MOVEMENTS AND HABITAT USE OF FEMALE LEOPARD SHARKS IN ELKHORN SLOUGH, CALIFORNIA

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ABSTRACT

MOVEMENTS AND HABITAT USE OF FEMALE LEOPARD SHARKS IN ELKHORN SLOUGH, CALIFORNIA

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From May 2003 to February 2005, 20 female leopard sharks (78 – 140 cm TL) were tagged with acoustic transmitters in Elkhorn Slough, California, and their movements and habitat use were examined using acoustic tracking techniques. Nine sharks were manually tracked for 20-71.5 h, and 11 sharks were monitored for 4-443 d using an array of acoustic receivers. Use of different regions in Elkhorn Slough by tagged sharks changed seasonally and was associated with changes in temperature, salinity, and dissolved oxygen. Sharks used Elkhorn Slough National Estuarine Research Reserve (ESNERR) extensively throughout the year, but especially during the spring and summer. ESNERR appeared to be important as both a foraging and nursery area, likely due to the abundance of intertidal mudflats. Movements and habitat use were tidally influenced, and likely were related to the distribution of important prey items in Elkhorn Slough.

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INTRODUCTION

Elasmobranchs are commonly found in shallow coastal areas such as bays and estuaries (Snelson & Williams 1981, Castro 1993, Simpfendorfer & Milward 1993, Schwartz 1995). Due to the high productivity of these environments, bays and estuaries play an important role in the life history of many sharks and rays (Springer 1967, Castro 1993, Simpfendorfer & Milward 1993), and have for at least 320 million years (Lund 1990). Because top-level predators are important in regulating marine ecosystems, especially in maintaining the stability of food webs, elasmobranchs are an important part of these communities (Kitchell et al. 2002, Bascompte et al. 2005).

One of the reasons bays and estuaries are important in the life history of many elasmobranchs is that they frequently function as nursery areas, especially for coastal species of viviparous sharks and rays (Springer 1967, Gruber et al. 1988, Martin & Cailliet 1988, Branstetter 1990, Castro 1993, Morrisey & Gruber 1993, Simpfendorfer & Milward 1993, Merson & Pratt Jr. 2001, Rechisky & Wetherbee 2003). Shallow habitats are relatively inaccessible for larger predators, such as adult conspecifics or larger species of elasmobranchs, which are a source of significant mortality for neonate and smaller elasmobranchs (Springer 1967, Van der Elst 1979). Also, these shallow areas contain a great abundance and diversity of prey for foraging and have warmer waters that may be conducive to rapid growth and improved physiological rates (Bushnell et al. 1989, Branstetter 1990, Castro 1993, Morrissey & Gruber 1993). These factors may increase survivorship and growth rates of neonate and juvenile elasmobranchs, which are important factors in cohort recruitment and strength (Branstetter 1990). Bass (1978) divided nursery areas into primary areas where parturition occurs and neonates reside for a period of time, and secondary areas where juveniles reside for a period of time. These areas may be geographically discrete or overlapping.

The leopard shark (*Triakis semifasciata*) is one of the most common nearshore sharks in California and is especially abundant in bays and estuaries in central and northern California. It is endemic to the Northeast Pacific and occurs from Mazatlan, Mexico to Willipa Bay, Washington (Miller & Lea 1972, Ebert & Ebert 2005). It is an opportunistic predator that feeds on a variety of benthic invertebrates and fishes, although it feeds primarily on fat innkeeper worms (*Urechis caupo*), small fishes, crustaceans, and clams (Russo 1975, Talent 1976, Barry et al. 1996, Kao 2000). They forage extensively in the intertidal zone (Webber & Cech Jr., Ackerman et al. 2000), and are physiologically suited to forage intertidally throughout the diel cycle (Miklos et al. 2003). Leopard sharks exhibit the life history traits typical of sharks and rays. They are relatively long-lived (up to 30 yrs), late maturing (about 7 yrs for males, 10 yrs for females), have long gestation times (10 – 12 mos), long generation times (22.35 yrs), and low fecundity (7 – 36 offspring) (Cailliet 1992, Smith 2001). As a result, demographic analyses indicate that they are susceptible to overfishing (Cailliet 1992, Kusher et al. 1992, Au & Smith 1997). They are fished commercially and recreationally, with the recreational fishery recently accounting for the majority of the leopard shark landings in California (Smith 2001).

Little is known about the large-scale movements and population structure of leopard sharks along the west coast of North America. Tag-recapture data indicate that although leopard sharks are capable of swimming long distances there is limited exchange between regional populations (Smith & Abramson 1990, Smith 2001). A leopard shark tagged in San Francisco Bay, CA was recaptured in Santa Monica Bay (approximately 600 km distance), CA after ten years at liberty (Smith 2001), and sharks tagged in San Francisco Bay have been recaptured in Elkhorn Slough, CA (approximately 150 km distance) and vice versa (Smith & Abramson 1990). A shark tagged with an acoustic transmitter on the coast of Santa Catalina Island, CA, swam to Carlsbad, CA, a distance of 105 km, in seven days (Hight 2005), indicating that these sharks also can cross deep water. This indicates that there is gene flow across distances of hundreds of kilometers, although the amount of exchange is limited. In San Francisco Bay, tag recapture data indicated that leopard sharks were mostly resident, but at least 10% of the sharks leave the bay during the fall and winter for coastal areas (Smith & Abramson 1990). The only published telemetry study of leopard sharks was conducted by Ackerman et al. (2000) in Tomales Bay, CA, which showed that the movements of leopard sharks were tidally influenced.

Elkhorn Slough is a shallow, highly productive seasonal estuary located at the head of Monterey Bay in central California (Figure 1), which is used extensively by elasmobranchs. Seven species of sharks and rays commonly inhabit Elkhorn Slough (Talent 1985). These include leopard sharks, bat rays (*Myliobatis californica*), shovelnose guitarfish (*Rhinobatos productus*), thornbacks (*Platyrhinoidis triseriata*), gray smoothhounds (*Mustelus californicus*), brown smoothhounds (*Mustelus henlei*), and round stingrays (*Urobatis halleri*). Currently leopard sharks, bat rays, and thornbacks are the most common species in Elkhorn Slough. In addition, torpedo rays (*Torpedo californica*), spiny dogfish (*Squalus acanthias*), and big skates (*Raja binoculata*) also have been recorded in Elkhorn Slough on several occasions (Carlisle et al. in review). Leopard sharks occur in the slough year round (Talent 1985), but are seasonally abundant during spring, summer, and fall (Barry 1983, Yoklavich 1991).

As has been documented in other estuaries, Elkhorn Slough serves as a nursery area for a number of these elasmobranchs. These include the leopard shark (Ackerman 1971, Barry 1983, Talent 1985), bat ray (Barry 1983, Talent 1985, Martin & Cailliet 1988), gray smoothhound (San Filippo 1995), and possibly the shovelnose guitarfish (Herald et al. 1960). The abundance and diversity of potential prey, warm water, and lack of large predators make Elkhorn Slough a suitable nursery area.

Elkhorn Slough has undergone substantial anthropogenic changes during the last 150 yrs, mainly through diking of marshlands for agricultural purposes, channel construction for habitat restoration, destruction of levees, and the creation of Moss Landing harbor in 1947 (Van Dyke & Wasson 2005). These changes have contributed to the severe erosion of the major sedimentary habitats and have had dramatic impacts on the Slough's biological communities (Van Dyke & Wasson 2005). Habitat alteration likely has impacted Elkhorn Slough's function as a nursery area. In the 1970s, tidal creeks were used as nursery areas by leopard sharks (Barry 1983), but those habitats have since experienced significant amounts of erosion, becoming wider and deeper (Van Dyke & Wasson 2005). In addition, habitat alteration has altered the abundance, distribution, and diversity of prey, which has impacted composition, abundance, and trophic patterns of the ichthyofaunal assemblage of the slough (Wasson et al. 2002, Yoklavich et al. 2002). The fish and invertebrate assemblages of the slough have decreased in diversity, and as a result, the diets of fishes have become less diverse as well. This is likely due to alteration of the substrate through erosion (Kvitek et al. 1996, Lindquist 1998, Yoklavich et al. 2002).

The feeding ecology of leopard sharks also has been impacted by changes in the slough. In the 1970's leopard sharks exhibited an ontogenetic shift in their diets, with smaller sharks (< 90 cm) primarily consuming small yellow shore crabs (*Hemigrapsus oregonensis*), and larger sharks eating a number of species of crabs, clams, fishes, fish eggs, and fat innkeeper worms. Fishes, crabs, and fat innkeeper worms were the most important prey items in the diet of larger sharks, although fat innkeeper worms were the single most important prey item (Ackerman 1971, Talent 1976). Most recently, Kao (2000) reported that the diet of leopard sharks was less diverse than in previous studies and that the ontogenetic shift in diet was no longer apparent as the diets of small and large sharks had converged upon fat innkeeper worms and fishes, with crabs and clams becoming minor components of the diet.

Kao (2000) suggested that the change in diet was a result of erosion and the impact of sea otters (*Enhydra lutris*) on the invertebrate community. Sea otters in Elkhorn Slough feed extensively on crabs and clams (Kvitek et al. 1988, Jolly 1997, Wilkins 2003), which might lead them into direct competition with leopard sharks. Fat innkeeper worms have increased in abundance since the 1970s (Kvitek et al. 1996), which may have lead to the increase in their importance in leopard shark diet.

Although much is known about biology of leopard sharks in Elkhorn Slough, patterns of movement, habitat use, and residency within the slough are unknown. Information about the spatial dynamics of leopard sharks is needed to gain a more complete understanding of how these top level predators use estuarine environments, which is important because as predators, leopard sharks can have important community wide effects in bays and estuaries (Brown et al. 1999, Stevens et al. 2000, Dill et al. 2003). In addition, because the modification of Elkhorn Slough is ongoing, it is important to identify critical habitats so that steps can be taken to preserve and restore potential essential fish habitat (defined as those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity). Information on habitat use and movements also would be applicable to other bays in central and northern California, which is useful because over 91% of California's coastal wetlands have been lost or heavily degraded (Larson 2001), and these regions are used extensively by leopard sharks.

Collecting the type of data needed to examine movements and habitat use of mobile marine organisms such as elasmobranchs has traditionally been difficult logistically and technologically, but acoustic telemetry is a tool that allows researchers to overcome this problem (Arnold & Dewar 2001). Most telemetry studies have been on coastal and pelagic species of elasmobranchs (McKibben & Nelson 1986, Gruber et al. 1988, Holts & Bedford 1993, Nelson et al. 1997, Goldman & Anderson 1999, Gunn et al. 1999), whereas fewer have been conducted on elasmobranchs in bays and estuaries. Telemetry studies conducted in bays and estuaries have indicated the importance of these regions as nursery areas (Holland et al. 1993, Morrissey & Gruber 1993, Heupel & Heuter 2001, Merson & Pratt Jr. 2001, Sims et al. 2001, Rechisky & Wetherbee 2003) as well as feeding areas (Teaf 1980, Ackerman et al. 2000, Matern et al. 2000, Cartamil et al. 2003).

In bays and estuaries, elasmobranchs exhibit diel and tidal patterns of movement. Diel patterns of movement have been observed on numerous occasions in elasmobranchs in coastal areas (Sciarotta & Nelson 1977, Standora & Nelson 1977, McKibben & Nelson 1986, Gruber et al. 1988, Klimley et al. 1988, Holland et al. 1993, Lowe et al. 1996, Nelson et al. 1997), but they have been rarely observed in enclosed bays or estuaries (Holland et al. 1993, Hopkins 1993, Matern et al. 2000). Tidal patterns of movement in bays and estuaries have been documented more frequently than diel patterns, and have been observed in leopard sharks (Ackerman et al. 2000), sandbar sharks (*Carcharhinus plumbeus*) (Huish & Benedict 1978), dusky sharks (*Carcharhinus obscurus*) (Medved & Marshall 1983), Atlantic stingrays (*Dasyatis sabina*) (Teaf 1980), cownose rays (*Rhinoptera bonasus*) (Smith & Merriner 1985) and spotted eagle rays (*Aetobatus narinari*) (Silliman & Gruber 1999). These tidally influenced movements generally have been attributed to foraging.

The main objectives of this study were to: 1) identify regions and habitats in Elkhorn Slough that are commonly used by female leopard sharks; and 2) examine patterns of movement and habitat use of female leopard sharks within Elkhorn Slough and how these vary with the tide. This research will increase our understanding of the ecology of leopard sharks and aid in the management and conservation of leopard sharks in central California through identification of critical habitats.

MATERIALS AND METHODS

Study Site

Elkhorn Slough, California is a shallow tidal wetland system located in central Monterey Bay (Figure 1). It is approximately 11 km long and extends eastward from the ocean about 6 km before turning north for an additional 5 km. It has a large central main channel and branching tidal creeks. These channels and tidal creeks are bordered by extensive mudflats and salt marsh composed primarily of pickleweed, *Salicornia virginica*. Together, the mudflats and salt marsh cover approximately 1,400 ha. The main channel is wider and deeper in the lower parts of the slough (200 m wide and 7.5 m deep at the mouth), but it narrows and becomes shallower in the upper regions (3 m wide and 1.5 m deep at Hudson's Landing). The Elkhorn Slough National Estuarine Research Reserve (ESNERR), which is part of NOAA's National Estuarine Research Reserve System and is managed by the California Department of Fish and Game (Caffrey et al. 2002, Caffrey & Broenkow 2002), occupies the southeastern part of the slough.

Substrates in Elkhorn Slough are primarily composed of organic-rich muds in the upper intertidal regions, a mix of organic-rich mud and inorganic muds and clays in lower intertidal regions, and predominately inorganic muds and clays in the subtidal areas (Malzone 1999). In the main channel, the sediments become less dense and consolidated further up in the slough (Malzone 1999). In the lower slough, much of the soft unconsolidated sediments have been scoured away, resulting in a more consolidated clay substrate (Kvitek et al. 1996).

Elkhorn Slough experiences mixed semidiurnal tides, with the strongest tides occurring in December and June and the weakest tides in March and September (Caffrey & Broenkow 2002). Temperatures increase in the spring and peak in the summer, after which they decrease to their lowest levels during the winter. Salinity decreases to its lowest levels in the winter due to winter rains, and the highest levels usually occur in summer due to evaporation, especially in upper parts of the slough. Dissolved oxygen generally is lower in areas further from the mouth, and seasonally the lowest levels are encountered in the late summer and fall, but also occur during periods of increased freshwater input.

Environmental conditions in the upper regions of Elkhorn Slough are more variable than the areas closer to the ocean. This is because a tidal prism, which in the 1970s was located approximately 5 km inland from the mouth, divides the slough into two distinct water bodies. The zone below the prism is similar to coastal waters and approximately 75% of its water volume is exchanged daily, whereas the water above the prism has a residence time of up to 300 d and generally has more variable environmental conditions (Broenkow 1977). In the regions below Hudson's Landing, temperatures can be as great as 27° C in the summer, and salinities can range from 37.7 ppt during the summer to 0 ppt during periods of increased runoff in the winter (Broenkow 1977, Caffrey & Broenkow 2002). In 2005 when data from Kirby Park were available, the temperature at Kirby Park ranged from 6.9° to 24.2° C (mean 16.9° C), salinity 0.9 to 36.4 ppt (mean 30.8 ppt), and dissolved oxygen approximately 0.5 mg l-1 to 15 mg l-1 (mean approximately 8.5 mg l-1). (NSF/MBARI LOBO Project, unpublished data available at http://www.mbari.org/lobo).

In ESNERR, conditions also are more variable than in the lower regions of the main channel. In 2003 and 2004, the temperature ranged from 8.9° to 24.1° C (mean 16° C), salinity 20.9 to 34.7 ppt (mean 31 ppt), and dissolved oxygen 0 to 15.8 mg l-1 (mean 6.9 mg l-1). The areas of the main channel closer to the ocean are less variable than the upper regions of the slough and ESNERR and are more similar to conditions found in the Monterey Bay. In 2003 and 2004, the temperature ranged from 9° to 21° C (mean 14° C), salinity 24.5 to 34.3 ppt (mean 32 ppt), and dissolved oxygen 3 to 15.6 mg l-1 (mean 7.6 mg l-1) (ESNERR unpublished data) (Appendix A).

Elkhorn Slough has changed greatly during the last several decades. The most dramatic period of change started around 1947 when the Army Corps of Engineers created Moss Landing Harbor. This opened up Elkhorn Slough to direct tidal flow, which had been a sluggish wetland system with muted tides. In addition, during the course of the following decades, several diked areas were reopened to tidal flow. This change in tidal dynamics greatly increased erosion and changed the slough from a depositional to an erosional area (Caffrey & Broenkow 2002). Elkhorn Slough would likely have filled in and become a dry alluvial valley with intermittent streams within 2000 – 3000 yr if Moss Landing Harbor had not been created (Schwartz 1984, Schwartz et al. 1986).

The increase in erosion is due to increased tidal flow and volume. The creation of the Elkhorn Slough National Estuarine Research Reserve (ESNERR) marsh restoration site in 1983 also had an impact on the slough as it increased the total volume of the Slough by 30% (Malzone & Kvitek 1994). Overall the tidal volume of Elkhorn Slough increased by greater than 200% since 1947 (Crampton 1994, Malzone 1999). The average cross section width of tidal creeks has increased from 2.5 m 1931 to 12.4 m 2003 (Van Dyke & Wasson 2005). The main channel has increased in width from 60 m in 1940 to 200 m in the 1990s, and the depth at the mouth of the slough has increased from 2 m in 1940 to 7.5 m in 2002 (Caffrey & Broenkow 2002). Tidal currents at the mouth of the slough have increased from around 40 – 60 cm/sec in the 1970 to up to 147 cm/sec in the late 1990s (Malzone 1999), and currents of up to 171 cm/sec have been recorded in Long Canyon (Caffrey & Broenkow 2002). These changes have made the channels and tidal creeks wider and deeper and have converted salt marsh into mudflats. As a result, degraded marshland and mudflats are now the primary habitats in Elkhorn Slough, whereas before the opening of Moss Landing Harbor in 1947, there were no deep channels or intertidal mudflats (Van Dyke & Wasson 2005).

Tagging

I captured and tagged leopard sharks at the mouth of the lagoon in ESNERR, in Long Canyon, and at Kirby Park (Figure 1). Monofilament gillnets of different length and mesh size (20 m x 2 m, 12.7 cm stretch mesh; 15 m x 1.5 m, 10.2 cm stretch mesh) were set perpendicular to shore to capture leopard sharks. When fishing in the main channel (Kirby Park), anchored bottom sets were used and nets were checked every 15-20 min. In ESNERR gillnets were strung across channels and the floats were monitored for any activity that would indicate an animal had become entangled in the net, at which point they were checked. All fish other than leopard sharks caught in the net were identified, sex determined, measured (TL or DW), tagged with an ID tag (Floy T-bar), and removed as rapidly and carefully as possible to reduce stress on the animal. In ESNERR, animals only remained in the net for the time it took to recover the net and remove the animal (approximately 5 min), whereas in the main channel animals tended to remain in the net longer because floats could not be directly observed. The maximum time animals were in the net was 15 min. All animals survived capture and appeared in good condition when released. Catch data were used to calculate catch-per-unit-effort (CPUE) (# leopard sharks per hour) to examine the relative abundance and sex ratios of leopard sharks during the different seasons (Winter: December through March; Spring: March through May; Summer: June through August; Fall: September through November) in ESNERR and the main channel.

I recorded sex and total length of all captured leopard sharks and then placed a Floy T-bar or oval tag in them which contained an ID number and phone number of Moss Landing Marine Laboratories before release. Only female leopard sharks were tagged with acoustic transmitters. Only females longer than 70 cm TL were tagged because Winter (1983) suggested that implanted tags should never be more than 2% of the fish's body weight, and based upon the weight of the acoustic tags and length-weight relationship of female leopard sharks (Carlisle et al. in review), sharks less than this size would be too small based upon this criterion.

Transmitters were implanted inside the peritoneal cavity because internal tags are more suited for longer-term studies when compared with external and gastrically placed tags. External tags have a number of effects on fish such as an increase in fouling (Thorstad et al. 2001), drag (McCleave & Stred 1975, Mellas & Haynes 1984, Lewis & Muntz 1984, Counihan & Frost 1999), and greater rates of shedding (Kohler & Turner 2001). Gastrically implanted transmitters often are regurgitated (Mellas & Haynes 1984, Holland et al. 1993). A review of tagging effects in elasmobranchs by Kohler and Turner (2001) indicated that external tags have shorter life expectancies, increased susceptibility to fouling in capture gear and vegetation, and can lead to substantial damage and restriction of growth in body and fin thickness during long-term experiments. Fouling is of special concern in Elkhorn Slough, because of the great amount of potential fouling material there.

After being removed from the net and measured, sharks were anesthetized by placing them in a solution (0.05 – 0.1 g/L) of tricaine methanosulfate (MS-222). Once respiratory movements noticeably slowed and the sharks ceased responding to stimuli, they were removed from the MS-222 solution and placed on their backs in a v-board and a constant flow of water was passed over their gills. A small axial incision (~3 cm) was made into the peritoneal cavity about 3 cm away from the midline and about two-thirds of the way between the pectoral and pelvic fins. Transmitters were coated in a 7:3 mixture of beeswax and paraffin wax in an effort to prevent transmitter rejection (Holland et al. 1999), and then washed in betadyne to sterilize them before implantation. The transmitters were then inserted into the abdominal cavity and gently pushed anteriorly. The incision was then cleaned with betadyne and closed using intermittent surgical sutures. The sharks were then returned to the slough and held until completely revived.

Sharks were tagged with continuous transmitters for active tracking or with coded transmitters for acoustic monitoring. For active tracking, sharks were tagged with continuous transmitters (Vemco model V16-5H, 16 x 92 mm, 16 g) that had unique operating frequencies ranging from 51 kHz to 75 kHz and pulse periods of either 1000 ms (estimated battery life 65 days) or 1500 ms (estimated battery life 95 days). The estimated battery life was conservative, often batteries operated up to 30% longer. For acoustic monitoring, sharks were tagged with 69 kHz coded transmitters (Vemco model V16-5H-R256, 16 x 92 mm, 16 g) with estimated battery lives of 425 days. The transmitters all had pulse train delays of 30-79 sec, meaning that each transmission of their unique coded ID occurs randomly between 30 and 79 seconds, which reduces the chance of signal collisions.

Active Acoustic Tracking

I used active tracking techniques to examine short-term small-scale movements of leopard sharks in Elkhorn Slough. After being tagged and released, sharks were allowed a minimum of 24 h to recuperate before tracking commenced. Sharks were tracked with a directional hydrophone and acoustic receiver (Vemco model VR-60) from a shallow-drafted skiff capable of entering shallow water (< 30 cm). Every 5 min, the boats position was recorded using a handheld GPS (Garmin eTrex Vista, WAAS enabled, < 3 m accuracy), and the bearing to the shark (a correction factor of 15° was used to adjust magnetic compass bearings to true north), signal strength, receiver gain setting, and time also were recorded. In more open areas, this was done twice in succession to get two intersecting lines of bearing for a single position. I used intersecting lines of bearing as often as possible because when combined with signal strength and gain setting, two lines of bearing provided better estimates of shark location.

In shallow, enclosed environments where mobility was limited and boat movement would likely influence the behavior of the shark, the estimated distance to the shark was based upon the signal strength, the gain setting of the receiver, and the physical setting (e.g., distance to shore). In these shallow, restricted areas, a maximum distance could be established based on the location of the shore, and the shark was always in close proximity to the boat, resulting in good estimates of distance. Whenever the receiver's gain was set to 0 and the signal strength was at or near 100% in every direction, the location of the boat was used as the position of the shark.

Every effort was made to not disturb the shark's behavior, and it appeared as if the sharks were not easily perturbed. When a shark was disturbed, it was immediately obvious as they would suddenly and rapidly move a short distance away before slowing down and exhibiting apparently normal behavior. This only happened on a few occasions and data collection only resumed after they resumed exhibiting more typical behavior. By using a pole to move the boat around whenever possible, and by limiting movements, any potential impacts on the shark's behavior were minimized.

VR-60 signal strength varied greatly with bottom topography, sea state, depth, weather, and other physical factors. Based upon trials, signals could be detected as far away as 1,000 m in the main channel, but was usually 400-600 m. In shallower habitats in ESNERR, the range of reception decreased slightly to 200-400 m. In shallow areas in inclement weather, or in eelgrass beds reception range was as low as 50 – 100 m. Despite fluctuating reception ranges, experience and a detailed knowledge of the geography of Elkhorn Slough allowed for high degree of confidence in estimated positions.

I tracked tagged sharks for six hours at a time. I chose to track animals in four distinct time periods: 00:00 – 06:00 h, 06:00 – 12:00 h, 12:00 – 18:00 h, and 18:00 – 00:00 h. Three replicate tracking sessions were then conducted for each six-hour block, for a total of 72 h of tracking per shark. The temporal allocation of these tracking sessions depended on weather, tide, and assistance from volunteers. As a result these replicate tracking sessions were conducted haphazardly to gather the predetermined amount of data as rapidly as possible.

I plotted positional fixes onto a geo-referenced map of Elkhorn Slough provided by the Monterey Bay National Marine Sanctuary's Sanctuary Integrated Monitoring Network, NOAA Coastal Services Center, and California State University Monterey Bay's Seafloor Mapping Laboratory and analyzed them using ESRI ArcView 3.2 and ArcGIS 9 GIS programs. Fixed kernel density utilization distributions (Worton 1989) were calculated using the Animal Movement Analysis Extension for ArcView 3.2 (Hooge & Eichenlaub 2000) to estimate the activity space of leopard sharks. The kernel density utilization (KUD) is a robust, nonparametric, probabilistic home range technique in which a probability density (a kernel) is assigned to each position recorded in a grid. Kernel density is then estimated at each grid intersection by averaging the density of all the kernels that overlap that point. Therefore, density estimates will be greater in areas with more positions than fewer (Seaman & Powell 1996). The program creates and plots isopleths representing the frequency of occurrence that describe the size and shape of the activity space and identify important core areas. The 95% probability contours, representing total activity space, and the 50% probability contours, representing core areas of activity, were calculated for each shark to describe an individual shark's spatial use. I also calculated KUDs for different tidal levels (low, intermediate, and high tidal levels) and periods of day (day, night) to determine if there were diel or tidal patterns of spatial use for each shark.

I examined habitat use using active tracking data. For the purposes of this study, habitat was classified according to depth of the bottom relative to mean lower low water (MLLW) as defined by the National Geodetic Survey (NGS). I defined eight habitats: < -3 m, -3 to -2 m, -2 to -1 m, -1 to -0.5 m, -0.5 to 0 m, 0 to 0.5 m, 0.5 to 1 m, >1 m. According to this classification system, subtidal substrates were all substrates below -0.5 m, whereas intertidal substrates were everything above -0.5 m. Because the intertidal zone is extensive in Elkhorn Slough, and because leopard sharks forage intertidally, I pooled substrates in and just below the intertidal zone into 0.5 m bins to get better resolution for estimating habitat use at shallower depths. I examined shark habitat use at low, intermediate, and high tidal levels because Elkhorn Slough is a dynamic tidal environment where the amount of habitat available fluctuates greatly based on tidal level. At low tidal levels, intermediate and high intertidal habitats (0.5 to 1 m and >1 m) were not available to the sharks because they were above the water line. At intermediate tidal levels only high intertidal habitats (>1 m) were not submerged and available for use, whereas at high tidal levels all habitat types were available.

The low, intermediate, and high tidal categories were defined based on tidal characteristics observed in the slough. During 2003 – 2004 the mean higher low tide was 0.6 m above MLLW whereas the mean lower high tide was 1.13 m. Based on these values, low tidal levels were classified as everything below 0.6 m, intermediate tidal levels as all tidal levels between 0.6 and 1.13 m, and high tidal levels were greater than 1.13 m.

Habitat use was examined in individual sharks and in two groups of sharks based upon the two different patterns of habitat use that were observed in ESNERR and the main channel. To determine if it was valid to group the sharks into these two groups, a principal components analysis (PCA) was conducted using the program Multivariate Statistical Package v. 3.13 (Kovach Computing Services). Because the type and amount of available habitat changes greatly during the tidal cycle, the PCA was conducted for low, intermediate, and high tidal levels. At low tidal levels, the PCA included six habitats (< 3 m, -3 to -2 m, -2 to -1 m, -1 to -0.5 m, -0.5 m to 0 m, and 0 to 0.5 m), at intermediate tidal levels the PCA included seven habitats (< 3 m, -3 to -2 m, -2 to -1 m, -1 to -0.5 m, -0.5 m to 0 m, 0 to 0.5 m, and 0.5 to 1 m), and at high tidal levels the PCA included all eight habitats (< 3 m through > 1 m). The data were log (x+1) transformed and Kaiser’s rule was used to determine which axes to extract.

For each tidal level I used linear regression to determine if there was a relationship between time tracked and number of habitats utilized. This was done to ensure that the length of time spent tracking sharks did not influence the number of habitats they used, which would further support pooling sharks into the two groups. The sharks were then grouped based on the results of the PCA and linear regression and their data pooled to examine general patterns of habitat use.

First, to test the null hypothesis that sharks were using habitats randomly, a G-test was performed for each tidal level on individual sharks and the two groups of sharks (Krebs 1999). Then a selection index (Krebs 1999, Manly et al. 2002), which is a measure of selectivity, and its confidence limits were calculated for each of the habitats during the different tidal levels. These calculations were conducted using the program-group Niche Measures in Programs for Ecological Methodology 2nd edition (Krebs 1999). Selection indices range from 0 to ∞, with values greater than one indicating selection and values less than one indicating avoidance. Finally, pair-wise comparisons between selection indices for the different habitats were conducted to test for differences in habitat use. To compensate for multiple pair-wise comparisons a Bonferonni correction was used.

I used positions obtained from active tracking to estimate rates of movement (ROM) of tagged sharks. I calculated ROM by taking the distance between consecutive positions and dividing it by the time that elapsed between positions. This method provides a conservative estimate because it assumes that the shark swims in a straight line between positions. ROM was calculated for individual sharks and presented as the mean ROM (± 95% CI) at different tidal levels, tidal ranges, and periods of the day (night, dawn, day, dusk) for the ESNERR and main channel group of sharks. Tidal range was used as a proxy for current velocity, because the magnitude of tidal currents was directly related to the change in tidal level (i.e. higher tidal change indicates higher current velocities). For period of day, dawn and dusk were defined as ± 1 hr from sunrise and sunset for all analyses.

Acoustic Monitoring

I used moored receivers to examine larger-scale spatial and temporal patterns of movements of leopard sharks in Elkhorn Slough. Six Vemco VR1 receivers, single channel automated receivers capable of detecting multiple coded transmitters, were moored to the bottom at strategic locations around the slough (Figure 2). The VR1's and their moorings were initially deployed in early September 2003 and recovered in February 2005. Receiver 1 was initially placed in the north part of Moss Landing Harbor, however it did not detect any sharks, so it was moved to axis of the lowermost part of the main channel in December 2003. Approximately once a month divers retrieved the receivers to be downloaded and cleaned. This occurred on site, and receivers were out of the water for approximately 10 min before being returned to their moorings. Every six months the receivers were recovered to replace the batteries and to be thoroughly cleaned, in which case the receivers were out of the water for a day.

VR1 receivers recorded tag transmissions, so when a shark swam within a receiver's range of reception, the shark's transmitter ID and the time of detection were recorded. Because VR1's provide a continuous record of the relative location of all tagged sharks, larger spatial and temporal patterns of movement can be observed than is possible using active tracking techniques. This is possible because the slough is essentially a linear system and the reception range of the receivers is greater than the width of the channel, so there is little chance that sharks can pass by receivers without being recorded. Movement across two adjacent receivers is needed to determine directionality of movement. Two receivers were placed in close proximity in the lower slough and at the mouth of ESNERR thus I knew if the sharks vacated the slough or entered ESNERR. The range of reception for individual receivers also varied with environmental conditions, but range testing indicated that the reception range was approximately 350-500 m, so a conservative estimate of 400 m was used in my analyses.

I divided the slough into 4 regions (lower slough, mid slough, upper slough, and ESNERR) based upon the placement of the VR1's and initial examination of patterns of movement (Figure 2). This allowed patterns of residency within these areas to be described. The area that was immediately east of the Moss Landing Harbor was defined as the low region (0.35 km^2). The area of the main channel between the lower and upper regions was the mid region (1.4 km^2). The uppermost part of the main channel was the upper region (1.25 km^2). The ESNERR and Long Canyon made up the ESNERR region (1.68 km^2). The entire lower region was almost completely covered by two receivers which meant that the probability of a shark passing by this region without being detected was almost zero, and allowed me to know if a shark vacated the slough. Once sharks moved outside the range of Receiver 2, it was then determined to be in the mid region until it was either picked up at Receiver 4 (ESNERR region) or Receiver 6 (upper region). The two receivers at the mouth of ESNERR (Receivers 4 and 5) allowed me to know when sharks entered and vacated ESENRR. If a shark was detected at Receiver 3 and Receiver 6 consecutively, followed by an extended period of time with no detections, and was then detected consecutively at Receiver 6 and Receiver 3, it was determined to have been in the upper region.

Based upon this system, the total proportion of time spent in each region was calculated for each individual shark, which was used as an estimate of the relative importance of the different regions. The observed proportion of time a shark spent in the different regions was compared with the predicted proportion of time they would spend in the regions if they were being used in proportion to their area. To determine if the observed time differed from the predicted time, a chi-square goodness of fit test was used. If there was a significant difference, the chi-square analysis was subdivided and conducted using the Yates correction for continuity (Zar 1999). This tests the difference between the observed and expected time each shark spent in an individual region. To examine seasonal pattern of regional use, the time each shark spent in each region was calculated for every month. These data were then combined and expressed as the mean proportion of time (± 95% CI) sharks spent in each region during each month.

To examine the role of tides on the general distribution of sharks in the slough, I assigned each detection at a receiver a time relative to the time of that day's lower low tide. Tidal information was obtained from the program Virtual Tide Stations in Elkhorn Slough (Watson 2005). The data were then pooled into hourly bins ranging from 13 h before the day's lower low tide to 13 h after, which encompassed the time between successive higher low tides. The data from all sharks were then combined and expressed as the mean proportion of receptions (± SE) in each hourly bin. This was done for each of the six receivers.

I also examined directionality of movements relative to tidal flow. For the purposes of this analysis, a movement is defined as any time the shark moved between any two receivers. Each movement was assigned to a category depending on the direction of movement relative to the direction of tidal flow during that movement. Movements were assigned to one of five categories: negative, positive, mixed, slack, and unknown. The negative and positive categories refer to rheotaxis, which is the orientation of an organism relative to a current. Positive rheotaxis is exhibited when an organism orients into a current, and negative rheotaxis is when an organism orients in the same direction as a current. A shark's movement was categorized as mixed if for approximately half of the movement the shark was exhibiting positive rheotaxis and the other half negative rheotaxis, as would occur when the tide changed while a shark was moving between receivers. The slack category encompassed movements that occurred entirely during slack tide (± 30 min from high or low tide), when currents would be weakest. The movement was assigned to the unknown category if it occurred over a period of time greater than one tidal cycle, making it impossible to assign the movement to any of the other categories. The data were pooled for each shark and expressed as the proportion of movements that occurred in each category. Movements between receivers 3 and 4 were not used due to the arrangement of the receivers.

Movements between receivers were examined to determine the potential relationship between tidal range and movements. All movements for an individual shark were assigned a tidal range value based on how much the tide level changed during the tidal stage in which the movement occurred. Movements during slack tide were not used. These data were expressed as the mean (± 95% CI) tidal range during which an individual shark's movements occurred relative to the mean (± 95% CI) tidal range during the time that shark was in Elkhorn Slough.

The relationship between number of movements and time of day also was examined. For each movement, the time halfway between the previous receiver's last detection and the next receiver's first detection was used as the time of movement. Each movement was assigned a time, and these were grouped into hourly bins for each shark. To examine the general trend across all sharks the mean (± 95% CI) for each hourly bin was calculated and expressed as a histogram. In addition, times of movement were grouped by period of day for each shark. To examine the general trend for all sharks, the mean (± 95% CI) for each period of day was calculated.

ROMs in the main channel also were examined using the acoustic monitoring data. This was done by calculating the time it took tagged sharks to move between receivers and dividing that by the distance between receivers. Distance between receivers was estimated using a conservative line of movement drawn down the axis of the channel from the edge of one receiver's estimated reception range to the edge of the neighboring receiver's range of reception. Movements between receivers 3 and 4, and 4 and 5 were not used because the placement of the receivers made it impossible to calculate reliable rates. ROM was calculated for all individuals, and then combined and expressed as the mean ROM (± 95% CI) relative to tidal range, direction of tidal flow, and period of day.

No statistical tests were performed on any of the active or passive movement data. This was due to violations in statistical assumptions that are inherent to these types of data, primarily violation of the assumption of independence and random sampling. For this reason 95% confidence intervals were calculated and presented because they often are good substitutes for statistical tests (Johnson 1999).

RESULTS

Catch-Per-Unit-Effort

In total, 103 leopard sharks, 31 thornbacks, 29 bat rays, 5 gray smoothhounds, 2 brown smoothhounds, 1 round stingray, and 1 shovelnose guitarfish were caught during sampling in 2003 and 2004. From September to October 2003, sampling only occurred in ESNERR (including Long Canyon). CPUE of leopard sharks was greatest in the spring and decreased by nearly 50% in the summer and fall, but sampling was limited and few leopard sharks were caught in the late fall (Table 1).

In ESNERR during 2004, CPUE of leopard sharks was greatest in the spring but it decreased by approximately 50% in the summer, and no fishing occurred in ESNERR in the fall (Table 1). The decrease in summer CPUE primarily reflects a lack of leopard shark catch in August. CPUE was high in June-July (1.04 fish hr-1 ± 0.43 SE), but in August it decreased to 0 despite repeated sampling efforts. For this reason, fishing in ESNERR was abandoned in fall, and sampling effort switched to Kirby Park in the main channel.

In the main channel during 2004, CPUE of leopard sharks was greater later in the year (Table 1). CPUE was lowest in the spring but it increased by 60% in the summer and increased greatly in the fall (> 700% relative to spring). The increase in CPUE in the main channel during the summer was due to increased catch rates at Kirby Park in August, and the high catch rate in the fall reflects very high catch rates at Kirby Park in September.

The sex ratio of the catches of leopard sharks varied greatly with region (Table 1). In 2003 and 2004, females strongly dominated the catch in ESNERR in the spring, summer and fall. In the main channel, only males were caught in the spring, but the sex ratio was closer to 1:1 in the summer and fall. This suggests that males did not occur to any great extent in ESNERR and that the number of females in the main channel increased in the late summer and fall.

Tagging

Nineteen sharks were tagged with acoustic transmitters between spring and fall of 2003 and 2004. All sharks were removed from the net within 2 to 15 min, and it took 3 to 12 min to anesthetize them. The only time sharks were out of the water was during surgery, which lasted from 4 to 10 min (mean 7.79 min ± 0.49 SE), although they had a constant flow of water passing over their gills. All sharks revived rapidly after surgery. The entire procedure, from capture to release took from 15 to 25 min, and all sharks swam away normally in apparent good condition.

There were no complications during any of the tagging procedures and all sharks were released in apparent good condition. However, complications arose for two sharks post-release. One shark tagged with a continuous transmitter in August 2004 at Kirby Park died shortly after release. The capture, surgery, and release of the shark were normal, but when located the next day the shark was not moving. It was collected the following day and a necropsy performed. There were no apparent physical causes of death. There were no internal injuries from implantation and the incision was still closed. August had the highest water temperatures of the year, ranging up to 24^{o} C. The day the tagging occurred also was extremely warm and sunny, and despite every effort it was impossible to provide adequate shade to the shark during the procedure. Based upon the circumstances and consultation with other researchers, the likely cause of death was a combination of thermal and tagging stress.

The other incident occurred when the sutures in shark 108 apparently ruptured after being tagged on April 27. After being released, it was caught twelve days later by the Pelagic Shark Research Foundation, and at that point most of its sutures had pulled out, and there were abrasions around the incision. It appeared as if the incision had ruptured at most several days after being released based on the amount of healing. The tag had not been expelled. The shark's liver had filled the opening, and despite the wound the shark was alive. I cleaned the wound, sutured it shut, and released the shark. Afterwards it remained in ESNERR for two days before leaving the reserve and moving around the main channel for the next ten days, at which point it reentered ESNERR and remained there for the rest of the study period. It was detected by Receiver 5 in ESNERR on several occasions during the next several months, and was detected with the VR60 on several occasions, indicating it survived this incident.

Active Tracking

Nine female sharks (one juvenile, eight adults) were tagged with continuous transmitters (Table 2). Sharks ranged in size from 91 to 132 cm TL (mean 119.4 cm ± 4.8 SE). Sharks 54, 60 and 63 were pregnant when they were tagged. Four of the sharks were tagged in ESNERR, one in Long Canyon, and three at Kirby Park when tagging operations shifted from ESNERR to Kirby Park in fall 2004. All tagged sharks vacated the slough by mid-November.

These eight sharks were actively tracked for 432 h (Figure 3). Total distance traveled by sharks was 9.9 to 68 km (mean 39.14 km ± 7.62 SE), and activity space (95% KUD) was 0.21 km^2 to 1.75 km^2 (0.92 km^2 ± 0.18 SE). The time each shark was tracked was 19.9 h to 71.4 h (mean 54 h ± 7.5 h SE). Sharks were primarily tracked in either ESNERR or the main channel, and did not tend to move between these regions with any frequency during the six-hour active tracking sessions.

The first shark tracked (shark 51, tagged 28 April 2003 in Long Canyon) was tagged externally and tracked immediately for 4 h, but was not relocated in the main channel despite intensive searching. At some point the shark shed the tag as it was found by the Pelagic Shark Research Foundation a month later in the vicinity of the lagoon in ESNERR. This indicates that it likely entered ESNERR shortly after being tagged, which I was not able to search due to not having a permit at that time.

On several occasions, sharks 60 and 63 moved into the lagoon in ESNERR which was usually inaccessible by boat. When this occurred, the lagoon (Figure 1) was monitored for the rest of the session to determine if the shark remained in the lagoon, and if possible the shark was tracked from land. On these occasions, when the shark could not be tracked from land and was out of range of the receiver, points for each five minute position were randomly allocated within the eastern part the lagoon that was out of the range of the hydrophone. The randomly generated points were only used in calculating kernel utilization distribution, which would give a conservative estimate of the areas being utilized.

Acoustic Monitoring

Eleven female sharks (3 juveniles, 8 adults) were tagged with coded transmitters (Table 3). Tagged sharks were 78 to 140 cm TL (mean 115.12 cm ± 6.25 SE). Sharks 102 and 105 were pregnant when they were tagged. Nine of the sharks were tagged in ESNERR and two were tagged at Kirby Park in late 2004 when tagging operations shifted to Kirby Park. All tagged sharks vacated the slough my mid-November, although one shark (Shark 107) returned for one day at the beginning of December after vacating 8 days earlier.

Sharks were acoustically monitored for 4 to 280 days (mean 117 days ± 101.88 SE). There were 70,525 detections at VR1 receivers. Of these, 3,876 detections were at Receiver 1, 15,006 detections were at Receiver 2, 11,529 detections were at Receiver 3, 3,476 detections were at Receiver 4, 15,771 detections were at Receiver 5, and 20,867 detections were at Receiver 6. Two sharks with coded transmitters were caught by recreational fisherman. Shark 105 was killed by bow hunters in the upper slough in the region above Kirby Park on 4 July 2004, and the tag was acquired and returned by the Pelagic Shark Research Foundation. Shark 103 was monitored moving around the slough for a month, but was last detected on 27 May 2004 at Receiver 6. The transmitter was later found beneath the dock at Kirby Park, a common fishing spot, so it was believed to be another fishing mortality.

The VR1 receivers revealed interesting patterns of movement in individual sharks. However, only the most important observations are reported. To see the results of individual sharks not mentioned here refer to appendices B – H.

Several of the sharks exhibited periodic movements up and down the main channel with the tides, most often during periods of greater tidal change, such as occurred around lower low tide. This was exemplified by the movements of shark 115 (Figure 4), which moved down to the lower slough (receivers 1 & 2) each day during the ebb tide prior to lower low tide, and then moved back to the upper slough (receiver 6) during the following flood tide. The movements of the other sharks generally followed this tidal pattern, although the movements of several of the sharks were not as periodic.

Shark 102 (Figure 5) and shark 105 (Figure 6) were pregnant when tagged and were monitored through the pupping period. Both of these sharks remained in ESNERR throughout the pupping period. In addition, shark 102 was the only shark that was monitored throughout an entire season, providing a continuous record of its movements during spring, summer and fall. Overall, shark 102 provided a good representation of how sharks were moving around the slough during different months.

Shark 100 (Figure 7) was the only shark of the three sharks tagged in 2003 to return the following year, and was the only shark in the study to vacate the slough for extended periods of time before returning. Shark 115, which was tagged in August 2004 and vacated the slough in mid-November 2004, was detected by a VR2 receiver from a different project (personal communication: Cyndi Dawson, Moss Landing Marine Laboratories) placed just outside the mouth of Moss Landing Harbor in Monterey Bay on

23 May 2005. The timing of the detection and the location of the receiver suggests that this shark also may have returned to Elkhorn Slough from the previous year.

Three juvenile leopard sharks (sharks 103, 104, and 108) were tagged on 27 April 2004 in ESNERR. Whereas shark 103 was caught by fishermen, the two other juveniles spent nearly the entire time in ESNERR until the receivers were removed in February 2005. Shark 104 did not vacate the reserve between the time it was tagged until the end of the study, but was only detected by Receiver 5 for the first month. This indicated that the shark may have died after May, so the VR60 was used to locate it intermittently through August, at which point such efforts ceased due to the belief that it was alive. The sutures on shark 108 ruptured after being released, but it survived the incident as previously described. Except for a week in mid May when it moved around the main channel, Shark 108 remained in ESNERR until February 2005, when the receivers were removed at the end of the study. It was detected intermittently by Receiver 5 through October, but after that it was not detected again. Although sharks 104 and 108 were alive as of August and October respectively, it is possible that the lack of detections in the fall and winter could be due to the sharks having died or their tags failing.

Regional Use

Based on data from the VR1 receivers, the amount of time leopard sharks spent in the four regions of Elkhorn Slough (low, mid, upper, and ESNERR) differed significantly from the predicted amount of time in ten of the eleven sharks (shark 103 $p < 0.025$, all other sharks $p < 0.001$, Figure 8). Leopard shark 101 was the only shark that did not differ significantly from the predicted times, likely because it was only monitored for approximately 4 days, the least time any shark spent in the slough after being tagged. The ESNERR region accounted for much of the differences between observed and predicted times spent in different regions. The time spent in the ESNERR region differed significantly from the predicted time in ten of the eleven sharks (two sharks < predicted, eight sharks > predicted). The time spent in the upper region of Elkhorn Slough differed significantly from the predicted time in seven sharks (five < predicted, two > predicted), whereas six sharks differed significantly in the mid region (all < predicted), and three sharks differed significantly in the low region (all < predicted).

If sharks were using the different regions in proportion to their area, leopard sharks would spend 7.4% of their time in the low region, 30.40% of their time in the mid region, 35.60% of their time in the ESNERR region, and 26.60% of their time in the upper region. Leopard sharks spent an average of 4.40% (± 1.53 SE) of their time in the low region, 13.50% (± 3.72 SE) in the mid region, 65.20% (± 9.91 SE) in the ESNERR region, and 16.90% (± 5.96 SE) in the upper region. ESNERR was the most heavily used region for eight of the sharks, whereas the upper region was the most heavily used region for two of the sharks.

The amount of time leopard sharks spent in the different regions of the slough changed seasonally (Figure 9). During fall 2003, ESNERR was used extensively, but use of this area decreased slightly later in the year just before the sharks vacated the slough. The average amount of time sharks spent in ESNERR ranged from 97% in September to 74% in November. Shark use of the mid region was greatest during November, when sharks spent an average of 14% of their time in that region. In 2004, a similar trend was observed where the ESNERR region was used extensively until later in the year at which point use of the regions in the main channel increased. In spring, tagged sharks spent the majority of their time in the ESNERR region, ranging from a mean of 78% in April to nearly 100% in May. The amount of time spent in ESNERR decreased slightly during summer from a mean of 82% in June to around 70% in July and August, but it was still the region where the tagged sharks spent the majority of their time. In fall, the average time sharks spent in ESNERR was between 42% in September to 52% in October. Whereas use of ESNERR decreased in fall, the upper and mid regions were used most intensively in fall. Use of the upper region was greatest in September, when sharks spent an average of 41% of their time in that region, and use of the mid zone was greatest in November, when they spent a average of 32% of their time in that region.

Rates of Movement and Activity Patterns

ROM from active tracking did not appear to be influenced by tidal level, tidal range, or period of day in sharks tracked in ESNERR. Sharks in ESNERR had a mean ROM of 0.59 km hr-1 (± 0.20 95% CI). ROM did vary depending on the tidal levels, period of day, and tidal range, but the variation was not great and I could detect no pattern. ROMs at different tidal levels ranged from a low of 0.43 km hr-1 (± 0.17 95% CI) at 0 – 0.25 m tidal levels to a high of 0.59 km hr-1 (± 0.35 95% CI) at 0.75 - 1 m tidal levels. ROMs during the different periods of the day ranged from a low of 0.53 km hr-1 (± 0.234 95% CI) during the day to 0.58 km hr-1 (± 0.32 95% CI) during the dawn. ROMs varied the most based on tidal range, but there was no pattern to the variation.

ROMs ranged from 0.38 km hr-1 (± 0.09 95% CI) when the tidal range was between 1.25 – 1.5 m to a high of 0.72 km hr-1 (± 0.41 95% CI) at 1.5 – 1.75 m tidal ranges.

In the main channel, active tracking and acoustic monitoring data were used to estimate ROMs. ROMs of sharks in the main channel were more influenced by tidal levels, tidal range, and period of day than for sharks tracked in ESNERR. Sharks in the main channel had a mean ROM of 0.60 km hr-1 (± 0.14 95% CI), which was nearly identical to that observed for sharks in ESNERR. The greatest ROM from active tracking was 3.5 km hr-1 for shark 75.

Based on the VR1 data, the mean ROM between receivers in the main channel was 1.24 km hr-1 (± 0.29 95% CI). ROMs calculated from VR1 receivers were consistently greater than those observed during active tracking. This could be influenced by the acoustic properties of the water column varying through time, which would influence signal propagation through the water column and range of reception of VR1 receivers. In addition, the distances sharks actually swam when moving between receivers could have been less than estimated since a conservative estimate of distance was used. Both of these factors could influence ROM estimates.

The difference in ROM estimates between active tracking and acoustic monitoring data in the main channel, however, is likely due to different scales on which these two techniques operate. On three occasions, leopard sharks were actively tracked making rapid, directional, long-distance movements in the main channel similar to the distance between Receivers 1 and 3. In every instance that directed movements were observed, the shark was located in the lowermost region of the slough when the tidal levels were low, and was tracked moving rapidly up the slough with the flooding tide. When exhibiting these directional movements, sharks moved more rapidly than usual. The mean ROM of these movements was 0.98 km hr-1 (± 0.21 95% CI, shark 75), 1.26 km hr-1 (± 0.32 95% CI, shark 75), and 1.81 km hr-1 (± 0.64 95% CI).

The lesser number of long-distance, directed movements observed during active tracking was due to the lack of correspondence between the timing of tracking sessions and tidal cycles. Due to the short nature of the active tracking sessions, it was unlikely that directed movements would be observed unless the tracking session corresponded exactly with a directed movement during tidal exchange. On a number of occasions during active tracking, I recorded initiations or conclusions of directed movements when sharks did move more rapidly than usual. Due to the similarity of ROM estimates between the three directed, long-distance movements observed during active tracking and the ROM estimates from VR1 data, the VR1 estimates appear to be valid and likely represent directed, long-distance movements.

Tidal Patterns of Activity in the Main Channel

ROM of sharks actively tracked in the main channel was influenced less by tidal height than by tidal range. While ROM was in general greater at lower tidal levels, this pattern was not strong. The highest ROM occurred at 0.25 to 0.5 m tidal levels (0.97 km hr-1 ± 0.87 95% CI). Other higher ROMs occurred at 0 to 0.25 m (0.73 km hr-1 ± 2.23 95% CI), 0.5 to 0.75 m (0.81 km hr-1 ± 0.46 95% CI), and 1.25 to 1.5 m (0.7 km hr-1 ± 0.71 95% CI) tidal levels. The lowest ROM occurred at 1.5 to 1.75 m tidal levels (0.46 km hr-1 ± 0.26 95% CI). ROMs of leopard sharks in the main channel indicated that they generally moved faster when tidal range was greater. The highest ROM (0.82 km hr-1 ± 0.82 95% CI) occurred when the tidal range was between 1.25 to 1.5 m. During the other categories of tidal range, ROM did not vary much. ROM ranged from 0.48 km hr-1 (± 0.08 95% CI) during 0.25 to 0.5 m tidal ranges to 0.6 km hr-1 (± 4.32 95% CI) during 1.5 to 1.75 m tidal ranges.

ROM between VR1's also indicated that sharks moved faster when tidal range was greater (Figure 10). They had the highest ROM (mean 1.29 km hr-1 ± 0.37 95% CI) when the tides were changing the most (> 1.5 m). This was faster than the lowest ROM (mean 0.8 km/hr ± 0.47 95% CI), which occurred when tides were changing the least (< 0.5 m).

Data from moored receivers indicated that sharks moved between receivers more when the tidal range was greater (Figure 11). For each shark except shark 107, the mean tidal range during which movements occurred was greater than the overall mean tidal range that occurred while that shark was in the slough. The mean tidal range during which sharks moved ranged from 0.08 to 0.32 m higher than the average tidal range.

The directionality of movements between receivers also was strongly influenced by the tide. Sharks moved with the tide (negative rheotaxis) 75.40% (± 0.08 95% CI) of the time and against the tide (positive rheotaxis) 20.10% (± 0.07 95% CI) of the time (Figure 12). Sharks exhibited negative rheotaxis during 64% to 94.50% of their movements. Shark 106 exhibited the strongest positive rheotactic movements; it moved against the tide 33.30% of the time. Only 2% of a shark's movements occurred at slack tide, whereas only 2% were in the mixed category and 0.7% in the unknown categories of movements.

The ROM between VR1's was greater when the shark was moving with the tidal current (Figure 13). Sharks moved fastest, an average of 1.56 km hr-1 (± 0.42 95% CI), when they exhibited negative rheotaxis, which was nearly twice as fast as when sharks exhibited positive rheotaxis (mean 0.81 km hr-1 ± 0.27 95% CI). Based on 95% CI, this difference appears to be significant. When they moved at slack tide, or when they exhibited a mix of positive and negative rheotaxis during movements, their ROM was similar to that exhibited during positive rheotaxis (mean 0.91 km hr-1 ± 0.4 95% CI during slack, 0.8 km hr-1 ± 0.47 95% CI during mixed).

The occurrence of sharks at the different VR1 receivers was strongly influenced by the tidal cycle (Figure 14). By examining a combination of the occurrence of sharks at different receivers with the movements of acoustically monitored sharks, I determined where sharks occurred along the length of the main channel at different tidal stages. Based on the time of detections at the different VR1 receivers, leopard sharks generally occupied the lower slough at lower tidal levels, the middle slough at intermediate tidal levels, and the upper slough at higher tidal levels. In addition movements up and down the slough were related to the extent of tidal change. During larger tidal exchanges sharks moved greater distances.

Based on the large number of detections at Receivers 1 and 2 within one or two hours of the day's lower low tide, sharks almost always occurred in the lower slough at or around low tides. At Receiver 1 there were secondary peaks at 12 h prior and 9 h following lower low tide. Both of these times coincided with higher low tides.

Sharks occurred at Receiver 3 over a wider range of times relative to lower low tide than was observed in the lower two receivers. Sharks were detected mainly from 4 h before the day's lower low tide to 11 h after it, which would correspond with higher low tide. The pattern of detections at Receiver 3 indicated that sharks were moving past or occurring around Receiver 3 during low to intermediate tidal levels. This pattern fits with the pattern of detections at Receivers 1 and 2. As sharks move down the slough before lower low tide and back up afterwards, they would pass by Receiver 3. Sharks would not always move to the lower region of Elkhorn Slough at lower low tide, as shown by large number of detections at Receiver 3 during lower low tide. These usually occurred when sharks did not move as far down the main channel during lower low tide, which generally occurred when the tidal range was not as great. When lower high tide was not as high, sharks would often not move further up the channel than Receiver 3 and would remain in the vicinity of that receiver, and when the tidal range was high and the sharks were moving greater distances, they would usually pass Receiver 3 around lower high tide when heading to the upper region of the main channel.

Sharks occurred at Receiver 6 over a wide range of times relative to lower low tide, more so than any of the other receivers. Sharks occurred most often at Receiver 6 around six hours after the day's lower low tide, which corresponds with lower high tide.

This indicates that sharks either moved past Receiver 6 into the upper region around lower high tide, or remained in the vicinity of Receiver 6 during periods of lower tidal range when they would not move as far up the main channel.

The occurrence of sharks at Receivers 4 and 5 was similar to what was observed at Receivers 1 and 2. Sharks were detected by Receiver 4 and 5 during the four hours on either side of lower low tide. Receiver 5 had a much stronger peak, however, right at lower low tide. The pattern of detections at Receivers 4 and 5 indicated that sharks were further up in ESNERR during higher tidal levels, and they only came to the entrance of ESNERR during the periods of maximum tidal current that occurred around lower low tides, similar to what was observed at Receivers 1 and 2.

Diel Patterns of Activity in the Main Channel

ROMs during active tracking were higher at night (0.69 km hr-1 ± 0.66 95% CI) than during other periods of the day based on active tracking. They moved slowest at dusk (0.52 km hr-1 ± 0.45 95% CI). The dawn (0.57 km hr-1 ± 0.31 95% CI) and the day (0.61 km hr-1 ± 0.21 95% CI) periods had intermediate values of ROM. Although there were differences in ROMs at different times of the day, these differences were not significant based on 95% CI.

ROMs between receivers also indicated that sharks moved fastest at night (Figure 15). Sharks moved 1.29 km hr-1 (± 0.29 95% CI) during the night, which was higher than during other periods. ROMs during dawn, day, and dusk were all roughly equivalent. During crepuscular periods, it ranged from 0.98 km hr-1 (± 0.33 95% CI) during the dawn to 1.05 km hr-1 (± 0.18 95% CI) during the dusk. During the day it was

1.07 km hr-1 (± 0.18 95% CI). These differences did not appear to be significant based on 95% CI.

Sharks in the main channel moved between receivers more often during the night than during other periods of the day (Figure 16). On average, 53.60% (± 0.15 95% CI) of a shark's movements occurred during the night, whereas during the day 31.70% (± 0.12 95% CI) of their movements occurred on average. Most of the movements that occurred at night occurred from midnight to dawn. Few movements occurred during dusk (4% ± 0.02 95% CI), whereas 10% (± 0.04 95% CI) of all movements recorded occurred at dawn.

Habitat Use

Kernel Utilization Distributions in ESNERR

Five sharks (51, 54, 57, 60 & 63) were actively tracked primarily in ESNERR, mainly during the spring and summer (Figure 17). The activity space of sharks tracked primarily within ESNERR ranged from 0.21 to 0.94 km^2 (mean 0.68 km^2 ± 0.13 SE), and did not appear to be influenced by period of day. During incoming tides, sharks moved out of deeper channels up onto intertidal mudflats as they flooded, and stayed up on the mudflats until the tide started to ebb. Once the water levels declined to a certain level, they vacated the mudflats and moved back to deeper channels where they remained until the tide started to rise again. These movements were regular and predictable.

Several (54, 60 & 63) sharks were pregnant when tagged. Shark 54 was pregnant when caught in 2003, but was primarily tracked in late July and early August, which was after pupping period. However, it appears as if the shark was mainly in ESNERR after being tagged. Permits to search in ESNERR were not obtained until July, and until then the main channel was searched regularly, and the shark was only located on two occasions. Presumably it was in ESNERR during this time since once tracking began in ESNERR it was rapidly located and regularly tracked in the reserve. Shark 60 was pregnant when tagged and was tracked during the pupping period, during which it was always found either in the lagoon or in the northeast channel. This shark strongly exhibited the previously described tidal pattern of movement when moving in and around the intertidal mudflats of the lagoon (Figure 18). Shark 63 also was pregnant when tagged and was tracked primarily during June, which was towards the end of the pupping period. It was mainly found in or around the lagoon until late June, after which it was primarily found around the entrance of ESNERR, the southwest channel, and in the first and second fingers of ESNERR.

Shark 57 was the only other shark actively tracked in 2003, and was tracked for relatively short period of time. It moved between the main channel and ESNERR more regularly than other sharks. During active tracking, it spent nearly equal times in ESNERR and the main channel, however, its pattern of habitat use in ESNERR was similar to the other sharks that were tracked in ESNERR. Shark 51 was tracked almost entirely during July. This shark was found mainly in south marsh earlier in the season, and later in the season was primarily found in the five fingers region, especially in the second finger.

Based on the activity spaces of the sharks tracked within ESNERR, there appeared to be a shift in the areas that sharks were using within ESNERR over the course of the season. In May and June, sharks almost exclusively occurred in the lagoon or in the northeast channel that leads to the lagoon, after that they were rarely found in the lagoon. From late June through August, sharks shifted to South Marsh, the southwest channel, and the five fingers region, the second finger in particular. Sharks were primarily tracked in the main channel from September to November, but when they were tracked in ESNERR during these months they were primarily found in either the northeast or southwest channel, although they were briefly tracked in south marsh and the first finger as well.

Kernel Utilization Distributions in the Main Channel

Three sharks were primarily tracked in the main channel during fall, and exhibited different patterns of movement than did sharks in ESNERR (Figure 19). They rarely were found on intertidal mudflats and their movements were not as influenced by the tides. Their activity space was greater than that of ESNERR sharks, ranging from 0.69 to 1.75 km^2 (mean of 1.32 km^2 ± 0.32 SE), but it did not appear to be influenced by period of day.

Shark 57A was tracked for a short period of time, and like sharks 57, which was also tracked for a relatively brief period of time in November 2003, it was found in ESNERR and the main channel, although its habitat use was similar to that of other sharks tracked in the main channel. Shark 54A was the only juvenile actively tracked. In late September and early October the shark was found at Hudson’s Landing in the upper slough. For the rest of the time it was found in the main channel ranging from just south of Kirby Park to the lowermost parts of the slough. Shark 75 was tracked in the main channel ranging from the lower-most regions of the slough up to Kirby Park. The bulk of tracking occurred in the area midway up the main channel, just off Long Canyon. The distribution of this shark was more influenced by tides than any other shark actively tracked in the main channel (Figure 20). In general as the tidal level increased this shark was usually found further up the main channel, which is similar to other sharks actively tracked in the main channel.

Regional Grouping of Sharks Based on Habitat Use

Because individual sharks exhibited different patterns of habitat use depending on whether or not they were tracked in ESNERR or the main channel, I pooled sharks for a group analysis of habitat use using principal components analysis (PCA) (Table 4) and linear regression. For high tidal levels, the first principal component exhibited a bipolar trend with the ESNERR group being negative, indicating use of shallower habitats, and the main channel group being positive, indicating use of deeper habitats (Figure 21). For intermediate tidal levels, the first principal component also exhibited a bipolar trend with the ESNERR group being negatively loaded, indicating use of shallow habitats, and the main channel group being positively loaded, indicating use of deeper habitats (Figure 22). For low tidal levels, the differences between the two groups were not as strong but were still apparent (Figure 23).

Linear regression analysis indicated that there was no significant relationship ($p > 0.05$) between time tracked and number of habitats utilized during high ($r^2 = 0.1$) or intermediate ($r^2 = 0.05$) tidal levels. For low tidal levels there was a significant relationship ($r^2 = 0.68$, $p < 0.025$). However, this relationship was due to the two sharks

(sharks 57 in the ESNERR group and 57A in the main channel group) which were tracked for the shortest duration (~20 h) indicating they were under sampled during low tidal levels. When these sharks were removed, there was no significant relationship ($r^2 = 0.009$, $p > 0.05$) at low tidal levels.

The results of the PCA and linear regression indicated that it was justified to pool the ESNERR and main channel sharks into groups at low (<0.6 m), intermediate (0.6 – 1.1 m), and high tidal levels (>1.1 m). However, habitat selection of sharks 57 and 57A were only examined individually at low tidal levels and were not included in the low tidal level group analysis due to their differences with the other sharks as shown by the linear regression. The difference between the ESNERR and main channel groups were most obvious at intermediate and high tidal levels. While the grouping was still apparent at low tidal levels, it was not as strong. This was due to sharks being restricted to a narrower range of habitats during low tides when they are all restricted to deeper habitats.

Overall habitat use in all individual sharks was significantly different than predicted based on habitat availability ($p < 0.0000$). In addition habitat use in the ESNERR and main channel groups also was significantly different than predicted ($p < 0.0000$). This indicated that neither individual sharks nor the ESNERR or main channel groups of sharks were using habitats randomly.

Habitat Use of Sharks in ESNERR

Individually, all sharks that were primarily tracked in ESNERR (51, 54, 57, 60, 63) showed a pattern of habitat use where they shifted from using deeper habitats during lower tidal levels to shallower ones during higher tidal levels. At high tidal levels these sharks used low intertidal mudflat habitats (-0.5 to 0 m and 0 to 0.5 m) almost exclusively. To see results for individual sharks, see appendices I – M.

The analysis of the pooled data from all sharks primarily tracked in ESNERR showed the same pattern as was observed in individual sharks. At low tidal levels sharks in ESNERR (sharks 51, 54, 60 & 63) primarily utilized intermediate subtidal habitats. The only habitat type that ESNERR sharks strongly used was the -2 to -1 m habitats (selection index (SI) 2.5 ± 0.29 95% CI) (Figure 24). Sharks used this habitat type significantly more than all other habitat types ($p < 0.001$). They also used the -1 to -0.5 and -0.5 to 0 m habitats more often than would be predicted, but based on 95% confidence intervals only the -0.5 to 0 m habitats appeared to be used significantly more than would be predicted. The -3 to -2 m habitats were used in proportion to their availability. Sharks in ESNERR avoided 0 to 0.5 m and <-3 m habitats, and used them significantly less than all of the other habitat types ($p < 0.001$).

At intermediate tidal levels ESNERR sharks (sharks 51, 54, 57, 60 & 63) increased use of shallower habitats, ranging from intermediate subtidal to low intertidal habitats. They used the -2 to -1 m (SI 2.08 ± 0.31 95% CI) and -0.5 to 0 m (SI 2.43 ± 0.36 95% CI) habitats most intensively, but the -0.5 to 0 m habitats were used significantly more than the -2 to -1 m habitats ($p < 0.025$) (Figure 25). The -3 to -2 m and -1 to -0.5 m habitats were also used, but not as often. The 0 to 0.5 m habitats were used in proportion to their availability. ESNERR sharks used the <-3 m and 0.5 to 1 m habitats significantly less than all other habitats ($p < 0.001$), and the 0.5 to 1 m habitats was used significantly less than the < -3 m habitats ($p < 0.001$).

At high tidal levels, when all habitats were available, sharks (sharks 51, 54, 57, 60, and 63) almost exclusively used habitats in the low intertidal. They used the -0.5 to 0 m habitats most frequently (SI 3.91 ± 0.43 95% CI), followed by the 0 to 0.5 m habitats (SI 2.31 ± 0.43 95% CI) (Figure 26). The -0.5 to 0 m habitats were used significantly more than the 0 to 0.5 m habitats ($p < 0.001$), and both of these habitats were used significantly more than all other habitat types ($p < 0.001$). The -1 to -0.5 m habitats were used in proportion to their availability, but all other habitats were avoided. The highest habitats (> 1 m) were the habitat type most avoided (SI 0.04 ± 0.04 95% CI), and it was used significantly less than all other habitat types ($p < 0.001$).

For sharks 60 and 63, the random points that were generated when they were in the lagoon were not included in this analysis. However, if these data were included it would have only strengthened the observed pattern. This is because the large majority of the substrate of the lagoon is between -0.5 to 0.5 m. Any use of the lagoon that was not included would have strengthened the selection of habitats between -0.5 to 0.5 m, which were the categories that were already highly used.

The low intertidal mudflats that leopard sharks used at intermediate and high tidal levels were primarily found along the northern and eastern boundary of ESNERR. Tagged sharks particularly used the lagoon, the northern part of south marsh, and the five fingers region, the second finger in particular. They were frequently observed making direct rapid directed movements of hundreds of meters across mudflats to these areas of low intertidal mudflats, where they would remain until tidal levels dropped, at which point they would make rapid directed movements back to the channel. These movements were regular and highly predictable.

Habitat Use of Sharks in the Main Channel

Individually, sharks tracked primarily in the main channel (57A, 54A & 75) exhibited a different pattern of habitat use than was observed in sharks tracked in ESNERR. Sharks tracked in the main channel primarily used subtidal habitats, although habitat use was tidally influenced to some extent. While they mainly used subtidal habitats at all tidal levels, use of shallower habitats increased at higher tidal levels. During high tidal levels, sharks used the lowest intertidal habitats, but only as much as would predicted if they were using habitats randomly. Use of intertidal habitats primarily represents the activity of shark 54A (Appendix O), which was the only juvenile shark actively tracked, when it was around Hudson's Landing in late September and early October. When it was at Hudson's Landing, even the channel was relatively shallow (rarely deeper than -1.5 m), and the shark did exhibit limited use of low intertidal mudflats. The general increase in use of shallower habitats at higher tidal levels was likely a result of sharks generally being further up the main channel during high tidal levels, which would lead to this increase in use of shallower habitats because the channel gets shallower with increasing distance from the ocean. To see results for individual sharks, see appendices N – P.

The analysis of the pooled data from all sharks primarily tracked in the main channel showed a similar pattern as was observed in the individuals. At low tidal levels sharks in the main channel (sharks 54A and 75) used deep subtidal habitats and avoided intertidal habitats (Figure 27). They most strongly used the < -3 m (SI 2.18 ± 0.31 95% CI) and -3 to -2 m (SI 1.72 ± 0.36 95% CI) habitats. They used < -3 m habitats significantly more than all the other habitats (p-values ranged from < 0.025 to < 0.001). They weakly used -1 to -0.5 m habitats and weakly avoided the -2 to -1 m habitats. However they avoided the -0.5 to 0 m habitats and strongly avoided the 0 to 0.5 m habitats (SI 0.1 ± 0.07 95% CI), which they used significantly less than all other habitats ($p < 0.001$).

At intermediate tidal levels main channel sharks (sharks 54A, 57A & 75) used habitats similar to those they used at lower tidal levels, although they did increase their use of shallower habitats (Figure 28). They used -3 to -2 m (SI 3.18 ± 0.4 95% CI) and < -3 m habitats (SI 2.2 ± 0.29 95% CI) intensively, but -3 to -2 m habitats were used most and were used significantly more than all other habitats ($p < 0.001$). -2 to -1 m and -1 to -0.5 m habitats were used, while -0.5 to 0 m habitats were avoided, but based on 95% confidence intervals use or avoidance of these habitats likely was not significantly different than would be predicted. The 0 to 0.5 m (SI 0.21 ± 0.09 95% CI) and 0.5 to 1 m (0.08 ± 0.05 95% CI) habitats were strongly avoided, and were used significantly less than all other habitats.

At high tidal levels main channel sharks (sharks 54A, 57A & 75) used shallower habitats than during lower tidal levels (Figure 29), but still did not use intertidal habitats to any great degree, although they did use low intertidal mudflats in proportion to their availability. They used -3 to -2 m (SI 3.27 ± 0.58 95% CI), -2 to -1 m (SI 2.24 ± 0.49 95% CI), and -1 to -0.5 m (3.12 ± 1.3 95% CI) habitats most intensively. These habitats were used significantly more than all other habitats ($p < 0.001$). They used < -3 m and -0.5 to 0 m habitats roughly in proportion to their availability. They avoided 0 to 0.5 m, 0.5 to 1 m, and > 1 m habitats, which they used significantly less than all other habitats (p-values ranged from < 0.005 to < 0.001).

DISCUSSION

Acoustic tracking of sharks in shallow geographically complex estuaries such as Elkhorn Slough is challenging, but the techniques that I developed worked well. The active tracking techniques allowed me to gather fine-scale information about movements and moored receivers provided broader scale temporal and spatial information about shark movements. While active tracking in very shallow areas, I minimized movements of the tracking boat and used a pole to move the boat whenever possible. This minimized the impact of the boat on leopard shark behavior. In general, leopard sharks did not appear to be easily perturbed. It was obvious when the presence of the boat did affect the behavior of the sharks being tracked, so suspect data could be discarded and steps could be taken to avoid such occurrences in the future.

During active tracking, I was able to consistently and reliably locate sharks in Elkhorn Slough. The slough could be thoroughly searched, and based on experience it seems very unlikely that a shark was in the slough if it was not located. The only areas I could not thoroughly search were the tidal creeks that branched off from the main channel. However, no shark was ever observed entering or leaving tidal creeks during active tracking, and there was no indication that they were extensively using tidal creeks based on acoustic tracking. That does not mean that they are not using these areas, but if they are, they do not seem to be using them extensively.

Residency, Seasonal Abundance, and Regional Use

Once female leopard sharks were in Elkhorn Slough, they rarely made forays into coastal waters. Based on acoustic monitoring, only two sharks (100 & 107) were observed to leave the slough and return during the same season, indicating that sharks rarely returned during the same season after they vacated the slough. Active tracking results also support the conclusion that leopard sharks largely remain within the slough once they enter it. When sharks were being actively tracked, they were consistently located. On every occasion when a shark was not located, it was not located again during the course of the study, indicating that it had left the slough or the tag had failed.

Based on acoustic monitoring, at least some leopard sharks exhibit seasonal site fidelity to the slough. Shark 100 returned to the slough after having left for the winter, and shark 115 likely did as well. This demonstrated that some individuals return to Elkhorn Slough on a seasonal basis. Seasonal site fidelity also has been observed in bat rays (Tomales Bay, CA: Matern et al. 2000, Hopkins & Cech Jr. 2003), lemon sharks (*Negaprion brevirostris*) (Bimini, Bahamas: Feldheim et al. 2002), and sandbar sharks (Delaware Bay: Merson and Pratt Jr. 2001).

The results of this study support previous findings that leopard sharks are seasonally abundant in Elkhorn Slough and that they generally leave enclosed bays and estuaries in the winter (Barry 1983, Talent 1985, Yoklavich et al. 1991, Smith & Abramson 1990). According to Talent (1985), leopard sharks occur in the slough year round in similar numbers. However, based on this study it seems likely that sharks caught in the winter are primarily transient.

The observed seasonal pattern of abundance is likely related to changing environmental conditions. Hopkins & Cech Jr. (2003) reported that temperature and salinity were the two most important factors determining the seasonal abundance of leopard sharks in Tomales Bay. They stated that when temperatures dropped below 10 – 12º C in the late fall and winter, leopard sharks left the bay, and that they returned in the early spring when temperatures increased to greater than 10 ºC.

This is similar to what I observed in Elkhorn Slough during this study. In 2003 and 2004, temperatures in Elkhorn Slough decreased to levels at or below 12 ºC in late November, and temperatures increased above 12 ºC starting in mid March. These time periods corresponded to times when tagged leopard sharks vacated the slough and when they returned. Except for the two juvenile leopard sharks that remained in ESNERR during winter of 2004, every leopard shark that was tagged exited the slough by mid to late November, and leopard shark catch rates declined later in the year as well, although no fishing occurred in the winter. Shark 100 returned to the slough in mid April, and shark 115 returned in mid May, but it is likely that leopard sharks started returning earlier than that because leopard shark catch rates were high in late March.

The use of different regions within Elkhorn Slough by female leopard sharks followed an interesting seasonal pattern. ESNERR was used intensively throughout the year, but especially during the spring and summer, which was during the pupping season. The intensive use of ESNERR in the spring and summer was likely tied to the abundance of leopard shark prey and its use as a nursery area, although leopard sharks also may have used this area due to increased temperatures that occur there. It is thought that leopard sharks behaviorally thermoregulate by using shallow warm areas to improve physiological and metabolic processes (Hight 2005), which may be why they use the warm waters of the slough and ESNERR in particular.

Use of ESNERR decreased in the late summer and fall, which is likely tied to changing environmental conditions. In the late summer and early fall, water temperature reached its highest levels (up to 24° C) and dissolved oxygen reached its lowest levels (to 1 mg l-1) in ESNERR, suggesting that conditions became stressful for the sharks. In a study on effects of hypoxia on three species of sharks, Carlson and Parsons (2001) considered dissolved oxygen levels below 5 mg l-1 as hypoxic, below this point sharks altered their swimming and respiratory behavior in response to decreased levels of dissolved oxygen. Going by this standard, conditions in ESNERR were frequently hypoxic in the late summer and early fall because mean levels of dissolved oxygen were consistently at or below 5 mg l-1 and the extremes were obviously less than that and it was not unusual for levels to decrease below 3 mg l-1.

Whereas leopard sharks continued to use ESNERR extensively throughout the time they were in Elkhorn Slough, the combination of decreased dissolved oxygen and greater temperatures in ESNERR may have increased the energetic cost of remaining in that area. As a result, leopard sharks may have increased their use of the main channel during this time. In fact, all adult sharks such as shark 102, that were being monitored during August ceased using ESNERR during that time and did not use ESNERR to any great extent for the rest of the year. Shark 100, however, returned to the slough in late September and remained exclusively in ESNERR, possibly because conditions had returned to more normal, less potentially stressful conditions by that time. This also may be why sharks monitored in 2003 spent more time in ESNERR in the fall than was observed in fall 2004. These sharks were tagged in the fall when conditions would have been less stressful, although low sample size, and individual and inter-annual variability also likely played a role.

Interestingly, the two tagged juveniles remained in ESNERR throughout the summer, fall, and winter. Assuming they had not died and their tags had not failed, their remaining in ESNERR could be related to age-specific differences in physiology similar to what have been reported for lemon sharks (Bushnell et al. 1989), the young of which are physiologically adapted to the more extreme environmental conditions found in shallow nursery areas, which they use extensively (Morrissey & Gruber 1993). However, there is no documentation of such physiological adaptations in young leopard sharks.

Sharks spent more time in the main channel regions late in the year. The upper region was the most heavily used in the main channel after sharks started spending less time in ESNERR. Sharks spent more time in the mid and lower region right before they left for the season. Active tracking supported this pattern. Activity spaces shifted from ESNERR in the spring and summer to the upper areas of the main channel in the early – mid fall. At that time, sharks were primarily tracked in the mid and lower region of Elkhorn Slough in the late fall before sharks vacated the slough for the season.

The increase in use of the lower and mid region of the main channel late in the year is likely tied to declining temperature and salinity in the upper region. The highest levels of freshwater input occur in the upper region, and areas in the upper slough and ESNERR that are shallower and further from the ocean experience more extreme conditions than areas in the lower and mid regions, which are more stable due to their proximity to the ocean (Caffrey & Broenkow 2002). As a result, when temperature and salinity levels decrease during the fall, they decrease more rapidly in the upper slough than they do in the more stable lower areas of the slough. Because leopard sharks are sensitive to decreased temperature and salinity (Hopkins & Cech Jr. 2003), they possibly move to the lower slough in the late fall after encountering rapidly dropping temperature and salinity levels in the upper slough and to a lesser extent ESNERR. Shortly thereafter sharks then vacate the slough for the winter.

Overall Rate of Movement

The ROM of 0.6 km hr-1 that was observed during active tracking was similar to those previously reported for leopard sharks. Ackerman et al. (2000) reported that leopard sharks moved approximately 0.52 km hr-1 (average of day and night rates). The rate observed in this study also was similar to those reported for bat rays (0.53 km hr-1) (Matern et al. 2000) and Pacific angel sharks (*Squatina californica*) (0.49 km hr-1) (Standora & Nelson 1977). Interestingly, the ROMs of sharks in the main channel and in ESNERR were nearly identical, which indicated that sharks were moving in a similar fashion in both regions while being actively tracked. These rates were slower than most other rates reported in coastal elasmobranchs, such as the lemon sharks, which moved at 1.19 km hr-1 (Sundström et al. 2001) and gray reef sharks (*Carcharhinus amblyrhynchos*) that moved at rates between 1.7 and 3.3 km hr-1 (McKibben & Nelson 1986). Leopard shark ROMs, however, were greater than the rates reported for several other coastal elasmobranchs. The Hawaiian stingray (*Dasyatis lata*) moved at approximately 0.25 km hr-1 (average of day and night ROM) (Cartamil et al. 2003), and the lesser spotted dogfish (*Scyliorhinus canicula*) moved at approximately 0.11 km hr-1 (average of individual's reported ROM) (Sims et al. 2001).

ROMs calculated from VR1 data were greater than those observed through active tracking, with an overall ROM of 1.24 km hr-1. This was likely due to the fact that movements between VR1 receivers were in general large-scale directed movements. The discrepancy between the rates of the directed long-distance movements observed by VR1s and the active tracking rates indicated that most of the movements during active tracking represented more meandering localized movements, possibly related to foraging or searching behavior. In general these VR1 rates were similar to ROMs reported for other coastal sharks. Lemon sharks have been reported as moving 1.19 km hr-1 (Sundström et al. 2001) and 1.67 km hr-1 (Gruber et al. 1988), blacknose sharks (*Carcharhinus acronotus*) at 1.14 km hr-1 (Carlson et al. 1999), juvenile sandbar sharks at 1.54 km hr-1 (Rechisky & Wetherbee 2003) and 1.21 km hr-1 (Medved & Marshall 1983), and juvenile scalloped hammerheads (*Sphyrna lewini*) at 1.24 km hr-1 (Holland et al. 1993). In addition, these ROMs were all well below the reported maximum sustainable swimming velocity of approximately 2.8 km hr -1 reported for similar sized leopard sharks (Graham et al. 1990)

Tidal Patterns of Activity

Tides are an important factor in the distribution of leopard sharks in Elkhorn Slough. Of the different factors that might influence patterns of movement of elasmobranchs in bays and estuaries, tides are likely to be one of the most important. Tides alter the amount of habitat available for use and cause considerable variability in currents, both of which would likely influence patterns of movement, especially because intertidal areas often are important foraging areas for leopard sharks. In addition, physical characteristics of the water column, such as temperature, salinity, and turbidity also may change as a result of tidal action, which could also influence movements.

The distribution of sharks within the main channel of Elkhorn Slough was influenced by the tides. Sharks were found in the lower slough at low tidal levels, in the mid slough at intermediate tidal levels, and in the upper slough at high tidal levels. The extent of the movement up and down the channel also was related to the tidal range. When tidal ranges and tidal currents were greater, the distance they moved up or down the main channel increased. Directed, long-distance movements up and down the slough often occurred around the day's lower low tide, which in Elkhorn Slough is when the strongest tidal currents occur (Caffrey & Broenkow 2002). Several sharks exhibited movements up and down the length of the slough that were highly periodic, often once a day, and were centered around the day's lower low tide. The fact that sharks in the main channel were frequently moving up and down the length of the main channel indicated that they were likely using the entire length of the slough.

The general distribution of sharks in ESNERR was also influenced by the tide, with the general pattern being similar to that in the main channel. Sharks generally were in upper parts of ESNERR away from the receivers over most of the tidal cycle and would usually only move down to the entrance of ESNERR around lower low tides. The greatest currents recorded in the slough (6.16 km hr-1) were recorded during ebb tide in Long Canyon, which is due to the fact that all of the water in ESNERR drains through

Long Canyon. Interestingly, despite possibly experiencing the strongest currents in the slough, sharks often remained in ESNERR for extended periods of time without departing or even being detected at Receiver 5. Sharks in ESNERR were actively tracked during these periods of greater tidal currents, and often they would swim against the current and remain in channels some distance from the entrance. When they did swim with the current towards the entrance, instead of continuing with the current and exiting the reserve, they would swim up another channel into the current. In general, sharks in ESNERR were frequently observed swimming against the current, even during periods of strong current.

Because most of the water drains from ESNERR during every lower low tide, sharks had to swim against strong currents to remain in ESNERR. If sharks moved with the currents, they would have left ESNERR regularly during these periods of greater tidal current. Indeed, when they did depart ESNERR it was almost always during these periods. That leopard sharks swam against the current to remain in ESNERR was different than occurred in sharks in the main channel, where they usually moved with the currents and frequently moved up and down the length of Elkhorn Slough during a tidal cycle. This indicated that the benefit of remaining in the ESNERR made the increased energetic cost of swimming against the current worthwhile, whereas sharks in the main channel are not as tied to any particular area and do not generally fight the current to remain in a particular area.

Leopard sharks in the main channel were more active when the tidal range, and therefore the tidal velocity, was greater. The increase in frequency of movements between receivers during greater tidal ranges indicated that sharks were making more directed, long-distance movements and moving greater distances when the tidal range was greater. The fact that leopard sharks moved faster when tidal range and current were grater was expected and similar to what was reported by Medved & Marshall (1983) for young sandbar sharks. The ROM of sandbar sharks, however, was not significantly different from those of passive drifting, which led Medved and Marshall to believe that the tidal current was responsible for much of the sharks' movement.

Leopard sharks making directed movements between receivers moved with the tide (negative rheotaxis), and when they moved with the tides their ROM was greater, which also was observed in young sandbar sharks (Medved & Marshall 1983). Leopard sharks in this study moved twice as fast when moving with the current, which was less than the two- to three-fold increase in ROM reported for young sandbar sharks when moving with the current (Medved & Marshall 1983). Dusky sharks (Huish & Benedict 1978) and Atlantic stingrays (Teaf 1980) also have exhibited negative rheotaxis in bays and estuaries. Cownose rays (Smith & Merriner 1985), spotted eagle rays (Silliman & Gruber 1999), southern stingrays (*Dasyatis americana*) (Gilliam & Sullivan 1993) and leopard sharks (Ackerman et al. 2000) all make tidal movements into shallower areas at high tides, so while it was not explicitly described their overall movements were likely with the tides. By moving with the currents, elasmobranchs use intertidal areas to forage while minimizing energy expenditure during movements (Teaf 1980, Ackerman et al. 2000).

Diel Patterns of Activity

While tide appeared to be the major factor influencing movements, time of day had less of an effect on the movements of leopard sharks. Sharks moved faster and more frequently between receivers during night, with the greatest number of movements occurring from midnight to dawn. Manly (1995) reported that acoustically tagged leopard sharks in Big Fisherman's Cove, Santa Catalina Island, CA were more active at night, likely due to foraging. Based on active tracking, leopard shark ROM was 0.69 km hr-1 at night, which was faster than during other periods of the day. This also was similar to what Ackerman et al. (2000) reported for leopard sharks. They reported that sharks moved 0.63 km hr-1 at night versus 0.40 km hr-1 during the day. Also, Ackerman et al. (2000) reported that ROMs were greatest between 00:00 h and 08:00 h, which corresponded with when sharks were moving between receivers most frequently during this study.

Many researchers have reported diel activity patterns in elasmobranchs and indicated that elasmobranchs are more active during crepuscular or nighttime hours. Amongst the different species that have been documented exhibiting crepuscular or nocturnal activity patterns were Pacific angel sharks (Standora & Nelson 1977), blue sharks (*Prionace glauca*) (Sciarotta & Nelson 1977), horn sharks (*Heterodontus francisi*) (Nelson & Johnson 1970), swell sharks (*Cephaloscyllium ventriosum)* (Nelson & Johnson 1970), gray reef sharks (McKibben & Nelson 1986), megamouth sharks (*Megachasma pelagios*) (Nelson et al. 1997), bigeye thresher sharks (*Alopias superciliosus*) (Nakano et al. 2003, Weng & Block 2004), lemon sharks (Gruber et al.

1988), bat rays (Matern et al. 2000), Hawaiian stingrays (Cartamil et al. 2003), lesser spotted dogfish (Sims et al. 2001), tiger sharks (Lowe et al. 1996), scalloped hammerhead sharks (Holland et al. 1993, Klimley et al. 1988), Cortez electric rays (*Narcine entemedor*) (Michael 1993), and California electric rays (Bray & Hixon 1978). Most of these movements or increases in activity have been attributed to crepuscular or nocturnal foraging behavior.

Habitat Use

Habitat use differed depending on whether sharks were in ESNERR or the main channel. Habitat use of sharks in the main channel did not appear to be strongly influenced by the tides, and they almost exclusively used subtidal habitats. Sharks in ESNERR extensively used intertidal habitats and their habitat use was strongly influenced by the tides. When available, sharks almost exclusively used lower intertidal habitats from -0.5 to 0.5 m while avoiding higher intertidal mudflats. Although they did move onto intertidal mudflats with the tide, they did not follow the advancing tide past these lower intertidal habitats. They did not passively ride the tide onto intertidal mudflats, instead they actively moved to the low intertidal habitats as soon as they were available and remained there until ebbing tides forced them back to the channels.

The influence of tide on habitat use has been documented in several elasmobranchs, and usually has been attributed to feeding. Leopard sharks have been reported to make tidally-influenced foraging movement (Ackerman et al. 2000), where they move in with the tide to forage in intertidal mudflats and then move back out with the receding tide. Atlantic stingrays were reported to move from deeper channels up onto intertidal mudflats with the incoming tide to forage (Teaf 1980). Cownose rays (Smith & Merriner 1985), spotted eagle rays (Silliman & Gruber 1999), and southern stingrays (Gilliam & Sullivan 1993) also have been reported to make tidal movements into shallower areas at high tides to feed. These patterns of tidally influenced habitat use are very similar to what was observed in sharks in ESNERR, indicating that the movements and habitat use of sharks in ESNERR are likely related to feeding.

Feeding Relative to Movements and Habitat Use

Because the movements of elasmobranchs are influenced by the availability of prey (Holland et al. 1993, Sims et al. 2001, Wetherbee et al. 2001, Heithaus et al. 2002, Rechisky & Wetherbee 2003), it is important to understand the distribution and abundance of leopard shark prey in Elkhorn Slough to put activity patterns and habitat use into context. The distribution and abundance of potential prey items varies throughout the length of Elkhorn Slough. In general, the diversity of invertebrates (Wasson et al. 2002) and fishes (Barry 1983, Yoklavich et al. 1991, Yoklavich et al. 2002) decreases with distance from the ocean. The abundance and diversity of fishes also varies temporally, increasing in spring, greatest in summer, and decreasing in the fall (Yoklavich et al. 1991, Yoklavich et al. 2002).

Because leopard sharks are opportunistic predators and potential prey can be found throughout Elkhorn Slough, they are able to feed throughout the slough. However, according to Kao (2000), leopard sharks in Elkhorn Slough primarily feed upon five main prey categories: decapod crabs (rock crabs: *Cancer* spp., yellow shore crabs), fat innkeeper worms, clams (gaper clams: *Tresus nutallii,* Washington clam: *Saxidomus* *nutalli*), polychaete worms (*Nereis* spp.), and fishes (staghorn sculpins: *Leptocottus armatus,* topsmelt: *Atherinops affinis,* northern anchovy: *Engraulis mordax,* shiner surfperch: *Cymatogaster aggregata*, and unidentified surfperches). The most important prey items were fat innkeeper worms and fishes. Many of these prey items were most abundant in specific regions of the slough.

Several important prey items are abundant in the lower main channel, and it is possible that the occurrence of leopard sharks in this region is tied to the availability of these prey items. The clams most commonly consumed by leopard sharks (gaper and Washington clams) are restricted to the sandier substrate of the lower slough. Rock crabs also are generally only found subtidally in the lower parts of the slough (Wasson et al. 2002). In the main channel, fat innkeeper worms are primarily found in the lower regions of the main channel. In these areas they are found intertidally and subtidally, although they are most abundant subtidally where they comprise up to 80% of the invertebrate biomass in areas (Jolly 1997). Although the overall diversity of fishes is highest in the lower channel, the only species that is abundant and fed extensively upon by leopard sharks is the shiner surfperch (Yoklavich et al. 1991, Yoklavich et al. 2002). The yellow shore crab is abundant throughout the length of the slough and in ESNERR (Wasson et al. 2002), and are typically most abundant in the low intertidal zone (Sliger 1982),

While the diversity of prey is lower in the mid and upper main channel relative to the lower main channel, there are a higher number of fish species that are important to the diet of leopard sharks in these regions than in the lower main channel, suggesting that leopard sharks may feed on these fishes in these regions. Topsmelt are most abundant in the mid slough, and shiner surfperch are abundant as well. In the main channel staghorn sculpins and northern anchovy are most abundant in the upper regions of the slough (Yoklavich et al. 1991, Yoklavich et al. 2002).

ESNERR has a high number of important prey items relative to the other regions of Elkhorn Slough, and the abundance of prey is likely why leopard sharks use this area so extensively. While the distribution and abundance of fat innkeeper worms in ESNERR has not been studied, they are present subtidally and intertidally (Kao 2000, Carlisle personal observation). However, fat innkeeper worms likely are more abundant in the low intertidal zone, which is generally where fat innkeeper worms are most abundant (Ricketts et al. 1985). Small (1986) reported that staghorn sculpins and northern anchovies dominated the ichthyofaunal assemblage in ESNERR, but that shiner surfperch and topsmelt also were present. These fishes are likely present in subtidal and intertidal habitats, as estuarine fishes move are known to move with the tides onto intertidal mudflats (Thomas & Connolly 2001, Morrison et al. 2002, Greenwood & Hill 2003, Dorenbosch et al. 2004).

It seems likely that the tidal pattern of habitat use in ESNERR is due to leopard sharks foraging intertidally, especially on fat innkeeper worms. That habitat use of leopard sharks is tidally influenced is not surprising as leopard sharks have been reported to move with the tide onto intertidal mudflats where they forage (Ackerman 1971, Talent 1976, Webber & Cech Jr. 1998, Ackerman et al. 2000, Kao 2000). The large number of apparent feeding pits in the lower intertidal zone indicated that leopard sharks (and/or other elasmobranchs) were foraging in this area. The importance of fat innkeeper worms is supported by Kao (2000), who reported that leopard sharks feed intensively upon fat innkeeper worms in ESNERR. Although fat innkeeper worms are of lesser caloric density per unit volume than fishes, Kao (2000) suggested that they were a more abundant and spatially reliable food source compared with fishes, so may be a more important food item where they are abundant.

It seems likely that the abundance of low intertidal mudflats is why ESNERR is used so extensively by female leopard sharks. The importance of intertidal mudflats is likely related to the high abundance of prey items, such as fat innkeeper worms, that occur in these habitats. The activity spaces of sharks tracked in ESNERR were smaller than those of sharks in the main channel, indicating that they likely foraged over smaller areas, which could be indicative of a high abundance of prey items. The importance of this area is demonstrated by the intensive use by sharks throughout the time that they are in the slough, and by the fact that sharks actively swim against the strong currents on a daily basis to remain in ESNERR for extended periods of time.

Whereas leopard sharks used intertidal mudflats intensively in ESNERR, leopard sharks in the main channel primarily used subtidal habitats, indicating that intertidal mudflats in the main channel are less important than those in ESNERR. This is likely because most of the intertidal mudflats are found in the upper slough. In the upper slough, the environmental conditions (temperature, salinity, dissolved oxygen) are more variable and extreme, the overall diversity of potential prey is lowest, and the amount of habitat varies greatly with tidal level. Most importantly, fat innkeeper worms are not found in the upper slough, so the primary intertidal prey is not found in the area of the main channel with most of the intertidal mudflats.

Because they are opportunistic predators and important prey items are found throughout the slough, leopard sharks are not restricted to feeding in any one region and likely feed throughout the main channel. The fact that activity spaces of sharks tracked in the main channel were greater than those of sharks tracked in ESNERR indicated that they forage over larger areas. However, because of the distribution of important prey, sharks need to move to particular regions to feed on particular important prey items. This is likely why sharks in the main channel move up and down the main channel so extensively.

Based on the distribution of prey items and the highly tidal nature of leopard shark movements in the main channel, it appears that instead of fighting currents to remain in a particular region as they did in ESNERR, likely due to the diversity and abundance of important prey items in that region, these sharks use the tidal currents to assist their movements along the length of the slough. By doing so, they would minimize the energetic costs of movement while maximizing the area over which they can move or forage. This allows them to more easily forage over the entire length of the main channel and gain access to the different prey items that are abundant in different areas of the main channel. For example, we know that leopard sharks feed during their brief visits to the lower slough that generally around lower low tide because they consume the clams and crabs that only occur there. Also, Kao (2000) reported that fish are an important prey item to sharks in the main channel, and the fact that the important fish prey that occur in the main channel are most abundant in the mid and upper slough indicated that sharks fed upon fishes in those areas.

By using the tides to facilitate movements, sharks can gain access to prey-rich areas while minimizing energy expenditure traveling to and from these areas. In addition, moving with the tide enables sharks to forage over larger areas. Ackerman et al. (2000) reported that by using the tide to facilitate movements into intertidal mudflats, leopard sharks could possibly conserve 6% of their total energy expenditure. Teaf (1980) theorized that the Atlantic stingray used its batoid body form to minimize energetic costs of movement by passively drifting with the tide into intertidal areas to forage. Medved & Marshall (1983) reported that young sandbar sharks passively rode the tide in Chincoteague Bay, VA, and that the only time they did not move with the tide was when they were in close proximity to menhaden (*Brevoortia tyrannus*). This indicated that these sharks may have used tidal currents to minimize energetic expenditures while searching for prey. Wetherbee et al. (2001) found similar tidally influenced movements in juvenile sandbar sharks in Delaware Bay.

Kao (2000) reported that leopard sharks fed on fishes in the main channel nocturnally. If leopard sharks are foraging on more mobile fish prey at night, especially in the main channel, this could be why leopard shark activity increased at night in the main channel. By feeding at night, leopard sharks are able to utilize their specialized olfactory, electrosensory and mechanosensory capabilities to aid in the capture of prey. This sensory advantage that elasmobranchs have over potential prey items is believed to be why many elasmobranchs forage nocturnally (Tricas 1982, Heithaus 2004).

It is possible that shark use of intertidal areas in the upper region was underestimated due to the limited sample size. Most of the observed use of intertidal mudflats in the main channel occurred during the tracking sessions of shark 54A at Hudson's Landing, although use of these habitats was not nearly as obvious as was observed in ESNERR. This indicates that use of intertidal habitats is indeed less in the main channel than in ESNERR, although again if more sharks were tracked, increased use of intertidal habitats could become apparent because based on acoustic monitoring sharks do spent large amounts of time in the upper region.

The apparent difference in feeding ecology between sharks in ESNERR and the main channel is not surprising given that the feeding ecology of leopard sharks varies by geographic area (Russo 1975, Talent 1976) and by site within a location (Webber & Cech Jr. 1998, Kao 2000). Webber & Cech Jr. (1998) reported that the feeding ecology of leopard sharks is site specific and reflects prey abundance. They reported that in Tomales Bay, leopard sharks foraged intertidally at an inner bay site, where they fed primarily on fat innkeeper worms, whereas at an outer bay site 6 km away they fed primarily on rock crabs, likely subtidally. They theorized that this was a result of differing abundances of prey at the two sites. As previously mentioned, Kao (2000) also reported that the diet of leopard sharks varied based on whether the sharks were in ESNERR or the main channel.

Overall leopard sharks are opportunistic benthic predators, and their diets likely reflect prey availability (Talent 1976, Webber & Cech Jr. 1998, Kao 2000). In addition, their diets in Elkhorn Slough have been shown to vary throughout the year so that they are not reliant on any one type of prey (Talent 1976). Because of this flexibility, they are able to feed in different areas of the slough throughout the year. It is not surprising that the feeding ecology of leopard sharks in ESNERR might be different from that of sharks in the main channel, because prey availability and habitat structure differ between the two regions, or that their feeding ecology might change seasonally.

Elkhorn Slough as a Nursery Area

Elkhorn Slough is a nursery area for leopard sharks (Ackerman 1971, Barry 1983, Talent 1985, Yoklavich et al. 1991, Carlisle et al. in review). As a result, the use of Elkhorn Slough by leopard sharks during the pupping period in the spring and summer is likely linked to reproductive activities. Ackerman (1971) stated that females give birth in the late spring and summer, probably beginning in mid to late May and peaking in June, and that some females contained fertilized eggs by early June, indicating that mating occurred shortly after birth. Talent (1985) reported that gravid females examined in April all had near-term young, and most females examined later in the summer contained recently fertilized eggs with little embryonic development, another indication that leopard sharks gave birth in Elkhorn Slough in the spring and early summer and mated shortly thereafter. This timing of parturition was supported by Ebert & Ebert (2005), who found that leopard sharks pupped in late May in Humboldt Bay. A possible mating event was witnessed in ESNERR by the author in early June in Elkhorn Slough, and leopard sharks have been observed mating off La Jolla in early August (Smith 2005), which supports the theory that mating occurs in the summer after parturition. Based on these studies, parturition in Elkhorn Slough likely occurs mainly in April – June, possibly peaking in May, and fertilization occurs shortly afterwards,

This study provides further evidence that Elkhorn Slough is an important nursery area for leopard sharks. Two pregnant female leopard sharks (102, 105) were acoustically monitored during this study, and each one of them remained almost exclusively in ESNERR for the duration of the pupping period. Similarly, shark 54 was pregnant when tagged, and although it was not actively tracked within ESNERR during the pupping period, it almost certainly was within ESNERR during the pupping period. This strongly indicates that these sharks gave birth within ESNERR. In addition, when shark 100 returned to the slough in April 2004, it was likely pregnant because leopard sharks have an annual reproductive cycle (Kusher et al. 1992). After entering the slough and spending 2 – 3 days in the main channel, the shark entered ESNERR and remained there for approximately 2 weeks before directly exiting the slough. This indicated that this shark returned to the slough, entered ESNERR to pup, and then departed after giving birth. The extensive use of ESNERR by pregnant sharks during the pupping period is strong evidence that ESNERR is a primary nursery area.

Within ESNERR, sharks intensively used low intertidal mudflats during the pupping period. This indicated that these habitats may have been where females gave birth in ESNERR. Leopard sharks have been observed giving birth in shallow areas in other areas. In Humboldt Bay, CA leopard sharks gave birth in low intertidal eelgrass beds (Ebert & Ebert 2005). Leopard sharks also have been observed giving birth in a shallow mudflat in Catalina Harbor, Santa Catalina Island, CA (Smith 2001). The lagoon, which has a large amount of low intertidal mudflats, in particular appears to be a specific area that is being used as a nursery area. Sharks (60 & 63) that were tagged and actively tracked in May and June were pregnant, and spent the entire pupping period in the lagoon or its immediate vicinity, which is evidence that they gave birth in the lagoon. After the pupping period, these sharks shifted their activity spaces from the lagoon to other areas, primarily south marsh and the five fingers area, and the second finger in particular. After June, none of the actively tracked sharks, including the ones that used that area extensively earlier in the year, frequented the lagoon with any regularity.

If leopard sharks do give birth in the lagoon, one possible explanation for the subsequent shift away from the lagoon is that it could be a way to minimize competition with neonates and the risk of consuming them. Cannibalism has been noted in a variety of shark species (Ebert 1991, Morrissey & Gruber 1993, Merson & Pratt Jr. 2001), including the leopard shark (Ackerman 1971) which, in addition to occasionally consuming neonatal leopard sharks, also feed on neonates of several other species of elasmobranchs (Russo 1975, Talent 1976). Minimizing the threat of predation from larger sharks, which is believed to be one of the major sources of mortality in elasmobranchs (Van der Elst 1979), is believed to be one of the primary functions of nursery grounds (Simpfendorfer & Milward 1993, Heupel & Heuter 2002). Not only are other species of sharks a possible threat, but adult conspecifics also might consume their own young.

Behavioral adaptations in adult females that increase the survival of neonates would be advantageous. One such behavioral adaptation could be to cease feeding when in nursery areas, as was reported by Springer (1960, 1967), who noted that female sandbar sharks and bull sharks (*Carcharhinus leucas*) stopped feeding when in nursery grounds and resumed feeding after moving to a different area after giving birth. Another example of a possible behavioral adaptation is to shift diets to minimize intraspecific competition as was suggested by Ebert & Ebert (2005). Ebert & Ebert (2005) reported that adult female leopard sharks fed primarily on fish eggs in Humboldt Bay before parturition, however, after they gave birth their diets shifted to crustaceans, which allowed neonates to feed on fish eggs without competing with adults. The observed decline in the use of the lagoon by female leopard sharks after the pupping period could represent a behavioral adaptation to maximize survivorship of neonatal leopard sharks. By shifting their activity space, adult females, or at least the ones that appeared to have given birth in that area, would reduce the risk of consuming neonatal leopard sharks and reduce intraspecific competition for prey items.

In the 1970s, the tidal creeks that branch off the main channel were used as nursery areas by leopard sharks during spring and summer (Barry 1983), but this appears to have changed. Since then, the tidal creeks have gotten wider and deeper, which affected their nursery function. There was no evidence of leopard sharks using tidal creeks from this study, so the importance of these habitats as nursery and foraging areas appears to have diminished. However, the role that was previously filled by tidal creeks had has been filled by ESNERR, which now appears to be the primary nursery habitat of the slough. That does not mean it is the only area in the slough that is being used as a nursery area, but there is no evidence of other areas of Elkhorn Slough currently being used in such a way. The fact that ESNERR is a nursery area for leopard sharks is quite remarkable considering that the reserve has only been open to marine waters and tidal flow since 1983, meaning that in less than 20 years this rehabilitated habitat has developed into a fully functioning nursery area for an upper level predator.

The importance of ESNERR may have increased soon after being opened to tidal flow. From 1951 to 1996, annual or biannual shark derbies occurred in Elkhorn Slough from May to July. Leopard shark catch during the derbies was consistent throughout the years until the mid-1980s, when it started to decrease. It decreased from approximately 30% of the catch in the 1970s to approximately 18% of the catch in the 1990s (Carlisle et al. in review). This timing of the decline corresponds with the creation of ESNERR. Although increased fishing pressure may have played a role in the decrease, the fact that female leopard sharks heavily used ESNERR during the time of year that the derbies occurred suggests that this decline may be a result of sharks being within ESNERR, therefore, being protected from the fishing effort.

In addition to being a primary nursery area, Elkhorn Slough also is a secondary nursery area for leopard sharks (Barry 1983, Carlisle et al. in review). During the Elkhorn Slough shark derbies, leopard shark catch was always strongly dominated by immature leopard sharks (Carlisle et al. in review). In addition, Talent (1985) and Barry (1983) reported that smaller leopard sharks were abundant in the spring and summer. This indicated that Elkhorn Slough functioned as a secondary nursery area at least during the warmer months of the year. This is supported by the fact that the two juvenile leopard sharks remained in ESNERR throughout the entire study. Morissey & Gruber

(1993) reported the juvenile lemon sharks used shallow areas as nursery areas to avoid predators and because the warmer waters may increase digestion and growth rates. Talent (1976) reported that because the diet of smaller leopard sharks were more restricted they may need a special environment where a particular food item is abundant, and Kao (2000) reported that smaller sharks fed exclusively on fat innkeeper worms in ESNERR. This indicated that juvenile leopard sharks may use ESNERR as a secondary nursery area due to the warmer water temperatures, lack of predators, and abundance of fat innkeeper worms. Why the two juveniles did not leave in the winter of 2004 is unknown. The VR60 was used to locate them occasionally until fall of 2004, at which point such effort ceased under the assumption that they were alive. It is possible, however, that they died or their tags failed afterwards. There is a small amount of illegal fishing that occurs along the western boundary of ESNERR, so it is also possible that they were caught by fishermen.

Leopard sharks exhibit a high degree of sexual segregation (Ackerman 1971, Ebert & Ebert 2005). Ackerman (1971) reported that the sex ratio of leopard sharks changed seasonally. From February to May the sex ratio was approximately 1:1, whereas from June through the rest of the year, it was usually around 2.5 females per male. Because leopard sharks mate shortly after giving birth in the spring and early summer (Ackerman 1971, Talent 1985, Ebert & Ebert 2005), this possibly indicates an influx of males into the slough for mating following parturition. Throughout this study, the catch of leopard sharks (and bat rays and thornbacks) in ESNERR was almost entirely female, whereas only male leopard sharks were caught in the main channel during the spring.

This suggests that most females were in the reserve during spring, likely pupping. However, in the summer and fall the sex ratio of the leopard sharks in the main channel was closer to 1:1. In addition, in the late summer when fishing in the main channel, small schools of adult leopard sharks were caught. These groups always had a sex ratio of 1:1. This suggested that females may mate in the main channel after giving birth. However, the possible mating event that was observed in ESNERR indicated that mating also may occur in that area.

Whereas leopard sharks are susceptible to overexploitation due to their life history characteristics, they also are vulnerable to loss of critical habitats in bays and estuaries. Leopard sharks use these areas extensively throughout their life, although they are of special importance because they are used as nursery areas. Because of this, it is important to identify critical habitats in these areas so that steps can be taken to protect them. Elkhorn Slough and ESNERR in particular are important leopard shark habitats. Continued habitat alteration is likely the greatest threat to leopard sharks in Elkhorn Slough. Rates of erosion in Elkhorn Slough are still very great, and ESNERR and the slough will continue to change, impacting the role that these areas play in the life history of leopard sharks and other species that occur in Elkhorn Slough. It appears as if low intertidal mudflats are of special importance as foraging and nursery areas for leopard sharks, and steps should be taken to preserve these habitats in Elkhorn Slough and other bays and estuaries along the coast of California. Because predators such as leopard sharks are important in regulating marine ecosystems through trophic interactions, and because these habitats are likely important to a variety of species, protecting low intertidal mudflats would likely have wide ranging benefits in terms of maintaining the biodiversity and health of bays and estuaries.

Conclusion

Leopard sharks are seasonally abundant in Elkhorn Slough during the spring through fall, and generally leave in the winter when temperature and salinity levels decrease. Once they are in the slough, females are largely residential and do not frequently move between the slough and coastal areas. Within the slough, there is a high degree of sexual segregation. Females are more abundant year round in ESNERR, whereas males are more abundant in the main channel in the spring, although sex ratios in the summer and fall in the main channel are nearly 1:1, which is possibly related to mating.

ESNERR is an important region of Elkhorn Slough that is used extensively by female leopard sharks throughout the year. Tidal creeks used to be important habitats for leopard sharks, but their utility has diminished as a result of habitat alteration. However, while intertidal habitats in the main channel were lost, new intertidal habitats were created during the formation of ESNERR, and leopard sharks shifted their habitat use accordingly. ESNERR is important as a foraging area and as a primary and possibly secondary nursery area. This is likely because ESNERR has an abundance of intertidal mudflats and prey, in particular fat innkeeper worms, is shallow, warm, and protected. At low tidal levels, sharks are restricted to channels, but as tidal levels increase they move out of the channels to forage on the intertidal mudflats. Sharks use low intertidal mudflats almost exclusively when they are available, indicating that these habitats are of particular importance as foraging and possibly pupping areas.

Leopard sharks use of ESNERR diminishes in the late summer or fall when dissolved oxygen is decreased and temperatures are increased, which causes sharks to spend more time in the main channel, which is more environmentally stable. When in the main channel, sharks exhibit different patterns of movement and habitat use. In particular, the foraging ecology of leopard sharks changes as they primarily use subtidal habitats and forage over larger areas. Use of intertidal mudflats is not as extensive in ESNERR, likely due to the absence of fat innkeeper worms in the upper main channel, which is where most of the intertidal mudflats are located in the main channel. Sharks also use the tide to assist their movements, which allows sharks to increase the area over which they can forage while minimizing the energetic costs of moving. Because they use the tides to assist their movements, they usually move during periods when the tidal currents are greatest, which allows them to move faster and further. These tidal movements up and down the main channel often occur with a high degree of periodicity, often every day around lower low tide. By using the tides they are more easily able to forage over the entire length of the main channel and gain access to the different prey items that are abundant in different areas of the main channel.

In the late fall, usually in October or November, use of the upper region and ESNERR diminishes as sharks spend more time in the lower regions of the main channel. This is likely because temperature and salinity decreases faster in the upper region, and ESNERR to a lesser extent, than in the lower regions of the main channel, which are more stable due to their proximity to the ocean. Once temperature and salinity levels drop to lower levels, male and female leopard sharks generally leave the slough for the winter, although juveniles may remain throughout the winter.

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Table 1. Summary of leopard shark catch-per-unit-effort (# sharks hr-1 ± SE) in ESNERR and the main channel in spring, summer, and fall of 2003 and 2004, and sex ratio for ESNERR and the main channel for both years combined. ESNERR region includes Long Canyon, and Main Channel includes all areas fished in the main channel, primarily around Kirby Park. Hours indicates total fishing time.

		Spring		**Summer**		**Fall**	
Year	**Region**	**CPUE**	**Hours**	**CPUE**	**Hours**	**CPUE**	**Hours**
2003	ESNERR	0.76 (±0.62)	7	0.42 (±0.41)	8.1	0.41 (±0.13)	18.75
	Main Channel	-	-	-	-	-	-
2004	ESNERR	0.92 (±0.28)	27.7	0.47 (±0.25)	35	-	-
	Main Channel	0.64 (±0.30)	25	1.05 (±0.40)	25.5	5.4 (±4.31)	5

		Spring		**Summer**		**Fall**	
Year	**Region**	**F:M Sex Ratio**	**Hours**	**F:M Sex Ratio**	**Hours**	**F:M Sex Ratio**	**Hours**
2003-2004	ESNERR	5.5:1	34.7	5:1	43.1	5:1	18.75
	Main Channel	0	25	0.75:1	25.5	0.87:1	5

Table 2. Summary data of nine female leopard sharks tagged with continuous transmitters and actively tracked in Elkhorn Slough, CA in 2003 and 2004. The table reports shark tag number, stage (A = adult, J = juvenile), date & location of tagging (LC = Long Canyon, E = ESNERR, KP = Kirby Park), length (TL = total length), time tracked (hours), number of blocks tracked (number of tracking sessions during the different pre-defined blocks of time, goal was n = 3, see text for more details), dates of tracking (if primarily occurred during a particular period of time this is indicated in parentheses), activity space (95% kernel utilization distribution – KUD), total distance traveled (km), and any important notes regarding individual sharks.

2003

Shark	Stage	Date Tagged (mm/dd/yy)	Tagging Location	TL (cm)	Hours Tracked	Blocks (0:00/6:00/12:00/18:00)	Dates Tracked (mm/dd/yy)	95% KUD (km2)	Total Distance Traveled (km)	Notes
51	A	04/28/03	LC	131	~ 4:00	0/0/1/0	04/28/03	NA	NA	Tag found in lagoon
54	A	05/12/03	LC	131	54:04	2/3/4/3	05/13/03 - 08/06/03 (July)	0.609	37.71	Pregnant
57	A	11/10/03	E	129	19:55	0/0/2/2	11/12/03 - 11/18/03	0.942	9.9	

2004

Shark	Stage	Date Tagged (mm/dd/yy)	Tagging Location	TL (cm)	Hours Tracked	Blocks (0:00/6:00/12:00/18:00)	Dates Tracked (mm/dd/yy)	95% KUD (km2)	Total Distance Traveled (km)	Notes
60	A	05/04/04	E	126.5	70:05	3/3/3/3	05/06/04 - 06/24/04 (May)	0.211	66.35	Pregnant
63	A	06/02/04	E	117	62:40	2/3/3/3	06/05/04 - 08/04/04 (June)	0.894	68.03	Pregnant
51	A	07/0704	E	132	61:05	3/3/3/3	07/08/04 - 09/16/04 (July)	0.726	33.23	
57A	A	09/02/04	KP	115	22:25	0/2/2/0	09/03/04 - 09/10/04	0.69	12.02	
54A	J	09/24/04	KP	91	70:35	3/4/4/4	09/25/04 - 11/12/04	1.752	39.92	
75	A	10/22/04	KP	114	71:25	3/3/3/3	10/23/04 - 11/12/04	1.502	45.98	

Table 3. Summary data of 11 female leopard sharks tagged with coded transmitters and passively monitored in Elkhorn Slough, CA in 2003 and 2004. The table reports shark tag number, stage (A = adult, J = juvenile), date & location of tagging (E = ESNERR, KP = Kirby Park), length (TL = total length), dates monitored (time from initial tagging to last detection, days indicates number of days the shark was actually in Elkhorn Slough during this time frame), total number of detections at VR1 receivers, and any important notes regarding individual sharks.

2003

Shark	Stage	Date Tagged (mm/dd/yy)	Tagging Location	TL (cm)	Dates Monitored (mm/dd/yy) (days)	Total Detections	Notes
100	A	08/29/03	E	127 cm TL	08/29/03 - 11/14/04 (132)	7472	Monitored during both years
106	A	09/09/03	E	124 cm TL	09/09/03 - 09/23/03 (14)	1280	
107	A	10/10/2003	E	135 cm TL	10/10/03 - 12/01/03(52)	3735	

2004

Shark	Stage	Date Tagged (mm/dd/yy)	Tagging Location	TL (cm)	Dates Monitored (mm/dd/yy) (days)	Total Detections	Notes
105	A	03/25/04	E	140 cm TL	03/25/04 - 07/4/04 (101)	11856	Pregnant, killed by bowhunter above Kirby Park
102	A	03/29/04	E	120 cm TL	03/29/04 - 11/13/04 (229)	9222	Pregnant
101	A	04/16/04	E	136 cm TL	04/16/04 - 04/20/04 (4)	862	
103	J	04/27/04	E	97 cm TL	04/27/04 - 05/27/04 (30)	5059	Fishing mortality
104	J	04/27/04	E	78 cm TL	04/27/04 - 02/03//05 (280)	512	Still in ESNERR at end of study
108	J	04/27/04	E	85 cm TL	04/27/04 - 02/03/05 (280)	5543	Still in ESNERR at end of study
109	A	08/13/04	KP	114 cm TL	08/13/04 - 11/10/04 (89)	11838	
115	A	08/20/04	KP	111 cm TL	08/20/04 - 11/13/04 (76)	13146	

Table 4. Results of principal components analysis for high, intermediate, and low tidal levels. Principal positive and negative variable loadings are indicated, along with habitats driving variable loadings.

Tidal Level	Principal Component	Percent of Variability	Eigenvalue	Positive Variable Loadings (Habitat)	Negative Variable Loadings (Habitat)
High	First	70%	0.012	0.475 (-3 to -2 m)	-0.716 (0 to 0.5 m)
				0.346 (-2 to -1 m)	-0.226 (-0.5 to 0 m)
				0.275 (< -3 m)	-0.103 (0.5 to 1 m)
	Second	24%	0.004	0.441 (0 to 0.5 m)	-0.832 (-0.5 to 0 m)
				0.286 (-3 to -2 m)	-0.101 (-2 to -1 m)
				0.126 (<-3 m)	-
Intermediate	First	66%	0.009	0.653 (< -3 m)	-0.464 (-0.5 to 0 m)
				0.440 (-3 to -2 m)	-0.289 (0 to 0.5 m)
				-	-0.277 (-2 to -1 m)
	Second	23%	0.003	0.769 (0 to 0.5 m)	-0.607 (-0.5 to 0 m)
				0.125 (0.5 to 1 m)	-0.104 (< -3 m)
Low	First	48%	0.007	0.573 (-3 to -2 m)	-0.420 (-1 to -0.5 m)
				0.523 (< -3 m)	-0.397 (-0.5 to 0 m)
				-	-0.233 (0 to 0.5 m)
	Second	31%	0.004	0.638 (-2 to -1 m)	-0.426 (0 to 0.5 m)
				0.389 (-3 to -2 m)	-0.370 (< -3 m)
				-	- 0.351 (-0.5 to 0 m)
	Third	16%	0.002	0.573 (-3 to -2 m)	-0.617 (< -3 m)
				0.291 (0 to 0.5 m)	-0.375 (-2 to -1 m)
				0.251 (-0.5 to 0 m)	-

Figure 1. Light detection and ranging (LIDAR) map of Elkhorn Slough. Important locations are indicated. Deeper areas are darker, with deep channels being black. Intertidal mudflats are shown in shades of gray, with lighter colors indicating shallower mudflats.

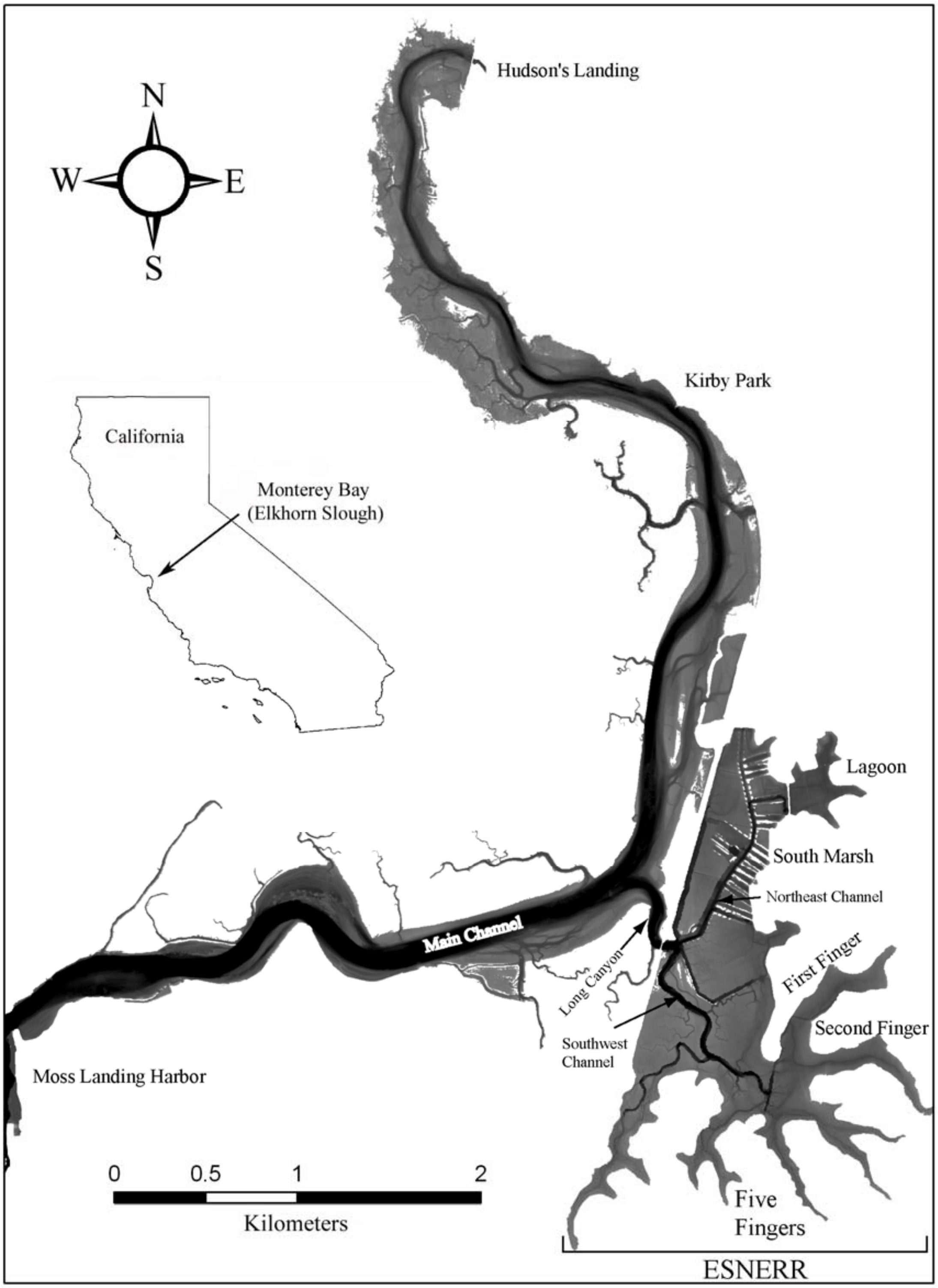

Hudson's Landing
N
W
E
S
Kirby Park
California
Monterey Bay
(Elkhorn Slough)
Lagoon
South Marsh
Northeast Channel
Main Channel
Long Canyon
First Finger
Second Finger
Southwest
Channel
Moss Landing Harbor
0
0.5
1
2
Kilometers
Five
Fingers
ESNERR

Figure 2. Elkhorn Slough showing locations of receivers (numbers 1 – 6) and the different regions of the slough (Low, Mid, Upper & ESNERR). Range of receivers is approximately 400 m.

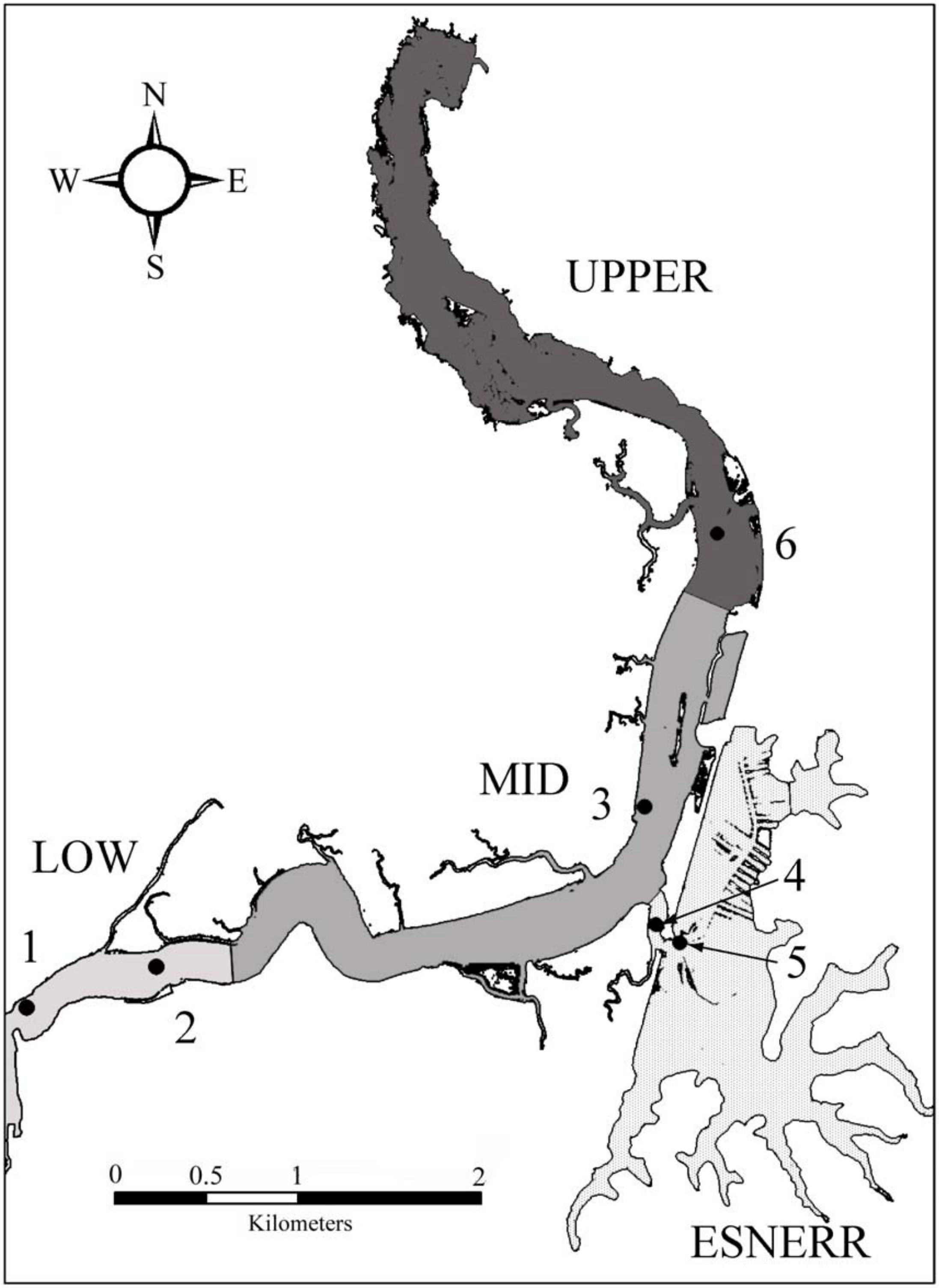

N
W
E
S
UPPER
6
MID
3
LOW
4
1
5
2
0
0.5
1
2
Kilometers
ESNERR

Figure 3. Elkhorn Slough showing all positions of female leopard sharks that were actively tracked in 2003 and 2004.

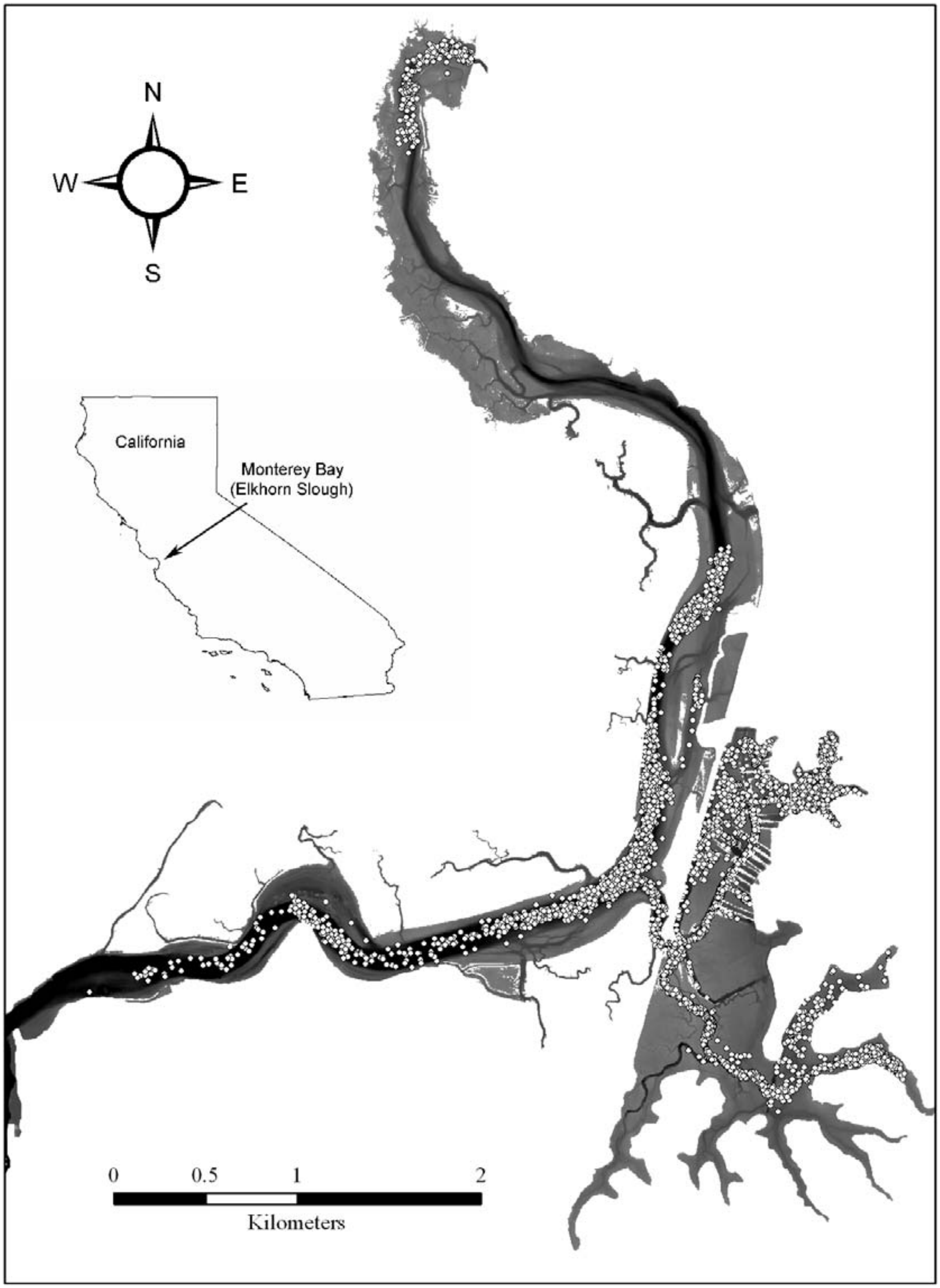
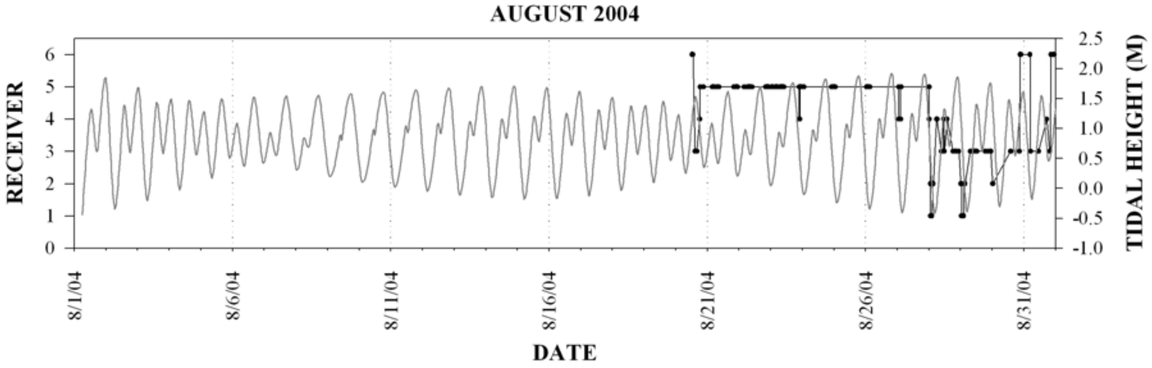
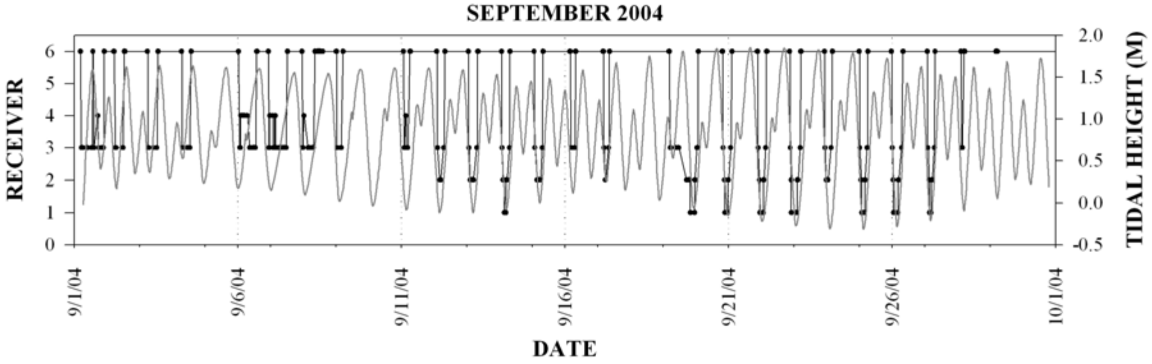
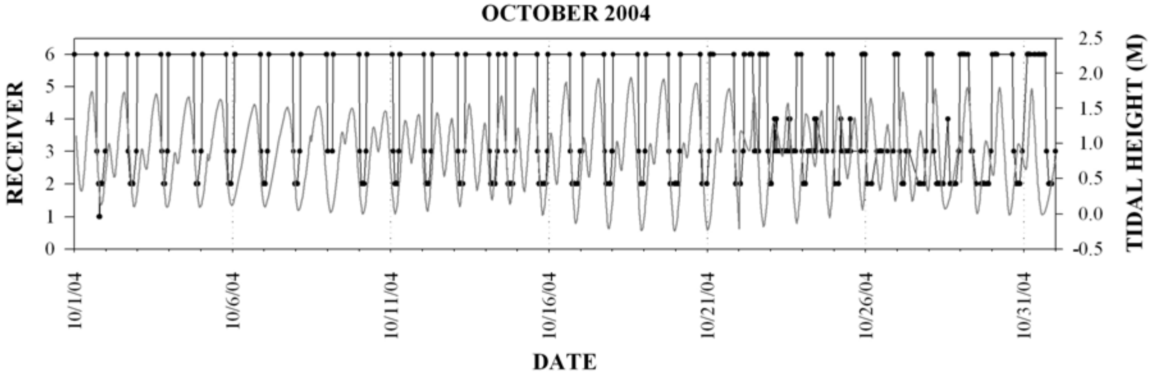

N
W
E
S
California
Monterey Bay
(Elkhorn Slough)
0
0.5
1
2
Kilometers

Figure 4. Movements of shark 115 among VR1 receivers. Left y-axis is receiver number, right y-axis is tidal height (m), and x-axis is date. Points indicate detections at a particular receiver. Light gray line represents tidal stage.


AUGUST 2004
RECEIVER
0
1
2
3
4
5
6
TIDAL HEIGHT (M)
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
8/1/04
8/6/04
8/11/04
8/16/04
8/21/04
8/26/04
8/31/04
DATE


SEPTEMBER 2004
RECEIVER
0
1
2
3
4
5
6
TIDAL HEIGHT (M)
-0.5
0.0
0.5
1.0
1.5
2.0
9/1/04
9/6/04
9/11/04
9/16/04
9/21/04
9/26/04
10/1/04
DATE


OCTOBER 2004
RECEIVER
0
1
2
3
4
5
6
TIDAL HEIGHT (M)
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
10/1/04
10/6/04
10/11/04
10/16/04
10/21/04
10/26/04
10/31/04
DATE

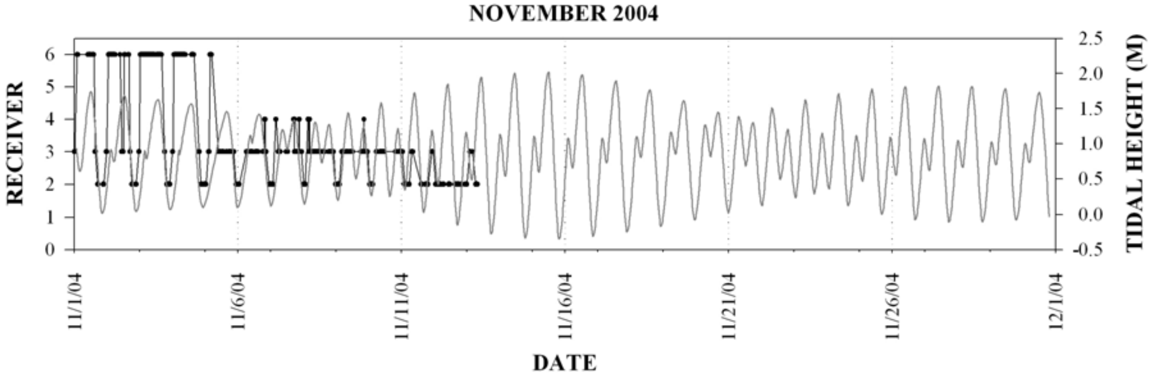
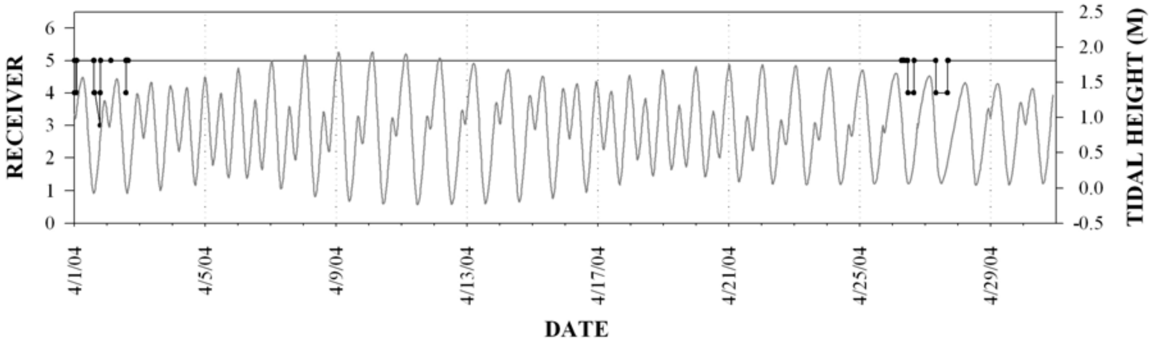
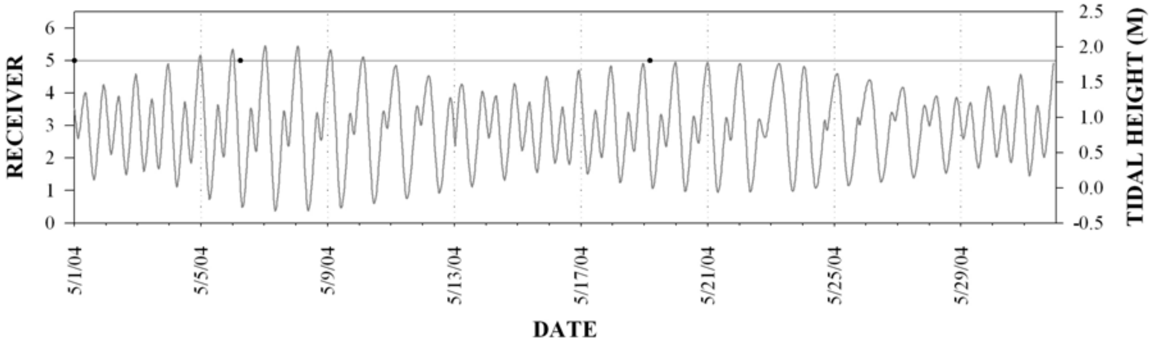

NOVEMBER 2004
RECEIVER
0
1
2
3
4
5
6
TIDAL HEIGHT (M)
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
11/1/04
11/6/04
11/11/04
11/16/04
11/21/04
11/26/04
12/1/04
DATE

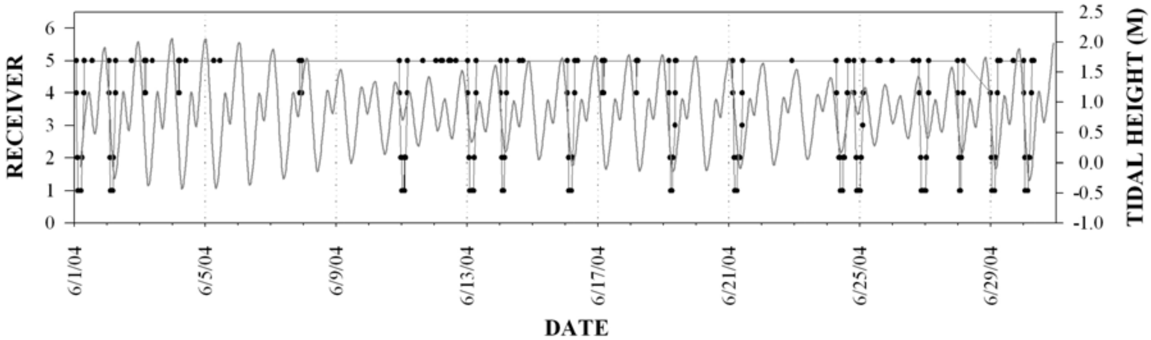
Figure 5. Movements of shark 102 among VR1 receivers. Left y-axis is receiver number, right y-axis is tidal height (m), and x-axis is date. Points indicate detections at a particular receiver. Light gray line represents tidal stage.



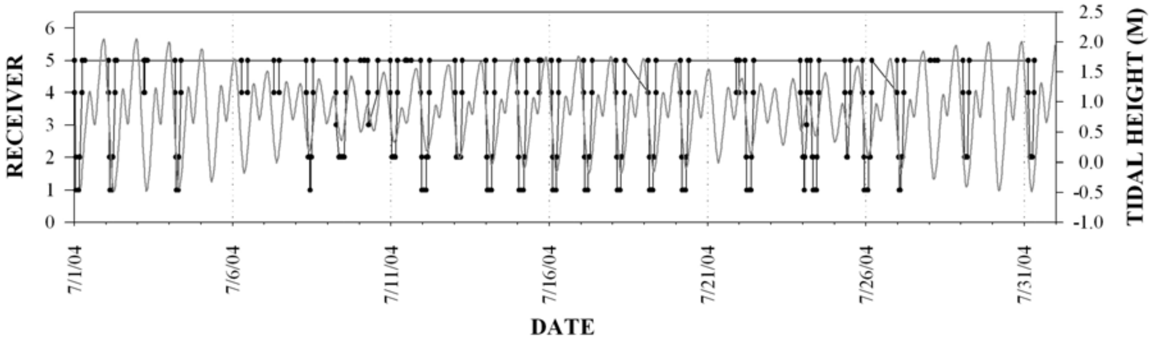
APRIL 2004



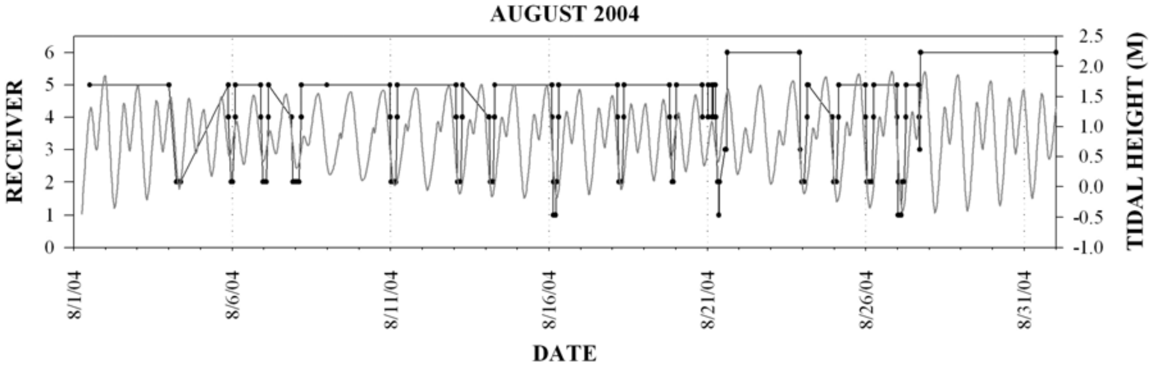
MAY 2004

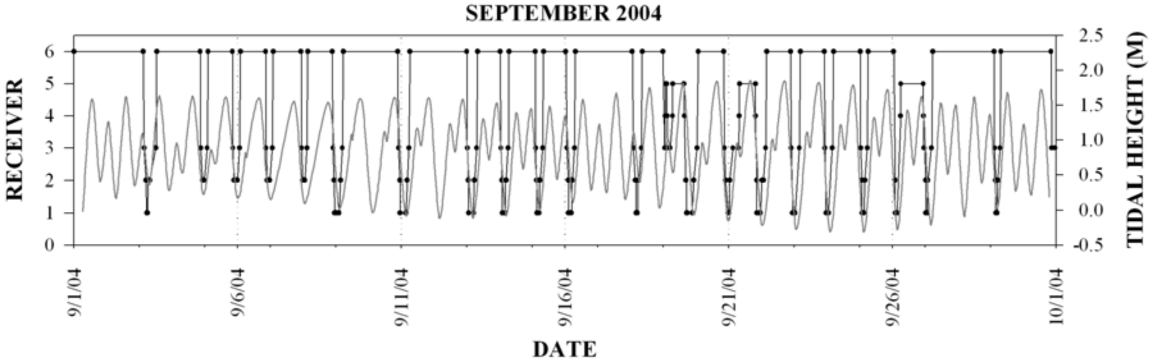


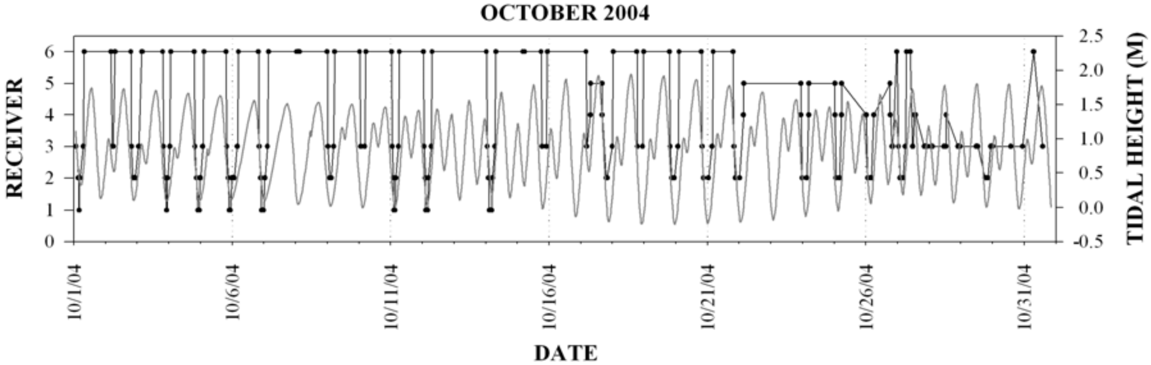
JUNE 2004



JULY 2004


AUGUST 2004


SEPTEMBER 2004


OCTOBER 2004

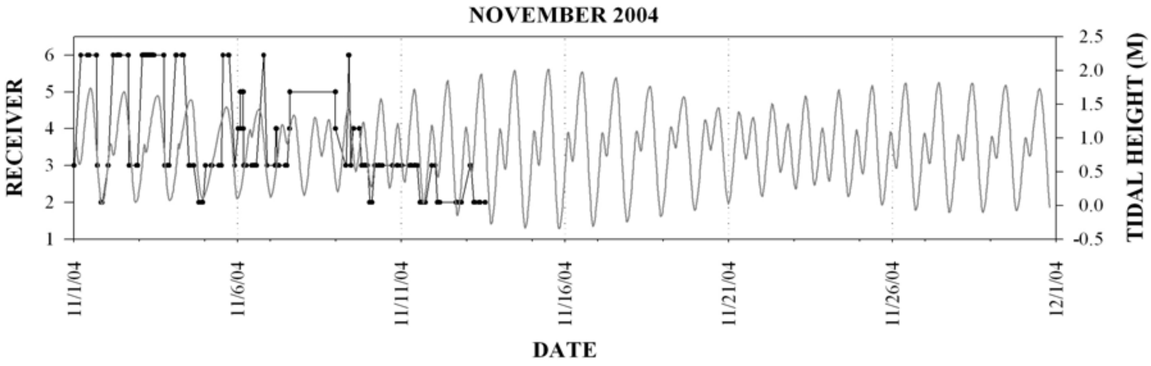
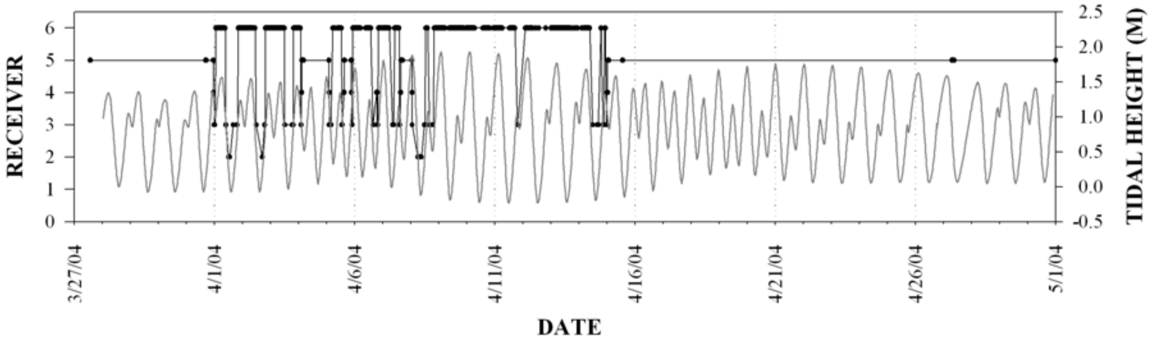
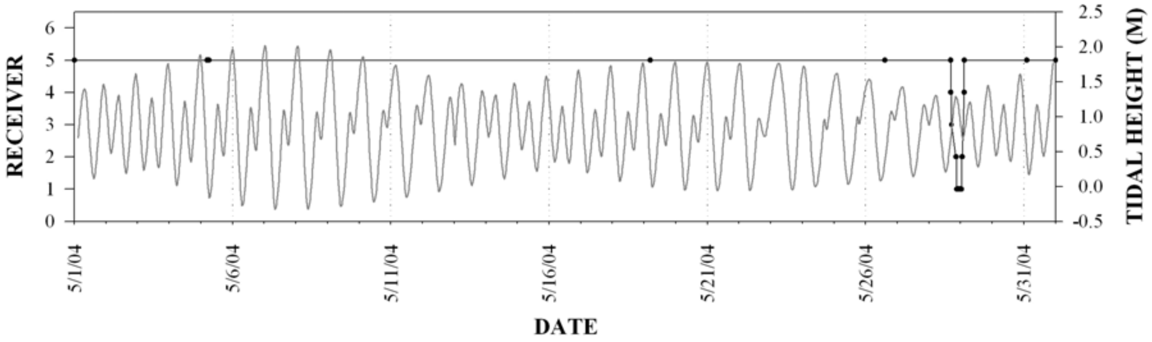

NOVEMBER 2004

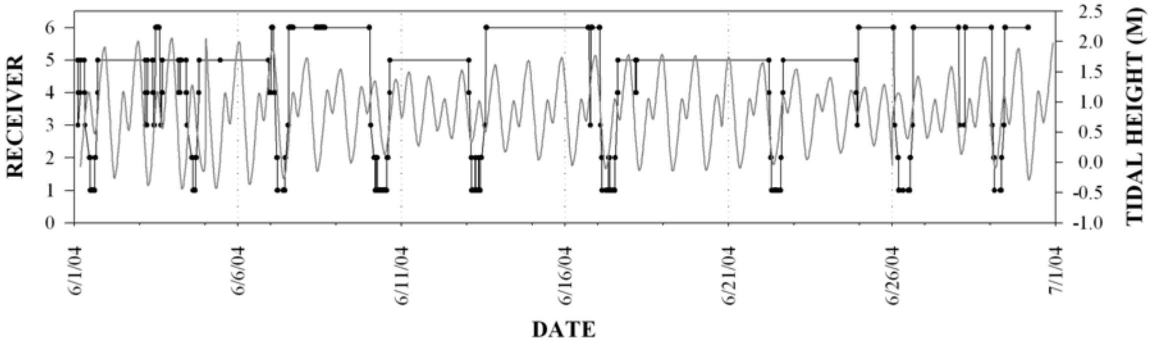
Figure 6. Movements of shark 105 among VR1 receivers. Left y-axis is receiver number, right y-axis is tidal height (m), and x-axis is date. Points indicate detections at a particular receiver. Light gray line represents tidal stage.



APRIL 2004



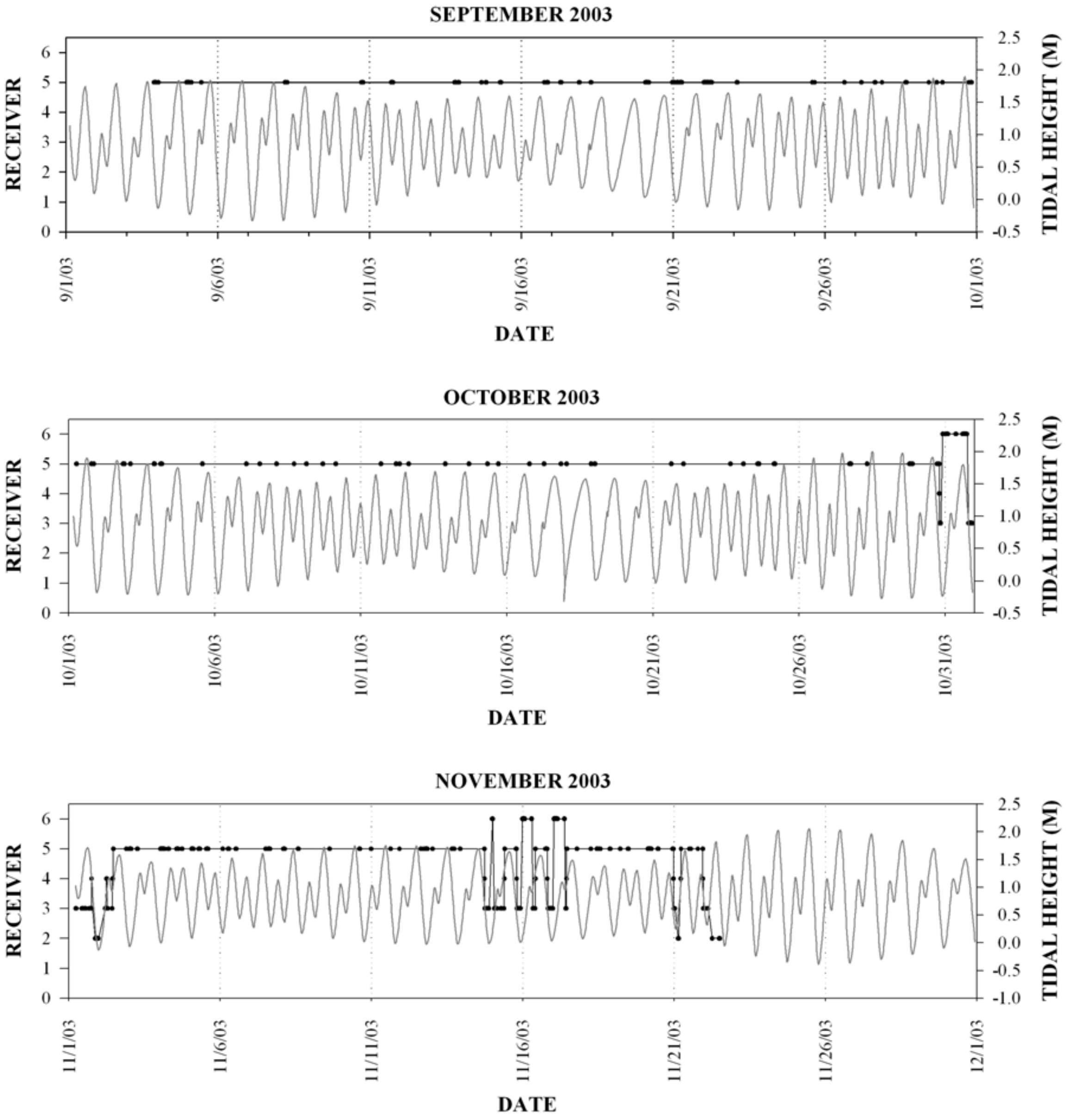
MAY 2004



JUNE 2004

Figure 7. Movements of shark 100 among VR1 receivers during 2003 (a) and 2004 (b). Left y-axis is receiver number, right y-axis is tidal height (m), and x-axis is date. Points indicate detections at a particular receiver. Light gray line represents tidal stage.

a


SEPTEMBER 2003
RECEIVER
0
1
2
3
4
5
6
TIDAL HEIGHT (M)
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
9/1/03
9/6/03
9/11/03
9/16/03
9/21/03
9/26/03
10/1/03
DATE
OCTOBER 2003
RECEIVER
TIDAL HEIGHT (M)
10/1/03
10/6/03
10/11/03
10/16/03
10/21/03
10/26/03
10/31/03
DATE
NOVEMBER 2003
RECEIVER
TIDAL HEIGHT (M)
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
11/1/03
11/6/03
11/11/03
11/16/03
11/21/03
11/26/03
12/1/03
DATE

b

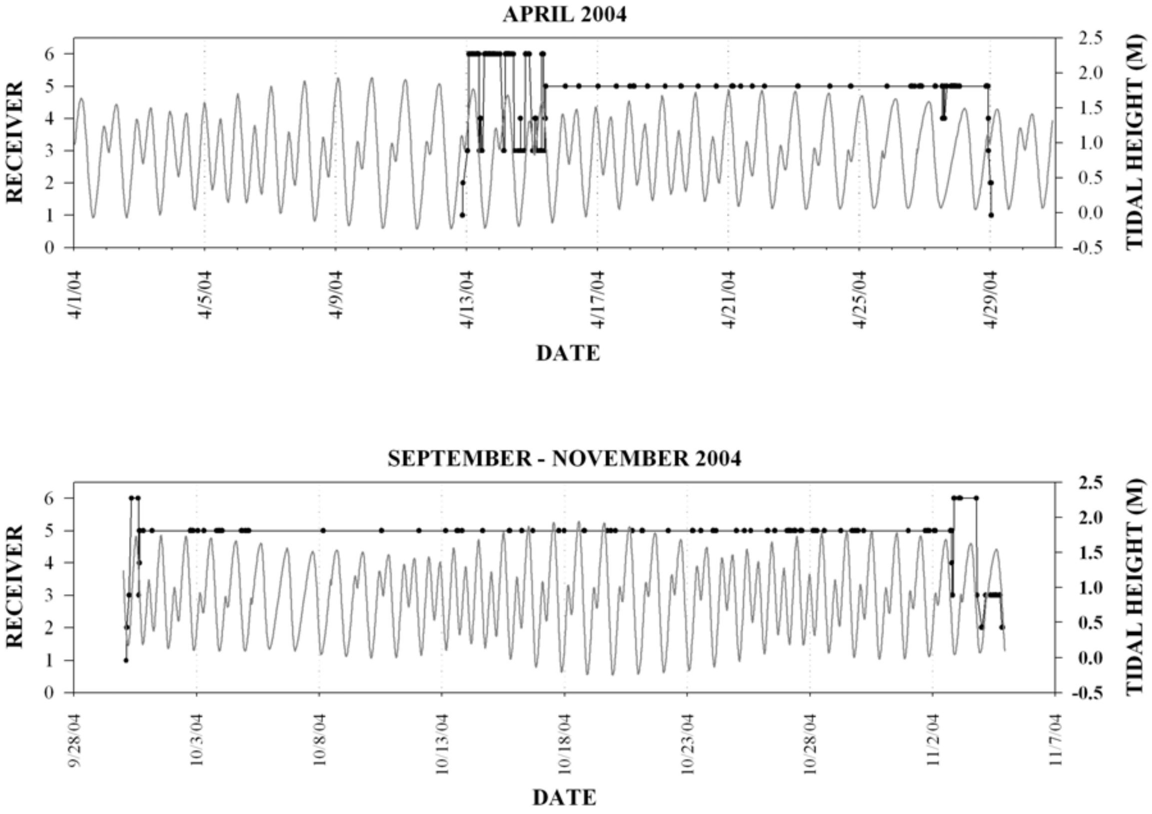

APRIL 2004
RECEIVER
TIDAL HEIGHT (M)
0
1
2
3
4
5
6
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
4/1/04
4/5/04
4/9/04
4/13/04
4/17/04
4/21/04
4/25/04
4/29/04
DATE
SEPTEMBER - NOVEMBER 2004
RECEIVER
TIDAL HEIGHT (M)
0
1
2
3
4
5
6
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
9/28/04
10/3/04
10/8/04
10/13/04
10/18/04
10/23/04
10/28/04
11/2/04
11/7/04
DATE

Figure 8. Proportion of time individual sharks spent in the different regions of Elkhorn Slough, asterisks indicate that time individual sharks spent in a particular region differed significantly from the predicted time they would spend in that region based on its area (* $= p < 0.05$; ** $= p< 0.005$; *** $= p < 0.001$).

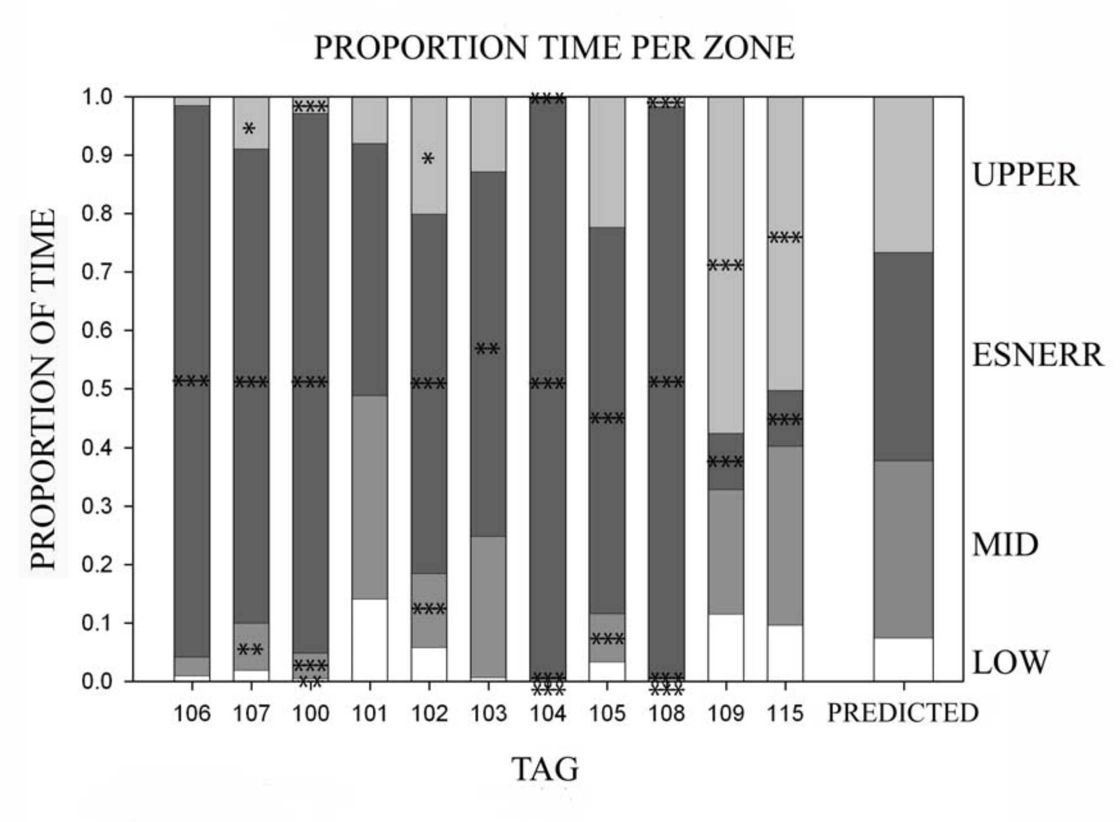

PROPORTION TIME PER ZONE
PROPORTION OF TIME
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
106
107
100
101
102
103
104
105
108
109
115
PREDICTED
TAG
UPPER
ESNERR
MID
LOW
*
**
***

Figure 9. Seasonal pattern of regional utilization of Elkhorn Slough. Values are the mean proportion (± SE) of time spent in each region by all sharks in the slough during a particular month. Number of sharks in the slough during each month is shown in parentheses after the month on the x-axis. All tagged sharks were absent from the slough in December, January, and February of 2003 and 2004.

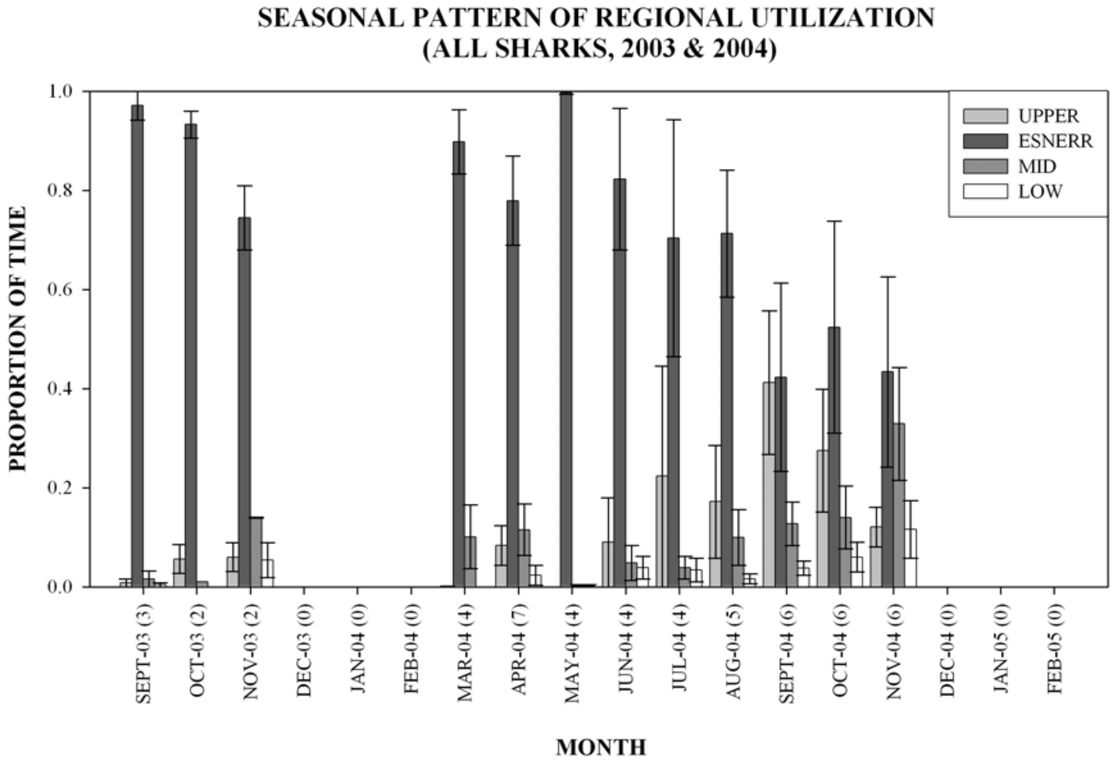
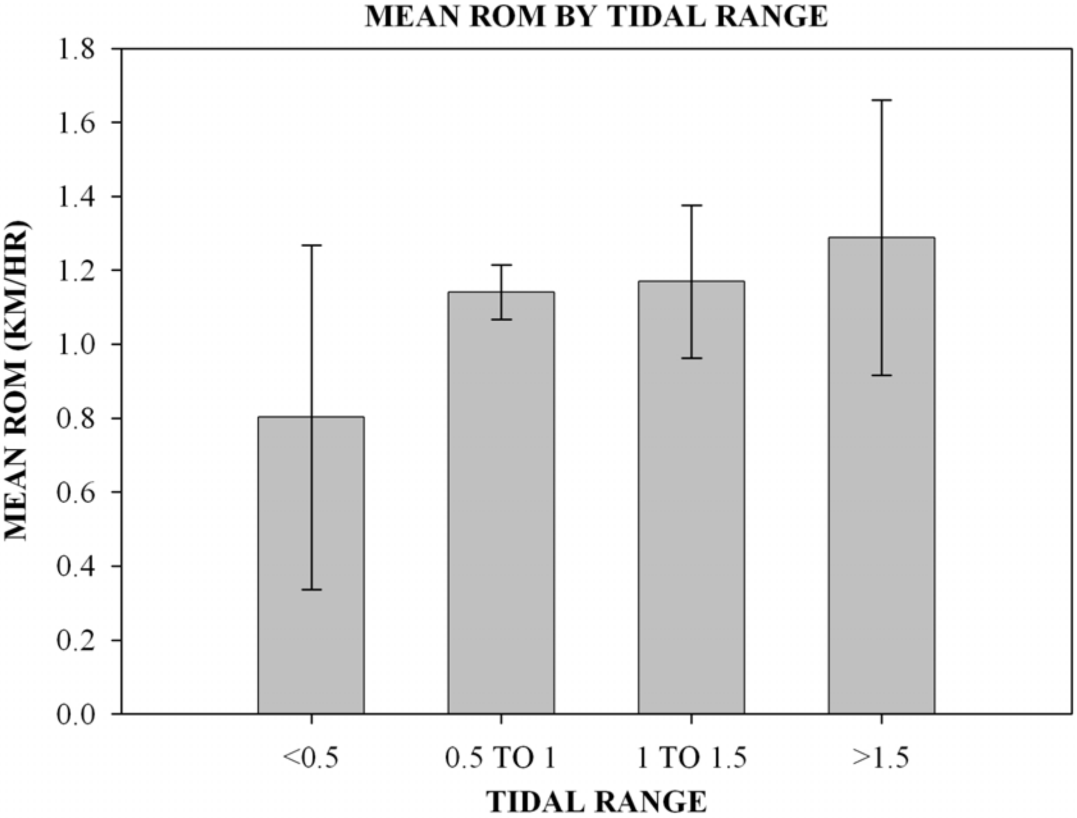

SEASONAL PATTERN OF REGIONAL UTILIZATION
(ALL SHARKS, 2003 & 2004)
PROPORTION OF TIME
1.0
0.8
0.6
0.4
0.2
0.0
UPPER
ESNERR
MID
LOW
SEPT-03 (3)
OCT-03 (2)
NOV-03 (2)
DEC-03 (0)
JAN-04 (0)
FEB-04 (0)
MAR-04 (4)
APR-04 (7)
MAY-04 (4)
JUN-04 (4)
JUL-04 (4)
AUG-04 (5)
SEPT-04 (6)
OCT-04 (6)
NOV-04 (6)
DEC-04 (0)
JAN-05 (0)
FEB-05 (0)
MONTH

Figure 10. Mean rate of movement (ROM) (± 95% CI) of acoustically monitored sharks (n = 10) between receivers relative to tidal range.



MEAN ROM BY TIDAL RANGE
MEAN ROM (KM/HR)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
<0.5
0.5 TO 1
1 TO 1.5
>1.5
TIDAL RANGE

Figure 11. Mean tidal range (• = mean during movements; vertical line = 95% CI) during which an individual shark's movements occurred relative to overall mean tidal range that occurred while that shark was in the slough (horizontal line = overall mean; box = 95% CI). Tidal range was used as a proxy for current velocity. Values are the difference between tidal range during movements and overall tidal range, so positive values indicate sharks moved more when tidal range (i.e. current velocity) was greater than average.

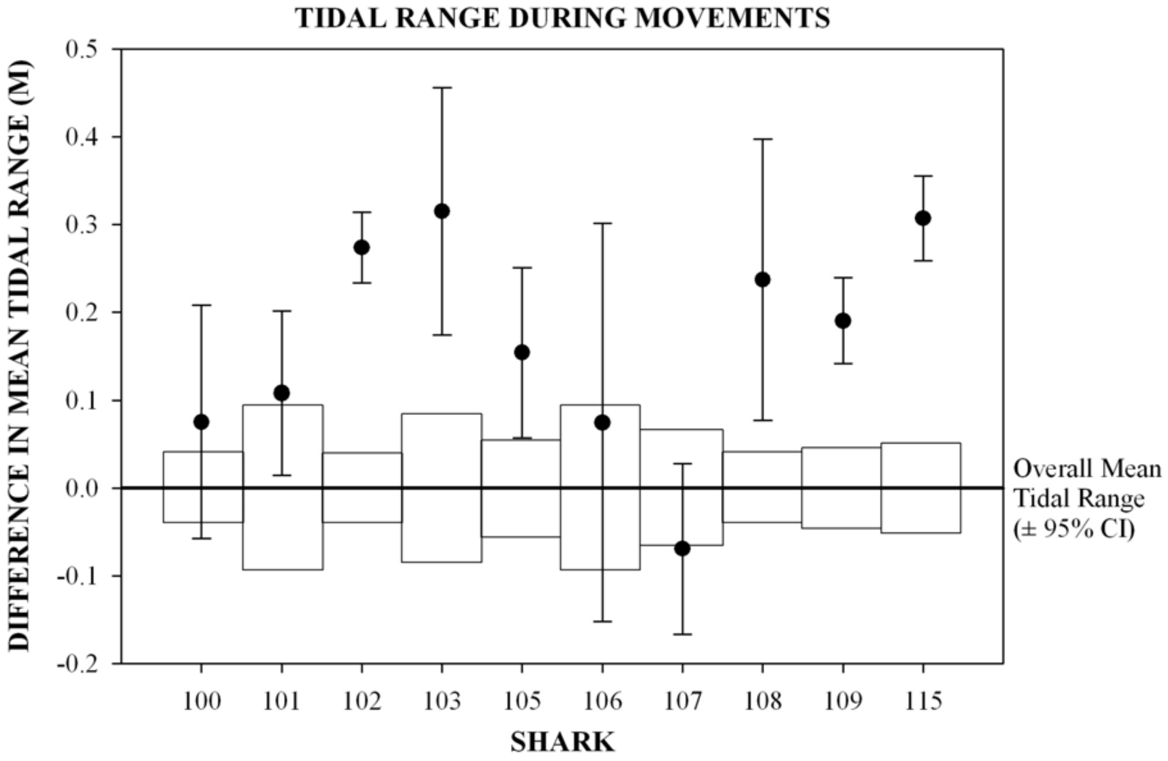

TIDAL RANGE DURING MOVEMENTS
DIFFERENCE IN MEAN TIDAL RANGE (M)
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
100
101
102
103
105
106
107
108
109
115
SHARK
Overall Mean
Tidal Range
(± 95% CI)

Figure 12. Movements of sharks between receivers relative to the direction of tidal flow. Negative rheotaxis: moves with current; positive rheotaxis: moves against the current; mixed: ~50% of movement was with current, ~50% against; slack: movement occurred entirely during slack tide (±1 from low tide); unknown: movement occurred over a period of time longer than a single tidal stage. The predicted column indicates proportion of movements that would occur in the different categories if the number of movements was proportional to the relative duration of each tidal stage. Note that unknown and mixed categories are indefinable so they are not included in the predicted column.

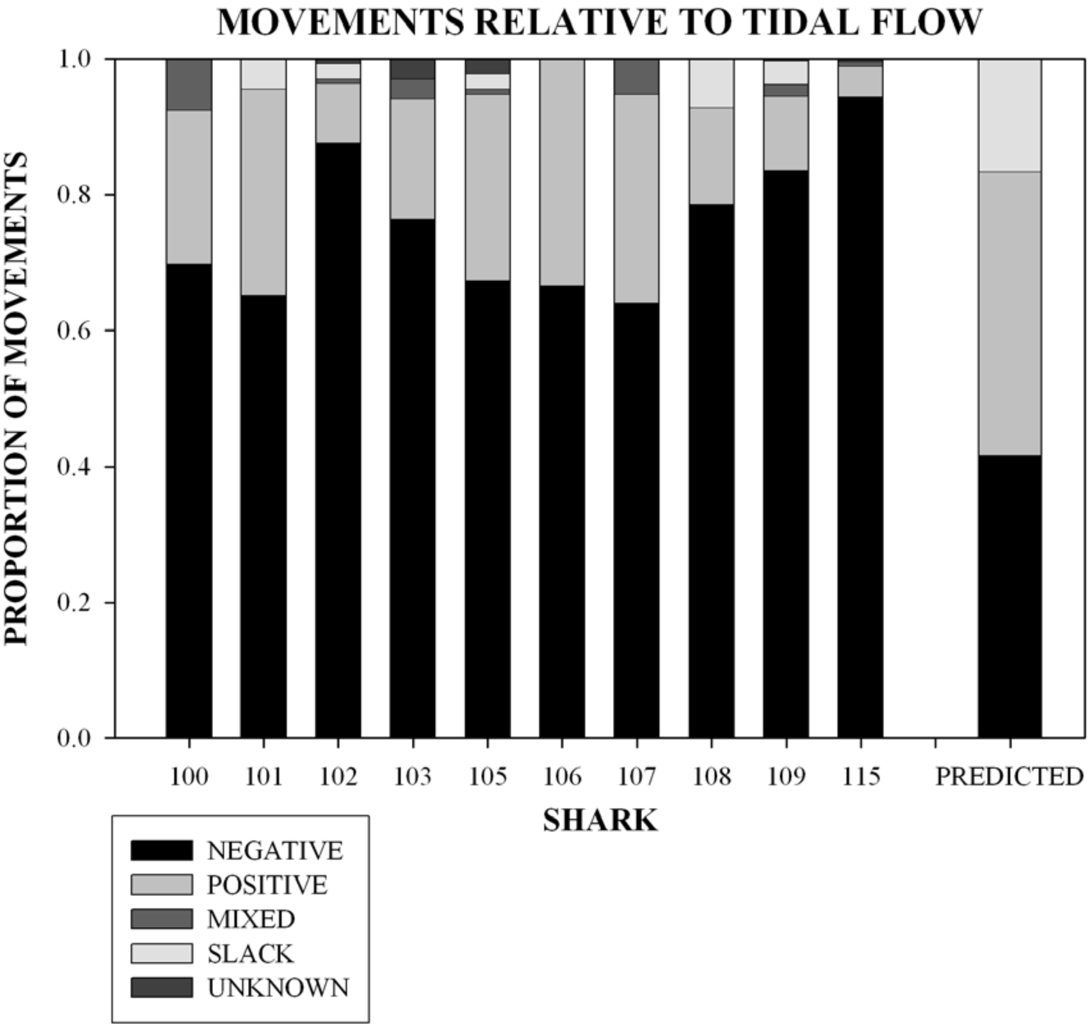

MOVEMENTS RELATIVE TO TIDAL FLOW
PROPORTION OF MOVEMENTS
0.0
0.2
0.4
0.6
0.8
1.0
100
101
102
103
105
106
107
108
109
115
PREDICTED
SHARK
NEGATIVE
POSITIVE
MIXED
SLACK
UNKNOWN

Figure 13. Mean rate of movement (ROM) (± 95% CI) (n = 10) between receivers relative to direction of tidal flow.

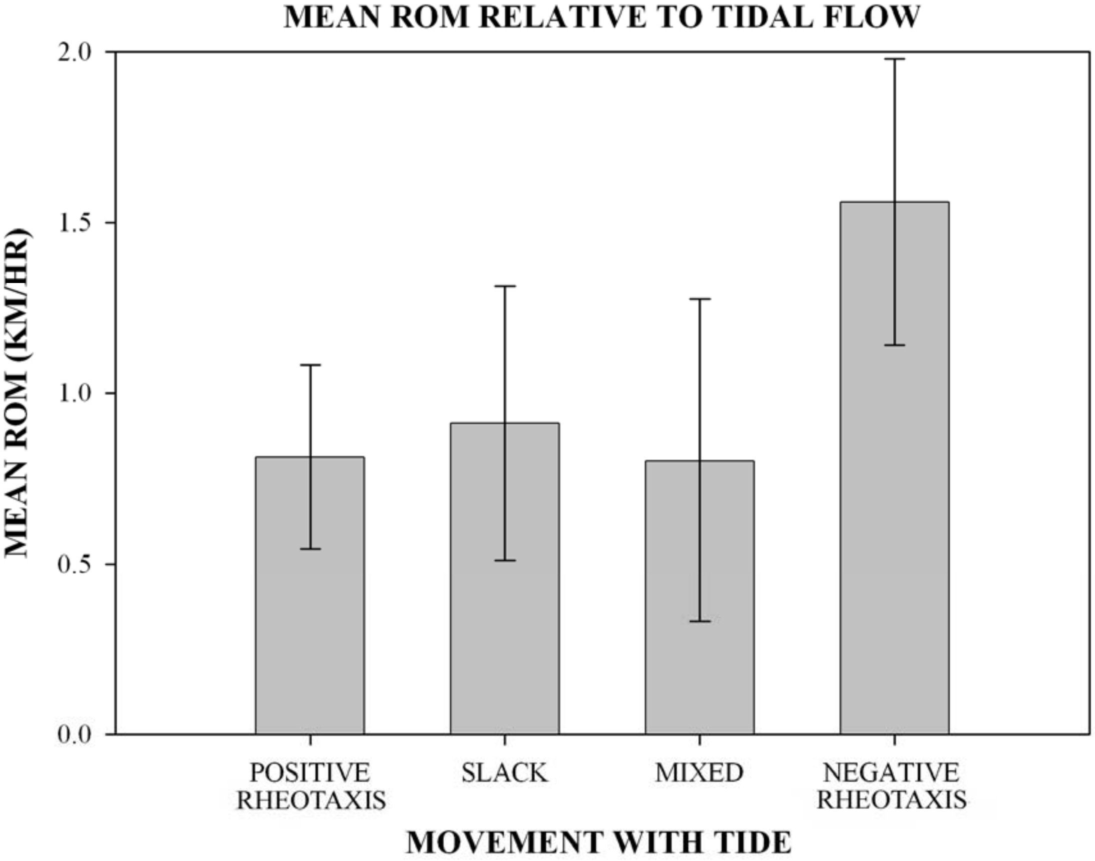

MEAN ROM RELATIVE TO TIDAL FLOW
MEAN ROM (KM/HR)
2.0
1.5
1.0
0.5
0.0
POSITIVE RHEOTAXIS
SLACK
MIXED
NEGATIVE RHEOTAXIS
MOVEMENT WITH TIDE

Figure 14. Time of detection at each receiver relative to tidal stage for main channel receivers (a) and ESNERR receivers (b). Left column shows receivers in the main channel of Elkhorn Slough, whereas the right column shows the receivers in ESNERR. Values are the hourly mean (± SE) proportion of receptions of all passively monitored sharks (n = 10) relative to each day's lower low tide (hour 0). Dashed line shows generalized tidal curve.

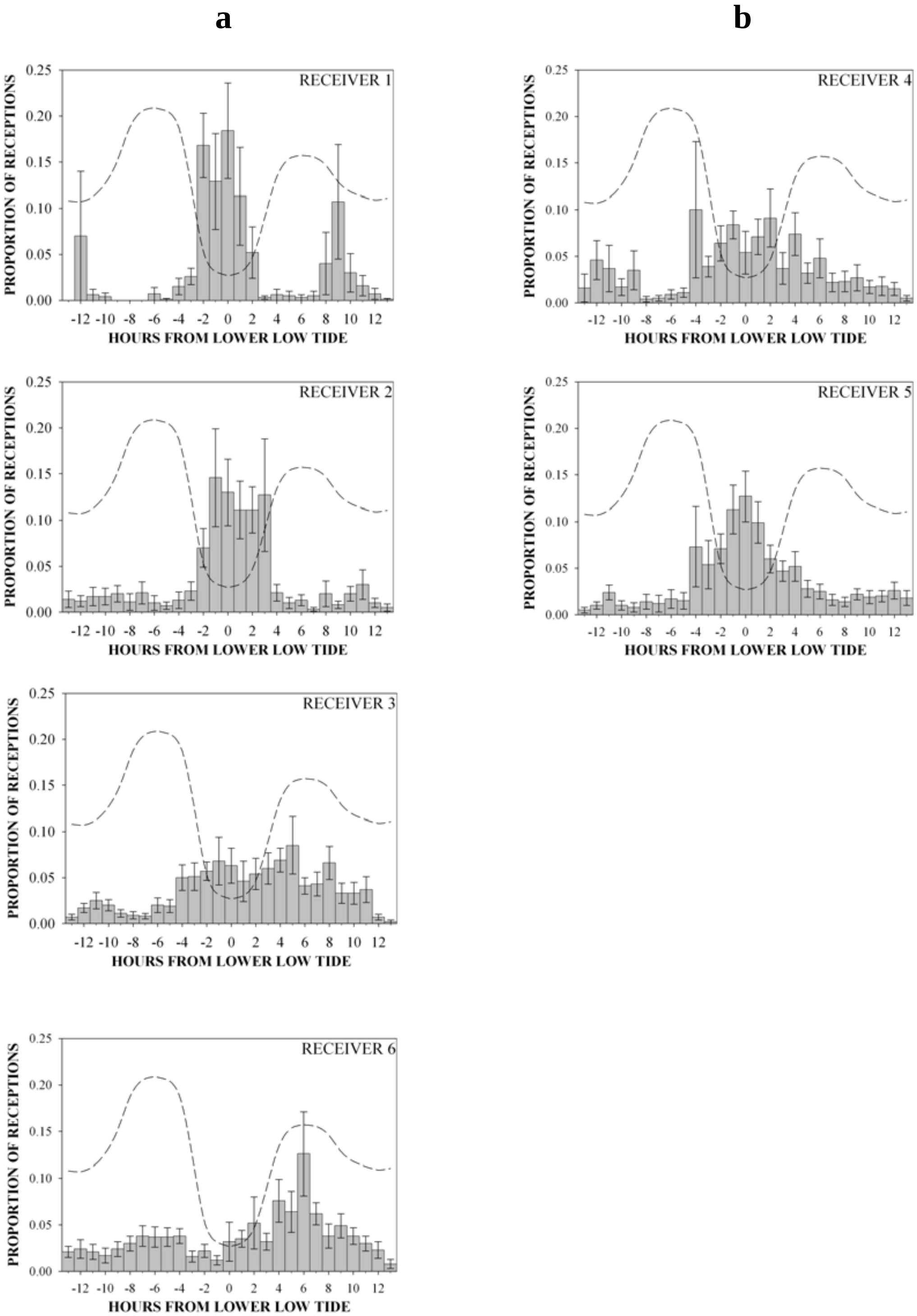

a
b
RECEIVER 1
RECEIVER 2
RECEIVER 3
RECEIVER 4
RECEIVER 5
RECEIVER 6
PROPORTION OF RECEPTIONS
0.00
0.05
0.10
0.15
0.20
0.25
HOURS FROM LOWER LOW TIDE
-12
-10
-8
-6
-4
-2
0
2
4
6
8
10
12

Figure 15. Mean rate of movement (ROM) (± 95% CI) (n = 10) between receivers relative to period of day.

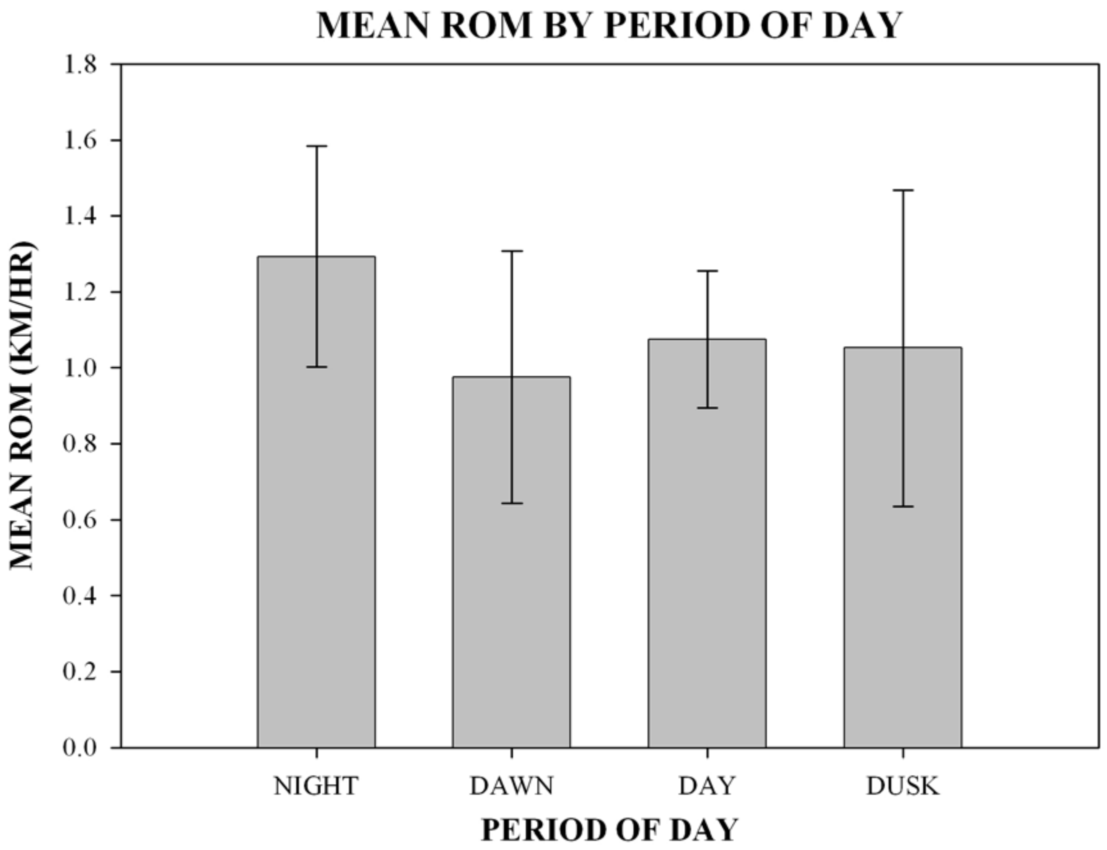

MEAN ROM BY PERIOD OF DAY
MEAN ROM (KM/HR)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
NIGHT
DAWN
DAY
DUSK
PERIOD OF DAY

Figure 16. Mean proportion of hourly movements (± 95% CI) (n = 10) between receivers of all passively monitored sharks relative to time of day. Dashed vertical lines indicate general crepuscular periods. Overall proportion of movements during different periods of day (night, dawn, day, dusk) is indicated in the upper part of the graph. The dotted line indicates the proportion of movements that would occur if sharks were moving equally during all hours.

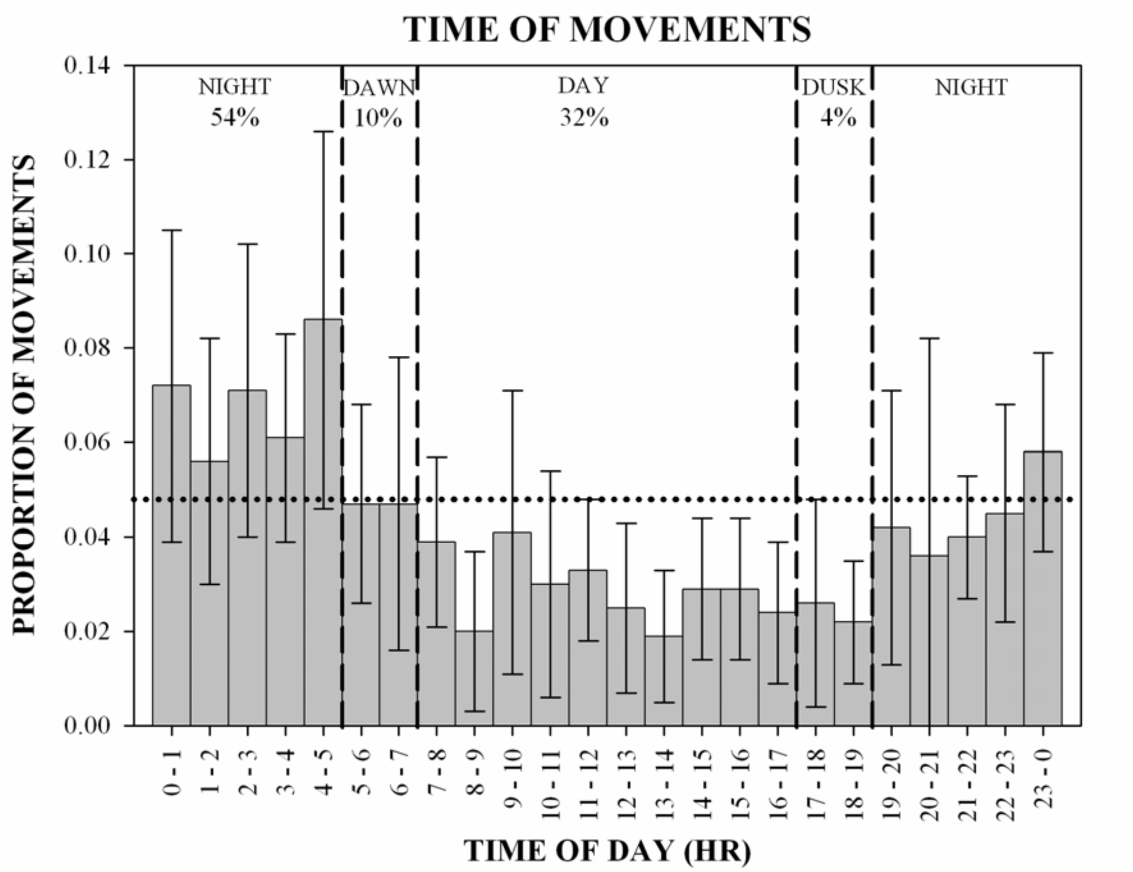
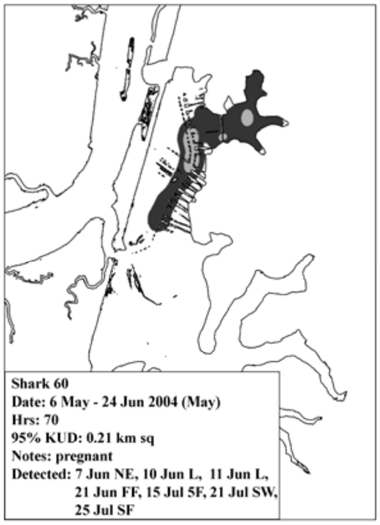
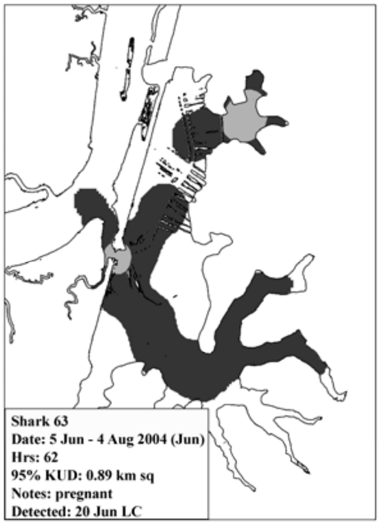

TIME OF MOVEMENTS
PROPORTION OF MOVEMENTS
TIME OF DAY (HR)
NIGHT
54%
DAWN
10%
DAY
32%
DUSK
4%
NIGHT
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0 - 1
1 - 2
2 - 3
3 - 4
4 - 5
5 - 6
6 - 7
7 - 8
8 - 9
9 - 10
10 - 11
11 - 12
12 - 13
13 - 14
14 - 15
15 - 16
16 - 17
17 - 18
18 - 19
19 - 20
20 - 21
21 - 22
22 - 23
23 - 0

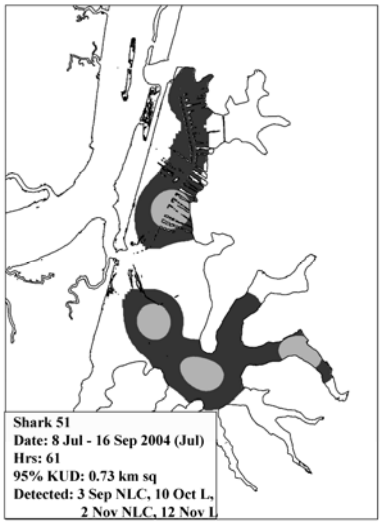
Figure 17. Kernel utilization distributions (KUD) for sharks tracked in ESNERR. Dark gray contour is the 95% KUD and light gray contour is the 50% KUD. Date: dates that sharks were tracked, followed by period when most of tracking occurred. Hrs: number of hours tracked. 95% KUD: area of 95% KUD. Notes: important details about individual sharks. Detected: dates when sharks were detected while tracking other sharks and abbreviations of locations where they were detected. Locations: L – lagoon, FF – first finger, SF – second finger, 5F – five fingers region, NE – northeast channel, SW – southwest channel, LC – Long Canyon, NLC – north of Long Canyon.



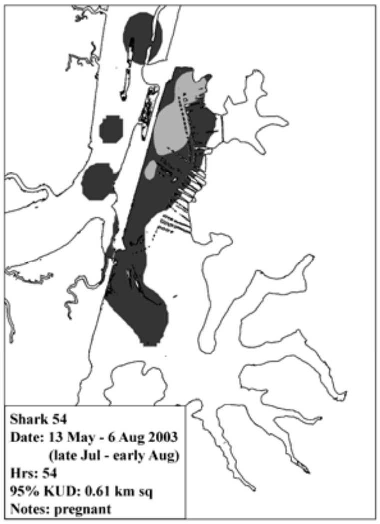
Shark 60
Date: 6 May - 24 Jun 2004 (May)
Hrs: 70
95% KUD: 0.21 km sq
Notes: pregnant
Detected: 7 Jun NE, 10 Jun L, 11 Jun L, 21 Jun FF, 15 Jul 5F, 21 Jul SW, 25 Jul SF



Shark 63
Date: 5 Jun - 4 Aug 2004 (Jun)
Hrs: 62
95% KUD: 0.89 km sq
Notes: pregnant
Detected: 20 Jun LC



Shark 51
Date: 8 Jul - 16 Sep 2004 (Jul)
Hrs: 61
95% KUD: 0.73 km sq
Detected: 3 Sep NLC, 10 Oct L, 2 Nov NLC, 12 Nov L



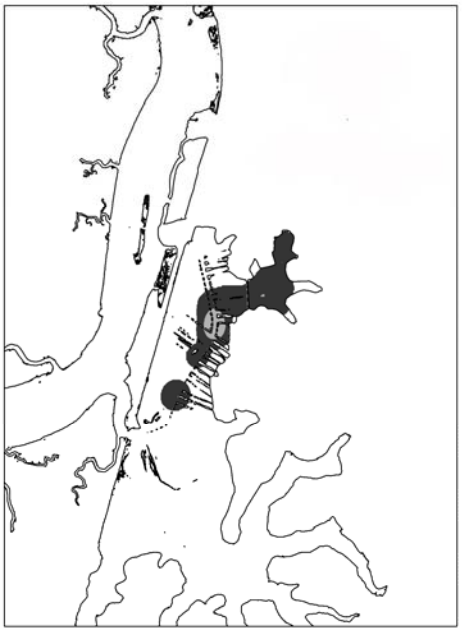
Shark 54
Date: 13 May - 6 Aug 2003 (late Jul - early Aug)
Hrs: 54
95% KUD: 0.61 km sq
Notes: pregnant

Shark 57
Date: 12 Nov - 18 Nov 2003
Hrs: 20
95% KUD: 0.94 km sq

Figure 18. Kernel utilization distributions (KUD) of shark 60 at low (a), intermediate (b), and high (c) tidal levels, showing tidally influenced movements from deeper channels at low tide to shallower intertidal areas at higher tidal levels. The dark gray contour is the 95% KUD whereas the light gray contour is the 50% KUD.

a

b



c

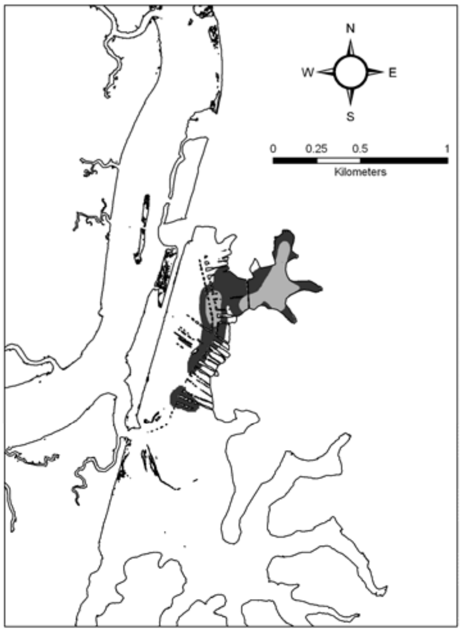
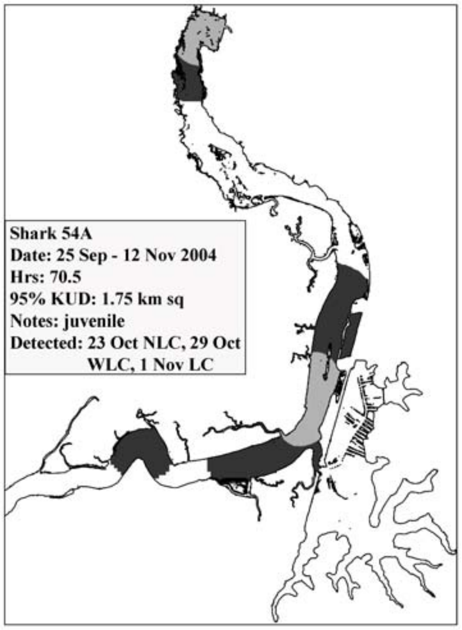
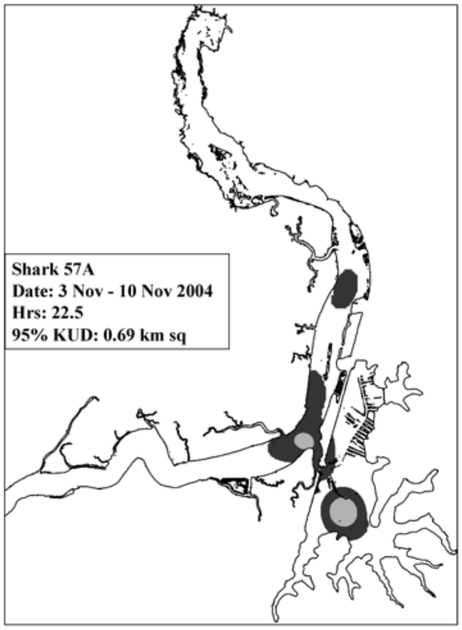


Figure 19. Kernel utilization distributions (KUD) for sharks tracked in ESNERR. Dark gray contour is the 95% KUD and light gray contour is the 50% KUD. Date: dates that sharks were tracked. Hrs: number of hours tracked. 95% KUD: area of 95% KUD. Notes: important details about individual sharks. Detected: dates when sharks were detected while tracking other sharks.and abbreviations of locations where they were detected. Locations: LC – Long Canyon, NLC – north of Long Canyon, WLC – west of Long Canyon.


Shark 54A
Date: 25 Sep - 12 Nov 2004
Hrs: 70.5
95% KUD: 1.75 km sq
Notes: juvenile
Detected: 23 Oct NLC, 29 Oct WLC, 1 Nov LC


Shark 57A
Date: 3 Nov - 10 Nov 2004
Hrs: 22.5
95% KUD: 0.69 km sq

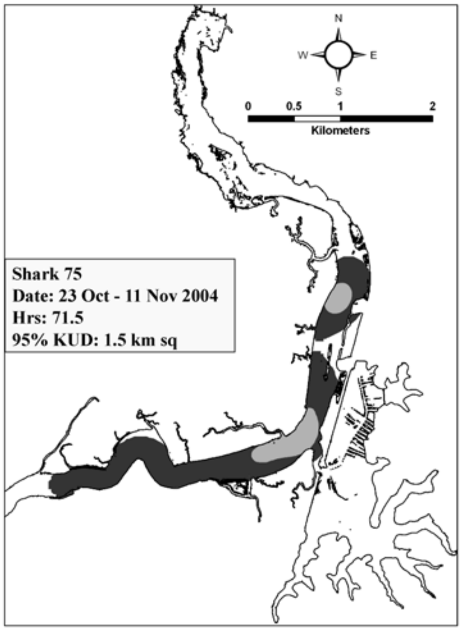

N
W
E
S
0
0.5
1
2
Kilometers
Shark 75
Date: 23 Oct - 11 Nov 2004
Hrs: 71.5
95% KUD: 1.5 km sq

Figure 20. Kernel utilization distributions (KUD) of shark 75 at low (a), intermediate (b), and high (c) tidal levels, showing tidally influenced movements from deeper channels at low tide to shallower intertidal areas at higher tidal levels. The dark gray contour is the 95% KUD whereas the light gray contour is the 50% KUD.

a

b

c

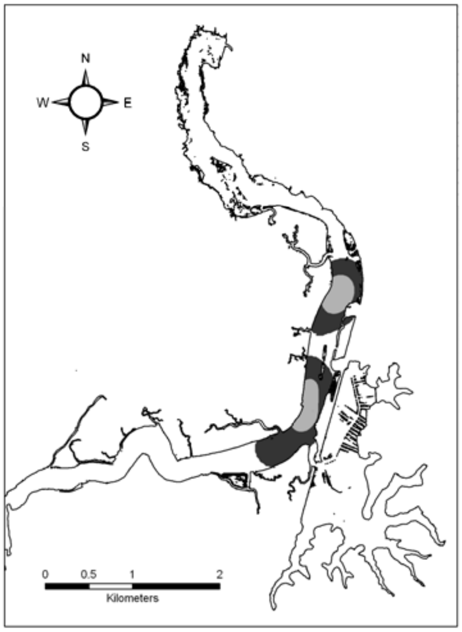


Figure 21. Ordination plot from PCA of habitat use of all sharks tracked during high tidal levels (>1.13 m). Points (•) represent sharks tracked in ESNERR, triangles (Δ) sharks tracked in the main channel. The percentage of the variation that is explained by each principal component is noted in the axis.

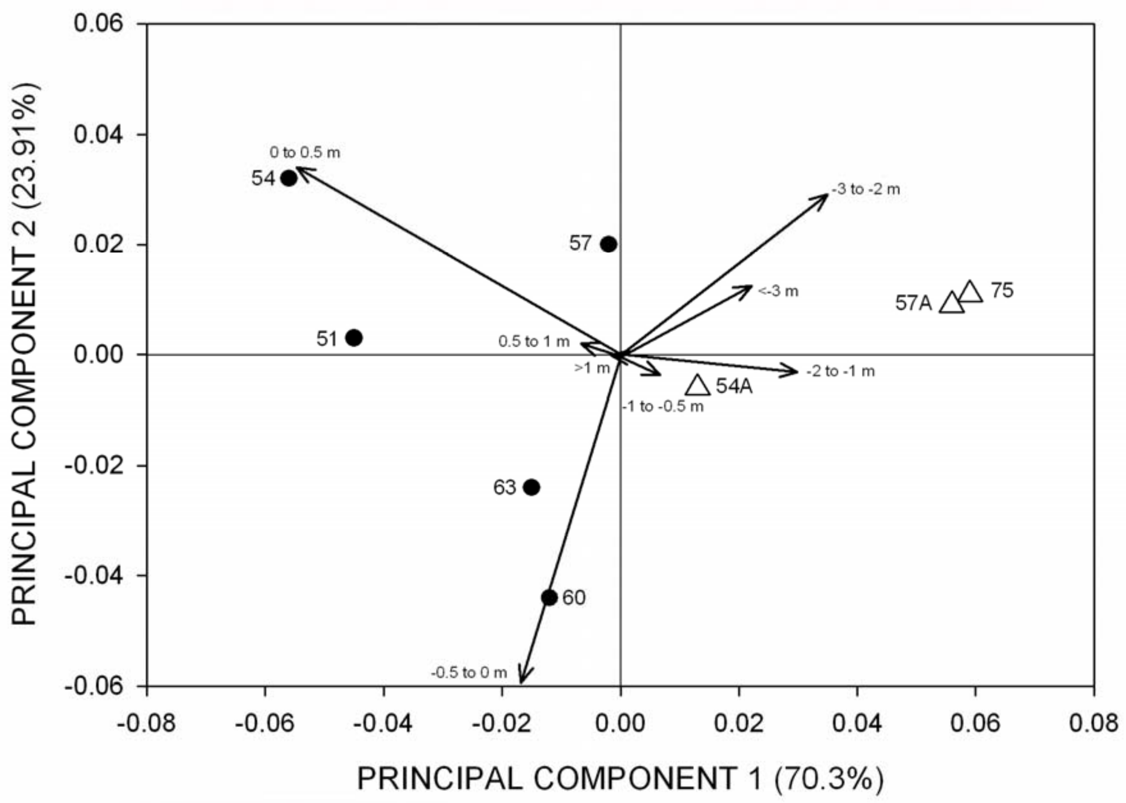

0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.06
-0.04
-0.02
0.00
0.02
0.04
0.06
0.08
PRINCIPAL COMPONENT 2 (23.91%)
PRINCIPAL COMPONENT 1 (70.3%)
0 to 0.5 m
54
57
51
63
60
-3 to -2 m
<-3 m
57A
75
0.5 to 1 m
>1 m
-2 to -1 m
54A
-1 to -0.5 m
-0.5 to 0 m

Figure 22. Ordination plot from PCA of habitat use of all sharks tracked during intermediate tidal levels (0.6 – 1.13 m). Points (•) represent sharks tracked in ESNERR, triangles (Δ) sharks tracked in the main channel. The percentage of the variation that is explained by each principal component is noted in the axis.

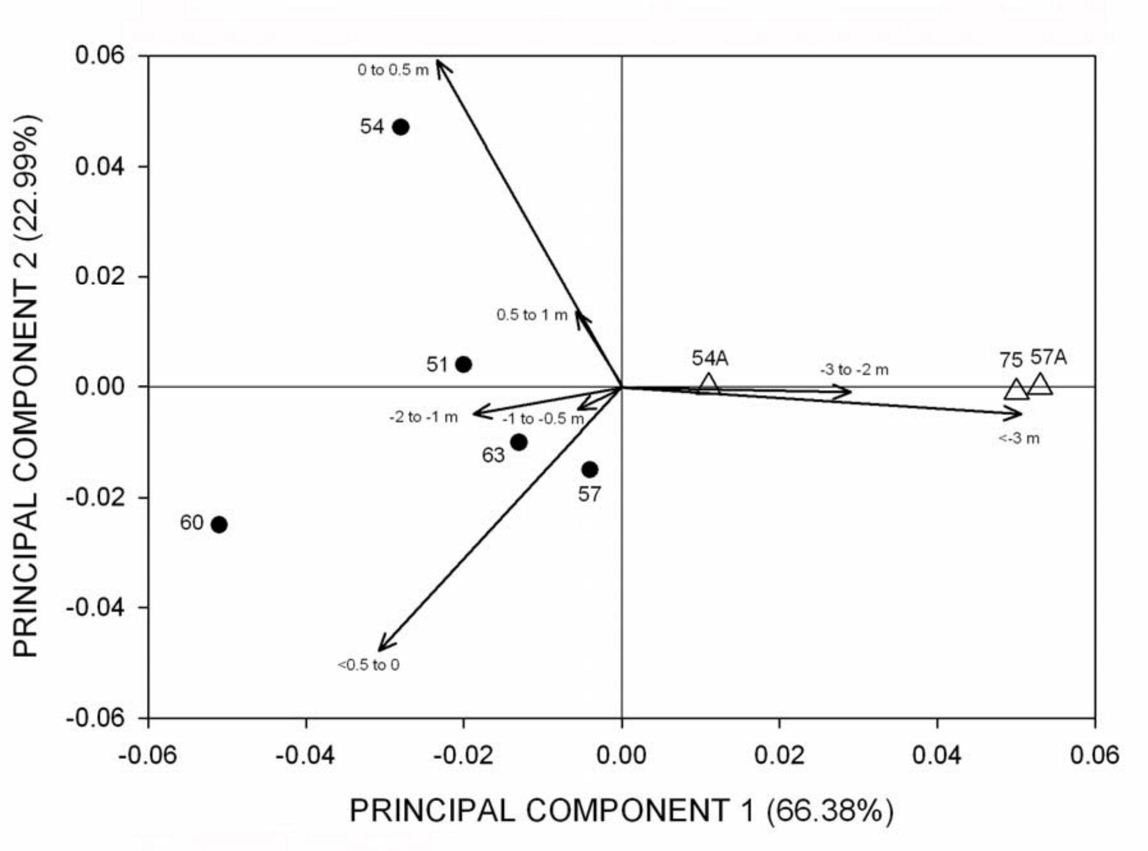

0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
PRINCIPAL COMPONENT 2 (22.99%)
-0.06
-0.04
-0.02
0.00
0.02
0.04
0.06
PRINCIPAL COMPONENT 1 (66.38%)
0 to 0.5 m
54
0.5 to 1 m
51
54A
-3 to -2 m
75
57A
-2 to -1 m
-1 to -0.5 m
<-3 m
63
57
60
<0.5 to 0

Figure 23. Ordination plot from PCA of habitat use of all sharks tracked during low tidal levels (< 0.6 m). Points (•) represent sharks tracked in ESNERR, triangles (Δ) sharks tracked in the main channel. The percentage of the variation that is explained by each principal component is noted in the axis.

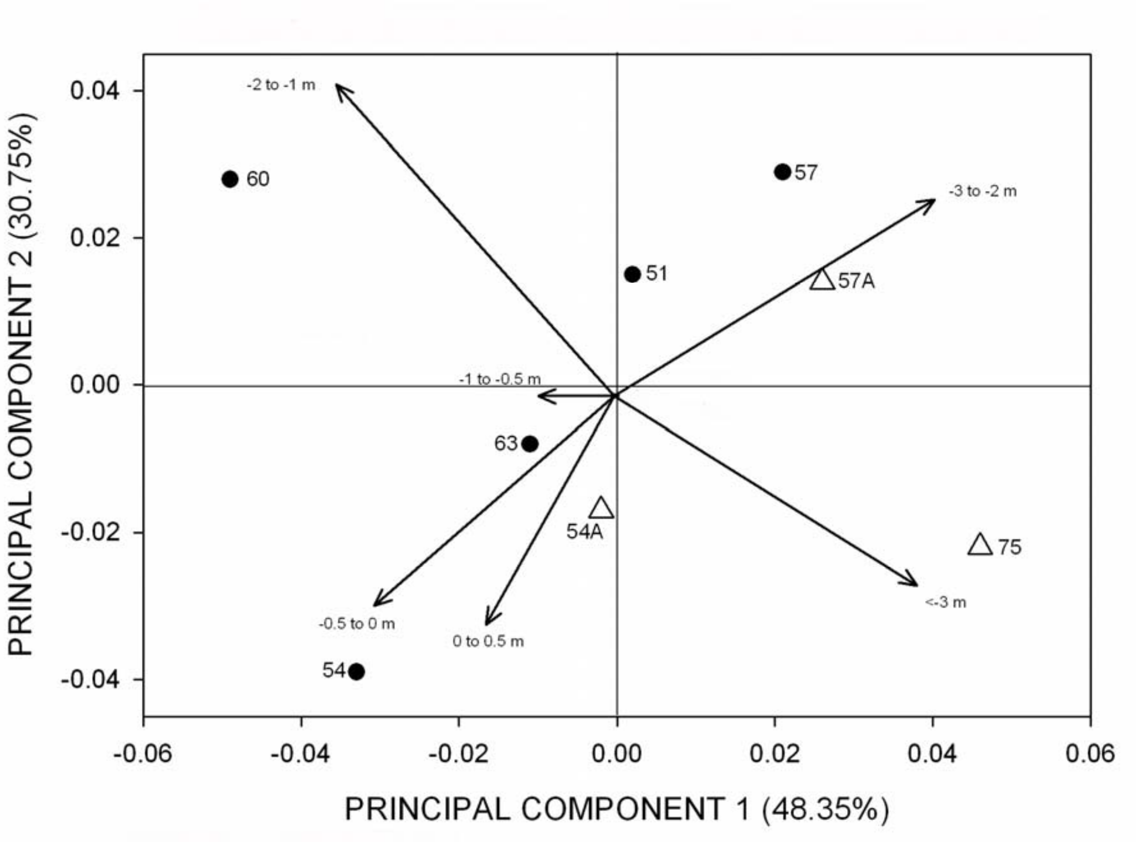
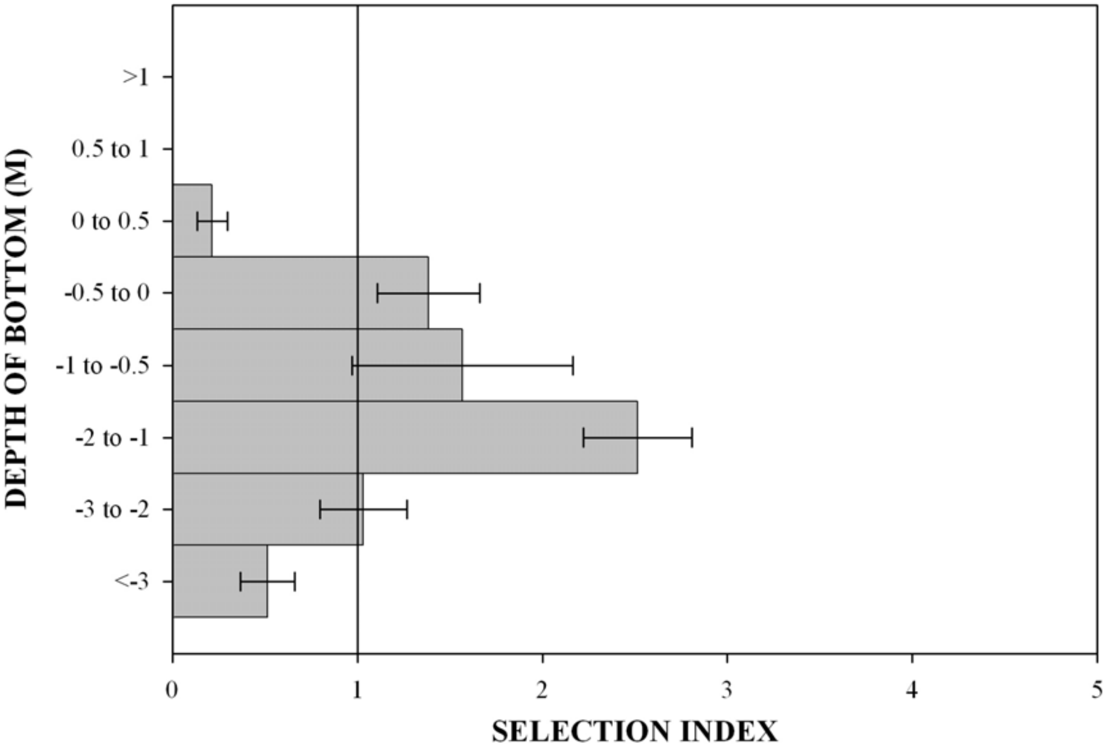
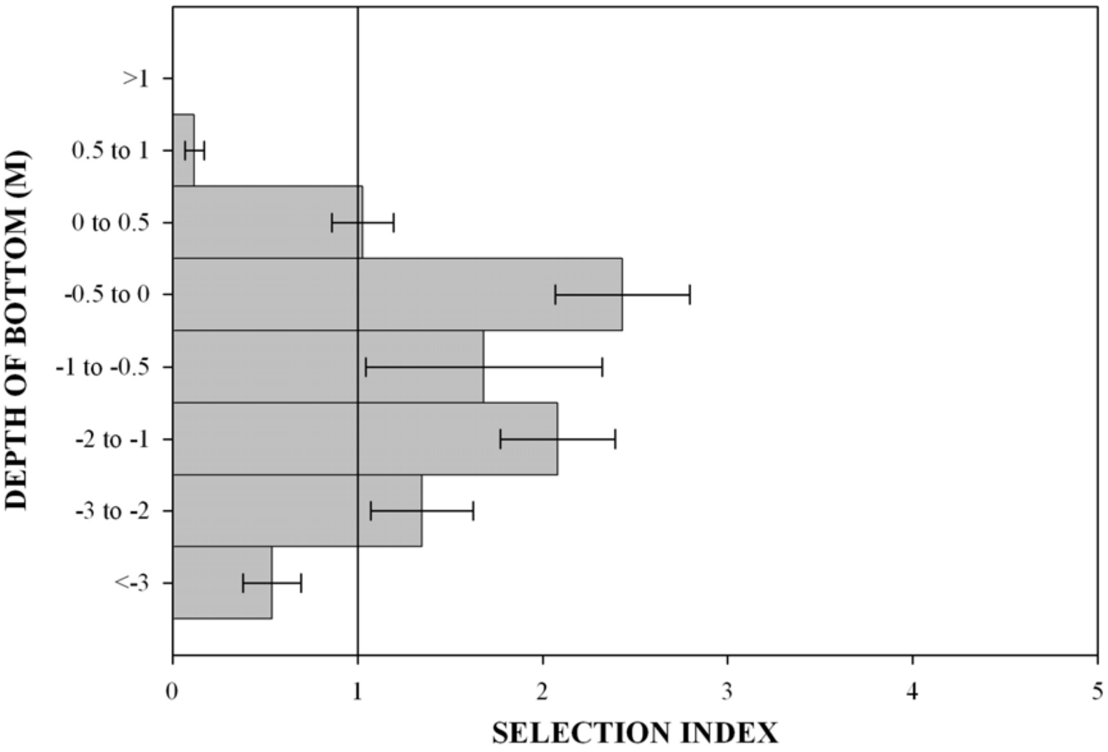

PRINCIPAL COMPONENT 2 (30.75%)
PRINCIPAL COMPONENT 1 (48.35%)
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.04
-0.02
0.00
0.02
0.04
0.06
-2 to -1 m
-3 to -2 m
-1 to -0.5 m
-0.5 to 0 m
0 to 0.5 m
<-3 m
60
57
51
57A
63
54A
75
54

Figure 24. Selection indices (± 95% CI) and pair-wise comparisons (with p values corrected using Bonferroni correction) between habitat categories for ESNERR sharks (n = 4) at low tidal levels (< 0.6 m). Selection index values > 1 indicate selection and values < 1 indicate avoidance. A value of 1 indicates that the shark is using that habitat type in proportion to its availability.



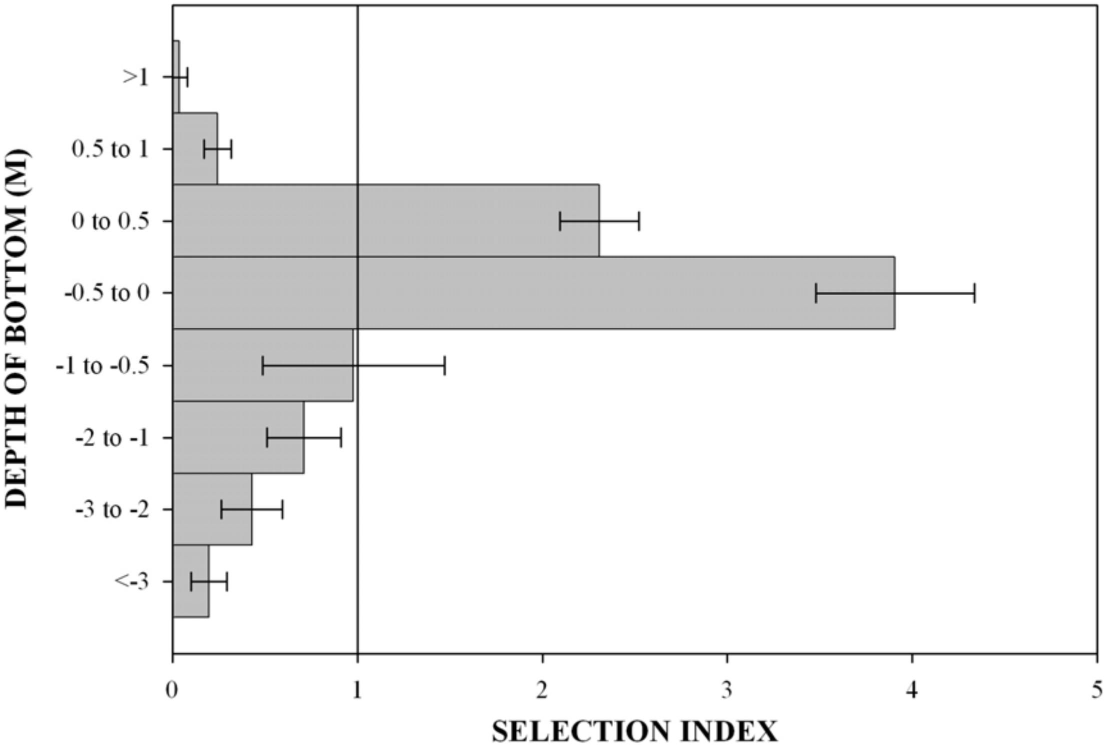
	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5
<-3	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-
-2 to -1	<0.001	<0.001	-	-	-	-
-1 to -0.5	<0.001	<0.025	<0.001	-	-	-
-0.5 to 0	<0.001	<0.005	<0.001	NS	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.001	<0.001	-

Figure 25. Selection indices (± 95% CI) and pair-wise comparisons (with p values corrected using Bonferroni correction) between habitat categories for ESNERR sharks (n = 5) at intermediate tidal levels (0.6 – 1.13 m). Selection index values > 1 indicate selection and values < 1 indicate avoidance. A value of 1 indicates that the shark is using that habitat type in proportion to its availability.



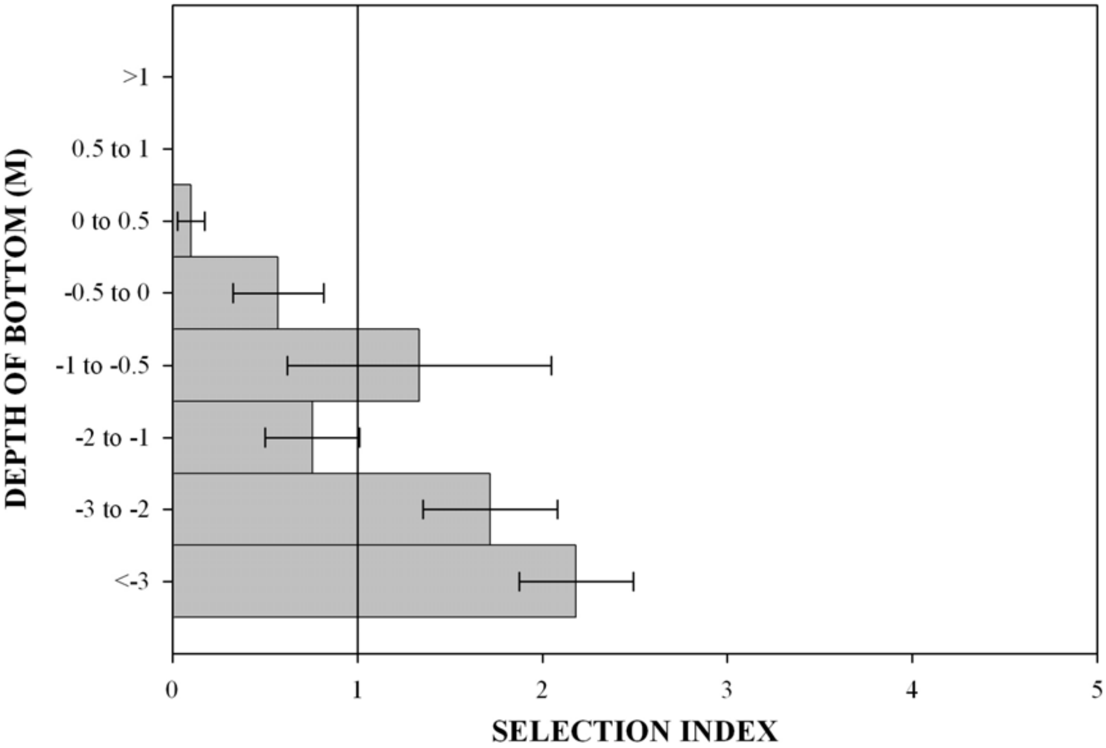
	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1
<-3	-	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-	-
-2 to -1	<0.001	<0.001	-	-	-	-	-
-1 to -0.5	<0.001	NS	NS	-	-	-	-
-0.5 to 0	<0.001	<0.001	<0.025	<0.01	-	-	-
0 to 0.5	<0.001	<0.025	<0.001	<0.01	<0.001	-	-
0.5 to 1	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-

Figure 26. Selection indices (± 95% CI) and pair-wise comparisons (with p values corrected using Bonferroni correction) between habitat categories for ESNERR sharks (n = 5) at high tidal levels (> 1.13 m). Selection index values > 1 indicate selection and values < 1 indicate avoidance. A value of 1 indicates that the shark is using that habitat type in proportion to its availability.



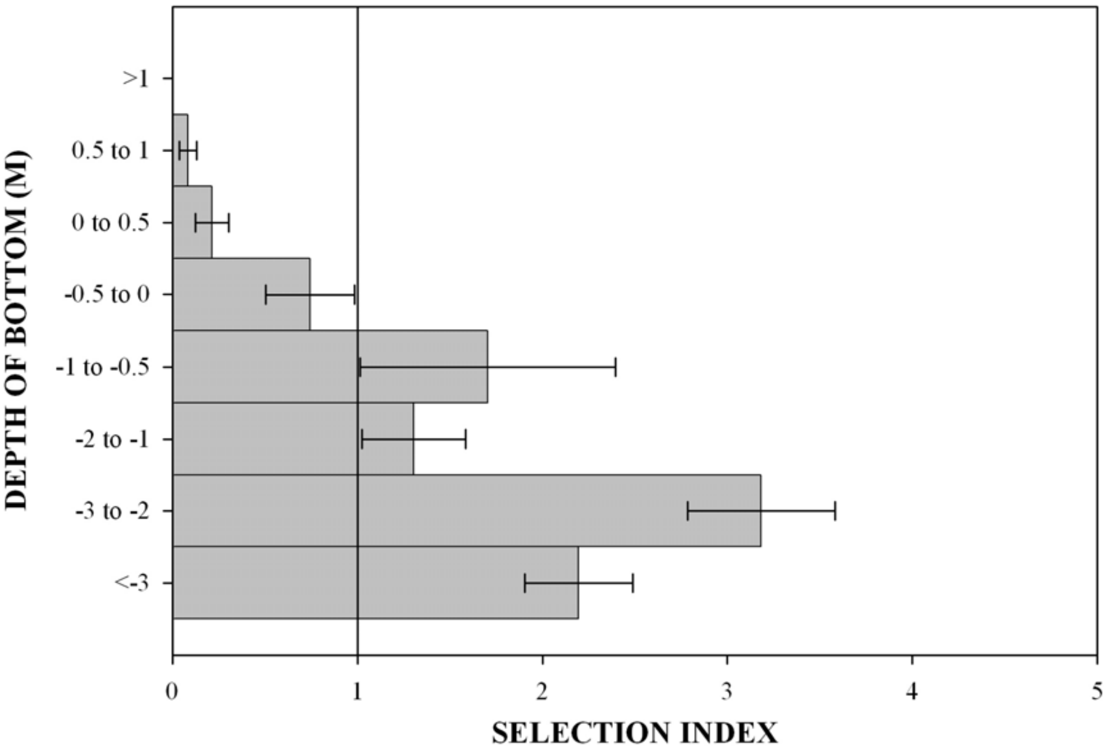
	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1	>1
<-3	-	-	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-	-	-
-2 to -1	<0.001	<0.005	-	-	-	-	-	-
-1 to -0.5	<0.001	<0.005	NS	-	-	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	<0.001	-	-	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.001	<0.001	-	-	-
0.5 to 1	NS	<0.005	<0.001	<0.001	<0.001	<0.001	-	-
>1	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-

Figure 27. Selection indices (± 95% CI) and pair-wise comparisons (with p values corrected using Bonferroni correction) between habitat categories for main channel sharks (n = 2) at low tidal levels (< 0.6 m). Selection index values > 1 indicate selection and values < 1 indicate avoidance. A value of 1 indicates that the shark is using that habitat type in proportion to its availability.



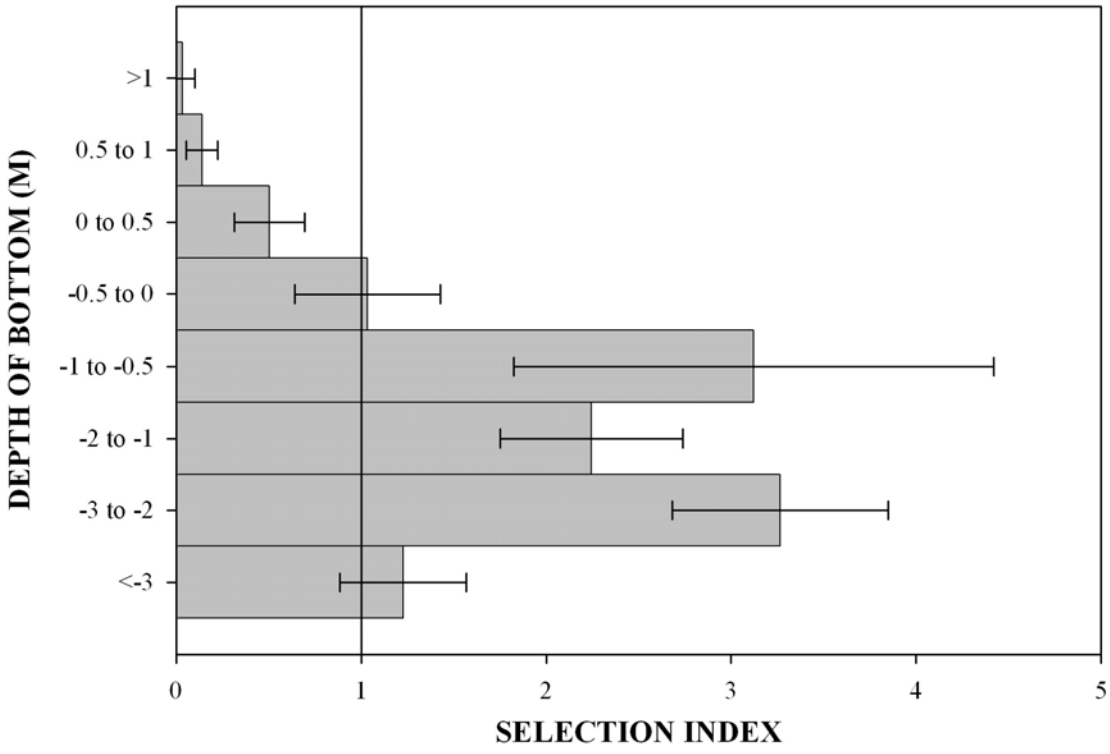
	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5
<-3	-	-	-	-	-	-
-3 to -2	<0.025	-	-	-	-	-
-2 to -1	<0.001	<0.001	-	-	-	-
-1 to -0.5	<0.005	NS	<0.05	-	-	-
-0.5 to 0	<0.001	<0.001	NS	<0.01	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.001	<0.001	-

Figure 28. Selection indices (± 95% CI) and pair-wise comparisons (with p values corrected using Bonferroni correction) between habitat categories for main channel sharks (n = 3) at intermediate tidal levels (0.6 – 1.13 m). Selection index values > 1 indicate selection and values < 1 indicate avoidance. A value of 1 indicates that the shark is using that habitat type in proportion to its availability.



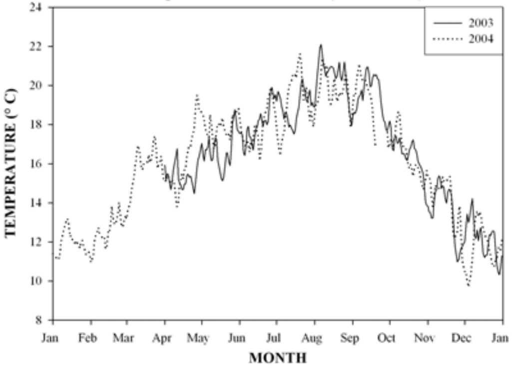
	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1
<-3	-	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-	-
-2 to -1	<0.001	<0.001	-	-	-	-	-
-1 to -0.5	NS	<0.001	NS	-	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	<0.001	-	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.001	<0.001	-	-
0.5 to 1	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-

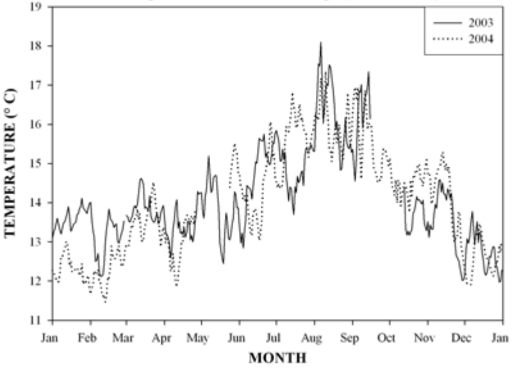
Figure 29. Selection indices (± 95% CI) and pair-wise comparisons (with p values corrected using Bonferroni correction) between habitat categories for main channel sharks ($n = 3$) at high tidal levels (> 1.13 m). Selection index values > 1 indicate selection and values < 1 indicate avoidance. A value of 1 indicates that the shark is using that habitat type in proportion to its availability.

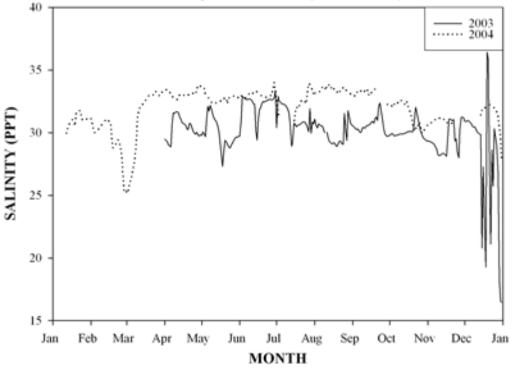


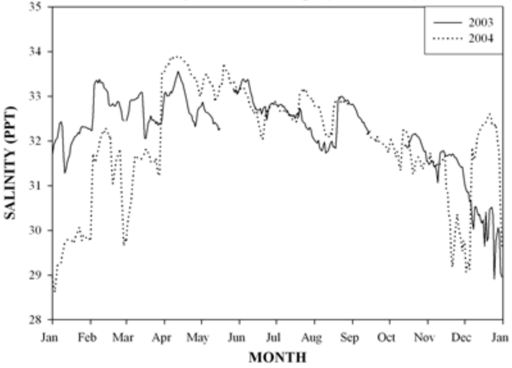
	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1	>1
<-3	x	-	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-	-	-
-2 to -1	<0.001	<0.005	-	-	-	-	-	-
-1 to -0.5	<0.001	NS	NS	-	-	-	-	-
-0.5 to 0	NS	<0.001	<0.001	<0.001	-	-	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.001	<0.005	-	-	-
0.5 to 1	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-	-
>1	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-

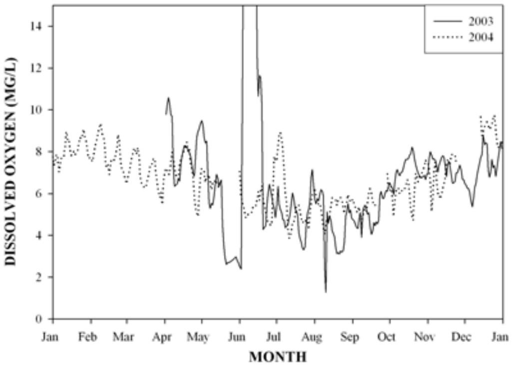
Appendix A. 2003 and 2004 environmental data from a monitoring station in south marsh in ESNERR and a monitoring station south of receiver 1 in the lower slough (ESNERR unpublished data).

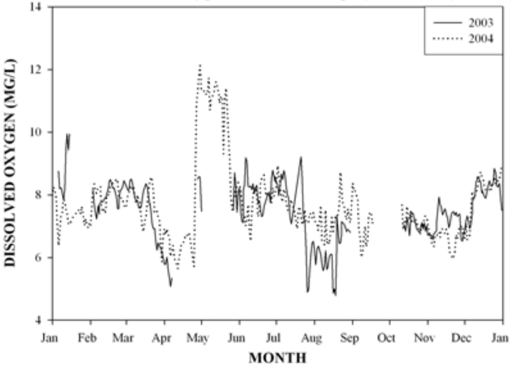

Temperature in ESNERR (2003 - 2004)


Temperature in Lower Slough (2003 - 2004)

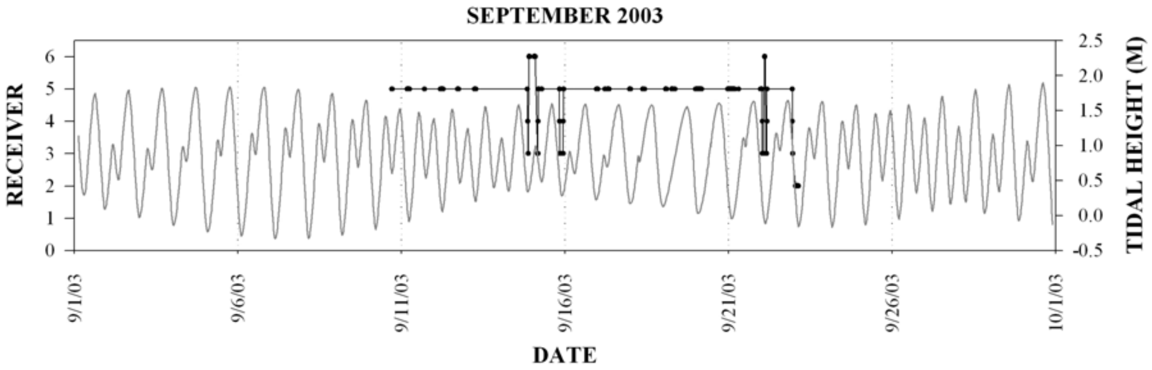

Salinity in ESNERR (2003 - 2004)


Salinity in Lower Slough (2003 - 2004)

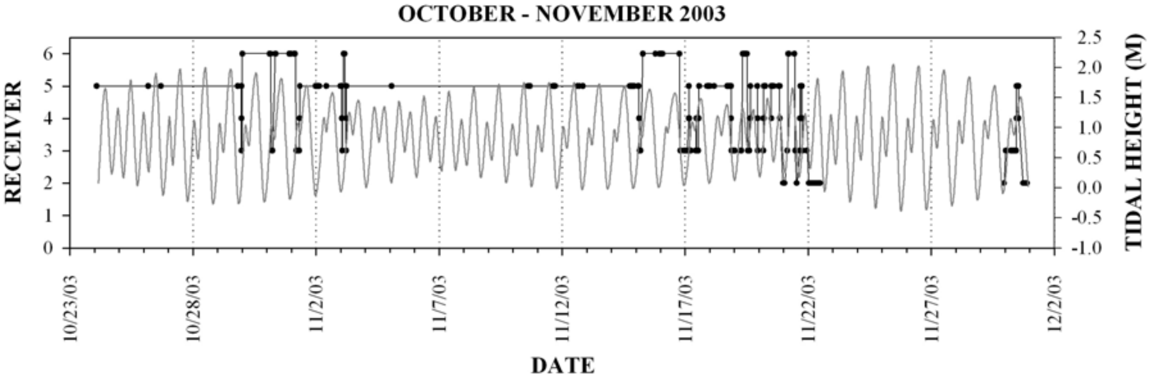

Dissolved Oxygen in ESNERR (2003 - 2004)


Dissolved Oxygen in Lower Slough (2003 - 2004)

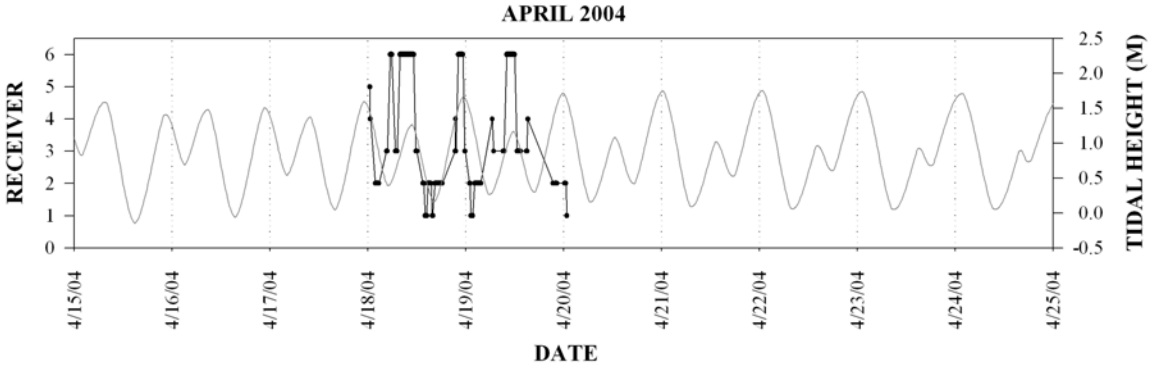
Appendix B. Movements of shark 106 among VR1 receivers. Left y-axis is receiver number, right y-axis is tidal height (m), and x-axis is date. Points indicate detections at a particular receiver. Light gray line represents tidal stage.


SEPTEMBER 2003
RECEIVER
TIDAL HEIGHT (M)
0
1
2
3
4
5
6
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
9/1/03
9/6/03
9/11/03
9/16/03
9/21/03
9/26/03
10/1/03
DATE

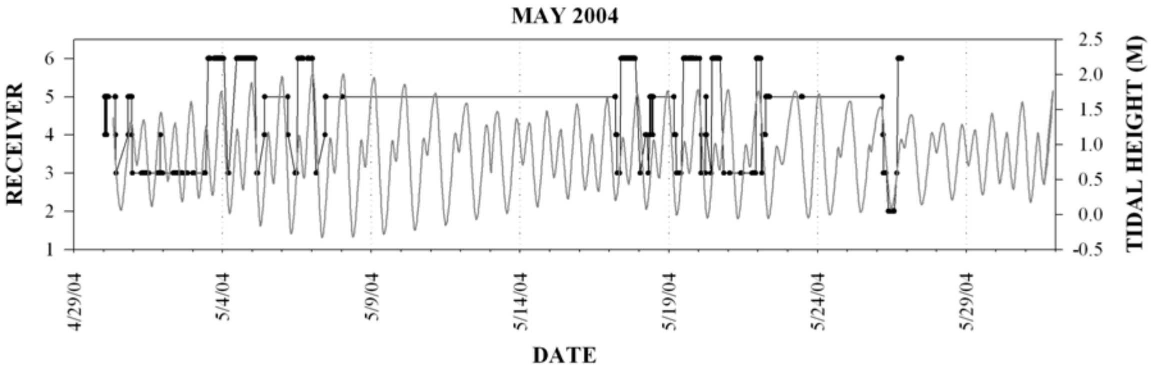
Appendix C. Movements of shark 107 among VR1 receivers. Left y-axis is receiver number, right y-axis is tidal height (m), and x-axis is date. Points indicate detections at a particular receiver. Light gray line represents tidal stage.


OCTOBER - NOVEMBER 2003
RECEIVER
0
1
2
3
4
5
6
TIDAL HEIGHT (M)
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
10/23/03
10/28/03
11/2/03
11/7/03
11/12/03
11/17/03
11/22/03
11/27/03
12/2/03
DATE

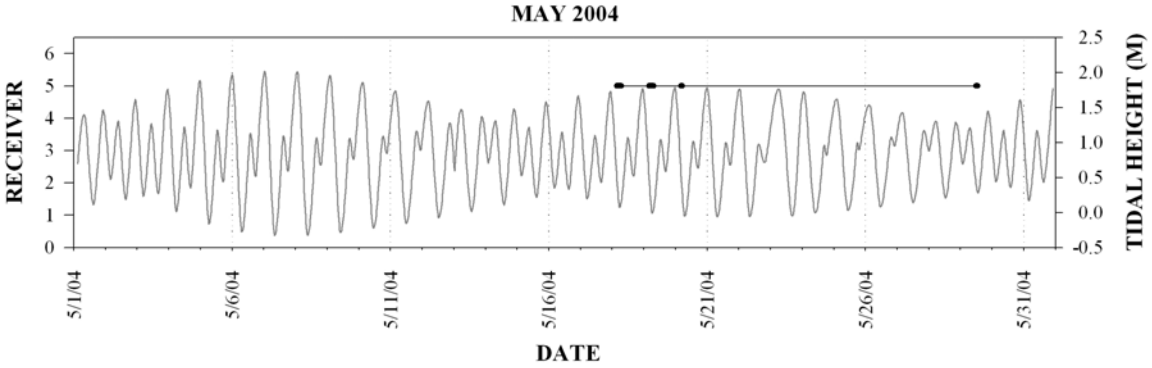
Appendix D. Movements of shark 101 among VR1 receivers. Left y-axis is receiver number, right y-axis is tidal height (m), and x-axis is date. Points indicate detections at a particular receiver. Light gray line represents tidal stage.


APRIL 2004
RECEIVER
0
1
2
3
4
5
6
TIDAL HEIGHT (M)
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
4/15/04
4/16/04
4/17/04
4/18/04
4/19/04
4/20/04
4/21/04
4/22/04
4/23/04
4/24/04
4/25/04
DATE

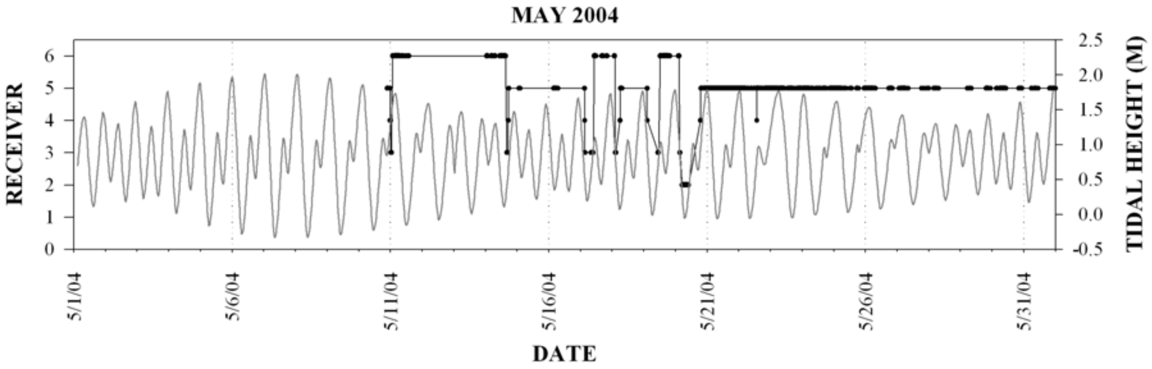
Appendix E. Movements of shark 103 among VR1 receivers. Left y-axis is receiver number, right y-axis is tidal height (m), and x-axis is date. Points indicate detections at a particular receiver. Light gray line represents tidal stage.

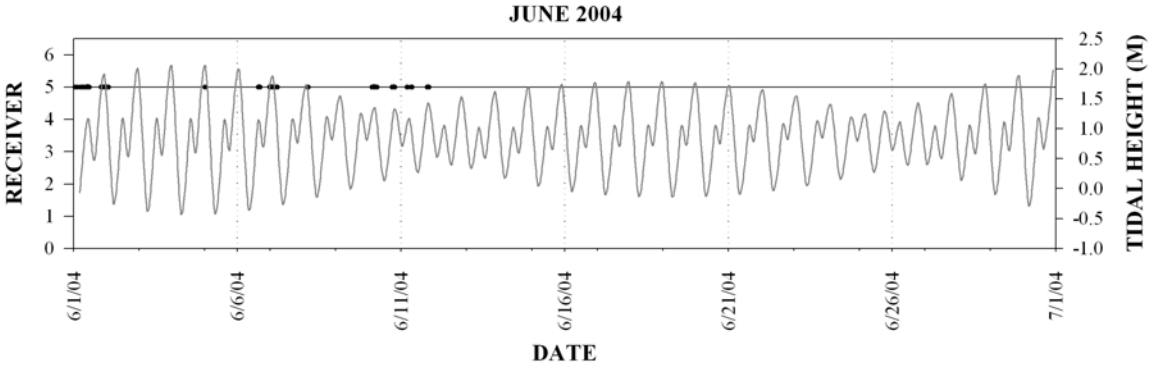

MAY 2004
RECEIVER
TIDAL HEIGHT (M)
DATE
1
2
3
4
5
6
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
4/29/04
5/4/04
5/9/04
5/14/04
5/19/04
5/24/04
5/29/04

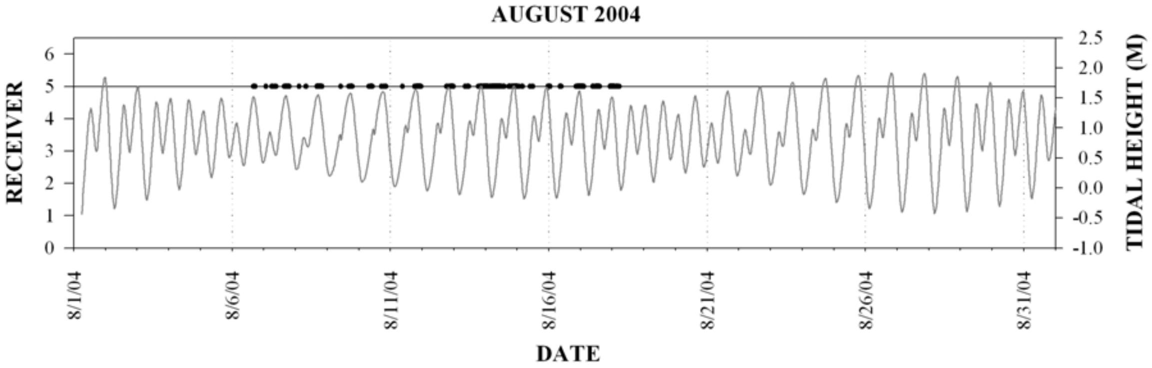
Appendix F. Movements of shark 104 among VR1 receivers. Left y-axis is receiver number, right y-axis is tidal height (m), and x-axis is date. Points indicate detections at a particular receiver. Light gray line represents tidal stage.

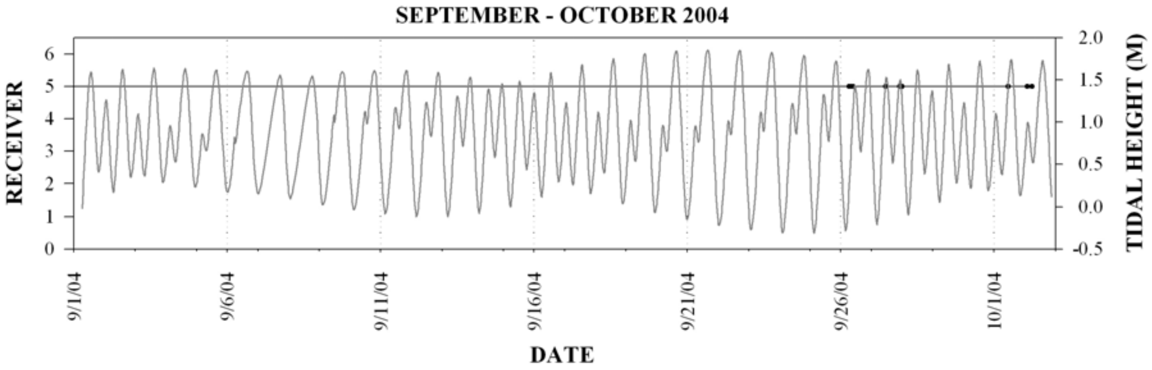

MAY 2004
RECEIVER
TIDAL HEIGHT (M)
DATE
0
1
2
3
4
5
6
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
5/1/04
5/6/04
5/11/04
5/16/04
5/21/04
5/26/04
5/31/04

Appendix G. Movements of shark 108 among VR1 receivers. Left y-axis is receiver number, right y-axis is tidal height (m), and x-axis is date. Points indicate detections at a particular receiver. Light gray line represents tidal stage.

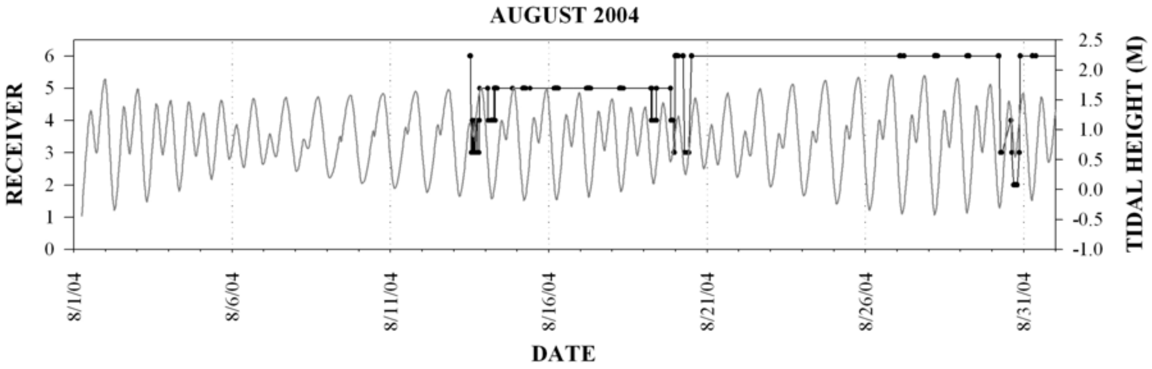

MAY 2004
RECEIVER
0
1
2
3
4
5
6
TIDAL HEIGHT (M)
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
5/1/04
5/6/04
5/11/04
5/16/04
5/21/04
5/26/04
5/31/04
DATE

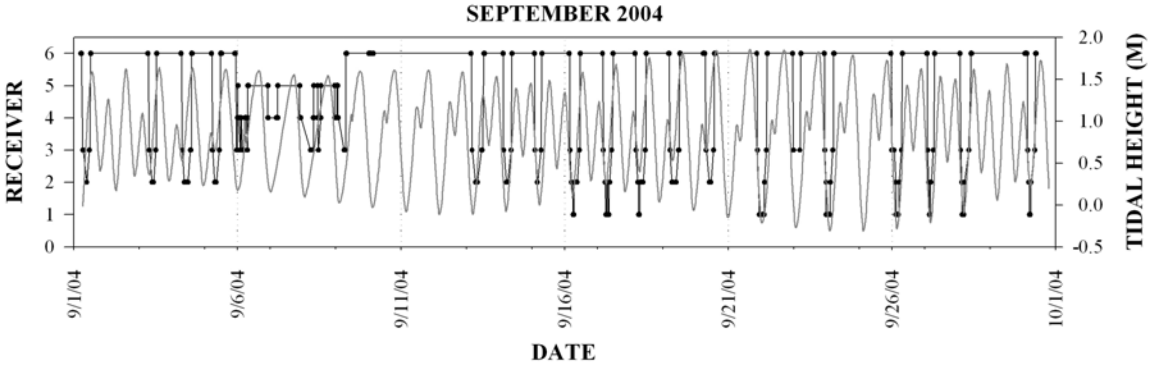

JUNE 2004
RECEIVER
0
1
2
3
4
5
6
TIDAL HEIGHT (M)
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
6/1/04
6/6/04
6/11/04
6/16/04
6/21/04
6/26/04
7/1/04
DATE

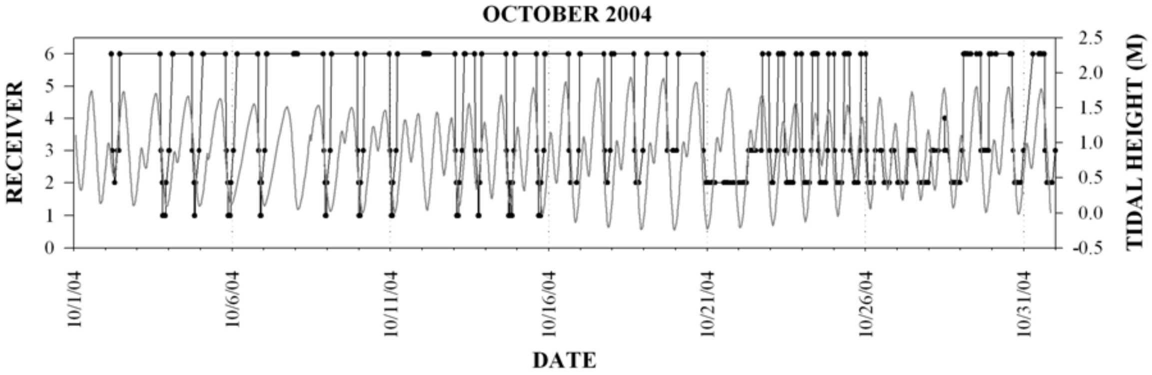

AUGUST 2004
RECEIVER
0
1
2
3
4
5
6
TIDAL HEIGHT (M)
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
8/1/04
8/6/04
8/11/04
8/16/04
8/21/04
8/26/04
8/31/04
DATE

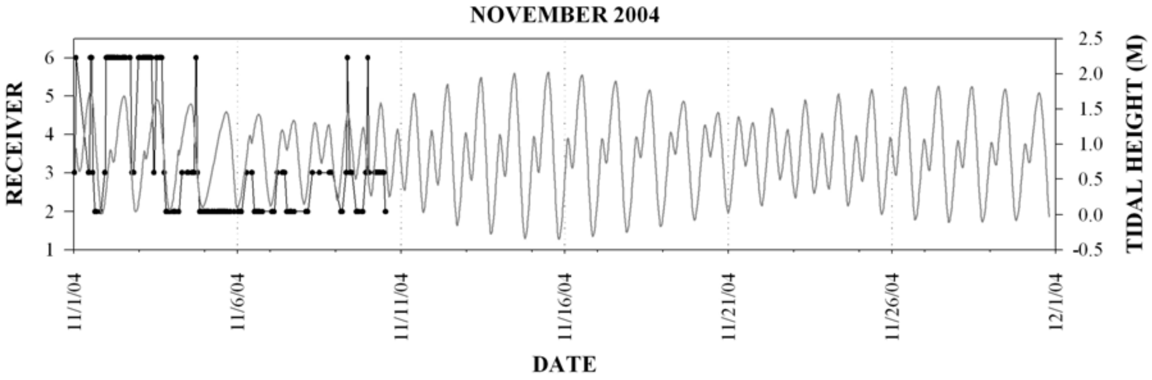

SEPTEMBER - OCTOBER 2004
RECEIVER
0
1
2
3
4
5
6
TIDAL HEIGHT (M)
-0.5
0.0
0.5
1.0
1.5
2.0
9/1/04
9/6/04
9/11/04
9/16/04
9/21/04
9/26/04
10/1/04
DATE

Appendix H. Movements of shark 109 among VR1 receivers. Left y-axis is receiver number, right y-axis is tidal height (m), and x-axis is date. Points indicate detections at a particular receiver. Light gray line represents tidal stage.


AUGUST 2004
RECEIVER
0
1
2
3
4
5
6
TIDAL HEIGHT (M)
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
8/1/04
8/6/04
8/11/04
8/16/04
8/21/04
8/26/04
8/31/04
DATE

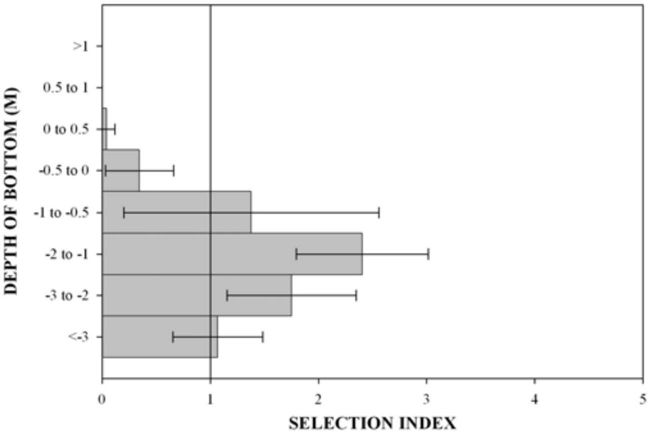

SEPTEMBER 2004
RECEIVER
0
1
2
3
4
5
6
TIDAL HEIGHT (M)
-0.5
0.0
0.5
1.0
1.5
2.0
9/1/04
9/6/04
9/11/04
9/16/04
9/21/04
9/26/04
10/1/04
DATE


OCTOBER 2004
RECEIVER
0
1
2
3
4
5
6
TIDAL HEIGHT (M)
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
10/1/04
10/6/04
10/11/04
10/16/04
10/21/04
10/26/04
10/31/04
DATE


NOVEMBER 2004
RECEIVER
1
2
3
4
5
6
TIDAL HEIGHT (M)
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
11/1/04
11/6/04
11/11/04
11/16/04
11/21/04
11/26/04
12/1/04
DATE

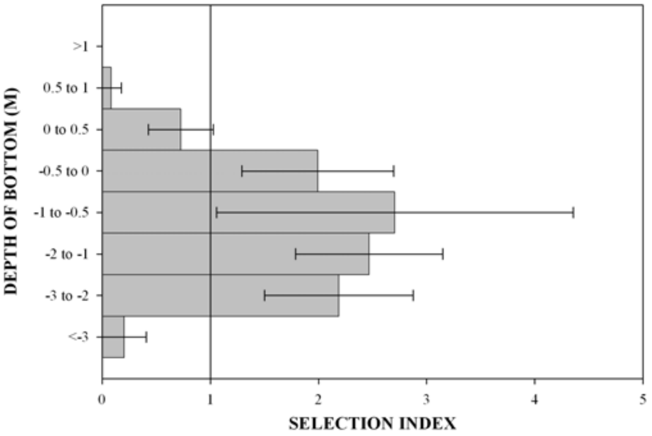
Appendix I. Selection indices (± 95% CI) and pair-wise comparisons (with p values corrected using Bonferroni correction) between habitat categories for shark 51 at (a) low, (b) intermediate, and (c) high tidal levels. Selection index values > 1 indicate selection and values < 1 indicate avoidance. A value of 1 indicates that the shark is using that habitat type in proportion to its availability.

a



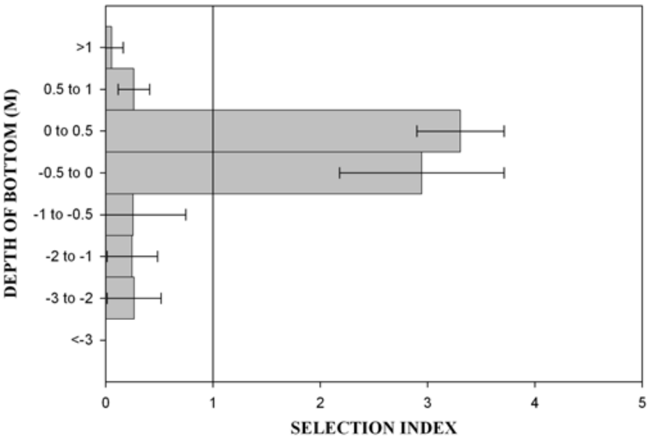
	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5
<-3	-	-	-	-	-	-
-3 to -2	<0.005	-	-	-	-	-
-2 to -1	<0.001	<0.005	-	-	-	-
-1 to -0.5	NS	NS	<0.05	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	<0.025	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.005	<0.025	-

b



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1
<-3	-	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-	-
-2 to -1	<0.001	NS	-	-	-	-	-
-1 to -0.5	<0.001	NS	NS	-	-	-	-
-0.5 to 0	<0.001	NS	NS	NS	-	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.005	<0.001	-	-
0.5 to 1	NS	<0.001	<0.001	<0.001	<0.001	<0.001	-

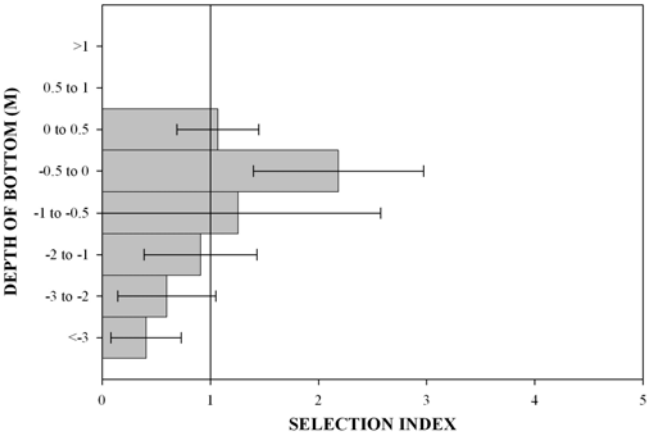
c



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1	>1
<-3	-	-	-	-	-	-	-	-
-3 to -2	<0.005	-	-	-	-	-	-	-
-2 to -1	<0.005	NS	-	-	-	-	-	-
-1 to -0.5	NS	NS	NS	-	-	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	<0.001	-	-	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.001	NS	-	-	-
0.5 to 1	<0.001	NS	NS	NS	<0.001	<0.001	-	-
>1	NS	<0.05	<0.05	NS	<0.001	<0.001	<0.005	-

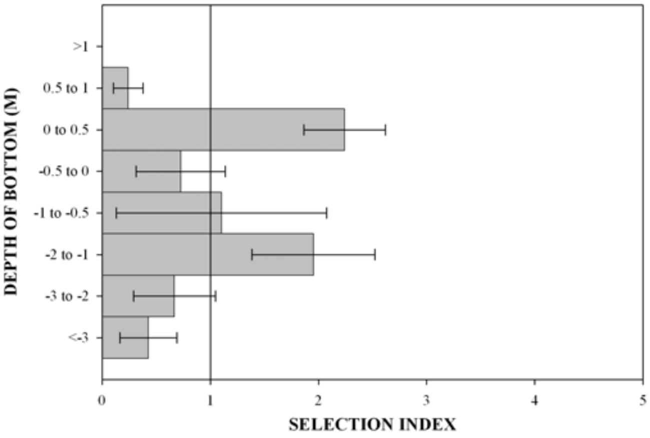
Appendix J. Selection indices (± 95% CI) and pair-wise comparisons (with p values corrected using Bonferroni correction) between habitat categories for shark 54 at (a) low, (b) intermediate, and (c) high tidal levels. Selection index values > 1 indicate selection and values < 1 indicate avoidance. A value of 1 indicates that the shark is using that habitat type in proportion to its availability.

a



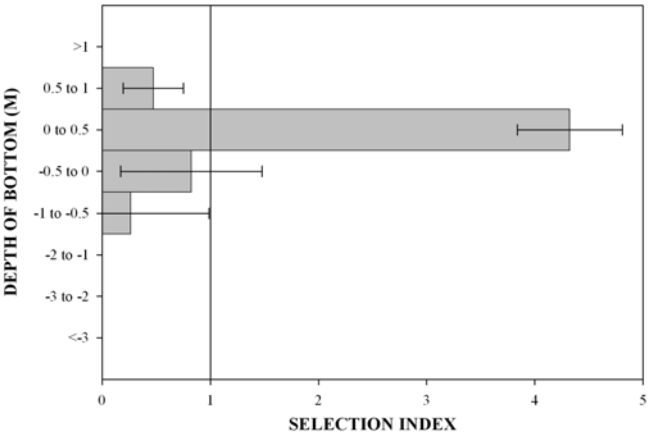
	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5
<-3	-	-	-	-	-	-
-3 to -2	NS	-	-	-	-	-
-2 to -1	<0.025	NS	-	-	-	-
-1 to -0.5	NS	NS	NS	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	NS	-	-
0 to 0.5	<0.001	<0.025	NS	NS	<0.001	-

b



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1
<-3	-	-	-	-	-	-	-
-3 to -2	NS	-	-	-	-	-	-
-2 to -1	<0.001	<0.001	-	-	-	-	-
-1 to -0.5	NS	NS	p<0.05	-	-	-	-
-0.5 to 0	NS	NS	<0.001	NS	-	-	-
0 to 0.5	<0.001	<0.001	NS	<0.005	<0.001	-	-
0.5 to 1	NS	<0.005	<0.001	<0.025	<0.005	<0.001	-

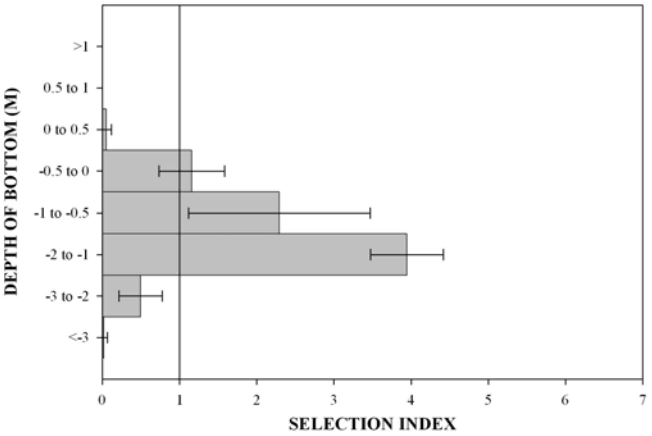
c



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1	>1
<-3	-	-	-	-	-	-	-	-
-3 to -2	NS	-	-	-	-	-	-	-
-2 to -1	NS	NS	-	-	-	-	-	-
-1 to -0.5	NS	NS	NS	-	-	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	NS	-	-	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.001	<0.001	-	-	-
0.5 to 1	<0.001	<0.001	<0.001	NS	NS	<0.001	x	-
>1	NS	NS	NS	NS	<0.001	<0.001	<0.001	-

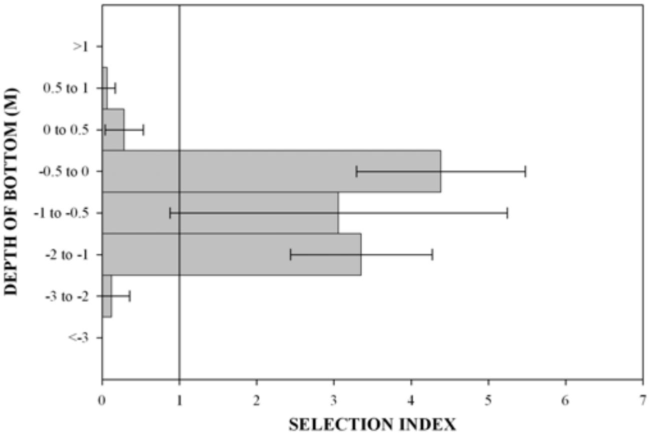
Appendix K. Selection indices (± 95% CI) and pair-wise comparisons (with p values corrected using Bonferroni correction) between habitat categories for shark 60 at (a) low, (b) intermediate, and (c) high tidal levels. Selection index values > 1 indicate selection and values < 1 indicate avoidance. A value of 1 indicates that the shark is using that habitat type in proportion to its availability.

a



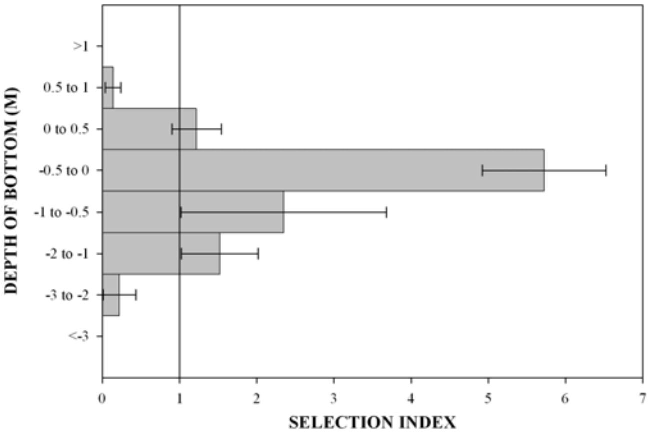
	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5
<-3	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-
-2 to -1	<0.001	<0.001	-	-	-	-
-1 to -0.5	<0.001	<0.001	<0.001	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	<0.01	-	-
0 to 0.5	NS	<0.001	<0.001	<0.001	<0.001	-

b



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1
<-3	-	-	-	-	-	-	-
-3 to -2	NS	-	-	-	-	-	-
-2 to -1	<0.001	<0.001	-	-	-	-	-
-1 to -0.5	<0.001	<0.001	NS	-	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	NS	-	-	-
0 to 0.5	<0.005	NS	<0.001	<0.001	<0.001	-	-
0.5 to 1	NS	NS	<0.001	<0.001	<0.001	<0.05	-

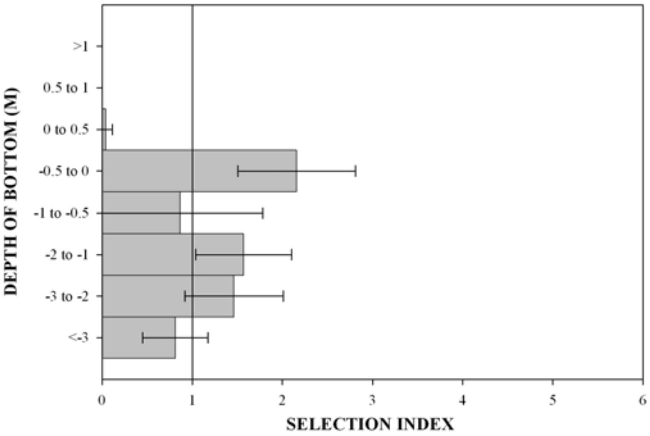
c



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1	>1
<-3	-	-	-	-	-	-	-	-
-3 to -2	<0.005	-	-	-	-	-	-	-
-2 to -1	<0.001	<0.001	-	-	-	-	-	-
-1 to -0.5	<0.001	<0.001	NS	-	-	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	<0.001	-	-	-	-
0 to 0.5	<0.001	<0.001	NS	<0.025	<0.001	-	-	-
0.5 to 1	<0.001	NS	<0.001	<0.001	<0.001	<0.001	-	-
>1	NS	<0.005	<0.001	<0.001	<0.001	<0.001	<0.001	-

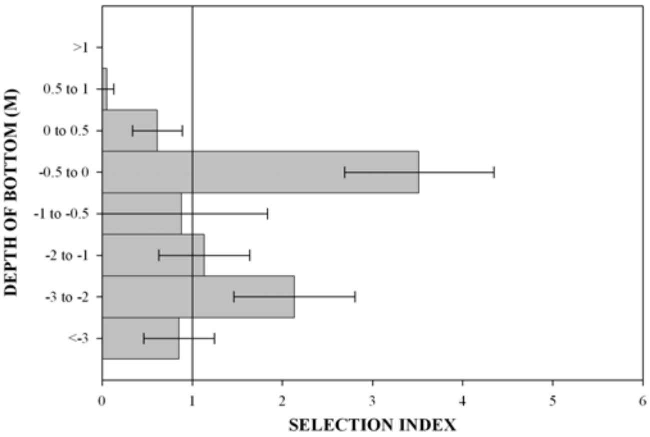
Appendix L. Selection indices (± 95% CI) and pair-wise comparisons (with p values corrected using Bonferroni correction) between habitat categories for shark 63 at (a) low, (b) intermediate, and (c) high tidal levels. Selection index values > 1 indicate selection and values < 1 indicate avoidance. A value of 1 indicates that the shark is using that habitat type in proportion to its availability.

a



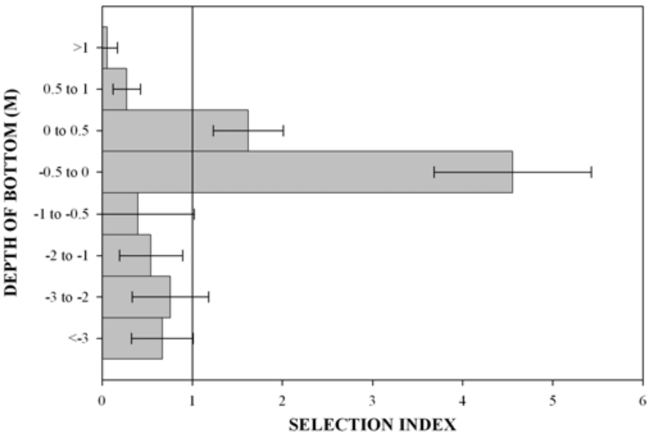
	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5
<-3	-	-	-	-	-	-
-3 to -2	<0.005	-	-	-	-	-
-2 to -1	<0.001	NS	-	-	-	-
-1 to -0.5	NS	NS	NS	-	-	-
-0.5 to 0	<0.001	<0.01	<0.025	<0.005	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.025	<0.001	-

b



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1
<-3	-	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-	-
-2 to -1	NS	<0.001	-	-	-	-	-
-1 to -0.5	NS	p<0.01	NS	-	-	-	-
-0.5 to 0	<0.001	<0.005	<0.001	<0.001	-	-	-
0 to 0.5	NS	<0.001	<0.025	NS	<0.001	-	-
0.5 to 1	<0.001	<0.001	<0.001	<0.025	<0.001	<0.001	-

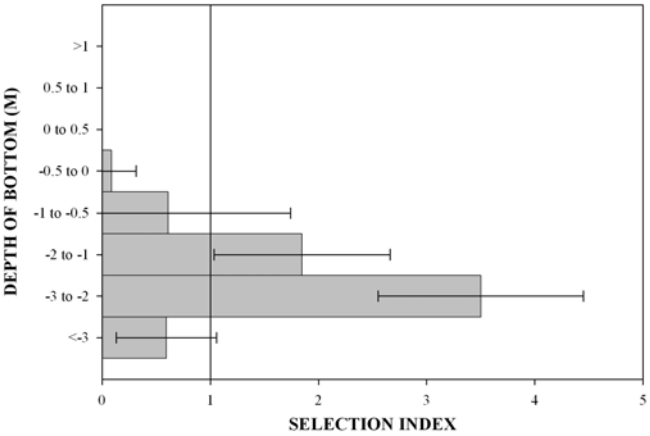
c



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1	>1
<-3	-	-	-	-	-	-	-	-
-3 to -2	NS	-	-	-	-	-	-	-
-2 to -1	NS	NS	-	-	-	-	-	-
-1 to -0.5	NS	NS	NS	-	-	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	<0.001	-	-	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.001	<0.001	-	-	-
0.5 to 1	<0.005	<0.005	<0.05	NS	<0.001	<0.001	-	-
>1	<0.001	<0.001	<0.001	NS	<0.001	<0.001	<0.005	-

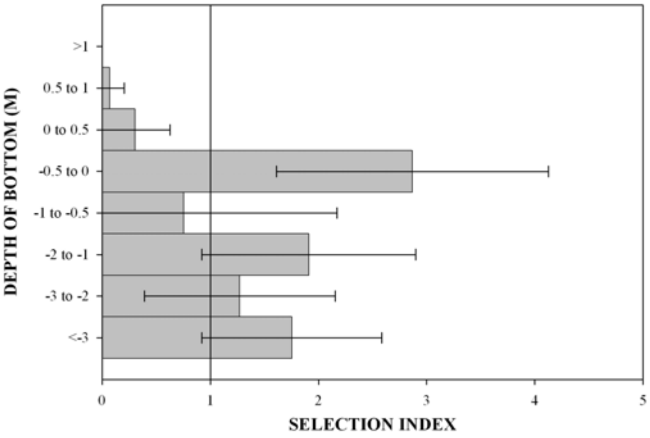
Appendix M. Selection indices (± 95% CI) and pair-wise comparisons (with p values corrected using Bonferroni correction) between habitat categories for shark 57 at (a) low, (b) intermediate, and (c) high tidal levels. Selection index values > 1 indicate selection and values < 1 indicate avoidance. A value of 1 indicates that the shark is using that habitat type in proportion to its availability.

a



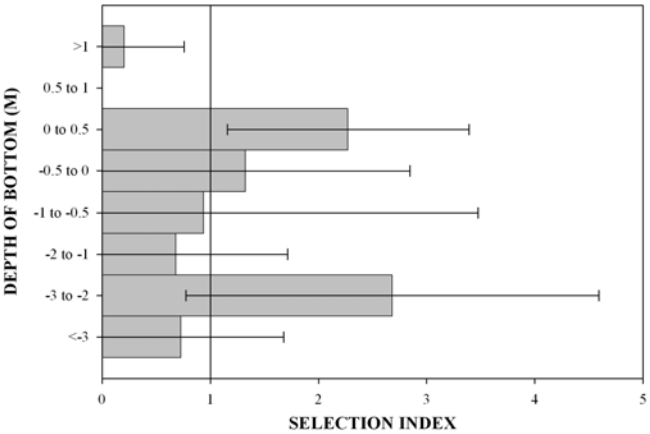
	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5
<-3	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-
-2 to -1	<0.001	<0.01	-	-	-	-
-1 to -0.5	NS	<0.001	<0.025	-	-	-
-0.5 to 0	<0.01	<0.001	<0.001	NS	-	-
0 to 0.5	<0.001	<0.001	<0.001	NS	NS	-

b



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1
<-3	-	-	-	-	-	-	-
-3 to -2	NS	-	-	-	-	-	-
-2 to -1	NS	NS	-	-	-	-	-
-1 to -0.5	NS	NS	NS	-	-	-	-
-0.5 to 0	<0.025	<0.005	<0.005	<0.005	-	-	-
0 to 0.5	<0.001	<0.005	<0.001	NS	<0.001	-	-
0.5 to 1	<0.001	<0.001	<0.001	NS	<0.001	NS	-

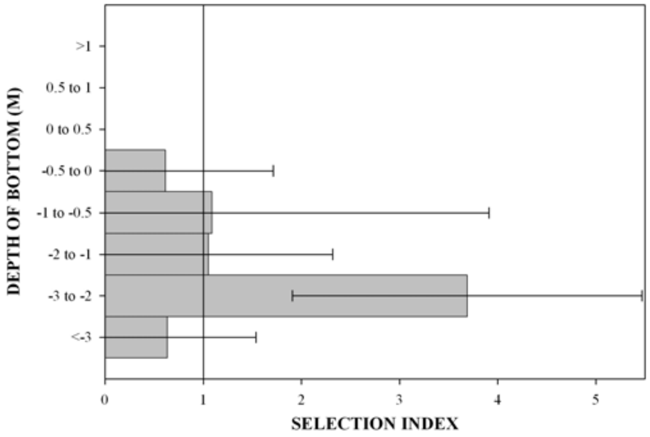
c



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1	>1
<-3	-	-	-	-	-	-	-	-
-3 to -2	<0.01	-	-	-	-	-	-	-
-2 to -1	NS	<0.01	-	-	-	-	-	-
-1 to -0.5	NS	NS	NS	-	-	-	-	-
-0.5 to 0	NS	NS	NS	NS	-	-	-	-
0 to 0.5	<0.001	NS	<0.005	NS	NS	-	-	-
0.5 to 1	<0.05	<0.001	NS	NS	<0.025	<0.001	-	-
>1	NS	<0.001	NS	NS	NS	<0.001	NS	-

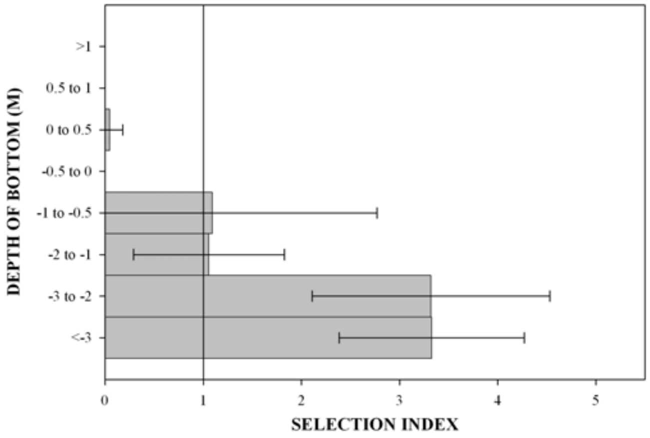
Appendix N. Selection indices (± 95% CI) and pair-wise comparisons (with p values corrected using Bonferroni correction) between habitat categories for shark 57A at (a) low, (b) intermediate, and (c) high tidal levels. Selection index values > 1 indicate selection and values < 1 indicate avoidance. A value of 1 indicates that the shark is using that habitat type in proportion to its availability.

a



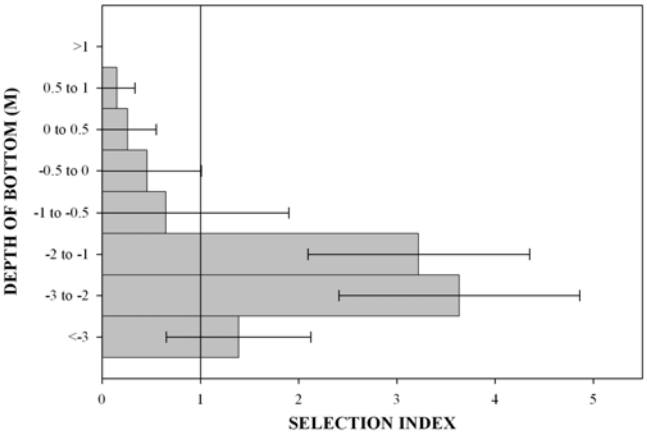
	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5
<-3	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-
-2 to -1	NS	<0.001	-	-	-	-
-1 to -0.5	NS	<0.025	NS	-	-	-
-0.5 to 0	NS	<0.001	NS	NS	-	-
0 to 0.5	NS	<0.001	<0.05	NS	NS	-

b



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1
<-3	-	-	-	-	-	-	-
-3 to -2	NS	-	-	-	-	-	-
-2 to -1	<0.001	<0.001	-	-	-	-	-
-1 to -0.5	<0.001	<0.005	NS	-	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	NS	-	-	-
0 to 0.5	<0.001	<0.001	<0.001	NS	NS	-	-
0.5 to 1	<0.001	<0.001	<0.001	NS	NS	NS	-

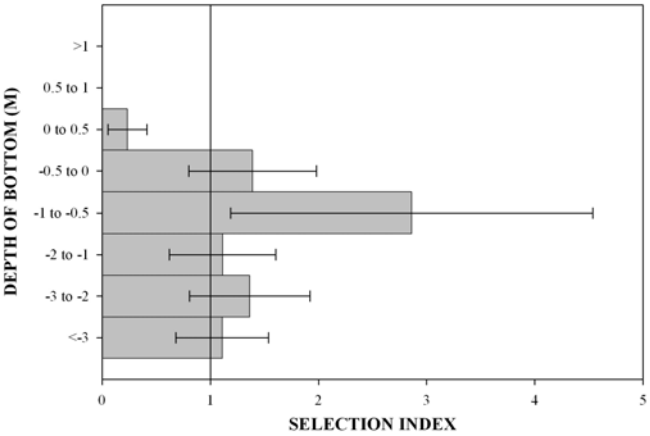
c



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1	>1
<-3	-	-	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-	-	-
-2 to -1	<0.001	NS	-	-	-	-	-	-
-1 to -0.5	NS	<0.001	<0.001	-	-	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	NS	-	-	-	-
0 to 0.5	<0.001	<0.001	<0.001	NS	NS	-	-	-
0.5 to 1	<0.001	<0.001	<0.001	NS	NS	NS	-	-
>1	<0.001	<0.001	<0.001	NS	<0.025	<0.025	<0.025	-

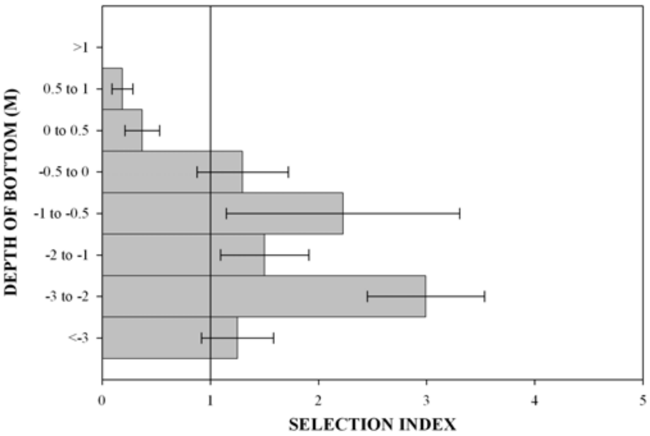
Appendix O. Selection indices (± 95% CI) and pair-wise comparisons (with p values corrected using Bonferroni correction) between habitat categories for shark 54A at (a) low, (b) intermediate, and (c) high tidal levels. Selection index values > 1 indicate selection and values < 1 indicate avoidance. A value of 1 indicates that the shark is using that habitat type in proportion to its availability.

a



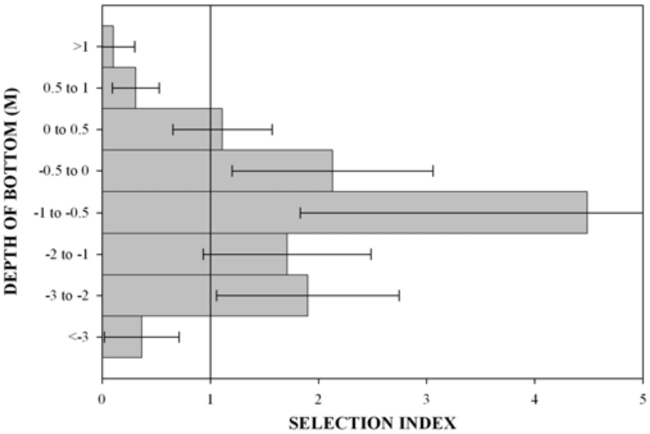
	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5
<-3	-	-	-	-	-	-
-3 to -2	NS	-	-	-	-	-
-2 to -1	NS	NS	-	-	-	-
-1 to -0.5	<0.01	<0.025	<0.01	-	-	-
-0.5 to 0	NS	NS	NS	<0.025	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.001	<0.001	-

b



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1
<-3	-	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-	-
-2 to -1	NS	<0.001	-	-	-	-	-
-1 to -0.5	<0.025	NS	NS	-	-	-	-
-0.5 to 0	NS	<0.001	NS	<0.05	-	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.001	<0.001	-	-
0.5 to 1	<0.001	<0.001	<0.001	<0.001	<0.001	p<0.01	-

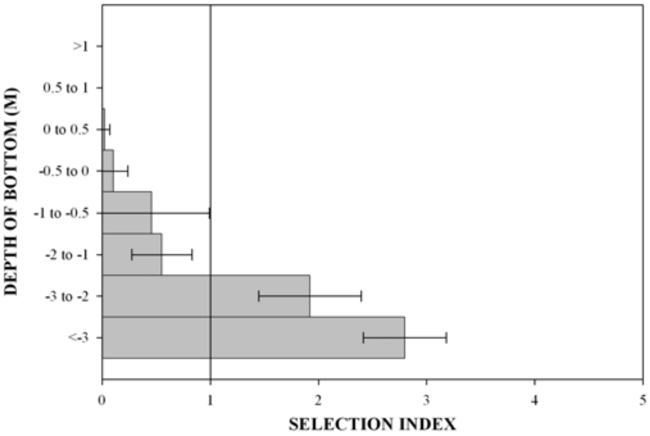
c



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1	>1
<-3	-	-	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-	-	-
-2 to -1	<0.001	NS	-	-	-	-	-	-
-1 to -0.5	<0.001	<0.01	<0.005	-	-	-	-	-
-0.5 to 0	<0.001	NS	NS	<0.025	-	-	-	-
0 to 0.5	<0.001	<0.025	<0.05	<0.001	<0.005	-	-	-
0.5 to 1	NS	<0.001	<0.001	<0.001	<0.001	<0.001	-	-
>1	NS	<0.001	<0.001	<0.001	<0.001	<0.001	NS	-

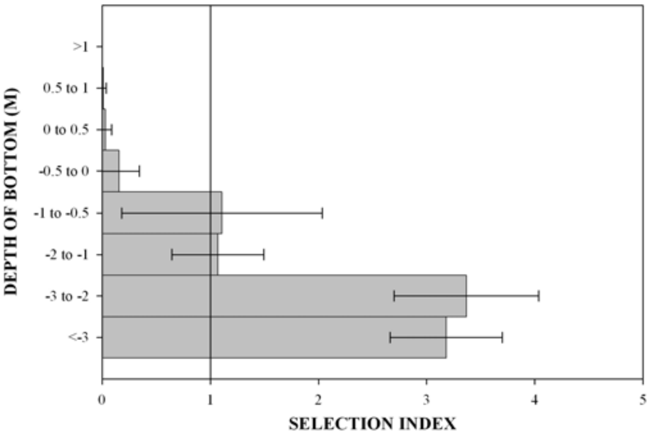
Appendix P. Selection indices (± 95% CI) and pair-wise comparisons (with p values corrected using Bonferroni correction) between habitat categories for shark 75 at (a) low, (b) intermediate, and (c) high tidal levels. Selection index values > 1 indicate selection and values < 1 indicate avoidance. A value of 1 indicates that the shark is using that habitat type in proportion to its availability.

a



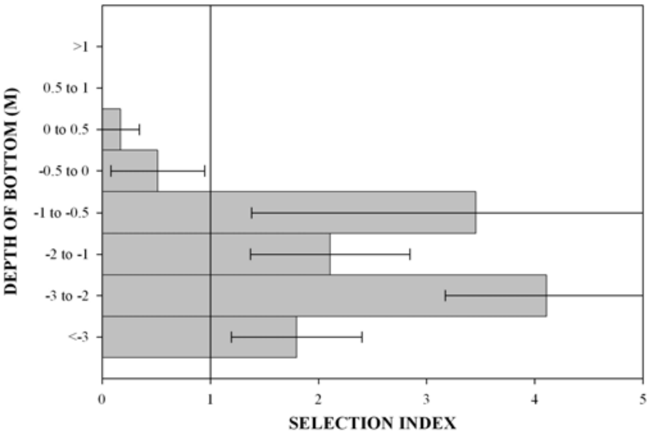
	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5
<-3	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-
-2 to -1	<0.001	<0.001	-	-	-	-
-1 to -0.5	<0.001	<0.001	NS	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	p<0.005	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.001	<0.001	-

b



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1
<-3	-	-	-	-	-	-	-
-3 to -2	NS	-	-	-	-	-	-
-2 to -1	<0.001	<0.001	-	-	-	-	-
-1 to -0.5	<0.001	<0.001	NS	-	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	<0.01	-	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.005	NS	-	-
0.5 to 1	<0.001	<0.001	<0.001	<0.005	<0.05	NS	-

c



	<-3	-3 to -2	-2 to -1	-1 to -0.5	-0.5 to 0	0 to 0.5	0.5 to 1	>1
<-3	-	-	-	-	-	-	-	-
-3 to -2	<0.001	-	-	-	-	-	-	-
-2 to -1	NS	<0.001	-	-	-	-	-	-
-1 to -0.5	<0.05	NS	NS	-	-	-	-	-
-0.5 to 0	<0.001	<0.001	<0.001	<0.001	-	-	-	-
0 to 0.5	<0.001	<0.001	<0.001	<0.001	<0.05	-	-	-
0.5 to 1	<0.001	<0.001	<0.001	<0.001	<0.005	<0.01	-	-
>1	<0.001	<0.001	<0.001	<0.001	<0.005	<0.01	NS	-