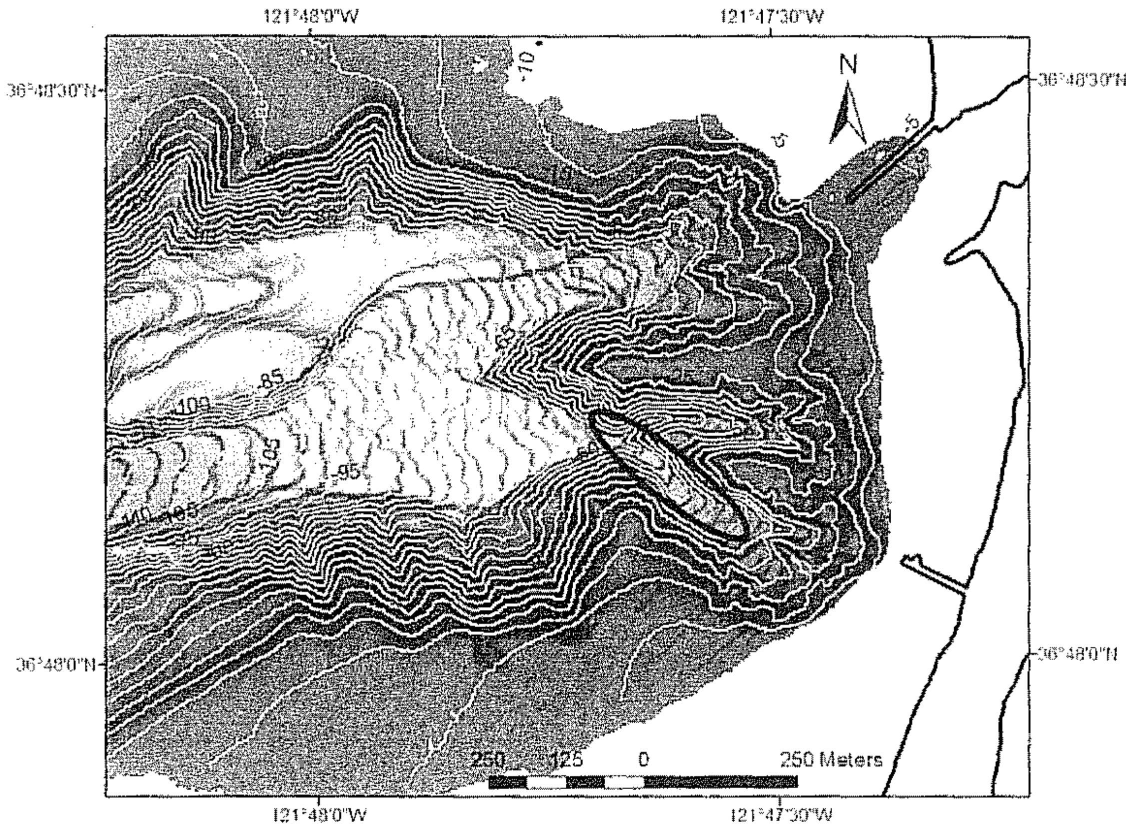


FIGURE 2. Close up of the head of the Monterey Canyon. Fishing operations took place within the circled area from March – August 2005. Five drop lines were deployed for 40 – 50 min sets. Contour lines are 5 m isobaths. Data were acquired, processed, archived, and distributed by the Sea Floor Mapping Lab of California State University Monterey Bay.

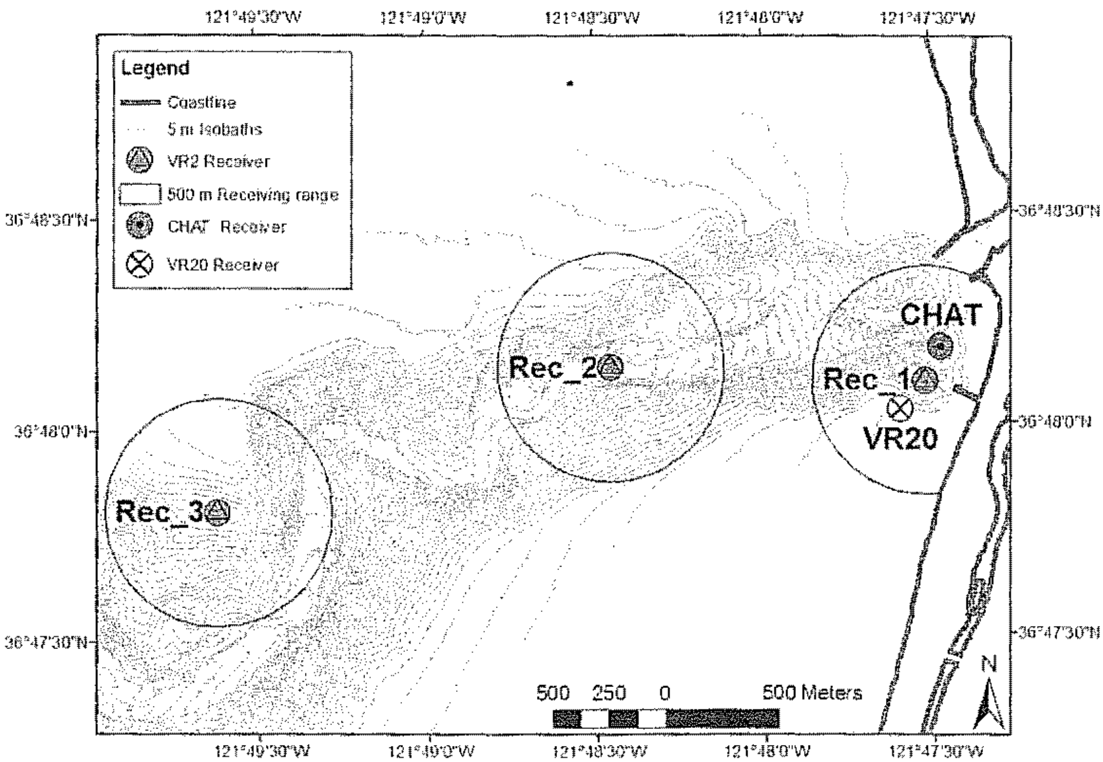


FIGURE 3. Locations of receivers moored in the axis of the Monterey Canyon. See Table 4 and text for detailed description of deployment dates.

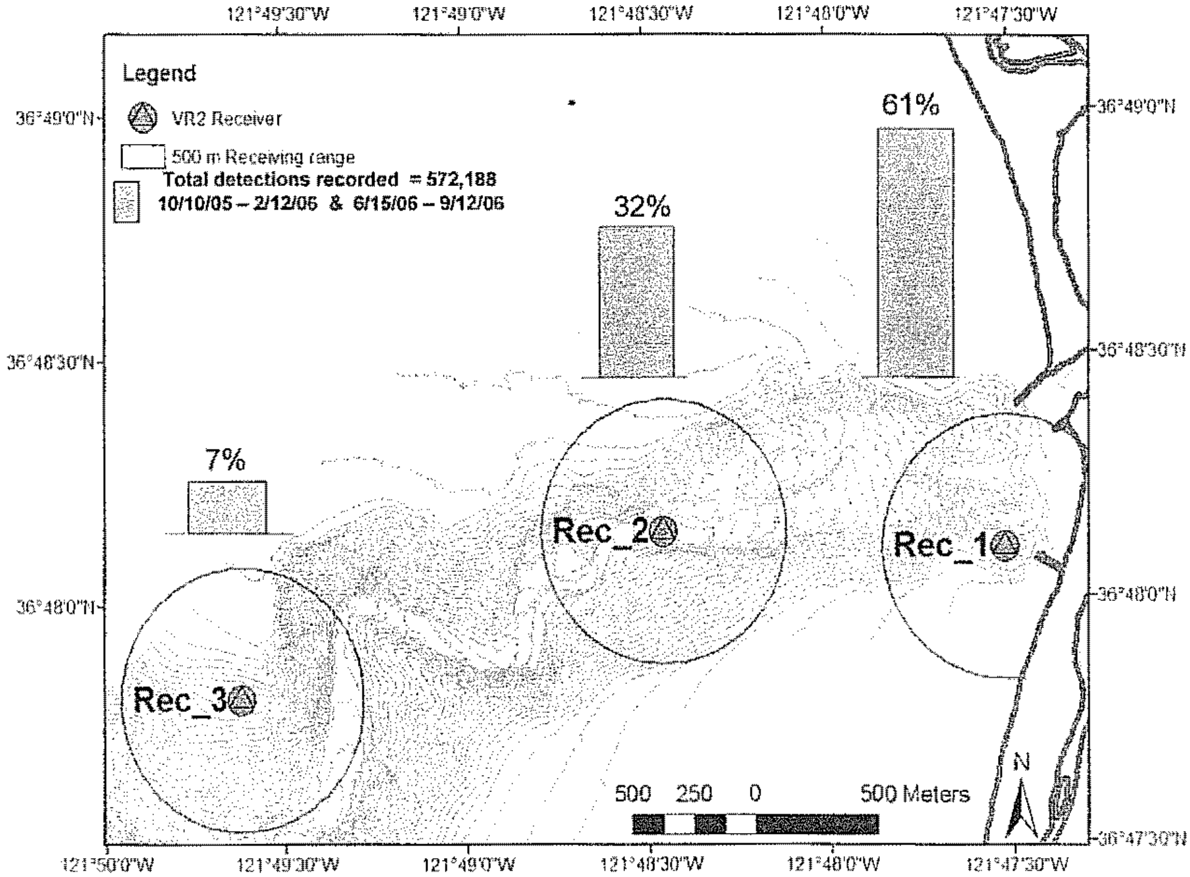


FIGURE 4. Location of VR2 receiver deployment locations with the percent of total detections recorded at each receiver for the 8 sharks with coded transmitters when all three receivers were deployed (10/10/05 - 2/12/06 & 6/15/06 - 9/12/06). Receivers in the array were lost during some periods during the study period and no data were collected during those times. The total detections for the two time period when all three receivers were deployed was 572,188.

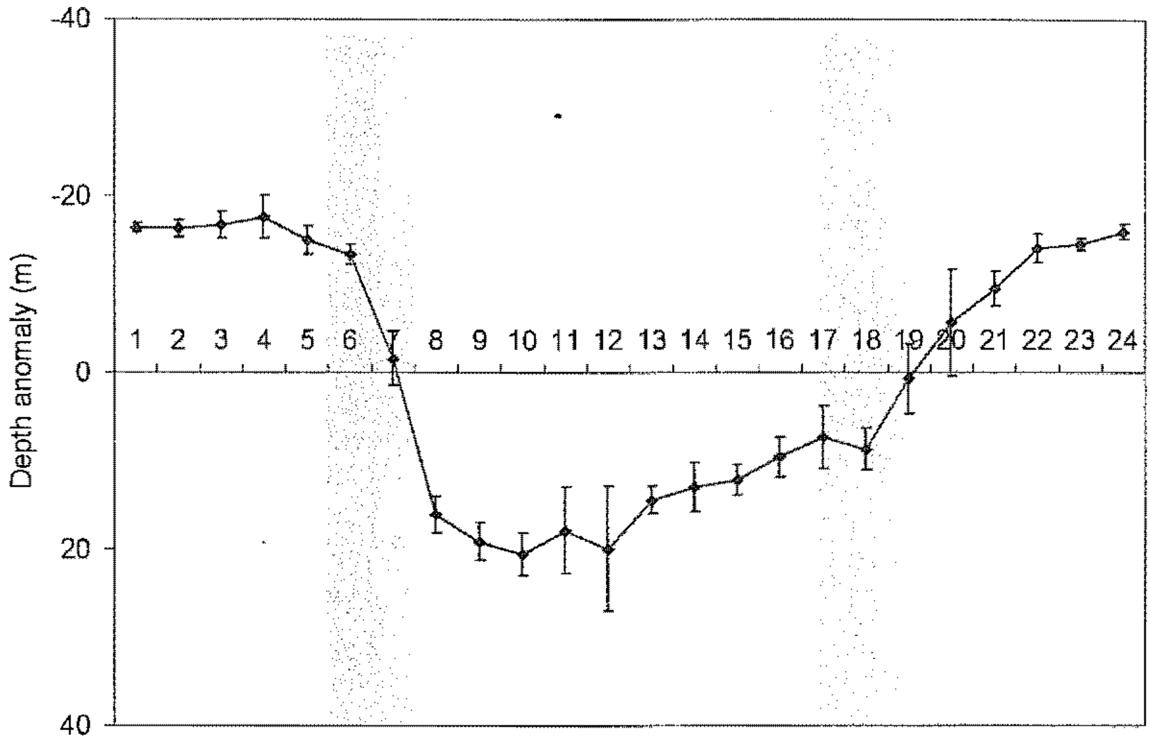


FIGURE 5. Mean depth anomaly for 2 male and 2 female sharks monitored with the VR20 receiver. The average depth for each shark was calculated for the entire monitoring period and then the average hourly depth was subtracted from that value. The grand mean was taken for all 4 sharks and is reported as the hourly mean depth anomaly ± SE. Dawn (0600 – 0800) and Dusk (1730 – 1930) are indicated by grey shading.

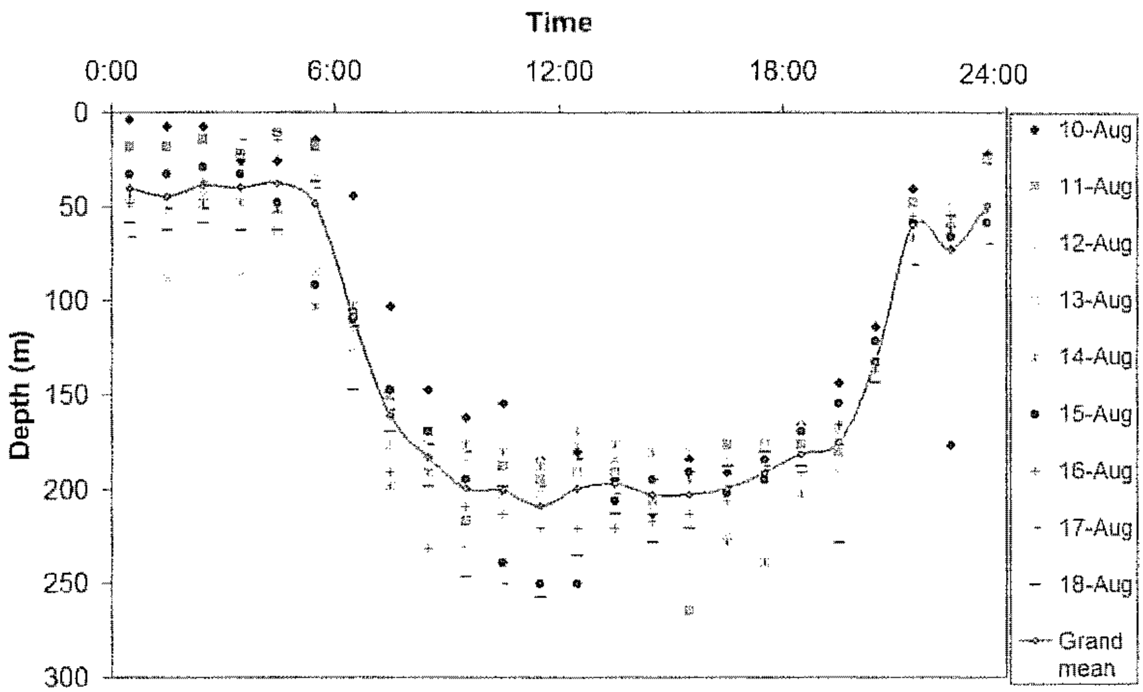


FIGURE 6. CHAT archival tag data for female prickly shark (Tag no. 15). The x-axis is 24 h time, 00:00 represents midnight and 24:00 represents midnight of the next day. The y-axis is the average hourly depth in meters of the tagged shark. Each of the nine series of data points has a unique symbol to indicate the day on which the data were collected. Each symbol represents the average depth of the shark for the previous hour. These data were archived into the CHAT tag memory and successfully uploaded when the shark was in range of the moored CHAT receiver.

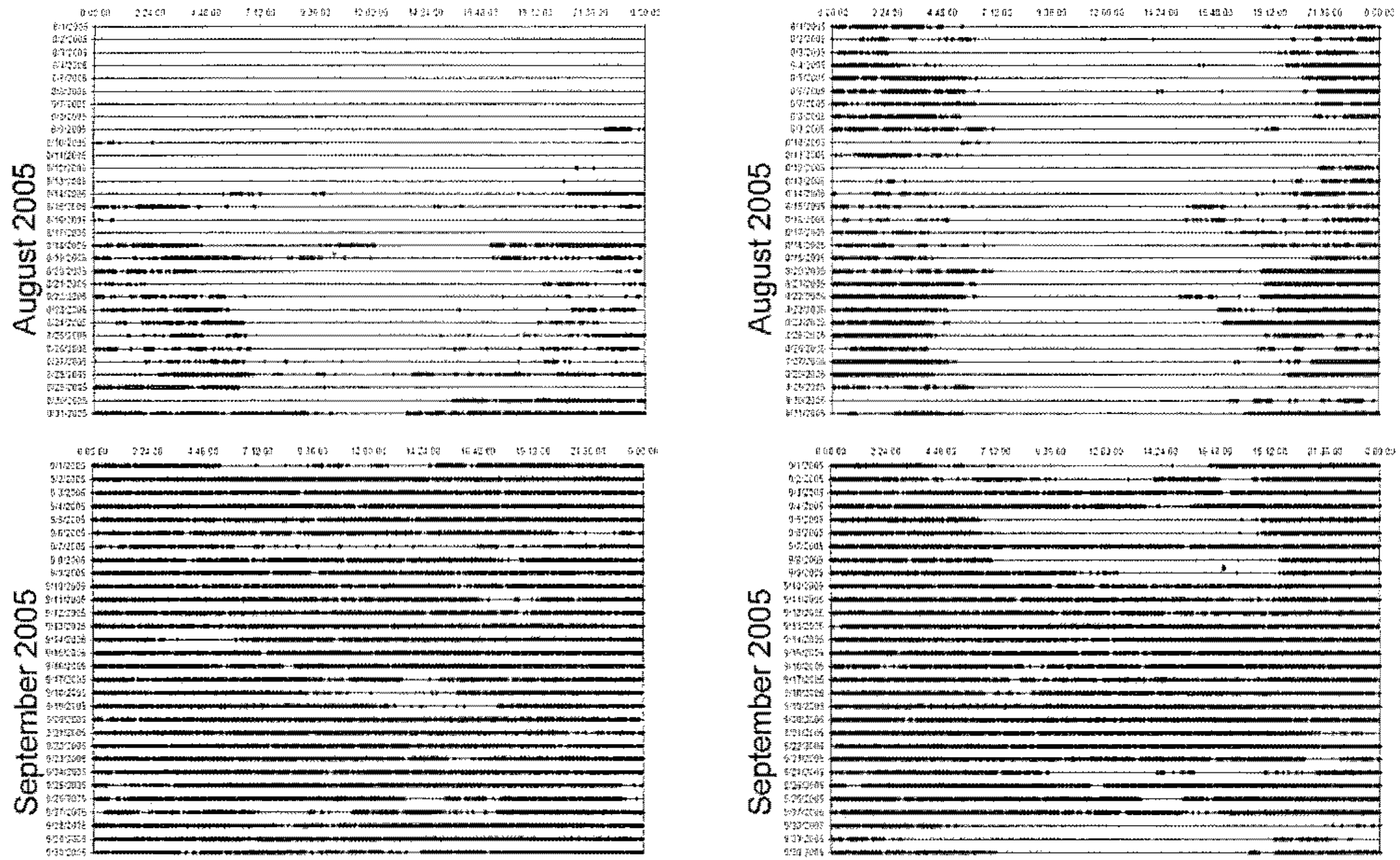


FIGURE 7. Representative monthly plots of signal detections at Receiver 1. Each symbol represents a detection of a tagged shark within the range of Receiver 1. The x-axis is a 24 h time period and the y-axis represents each day of the month. Representative plots on the left are from a female (Tag no. 8) and plots on the right are from a male (Tag no. 5). The upper set of plots illustrate the inshore/offshore habitat use pattern and the lower plots represent the residency at the head of the canyon habitat use pattern.

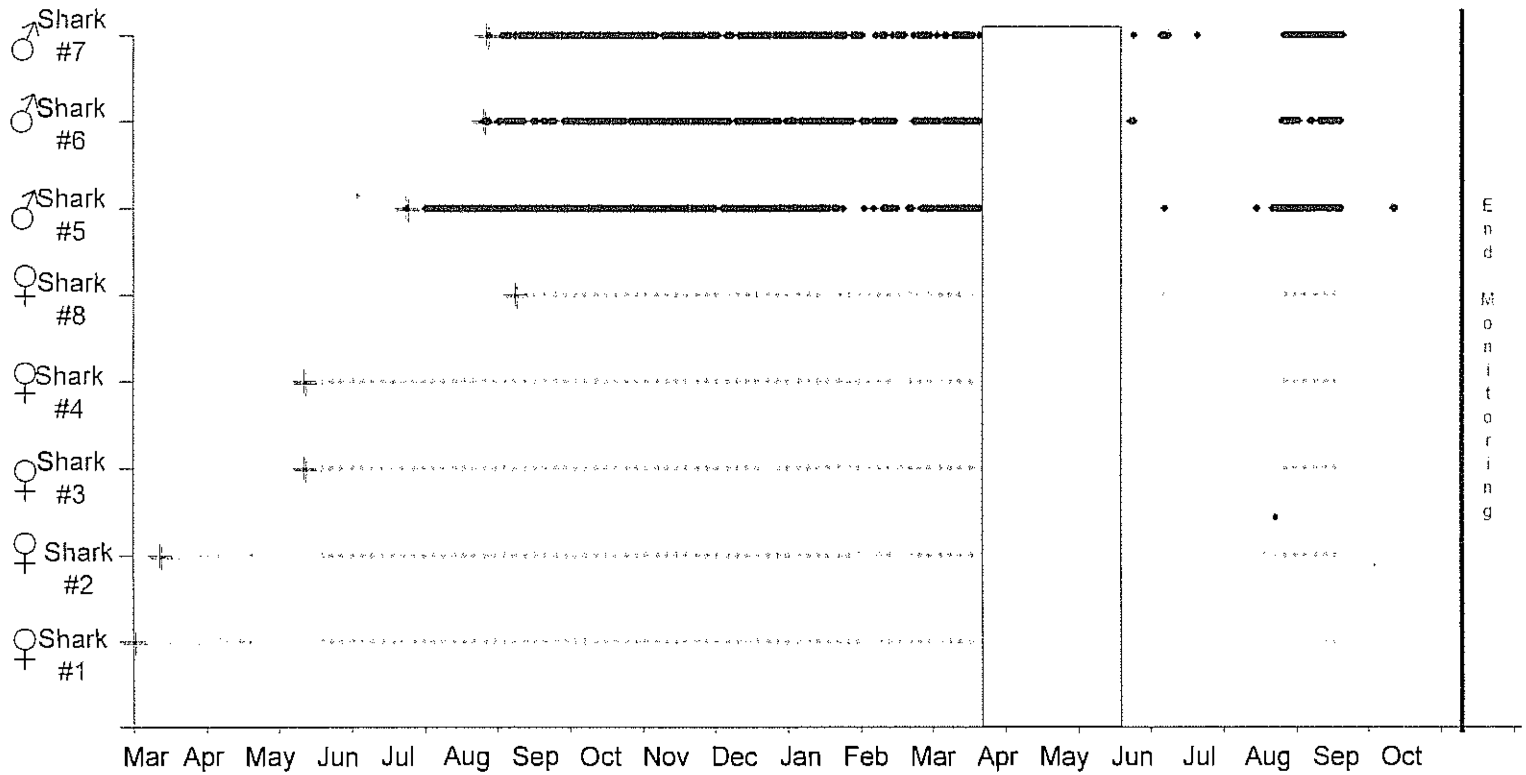


FIGURE 8. Seasonal habitat uses of sharks at the head of the Monterey canyon (< 80 m depth). Each symbol indicates a day in which Receiver 1 recorded the presence of an individual shark at the head of the canyon at least twice during that day. The plus signs indicate the date the shark was tagged. The shaded box indicates a period of time where the receiver was missing from 22 February – 20 April 2006 and the solid dark vertical line indicates when the receiver was pulled at the end of the study on 13 September 2006. Sharks no. 1 – 4 & 8 are females and sharks no. 5 – 7 are males.

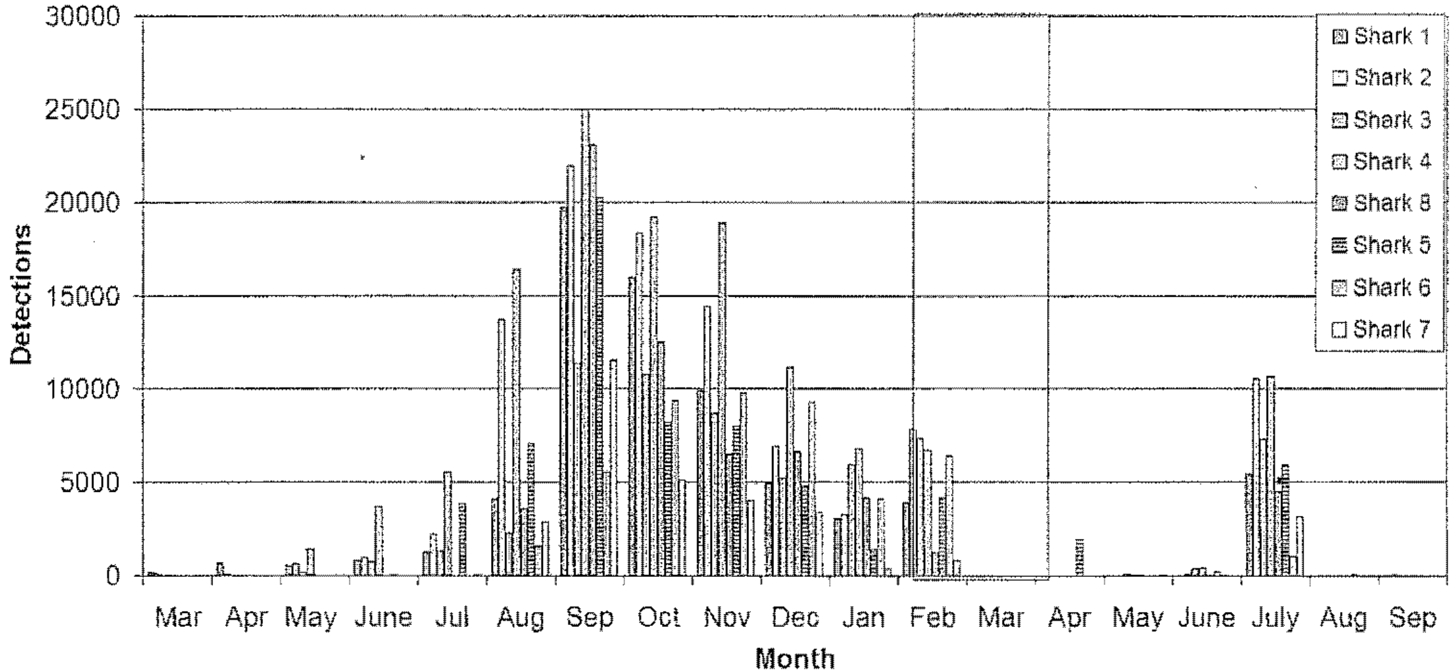


FIGURE 9. Total detections of signals recorded at Receiver 1 moored at the head of the Monterey Canyon by month. Sharks were tagged between 1 March 2005 and 10 August 2005. The shaded box indicates a period of time in which Receiver 1 was missing (22 February – 20 April 2006). The detections in the chart for February 2006 and April 2006 were recorded prior to 22 February 2006 and after 20 April 2006 when there was a working receiver deployed.

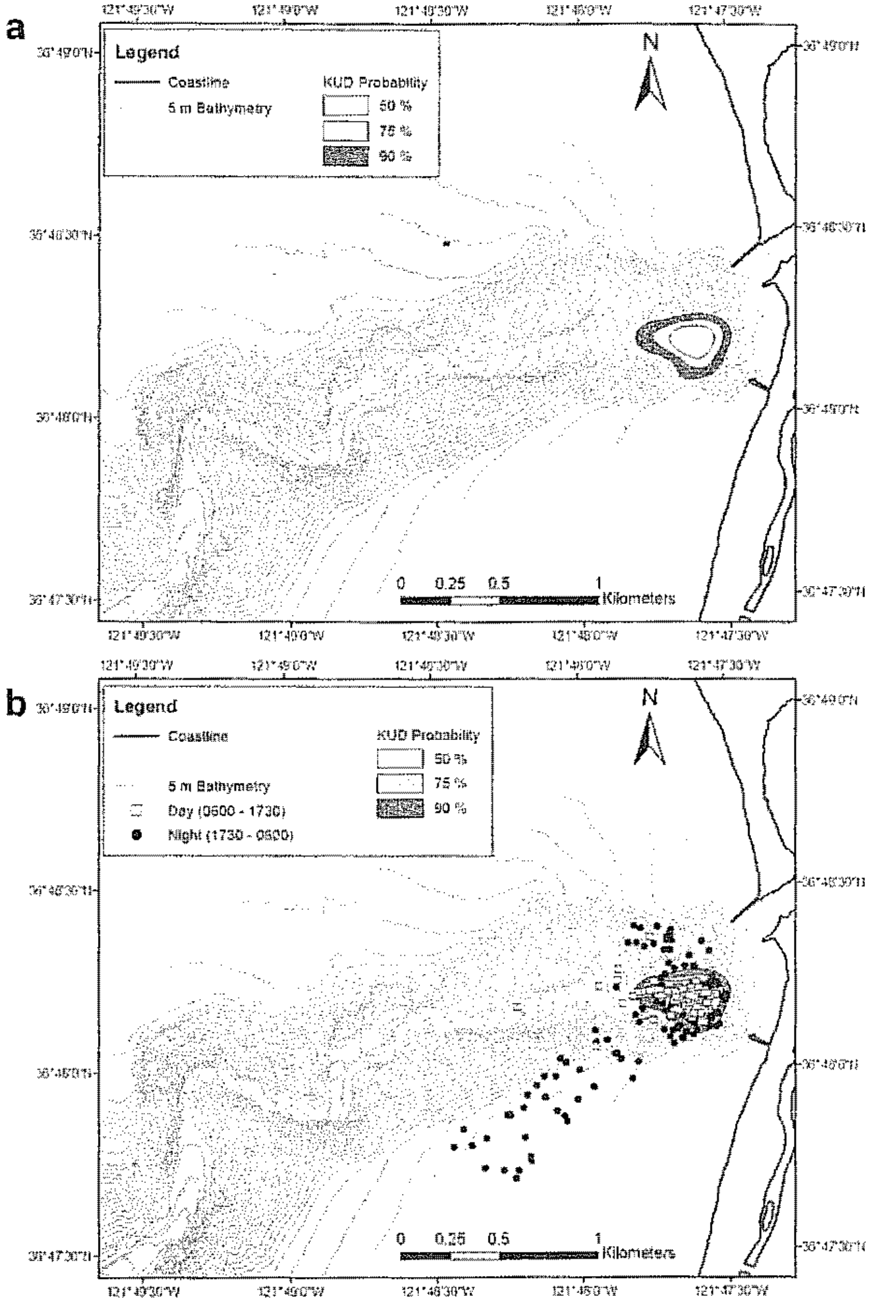


FIGURE 10. (a) The 50, 75, & 90% kernal utilization distributions (KUD) for a 220 cm (TL) female prickly shark (Tag no. 10). (b) Individual locational fixes obtained by manual tracking of shark no. 10 are shown for Day (0600 – 1730 h) and Night (1730 – 0600 h) tracking periods. Dark gray contour is the 90% KUD, the lighter gray contour is the 75% KUD, and the white contour is the 50% KUD.

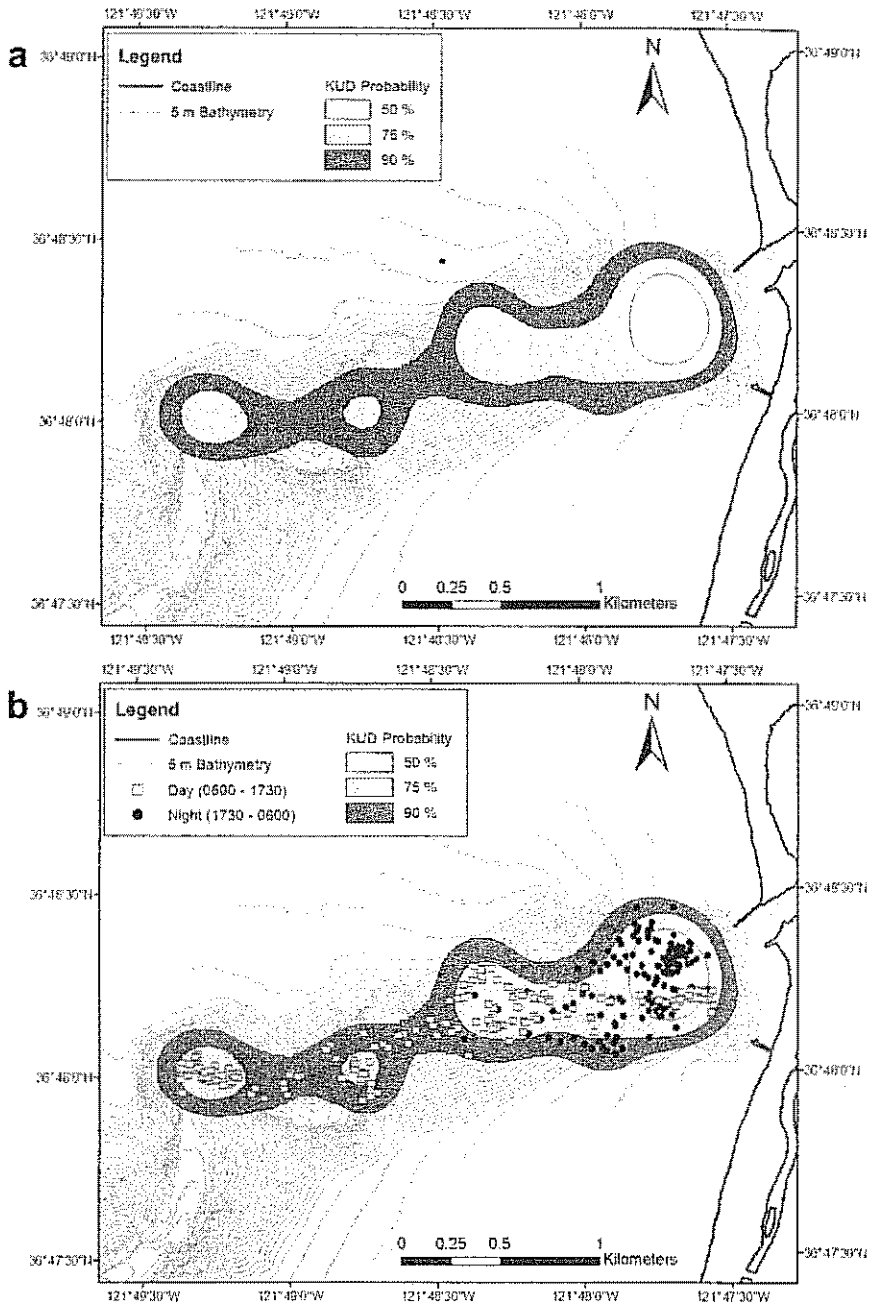


FIGURE 11. (a) The 50, 75, & 90% kernal utilization distributions (KUD) for a 178 cm (TL) male prickly shark (Tag no. 11). (b) Individual locational fixes obtained by manual tracking of shark no. 11 are shown for Day (0600 – 1730 h) and Night (1730 – 0600 h) tracking periods. Dark gray contour is the 90% KUD, the lighter gray contour is the 75% KUD, and the white contour is the 50% KUD.

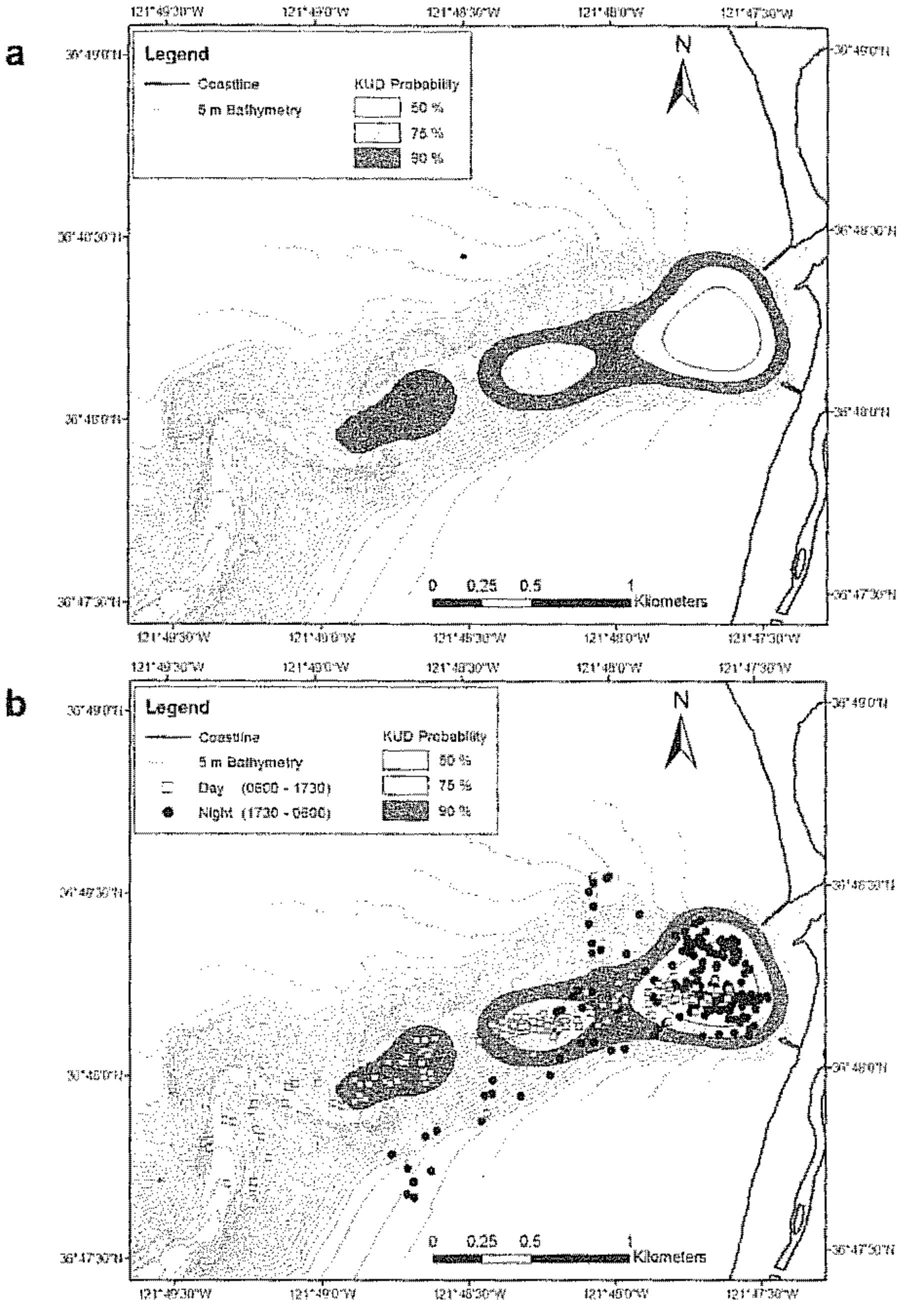


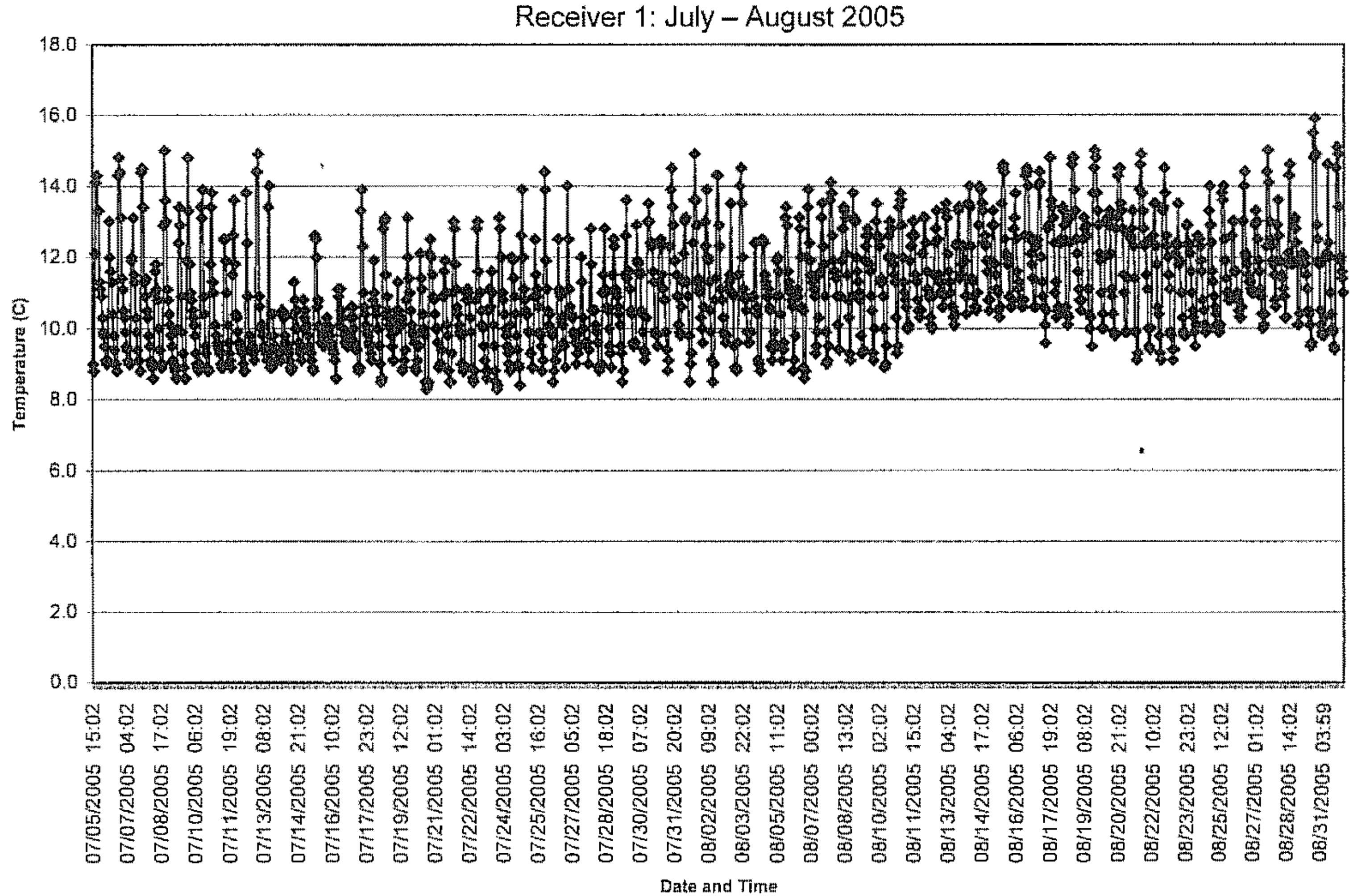
FIGURE 12. (a) The 50, 75, & 90% kernal utilization distributions (KUD) for a 184 cm (TL) male prickly shark (Tag no. 12). (b) (b) Individual locational fixes obtained by manual tracking of shark no. 12 are shown for Day (0600 – 1730 h) and Night (1730 – 0600 h) tracking periods. Dark gray contour is the 90% KUD, the lighter gray contour is the 75% KUD, and the white contour is the 50% KUD

APPENDICES

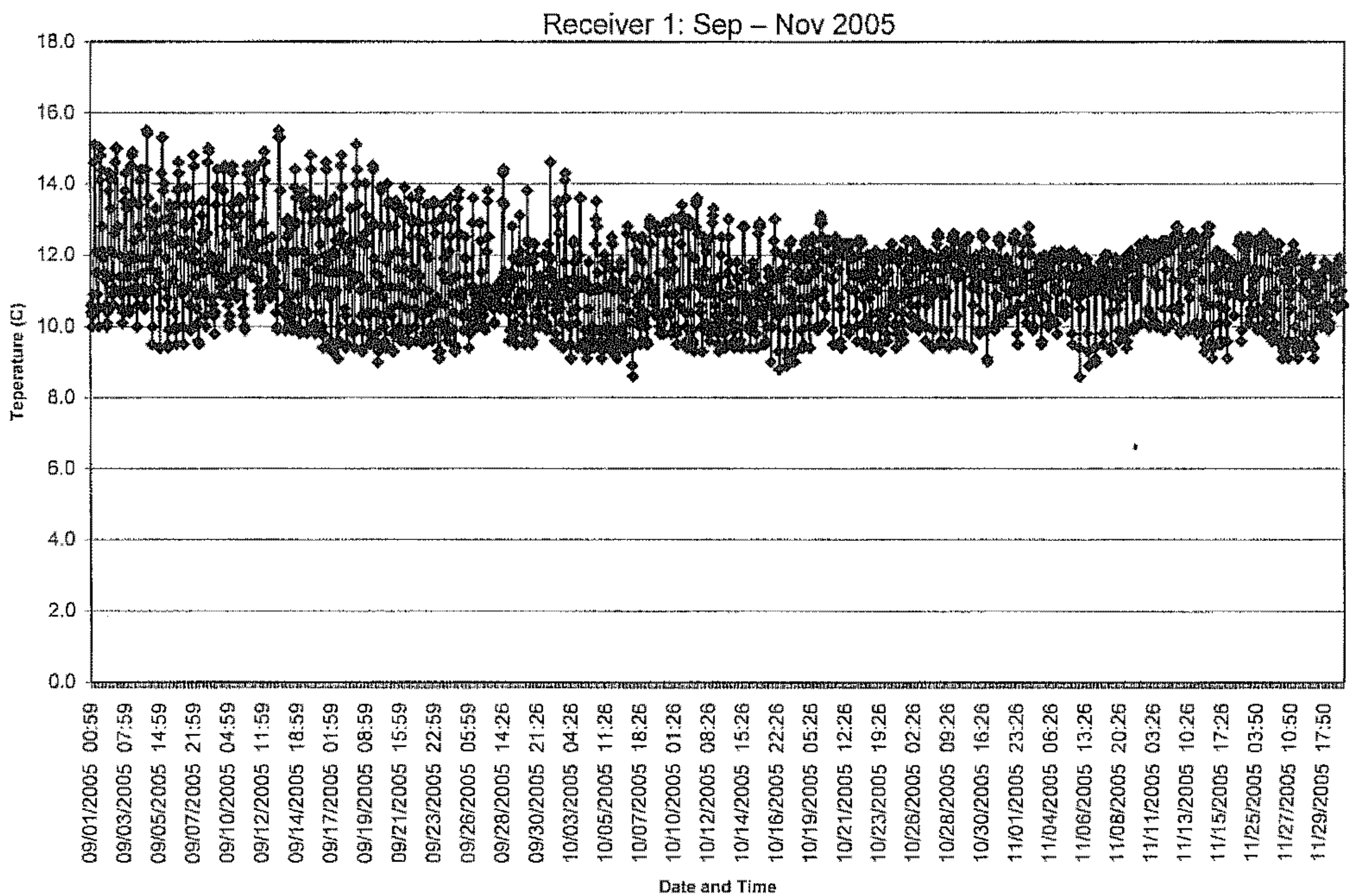
APPENDIX 1 - Detailed acoustic and external tag information

Study Shark ID	Serial #	Tag ID or Code	Freq. (kHz)	Depth sensor	Tracking type	Sex	Total Length (cm)	Date deployed	VIMS external tag	Battery dies
1	9501	5	69	No	VR-2	F	217	3/1/2005	none	2/10/2009
2	9503	7	69	No	VR-2	F	225	3/12/2005	171015	2/21/2009
3	9054	8	69	No	VR-2	F	190	5/12/2005	none	4/23/2009
4	9500	4	69	No	VR-2	F	184	5/12/2005	171013	7/25/2006
9	1793B	2	63	Yes	VR-60, VR-20	F	250	5/13/2005	none	8/23/2005
5	9497	1	69	No	VR-2	M	176	6/24/2005	171014	9/6/2006
13	4731B	15	32.8	Yes	CHAT	F	270	7/26/2005	171016	7/26/2006
14	5005B	31	32.8	Yes	CHAT	F	225	7/27/2005	171018	7/27/2006
6	9499	3	69	No	VR-2	M	170	7/27/2005	171017	10/9/2006
7	1790B	34	69	No	VR-2	M	200	7/28/2005	171020	7/28/2006
15	5006B	47	32.8	Yes	CHAT	F	198	8/9/2005	171022	8/9/2006
8	9498	2	69	No	VR-2	F	175	8/9/2005	171021	10/22/2006
10	1795B	4	78	Yes	VR-60, VR-20	F	220	8/10/2005	171012	11/18/2005
11	1794B	3	75	Yes	VR-60, VR-20	M	178	8/10/2005	171019	11/18/2005
12	1792B	12	54	Yes	VR-60, VR-20	M	184	8/10/2005	171023	11/18/2005
N/A	External tag ONLY					M	164	8/10/2005	171024	N/A
N/A	External tag ONLY					M	177	10/9/2006	171027	N/A
N/A	External tag ONLY					M	181	10/9/2006	171032	N/A
N/A	External tag ONLY					M	172	10/9/2006	171033	N/A

APPENDIX 2 - Temperature data collected at Receivers 1 and 3

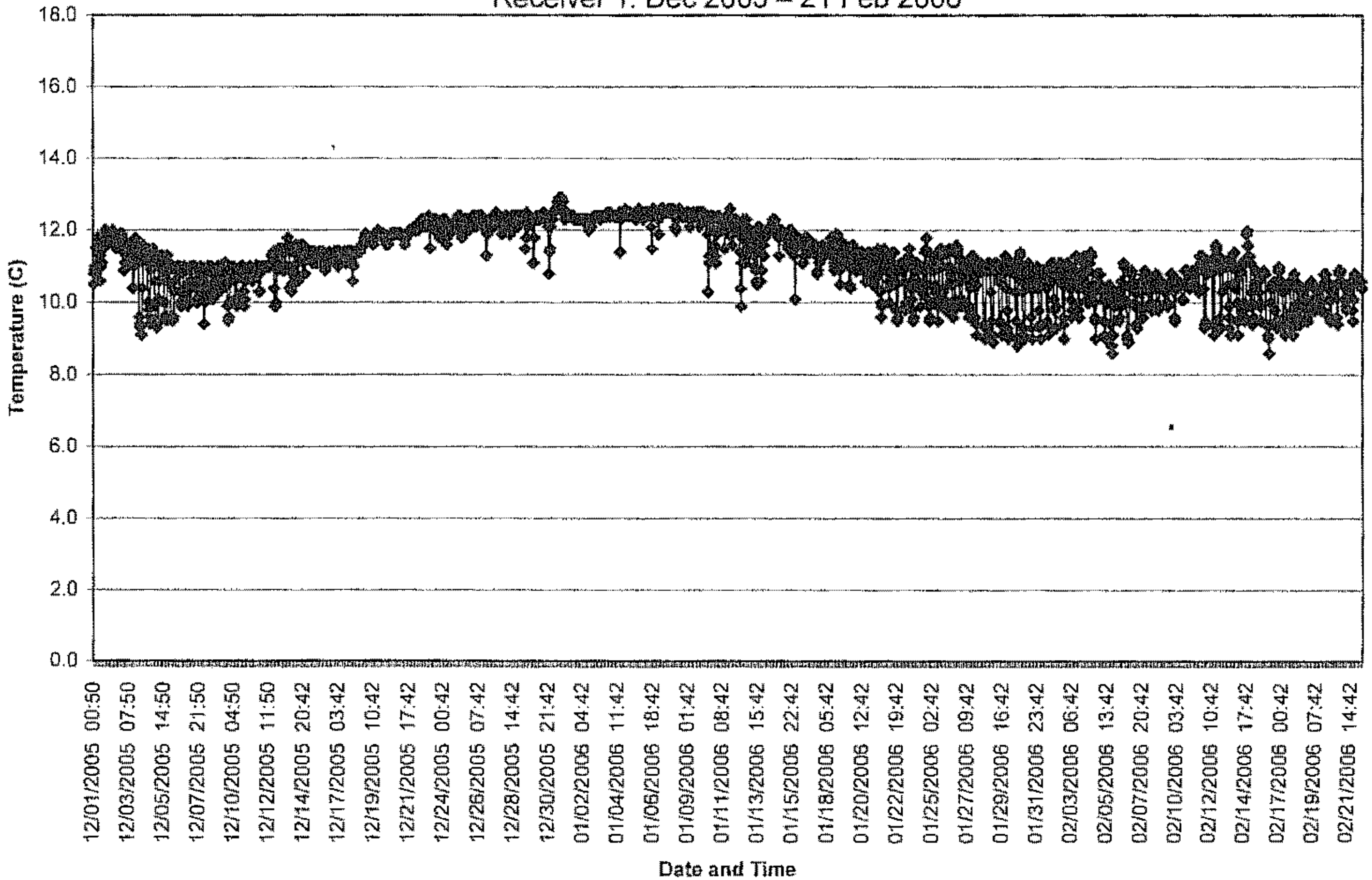


APPENDIX 2 - Continued



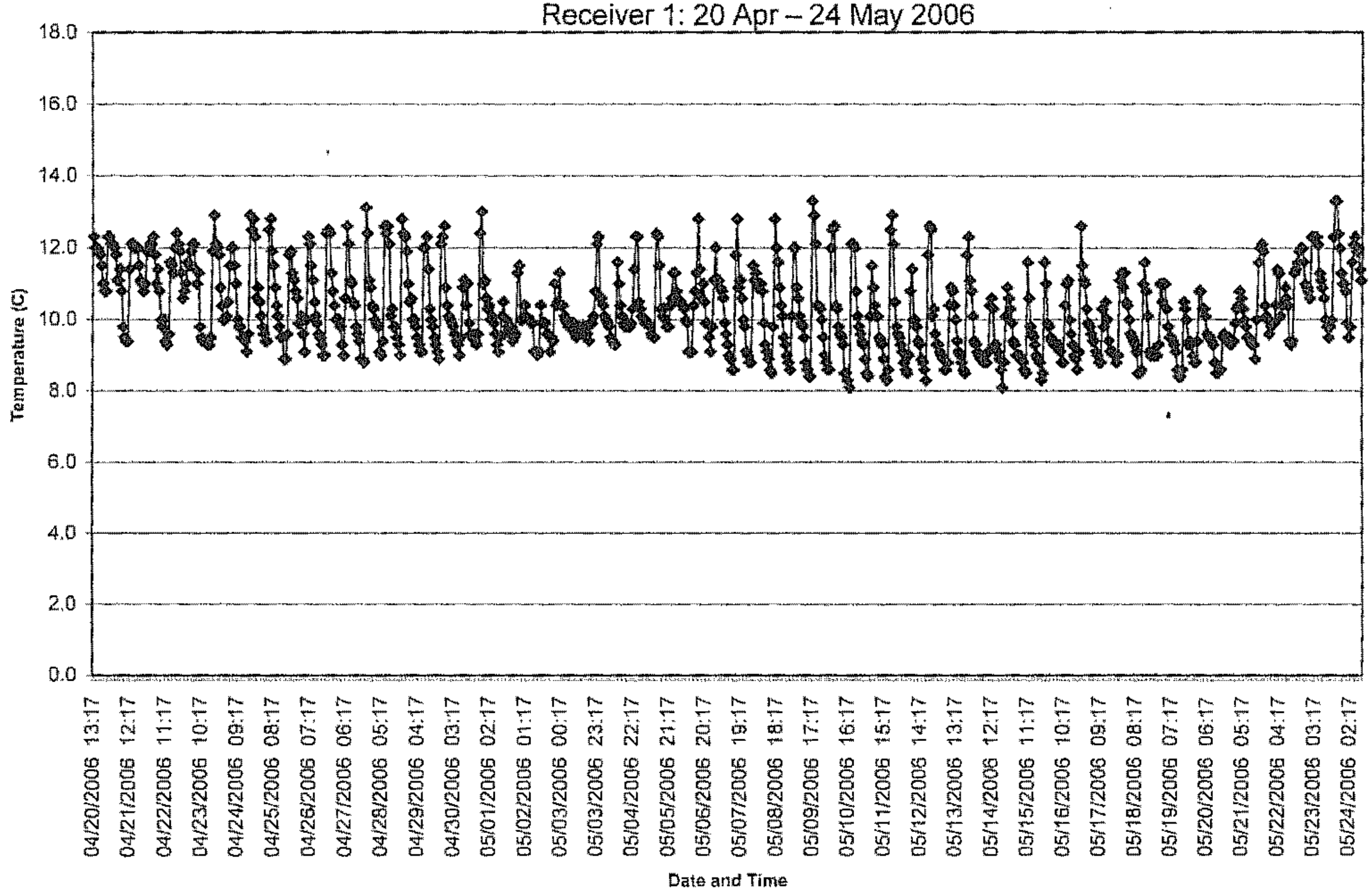
APPENDIX 2 - Continued

Receiver 1: Dec 2005 – 21 Feb 2006

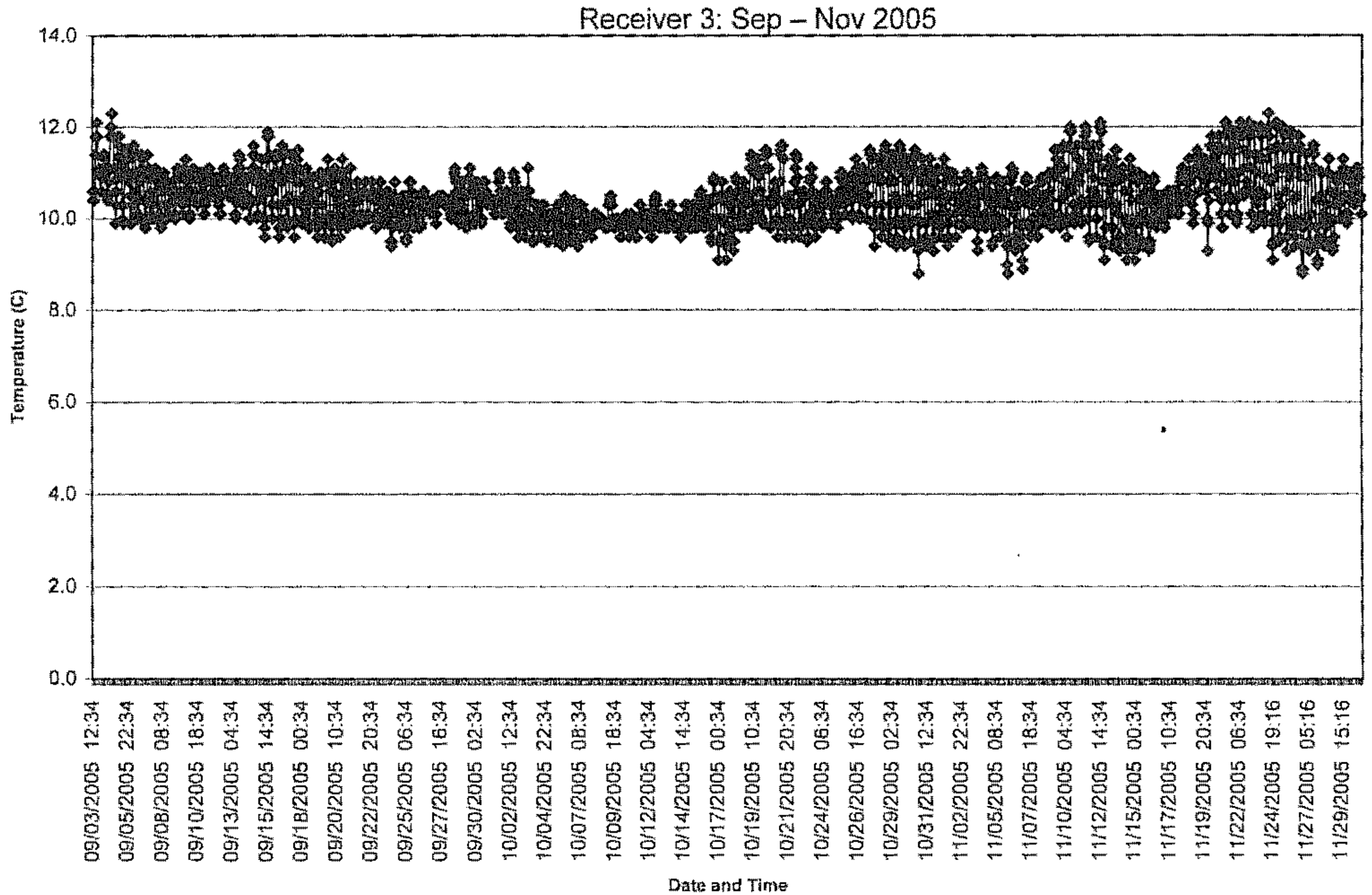


APPENDIX 2 - Continued

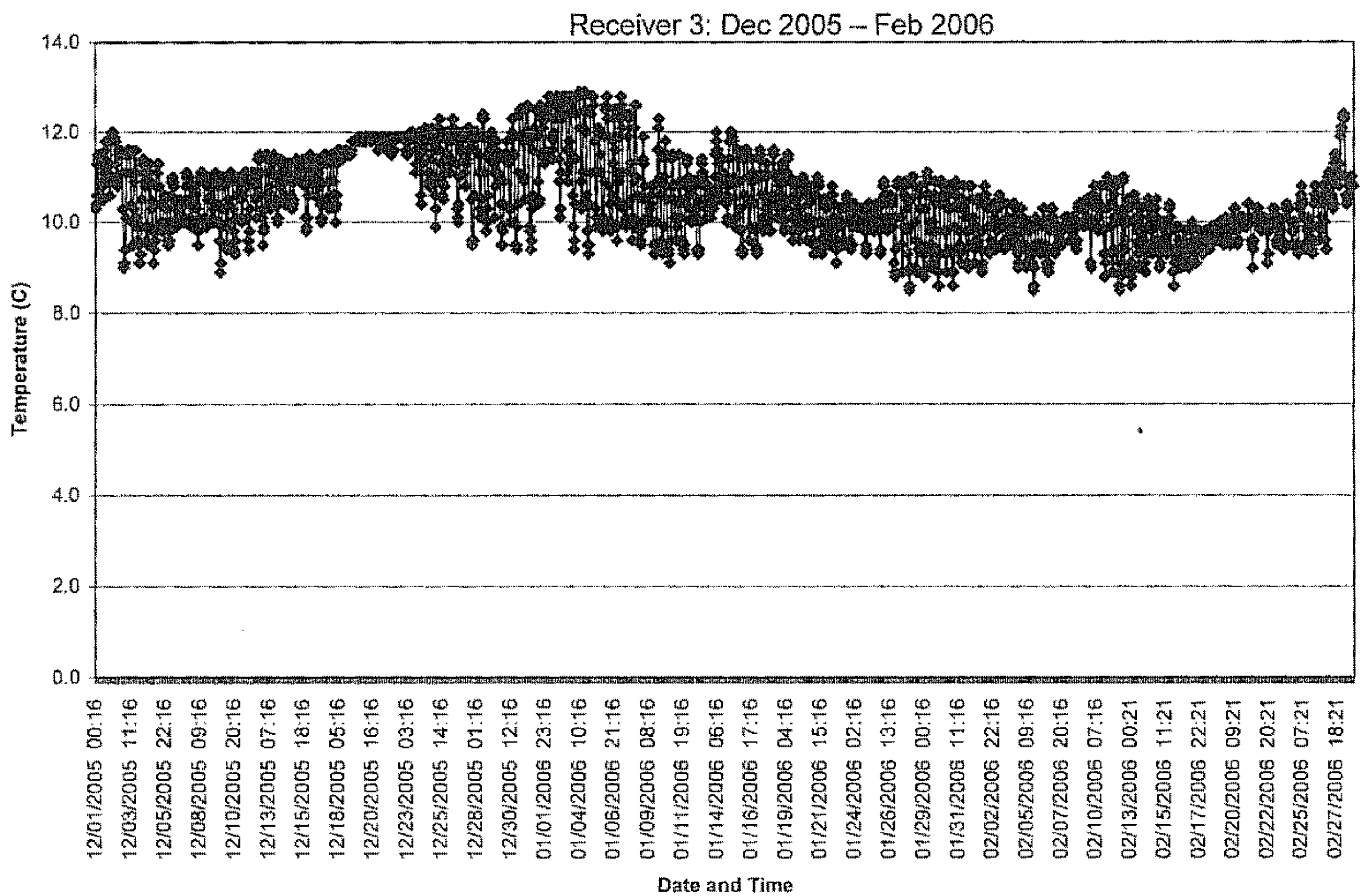
Receiver 1: 20 Apr – 24 May 2006



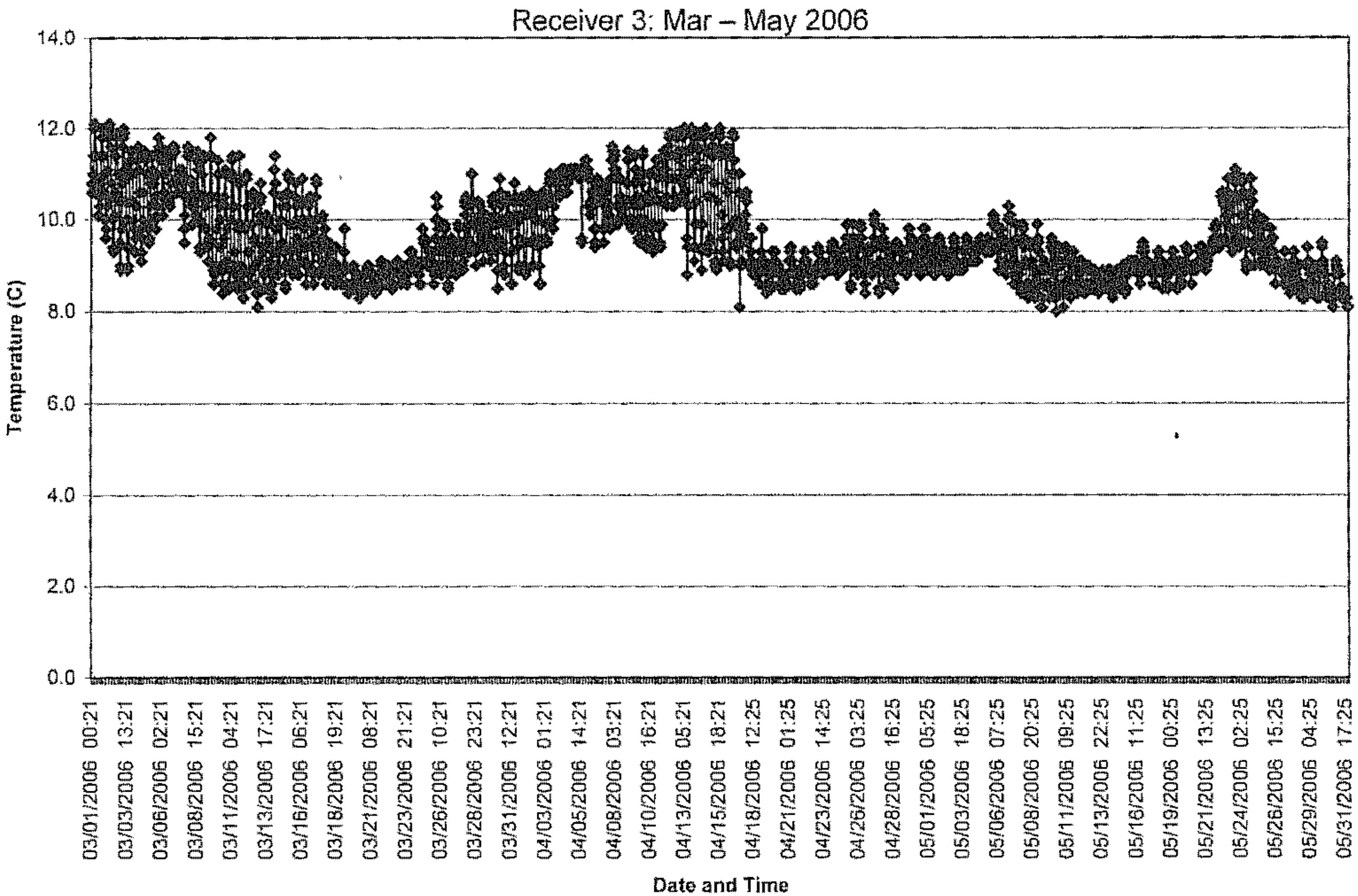
APPENDIX 2 - Continued



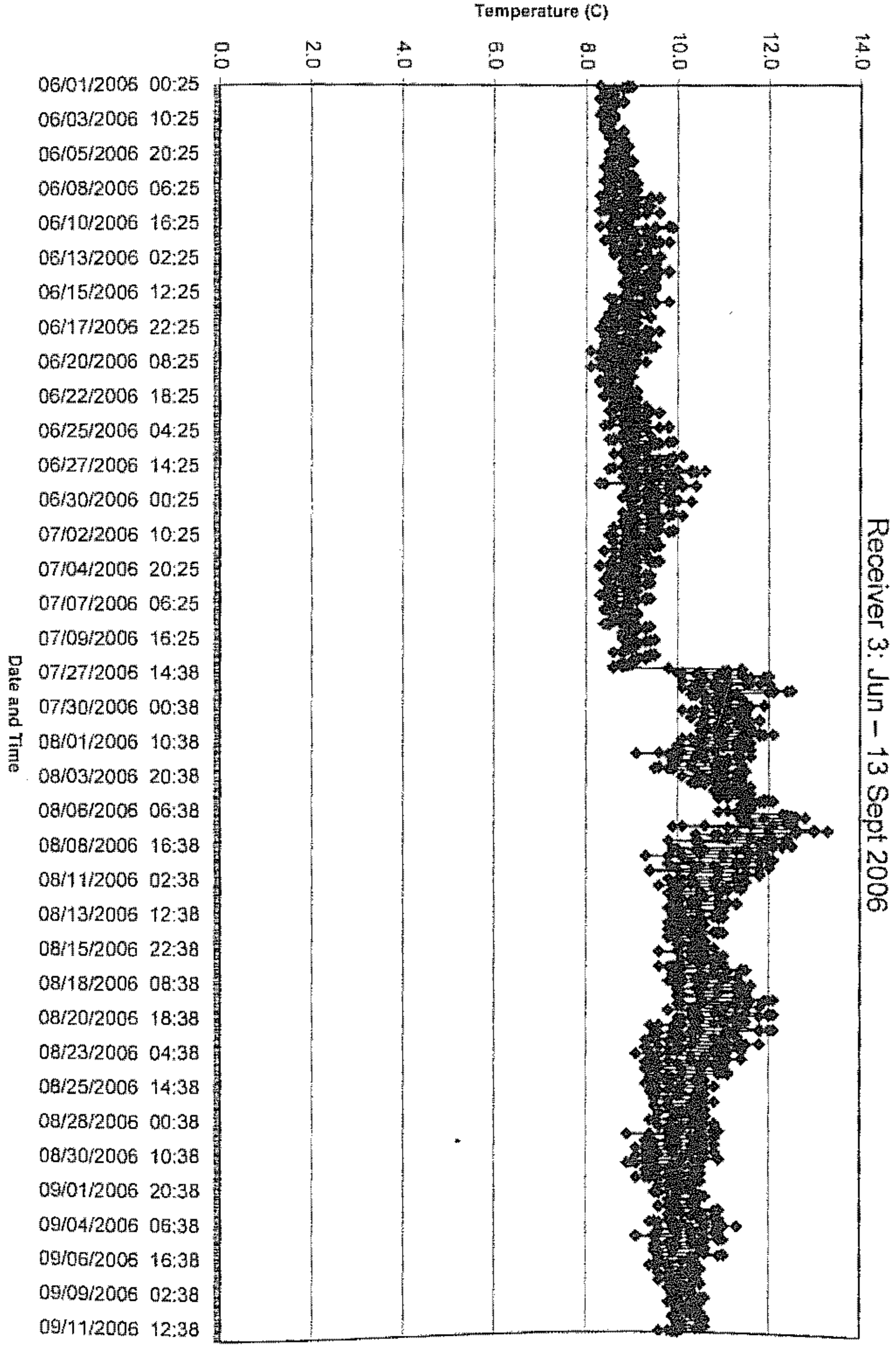
APPENDIX 2 - Continued



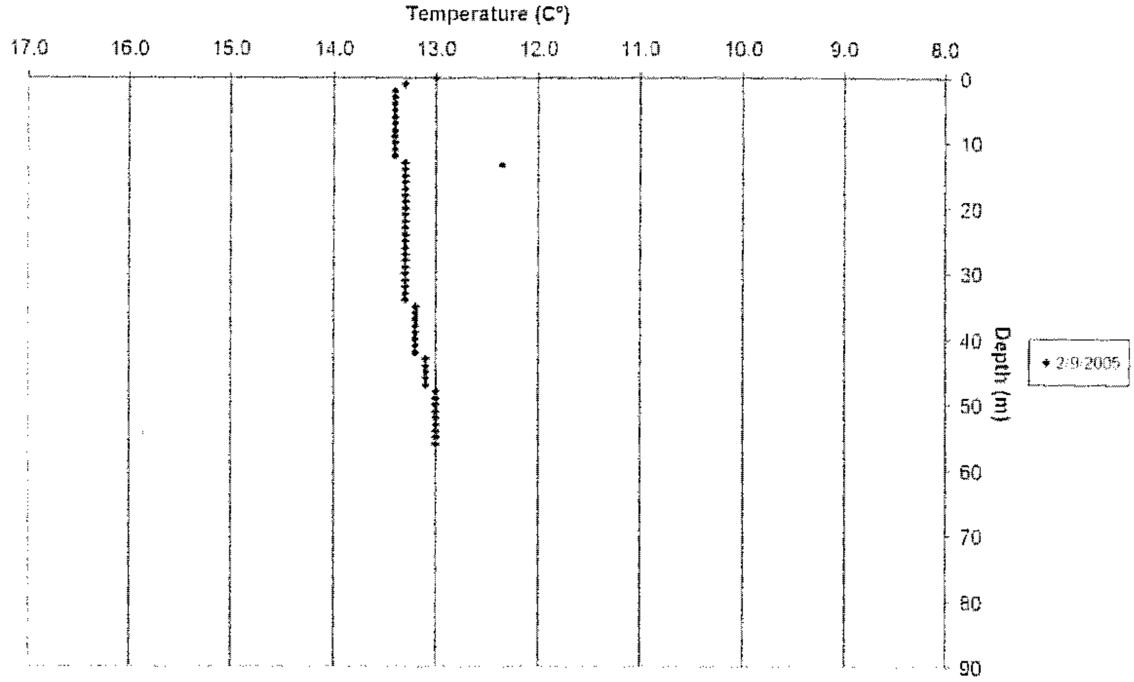
APPENDIX 2 - Continued

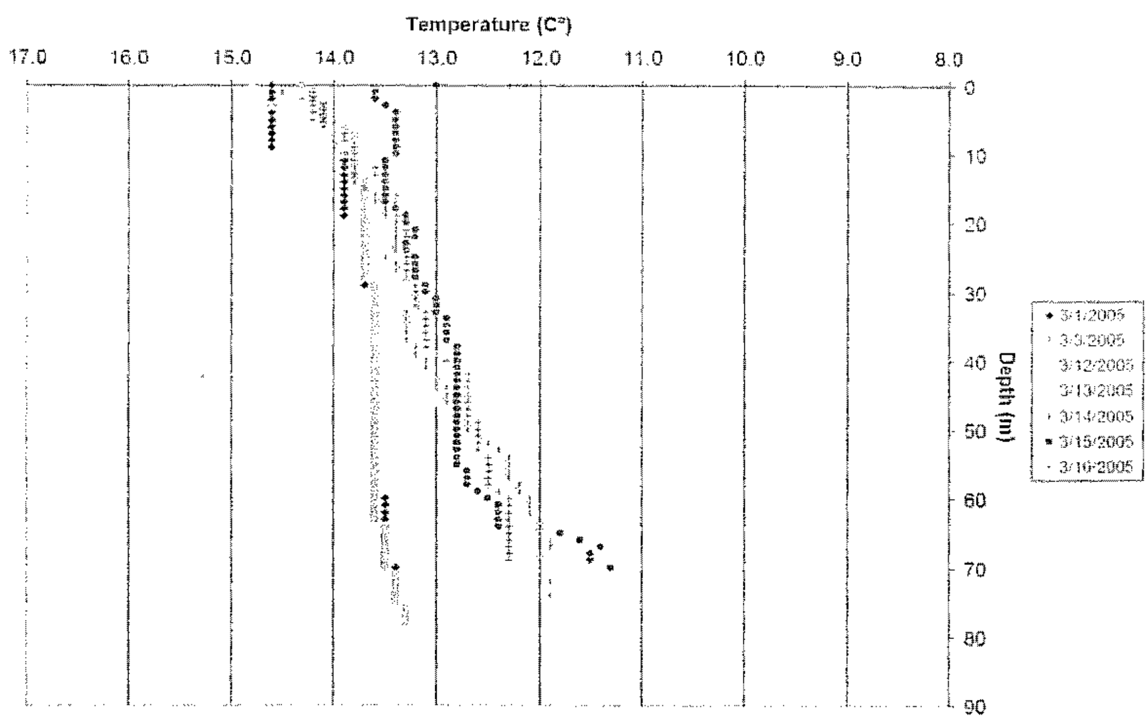


APPENDIX 2 - Continued

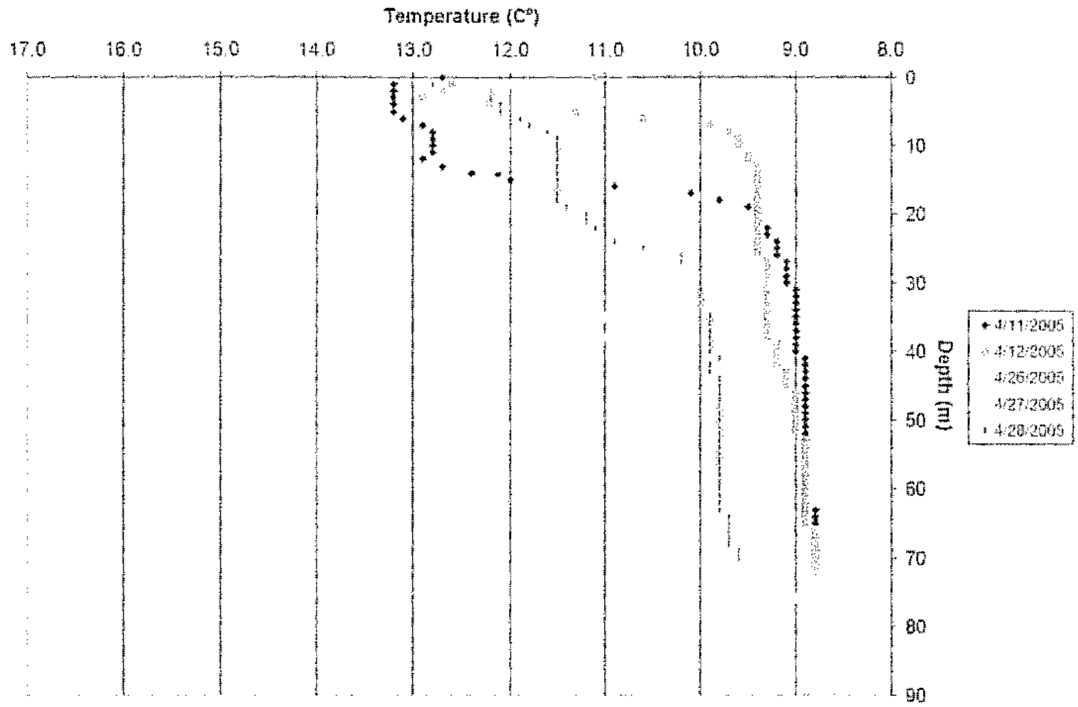


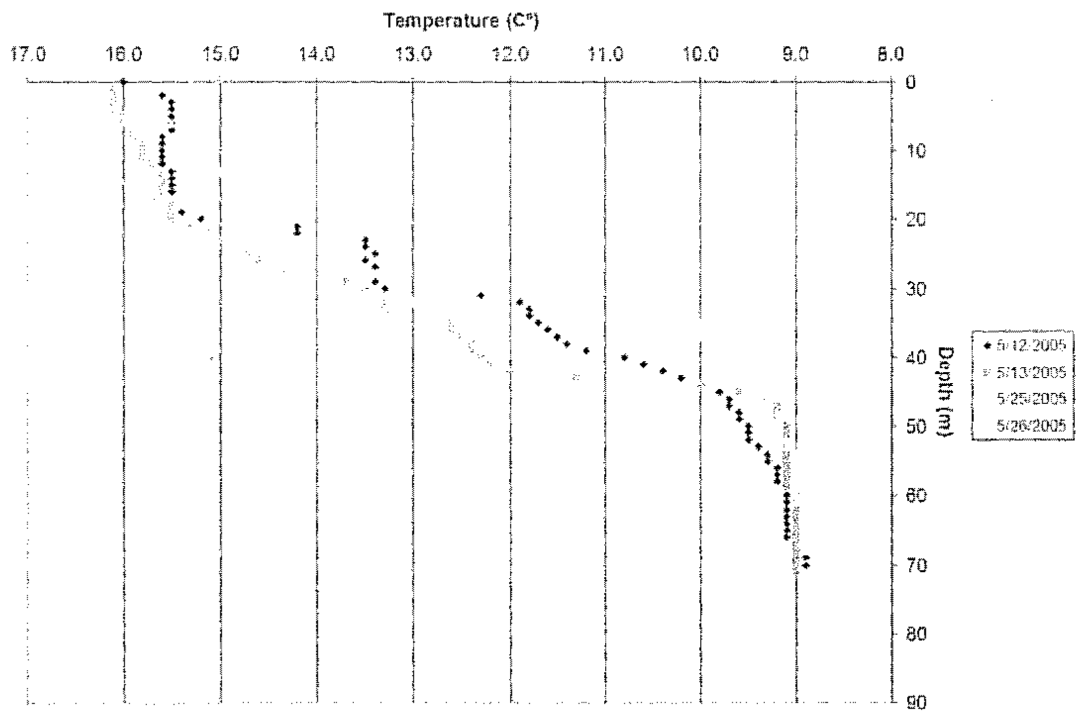
APPENDIX 3 - Temperature profile of the water column during fishing operations





APPENDIX 3 - Continued





APPENDIX 3 - Continued