MIGRATION AND HABITAT UTILIZATION IN LAMNID SHARKS

A DISSERTATION SUBMITTED TO THE DEPARTMENT OF BIOLOGICAL SCIENCES AND THE COMMITTEE ON GRADUATE STUDIES OF STANFORD UNIVERSITY IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

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Abstract

Understanding the movements, habitat utilization, and life history of high trophic level animals is essential to understanding how ecosystems function. Furthermore, large pelagic vertebrates, including sharks, are declining globally, yet the movements and habitats of most species are unknown. A variety of satellite telemetry techniques are used to elucidate the movements and habitat utilization of two species of lamnid shark. Salmon sharks used a subarctic to subtropical niche, and undertook long distance seasonal migrations between subarctic and subtropical regions of the eastern North Pacific, exhibiting the greatest focal area behavior in the rich neritic waters off Alaska and California, and showing more transitory behaviors in pelagic waters where productivity is lower. The timing of salmon shark aggregations in both Alaska and California waters appears to correspond with life history events of an important group of prey species, Pacific salmon. The enhanced expression of excitation-contraction coupling proteins in salmon shark hearts likely underlies its ability to maintain heart function at cold temperatures and their niche expansion into subarctic seas. Adult white sharks undertake long distance seasonal migrations from the coast of California to an offshore focal area 2500 km west of the Baja Peninsula, as well as Hawaii. A full migration cycle from the coast to the offshore focal area and back was documented. During the offshore migration, white sharks frequently swam at the surface. Sharks remained in the offshore focal area for up to 167 d, where they exhibited a broad depth distribution with intensive oscillatory behavior, possibly associated with feeding or mating. Young-of-the-year sharks remained south of Point Conception whereas one three-year-old shark moved north to Point Reyes, California. All juvenile white sharks displayed a diel change in behavior, with deeper mean positions during dawn, day and dusk than during night. Juvenile white sharks are captured as bycatch in both US and Mexican waters, suggesting that management of fishing mortality should be of increased concern. The ability of lamnid sharks to undertake rapid long distance migrations is essential in enabling them to integrate the productivity of distant regions.

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1 Introduction

1.1 Endothermic fishes

In the evolution of fishes, systemic endothermy arose independently in divergent lineages. Within the teleost fishes, endothermy has evolved at least two times within the suborder Scombroidei (Block et al. 1993); while within the Chondrichthyan fishes, endothermy occurs within the Lamniformes (Carey and Teal 1969; Carey 1971; Bernal et al. 2001; Donley et al. 2004). Sharks of the family Lamnidae (Carey 1982b) comprise the white, mako, porbeagle and salmon sharks (Compagno 1984). Measurement of tissue temperatures indicate that the salmon and porbeagle sharks are the most endothermic member of the lineage (Carey and Teal 1969; Goldman et al. 2004). The Alopiidae (thresher sharks) are closely related to the Lamnidae (Naylor et al. 1997) and some species possess specializations to retain metabolic heat in the cranial regions (Block and Carey 1985; Tubbesing and Block 2000; Weng and Block 2004) and slow-twitch swimming muscles (Carey 1982b). In both teleosts and sharks, the orders that contain warm fishes also have sister taxa that are ectothermic, offering a unique system for the comparative study of the evolution and ecology of endothermy.

The lamnid sharks are among the largest predatory sharks, and exceed other elasmobranchs in their trophic level (Froese and Pauly 2002), metabolic rates (Graham et al. 1990), swimming speeds (Carey and Teal 1969) and geographic distributions. The remarkable capability of lamnid sharks to maintain oxidative tissue temperatures above ambient (Carey and Teal 1969; Carey et al. 1985; Goldman et al. 2004) has been proposed as a key physiological feature underlying the group's dominant ecological position in the world's oceans.

The biology of lamnid and alopid sharks has been challenging to study. Most of our knowledge is based on the study of dead specimens, fishery data and short term or local scale observations of sharks (Burne 1924; Strasburg 1958; Carey et al. 1982; Klimley 1985; Klimley et al. 2002). Fisheries-based studies typically measure the occurrence of sharks in relation to sea surface temperature (Strasburg 1958; Nakano

and Nagasawa 1996) so the exact thermal environment experienced by the animals remains unknown. The locations of breeding areas and pupping locations are little known for these species (Compagno 1984; Pardini et al. 2001).

The use of new electronic tagging technologies to track pelagic animals has yielded numerous insights into the biology of animals such as Atlantic and Pacific bluefin tunas (Block et al. 2001; Inagake et al. 2001), elephant seals (DeLong et al. 1992; Le Boeuf 1994) and marine birds (Weimerskirch et al. 1995; Tuck et al. 1999; Weimerskirch et al. 2002). Deployments of electronic tags on lamnid and alopid sharks have already produced surprising revelations (Boustany et al. 2002; Goldman et al. 2004; Bonfil et al. 2005; Weng et al. 2005; Bruce et al. 2006; Domeier and Nasby-Lucas 2006). Enhanced knowledge of the long-range movements and aggregation areas of these species will improve our understanding of their life history, and of their relations to the physical and biotic environment.

1.2 The phylogeny of the order Lamniformes

The order Lamniformes are in the class Chondrithchthyes (cartilaginous fishes) and in the superorder Galeomorphii, which also contains the orders Heterdontiformes (bullhead sharks), Orectolobiformes (carpet sharks) and Carcharhiniformes (ground sharks) (Compagno 1999). The Lamniformes are represented by seven living families of sharks (Compagno 1999): the goblin sharks (*Mitsukurinidae*), the sand tiger sharks (*Odontaspididae*), the crocodile sharks (*Pseudocarchariidae*), the megamouth sharks (*Megachasmidae*), the thresher sharks (*Alopiidae*), the basking sharks (*Centorhinidae*) and the mackerel sharks (*Lamnidae*). The oldest fossils of the Lamniformes have been found in the lower Cretaceous, and are 124 to 140 million years old (Maisey 1984; Cappetta 1987). Present day lamniforms appear to be a relict of a much greater diversity that peaked in the upper Cretaceous and has gone through a number of contractions, and are therefore derived from divergent lineages (Naylor et al. 1997).

The present understanding of the phylogeny of the Lamniformes is drawn from paleontological, morphological and molecular investigations (Figure 1-1). There is currently debate about the relationships within this group. Morphological (Compagno 1990) and molecular (Naylor et al. 1997) evidence indicates that *Cetorhinidae* (a

monotypic family containing the basking shark), among the largest of extant elasmobranchs, is the sister taxa to the Lamnidae. Paleontological and morphological investigations suggest the family Alopiidae is the sister group (Maisey 1984); (Compagno 1990).

1.3 The biology of lamnid sharks

The sharks of the family Lamnidae are apex pelagic predators occupying ranges throughout the polar, temperate and tropical oceans (Castro 1983). The extant members of the Lamnidae are the shortfin mako shark (Isurus oxyrhincus), the longfin mako shark (Isurus paucus), the white shark (Carcharodon carcharias), the salmon shark (Lamna ditropis) and the porbeagle shark (Lamna nasus) (Compagno 1984). The lamnid sharks possess the striking ability to maintain warm body temperatures (Carey and Teal 1969) and their endothermy may underlie many of their ecological traits, including long distance migrations (Casey and Kohler 1990), wide thermal tolerance (Carey et al. 1982; Nagasawa 1998; Goldman et al. 2004), high performance swimming (Carey and Teal 1969; Graham et al. 1990) and trophic specializations on large, fast prey species (Tricas 1985; Nagasawa 1998). The alopid sharks are closely related to the lamnid sharks (Compagno 1990; Naylor et al. 1997), and the family contains three species, the common thresher (Alopias vulpinus), the pelagic thresher (Alopias pelagicus) and the bigeye thresher (Alopias superciliosus). They occupy pelagic, neritic, and occasionally shallow coastal waters throughout the tropics and subtropics (Gruber and Compagno 1981; Castro 1983).

Based on the extent of anatomical specialization and the elevation of oxidative tissue temperatures measured in freshly captured specimens, (Carey et al. 1985) ranked *Lamna* as the most endothermic genus, followed by *Carcharodon* then *Isurus*. The latitudinal distributions of the lamnids follow a consistent pattern, with the two *Lamna* species occupying the highest latitudes and *Carcharodon* and *Isurus* occupying warmer ranges (Compagno 1984).

1.3.1 Lamna

The salmon shark, *Lamna ditropis* (Hubbs and Follett, 1947), is the least studied of the sharks of the family Lamnidae (Anderson and Goldman 2001). It reaches over 3 m in length, has a stout body, short snout, conical teeth with cusplets, secondary caudal keels, and blotches on the ventral surface (Compagno 1984). The external morphology of the salmon shark is partially described (Nakaya 1971) and its cranial vascular anatomy has been examined (Tubbesing and Block 2000). Fecundity, development and growth have been investigated (Paust and Smith 1986; Nagasawa 1998) and its population abundance estimated in the western Pacific (Shuntov et al. 1993b; Shuntov et al. 1993a; Nagasawa 1998). Although the name salmon shark implies that it forages on salmon, studies of the gut contents indicate that they feed on a varied diet of Pacific salmon, herring, squid and a variety of benthic fishes (Sano 1960; Paust and Smith 1986; Nagasawa 1998).

Salmon sharks have been captured over much of the north Pacific (Strasburg 1958; Nakano and Nagasawa 1996; McKinnell and Seki 1998) and have been observed between 65 °N (Compagno 1984) and 35 °N (Strasburg 1958). Limited conventional tagging has been conducted for the salmon shark with a small number of short term, local recaptures (Nagasawa 1998). Salmon sharks can maintain temperature elevations up to 21°C in the body core (Goldman et al. 2004). Fishery, acoustic and electronic tagging studies show occupancy in waters between 3.5 and 22 °C and long distance movements within the Pacific Ocean (Strasburg 1958; Neave and Hanavan 1960; Nakano and Nagasawa 1996; Nagasawa 1998; Hulbert 2005; Weng et al. 2005).

Areas of parturition and nursery have been inferred from the capture of near-term pregnant females and juveniles. Young of the year salmon sharks and pregnant females are found in the waters of northern Japan (Nagasawa 1998) and California (Goldman and Musick, unpublished), indicating the existence of at least two pupping areas. Juveniles are found across the north Pacific in a band to the north of the

subarctic boundary (40-45°N) suggesting a large nursery area (Nakano and Nagasawa 1996).

1.3.2 Carcharodon

The white shark, *Carcharodon carcharias* (Linnaeus, 1758), grows to over 6m, has a stout body, a long snout, flat, wide, serrated teeth and a single caudal keel on each side (Compagno 1984). White sharks live in warmer waters than Lamna and range through temperate and tropical waters (Compagno 1984). Recent satellite tracking results show oceanic residency for up to half the year (Boustany et al. 2002). The white shark has been captured up to 52 °N (Pike 1962) and in tropical waters (Compagno 1984). Local-scale movements, feeding behaviors and predator-prey relations have been documented for the white shark (Tricas and McCosker 1984; Strong et al. 1992; Anderson and Goldman 1996; Long 1996; Long et al. 1996; Pyle et al. 1999; Klimley et al. 2001a; Klimley et al. 2001b). The white shark feeds on both fishes and marine mammals (Compagno 1984; Tricas and McCosker 1984). Aggregations of white sharks near pinniped colonies have been documented in a number of areas, including northern California (Ainley et al. 1985; Klimley 1985; Goldman and Anderson 1999), southern Australia (Bruce 1992), eastern Canada (Brodie and Beck 1983) and South Africa (Ferreira and Ferreira 1996).

The limited data obtained to date using electronic tagging suggest that white sharks occupy waters with sea surface temperatures ranging from 4 to 25 °C (Lowe and Goldman 2001; Boustany et al. 2002) and frequently swim in the thermocline (Carey et al. 1982). A long term track obtained using a pop-up satellite tag shows that a white shark spent a third of the day below 300 m and experienced temperatures as cool as 4.8 °C, demonstrating an ability to inhabit cold waters for extended periods (Boustany et al. 2002). The white shark has deep muscle temperature elevations of up to 5°C (Carey et al. 1982) and an average stomach temperature elevation of 10.8°C in 15 to 18°C waters (Carey et al. 1982; McCosker 1987; Goldman 1997).

The majority of white shark acoustic tracking studies are short-term, local-scale studies necessitated by the limitations of acoustic tracking (McCosker 1987; Strong et

al. 1992; Goldman 1997; Klimley et al. 2001a; Klimley et al. 2002). Conventional tagging studies are few (Casey and Kohler 1990; Bruce 1992; Strong et al. 1992; Strong et al. 1996; Kohler and Turner 2001) and have recorded one movement greater than 1000 km (Kohler and Turner 2001). The presence of white sharks in near-shore areas is strongly seasonal, but little information exists regarding where they are during the rest of the year.

Recent satellite telemetry studies of white sharks have revealed surprising movements and an enormous geographic range. Boustany et al. (2002) demonstrated that white sharks tracked from the central California coast moved into an offshore region between Hawaii and Baja, as well as to the Hawaiian Islands. Bonfil et al. (2005) reported a transoceanic migration from South Africa to western Australia and back, as well as fine-scale coastal movements in South Africa and Mozambique. Bruce et al. (2006) showed that white sharks make long distance movements along the west, south and east coasts of the Australian continent, and reported one shark moving from South Australia to the north island of New Zealand.

Breeding, pupping and population structure are unknown for the white shark. The long range movements of white sharks evident from recent electronic tagging studies (Boustany et al. 2002; Bruce et al. 2006; Domeier and Nasby-Lucas 2006) raises the possibility that distant coastal populations may actually be part of basin-scale metapopulations. Genetic evidence from maternally-inherited markers has suggested that males disperse over much greater areas that females (Pardini et al. 2001). Size segregation in fishery captures of white sharks in California has led to the hypothesis that pupping occurs south of Point Conception, and that sharks move north of Point Conception upon reaching about 1.7 m in total length (Klimley 1985) but no direct evidence of pupping or breeding has been found.

1.3.3 Isurus

The shortfin mako shark, *Isurus oxyrinchus* (Rafinesque, 1809) grows to 4 m, has a spindle-shaped body, long conical snout, blade-like teeth without serrations or cusplets, and a single long caudal keel (Compagno 1984). It has a worldwide pelagic distribution in temperate and tropical seas (Garrick 1967). The shortfin mako feeds on

pelagic and demersal fishes including scombrids and sharks, with lesser portions of squid, turtles and mammals (Stillwell and Kohler 1982; Compagno 1984; Vaske-Junior and Rincon-Filho 1998). Genetic data suggest a worldwide panmictic stock for the shortfin mako (Heist et al. 1996). Shortfin mako sharks have been acoustically tracked showing adult occupancy of waters ranging from 9 to 24 °C, a preference for the thermocline (Carey et al. 1981; Klimley et al. 2002) and less diving behavior than white sharks, reaching 500 m and 13 °C (Carey and Scharold 1990; Klimley et al. 2002; Sepulveda et al. 2004). Acoustic tracking of the shortfin mako showed stomach temperature elevations of up to 8 °C in waters of 17 °C (Carey et al. 1981) and 4 to 10°C in water temperatures of 11 to 27°C, with higher temperature elevations in cooler waters (Carey and Teal 1969).

1.4 Endothermy

1.4.1 Endothermy in distant lineages

Endothermy has evolved independently numerous times in vertebrates. Mammals, birds and some fishes share the ability to maintain warm body temperatures via elevations in metabolism coupled with reductions in conductance (Bennett 1979; Block *et al.* 1993). Some reptiles, insects and plants are capable of periods of thermogenesis that elevate body temperatures (Nagy et al. 1972; Van Mierop and Barnard 1978; Bennett 1979; Heinrich 1987; Slip and Shine 1988; Paladino et al. 1990; Block et al. 1993). All mammals and birds are endothermic, but in other vertebrates the condition is extremely rare due to the high metabolic expense, and the challenges of reducing heat loss to the environment. In the birds and mammals endothermy is a primitive trait, so there are no living outgroups that can be used in comparative studies of endothermy. In fishes, endothermy is a derived trait, offering systems in which comparative studies can be conducted using living species (Block et al. 1993; Block and Finnerty 1994). Endothermy in fishes evolved independently in elasmobranchs and teleosts, lineages that last shared an ancestor in the Silurian, more than 400 million years ago (Carroll 1988). An endothermic animal derives most of its heat content from metabolism rather than from the environment, while an ectotherm's thermal budget is dominated by heat flux between the body and the environment (Withers 1992). In an endothermic animal metabolic heat production is high enough, and conductance low enough, to raise body temperature above that of the environment at steady state. Ectotherms are in thermal equilibrium with the environment at steady state. At the cellular level all endotherms have higher oxidative demand per gram of tissue than ectotherms (Else and Hulbert 1985). Ectotherms and endotherms both regulate their body temperatures via behavioral and vascular adjustments. Endotherms, in general, have evolved more sophisticated mechanisms (blubber, fur, fat) for reducing whole body conductance.

Endothermy has profound consequences for the thermoregulatory capabilities of animals, and the physical mechanism of thermoregulation is different for endotherms and ectotherms. Endotherms can regulate body temperature both by changing metabolic heat production and by changing conductance (Withers 1992). Ectotherms can regulate body temperature only by moving to more favorable thermal environments. Hence, endotherms can maintain thermal excess at steady state, while ectotherms cannot.

The strategies used by different taxa to achieve endothermy vary in the relative contributions of elevated metabolic rate and reduced conductance. All endothermic vertebrates have specializations to reduce conductance, via fur, feathers, blubber or counter-current heat exchangers, but some taxa have much greater elevations of aerobic capacity and metabolic rate than others. Mammals and birds have elevated aerobic capacity and metabolic rates three to ten times greater than reptiles of similar body mass (Crompton et al. 1978; Bennett 1979; Block 1991; Hayes and Garland 1995). Tunas have metabolic rates two to three times that of similar sized fishes (Dewar and Graham 1994). In contrast to birds and mammals, the leatherback turtle has only a modest increase in metabolic rate over similar ectotherms, while its great size and circulatory specializations confer a very low conductance (Frair et al. 1972; Paladino et al. 1990).

1.4.2 Endothermy in fishes

The major differences in vascular architecture between endothermic and ectothermic fishes caught the attention of early researchers, but the connection between these features and elevated body temperatures was not made immediately. The existence of *retia mirabilia* in tunas and lamnid sharks has been known since 1835 when (Eschricht and Muller 1835) published a detailed study of these structures in bluefin tuna (*Thunnus thynnus*), and a brief description of the suprahepatic and orbital *retia* in the porbeagle shark. Fishermen have long known that tunas are warm and (Davy 1835) published information revealing the temperature elevation in recently killed specimens of a variety of species, but the link between *retia* and warmth was not evident at this time. (Burne 1924) presented an in-depth description of the vascular anatomy of the porbeagle shark that included descriptions of structures in the muscle, viscera, cranial cavity and kidney. Simultaneously (Kishinouye 1923) provided a detailed description of the counter-current heat exchangers and vascular anatomy in the Thunnini and proposed a connection between retia and above-ambient body temperatures. (Carey and Teal 1969) were the first to make accurate measurements of body temperatures in lamnid sharks and proposed that the countercurrent heat exchangers are integral to the rentention of metaoblic heat observed in various body tissues.

Endothermic teleosts fall within one suborder, the Scombroidei, containing billfishes and tunas. Systemic and cranial endothermy are recognized as distinct forms of endothermy in fishes, and each has evolved independently in different lineages (Carey 1982b; Block et al. 1993; Block 1994; Block and Finnerty 1994). Systemic endothermy exists only in the Thunnini (*Thunnus, Euthynnus* and *Allothunnus*), involving elevation of metabolic rate, centralized slow-twitch muscle and the presence of *retia mirabilia* associated with the viscera, oxidative muscles and cranial circulation (Eschricht and Muller 1835; Carey and Teal 1966; Freund 1999). Cranial endothermy is hypothesized to have evolved independently in the billfishes (Xiphidae, Istiophoridae) and the scombrid butterfly mackerel, *Gastrochisma* (Block et al. 1993). Elevation of temperature above ambient has been measured in the brain, viscera and

muscles of scombrids (Davy 1835; Carey 1971; Linthicum and Carey 1972; Carey and Lawson 1973; Graham 1975; Carey 1982b) and in the eyes and brains of billfishes (Carey 1982a; Block 1983).

Among the class Chondrichthyes, anatomical specializations that reduce whole body thermal conductance are present in the Lamniformes (Lamnidae, Alopiidae) and possibly Myliobatiformes (Mobulidae, devil rays). Elevated body temperatures occur in the lamnid sharks, which have centralized slow-twitch muscles, and retia associated with the slow-twitch muscles, viscera and crania (Burne 1924; Carey and Teal 1969). Elevation of body temperature in tissues including the brain, viscera and slow-twitch muscle has been demonstrated in white sharks, shortfin mako, longfin mako, porbeagle and salmon sharks (Carey et al. 1981; Carey et al. 1982; Block and Carey 1985; Carey et al. 1985; Tubbesing and Block 2000; Anderson and Goldman 2001). Cranial endothermy is indicated by the presence of orbital *retia mirabilia* in the alopid sharks (Carey 1982b; Weng and Block 2004) and the mobulid rays (Schweitzer and Notarbartolo Di Sciara 1986; Alexander 1995; Alexander 1996), though measurements of cranial temperature have not been made. The alopid sharks may show limited systemic endothermy, based on centralization of slow-twitch muscle, the presence of rudimentary muscle retia (Carey 1982b; Bone and Chubb 1983) and the measurement of a 4°C temperature elevation in centralized slow-oxidative muscle for one freshly killed specimen (Carey 1971). Further studies of the anatomy and physiology of the Alopiidae are needed to understand the nature of endothermy in this group. They may represent the first stages toward the more complete Lamniform condition.

The benefits of endothermy in fishes are thought to include increased mechanical power in warm muscle tissues (Altringham and Block 1997), accelerated digestion in warm viscera (Carey et al. 1984), and buffering from ambient temperature change (Carey et al. 1985). Body temperatures that are buffered from ambient temperature fluctuations allow enzymes to be optimized to a narrower temperature range (Hochachka and Somero 1984) and maintain consistent function of visual and neural systems (Konishi and Hickman 1964; Friedlander et al. 1976; Prosser and Nelson

1981). Systemic and cranial endotherms appear to dive rapidly through the thermocline or occupy cool waters for extended periods of time (Carey and Robison 1981; Holland et al. 1992; Block et al. 1993; Gunn and Block 2001) and this ability may be advantageous in accessing deeper prey resources, extending search volume, or in entering productive high latitude regions.

1.4.3 Cardiac function

In a review of cardiac function across fish species, Farrell (1991) stated a general rule that cardiac output, the product of heart rate and stroke volume, is primarily volume-modulated in fishes and frequency-modulated in mammals. The author noted that tunas, the high performance teleosts, break this rule and have mammal-like cardiac qualities, with their large frequency range and exceptional maximal heart rates. The enhanced cardiac function of tunas may underlie their ability to occupy both cold and warm water habitats and make rapid vertical excursions through the thermocline. Studies of cardiac performance in lamnid sharks are few, and it is not known if their hearts are similarly specialized for high heart rates.

High cardiac capacity in mammalian and tuna hearts and lesser performance in the hearts of lower vertebrates is related primarily to mechanisms of cardiac calcium cycling (Shiels et al. 2002, Landeiera et al. 2004). Reptiles, amphibians and most teleost fishes rely primarily on extracellular calcium stores in cardiac muscle to bring about contraction of the myofibrillar apparatus, and it is the low rate of calcium flux that is thought to keep heart rates low in ectothermic fishes (Farrell 1991; Blank et al. 2002). A key specialization for high heart rates in mammals is the use of internal calcium stores in the sarcoplasmic reticulum (SR) of cardiac myocytes (Bers 2002). Extracellular calcium entering the cells induces these SR stores to release (calciuminduced calcium release), such that contraction occurs sooner. Relaxation is accelerated due to the reduced diffusion distances to the internal stores. Some coldadapted fishes have SR calcium stores that may help to maintain cardiac output at low temperatures (Tiitu and Vornanen 2002). Recent work in our laboratory has identified SR calcium stores in tuna myocytes, providing a mechanism for high maximal heart rates (Freund 1999; Blank et al. 2002; Shiels et al. 2002; Blank et al. 2004; Landeira-

Fernandez et al. 2004). The lamnid sharks are considered to be the high performance elasmobranchs, but no study has examined the role of internal calcium stores in cardiac myocyte function.

Specializations that enhance maximal heart rates may provide clues as to how lamnid sharks and tunas maintain cardiac output through large changes in ambient temperature (Brill and Bushnell 2001; Blank et al. 2002). Heart rate decreases as heart tissue temperature falls (Farrell 1991; Brill and Bushnell 2001; Blank et al. 2002; Blank et al. 2004), and in all fishes, including lamnid sharks and tunas, heart temperature is tightly coupled to ambient temperature. Blood passing through the gills comes to complete thermal equilibrium with ambient water due to the high surface area of blood vessels (Stevens and Sutterlin 1976), and this blood then enters the cardiac circulation without passing through any *retia* (Carey et al. 1981). When an ectothermic fish enters cooler waters, the oxygen demand of its body falls along with heart rate. When an endothermic fish enters cooler waters its heart rate falls due to cold induced bradycardia, while the oxygen demands of its tissues remain relatively constant, presenting a paradox as to how the heart maintains oxygen delivery (Blank et al. 2002; Morrissette et al. 2002; Blank et al. 2004; Landeira-Fernandez et al. 2004). Warm temperatures may also challenge the ability of an endothermic fish to delivery adequate oxygen, because stroke volume decreases and high heart rates occur that may be difficult to sustain. In both cold and warm waters, enhanced calcium cycling machinery in the myocytes could maintain cardiac output.

1.4.4 The evolution of endothermy

Research into the evolution of endothermy in vertebrates has highlighted a number of hypotheses regarding the selective pressures that drove it, among the most prominent being selection for increased aerobic capacity (Bennett 1979) and niche expansion (Crompton et al. 1978; Bennett 1979). While less information is available for sharks, it appears that the evolution of endothermy may have occurred differently in this lineage than in mammals, birds and tunas, with large body size being a precursor to other endothermic traits.

The aerobic capacity hypothesis (Bennett 1979) states that pressure for higher sustained locomotion speeds resulted in selection for higher maximum oxygen use and delivery (VO_2) in the form of greater lung surface area, higher blood pressure, more hemoglobin and more mitochondria. A key assumption of the aerobic capacity hypothesis is that VO_2 and basal metabolic rate (BMR) are somehow intrinsically linked, such that BMR rose in consequence to selection for higher VO_2 . The benefits of increased endurance, such as competitiveness in foraging, predation, escape and mating, co-occurred with these specializations, such that they were favored by natural selection. Thus, higher metabolic rate was a preadaptation that enabled the later development of endothermy.

The niche expansion hypothesis (Crompton et al. 1978) states that ectothermic terrestrial animals became torpid and less active at night as temperatures dropped, leaving a vacant nocturnal niche.

Animals with the ability to maintain body temperatures slightly higher than nocturnal temperatures (25 to 30 °C) were able to invade this niche. It is critical to note that the niche expansion hypothesis is founded upon the thermoregulatory hypothesis; that gradual or incremental increases in metabolic rate led to increases in body temperature and enabled independence of body temperature from ambient temperature via changes in heating and cooling rates. More constant body temperatures allowed benefits such as temperature-optimized enzyme activity, consistent neural and visual performance or thermal niche expansion.

Block *et al.* (1993) used the phylogeny of scombroids to perform a comparative analysis of the evolution of traits associated with endothermy in this lineage, finding that the evolution of systemic endothermy in tunas was preceded by elevated aerobic capacity (Block and Finnerty 1994; Freund 1999). Studies of citrate synthase in sharks suggest that aerobic capacity is not elevated in slow-twitch muscles of lamnids as compared to active ectothermic sharks (Dickson et al. 1993). Since slow-oxidative swimming muscles are presumably the major source of metabolic heat, lamnid endothermy may not be consistent with the aerobic capacity hypothesis of Bennett

(1979). Hence, factors that reduce conductance may have set the stage for endothermy in this group. Increased body size makes ectothermic fishes more resilient to changes in ambient temperature (Frair et al. 1972; McGowan 1979; Carey 1982b; Carey and Gibson 1987) and large ectothermic sharks have been shown to alter thermal conductivity during dives into cold water, presumably by reducing blood flow to the periphery (Carey and Scharold 1990; Block 1991).

A selective pressure may favor traits that are preadaptations to different traits for which no selective mechanism exists. This mechanism is invoked to explain mammalian endothermy by Bennett *et al.* (1979) by supposing that selection for faster locomotion favored traits that later facilitated endothermy. In the *Thunnus* lineage the centralization of red muscle may have occurred in response to selection for a thunniform swimming mode, but preadapted these species for endothermy by centralizing a major metabolic heat source (Block 1991; Block and Finnerty 1994). Similarly, large body size may have been under selection in the ancestors of lamnid sharks due to increases in prey size. The low conductance of a large body may have facilitated the evolution of mechanisms for reducing conductivity, such as the insertion of counter-current heat exchangers into the cranial circulation. Comparisons of the endothermic capacities of juvenile and adult lamnid sharks will reveal whether large body size is a necessary component of lamnid endothermy.

1.5 Electronic tagging technologies

The ability to examine the biology of large pelagic animals has been rapidly enhanced by the recent development of electronic tagging and tracking technologies (reviewed in Block and Gunn, 2001). Archival tags log data on-board and must be physically recovered in order to retrieve the data. Electronic tags that transmit data to satellites allow the tracking of species that are difficult to recapture, and are ideal for the study of large, rare animals such as pelagic sharks. Satellite-based tags were originally developed for the study of air breathing animals such as birds (Jouventin et al. 1994), turtles (Renaud and Carpenter 1994; Polovina et al. 2000) and marine mammals (McConnell et al. 1992b) since the antenna of the tag must be exposed in air to transmit to a satellite. Only recently have these technologies been applied to the

study of fishes (Block et al. 2001; Boustany et al. 2002; Goldman et al. 2004; Block et al. 2005; Hulbert 2005; Bruce et al. 2006; Domeier and Nasby-Lucas 2006).

Species that spend time at the surface can be tracked with tags that transmit to satellites while attached to the animal, allowing near real-time tracking and data recovery. The present study is using a satellite tag that can be attached to the first dorsal fin of a shark (SPOT2–4, Wildlife Computers). The SPOT tag can transmit position and temperature data (but not depth) when it is exposed in air, as determined by a conductivity switch.

The pop-up satellite archival tag (PSAT) was developed for pelagic fishes that do not spend significant time at the surface and cannot be tracked via radio transmissions to satellites. The PSAT gathers depth, ambient temperature and light data, remaining attached to the fish for a preprogrammed duration, then electolytically corrodes a metal link to release from the animal and float to the surface (Block et al. 1998a). Data are not received during the track, but are transmitted in summary form to the Argos system after the tag floats to the surface. Data on the animal's behavior and environment are collected by the tag, summarized, and transmitted to the laboratory via the Argos satellite system.

The light measurements taken by electronic tags can be used to estimate geoposition, which was first accomplished in the tracking of elephant seals (DeLong et al. 1992; Hill 1994). The current techniques for light-based geolocation have been greatly improved for tracking fishes. Longitude is estimated for each day by converting light curves into estimates for local noon or midnight (Ekstrom 2002; Hill and Braun 2002). Latitude is estimated by comparing sea surface temperature measured by the tag with that measured by satellite sensors, along the light-based longitude estimation (Teo et al. 2004). Light-based geolocation provides daily positions with errors on the order of 100 km (DeLong et al. 1992; Gunn et al. 1994; Block et al. 1998b; Welch and Eveson 1999; Musyl et al. 2001; Teo et al. 2004). Errors in light-based geolocation for free-ranging pelagic fishes have been quantified in double-tagging studies using PSAT and SPOT tags (Teo et al. 2004). The Argos position obtained from the SPOT tag was compared to the light- and temperature-

based position for the same day, over multiple days and multiple animals, to obtain error estimates.

The Argos system comprises modules attached to the NOAA polar-orbiting weather satellites that receive transmissions from satellite tags, earth receiving stations that accept data from satellite modules, and Service Argos processing centers that distribute data to users via the Internet. The geoposition of a satellite tag is estimated based on the Doppler shift of tag's radio frequency as the satellite flies overhead. As a satellite approaches the tag, the frequency it receives is higher than the tag's transmitted frequency, and when the satellite has passed overhead and is moving away from the tag, the received frequency is lower. Location quality codes are provided with stated RMS errors of: quality 3, <150 m; quality 2, <350 m; quality 1, <1000 m; and qualities 0, A, B, no accuracy provided. Independent studies published in the literature have provided route mean square error estimates for Argos positions, averaging 7.5 km for location quality B and lower errors for better location qualities (Hays et al. 2001; Vincent et al. 2002).

In this study, I use a variety of electronic tagging technologies and synoptic oceanographic tools to elucidate the spatial and physiological ecology of two lamnid shark species. By measuring the breadth of the spatial and thermal niches of these organisms, while also investigating their physiological adaptations to cold and high cardiac performance, we will better understand how they are able to undertake their wide-ranging ecological strategies. We must know the habitat utilization and movements of these upper trophic level organisms in order to understand their roles in marine ecosystems, and the cascading effects that large changes in their populations via fisheries and other anthropogenic factors may have. Specific knowledge of distribution, movement and behavior will also allow more effective management and conservation of these species, one of which, the white shark, is thought to be threatened. Furthermore, by understanding how these organisms utilize the diverse oceanographic environment, we will improve our ability to anticipate changes in the face of environmental variation.

The findings of the thesis are organized in the central four chapters. In chapter two I document the long distance seasonal migrations of salmon sharks, together with their specializations in cardiac physiology. In chapter three I show that adult and subadult white sharks utilize both neritic and pelagic waters on a predictable, seasonal basis, foraging while nearshore and potentially giving birth or mating while in an oligotrophic offshore aggregation area. In chapter four I show, through studies of juvenile white sharks, that both thermal niche and geographic range increase ontogenetically in this species, and that juveniles may move latitudinally with the seasons to avoid cold temperatures. In chapter five I revisit the migration cycle of salmon sharks, demonstrating that movements occur seasonally but not for the purpose of avoiding cold winters, and that the regions of the ocean utilized most intensively have the highest productivity.



Figure 1-1 Phylogeny of the order Lamniformes.

Maisey (1984) used paleontological data, concluding that the Lamnidae and Alopiidae are sister clades. Compagno (1990) used morphological studies of living lamniforms, finding that *Cetorhinus*, the basking shark, is closest to the Lamnidae, with the alopids being the next clade. Naylor *et al.*'s (1997) genetic study agrees with Compagno in most respects, although the molecular tree is poorly resolved.
2 Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks¹

2.1 Introduction

Sharks are threatened by fishing around the world (Stevens et al. 2000) and biological knowledge is urgently needed to design management strategies. Sharks have been tracked using short-term acoustic telemetry (Carey et al. 1982) and towed satellite tags on large, slow moving basking and whale sharks (Priede 1984; Eckert and Stewart 2001). Pop-up satellite archival tags (PAT) have been used to track sharks, however geolocations have root mean square errors of 0.89° of longitude and 1.47° of latitude (Boustany et al. 2002; Sims et al. 2003; Teo et al. 2004). In this study, we use a Smart Position Only Tag (SPOT), designed with a small Argos transmitter that permits direct attachment to the shark's dorsal fin (Figure 2-1). This tag enables the tracking of sharks with near real-time positions for multiple years (Table 2-1). SPOT tags greatly improve geopositioning for gill-breathing vertebrates as 59% of salmon shark positions have errors under one km based on Argos accuracies (Table 2-2).

2.2 Materials and methods

The movements of salmon sharks (*Lamna ditropis*) were monitored using SPOT and PAT tags (Wildlife Computers, Redmond, WA, USA). SPOT tags provided Argos geopositions and PAT tags recorded pressure, ambient temperature and light. Several hardware versions of the tags were used during the course of the experiments. In 1999 we tagged two salmon sharks with PAT1 tags. In 2002 we used the SPOT2 and PAT2 tags; in 2003 we used SPOT2, SPOT3 and PAT3 tags; and in 2004 we used SPOT4 and PAT4 tags. Accuracy and resolution of electronic tag sensors is available from the manufacturer's website (www.wildlifecomputers.com). All study animals are detailed

¹ The content of this thesis chapter is based on a published article: Weng et al. 2005, Satellite Tagging and Cardiac Physiology Reveal Niche Expansion in Salmon Sharks. Science 310: 104-106

in Table 2-1. We tagged 51 individual salmon sharks in Prince William Sound (PWS), Alaska. Twenty-one were double-tagged with SPOT and PAT; 17 with SPOT only; 10 with PAT only; and three with tags that failed to report data. A total of five tagged sharks were recaptured in PWS, two after more than a year, confirming fidelity to the region after long-distance migrations. Shark #37374 was recaptured during our 2003 research cruise after 396 days at liberty, within one km of the previous year's tagging location. The animal was re-tagged and released. Shark #41669 was recaptured near Valdez, AK after 688 days at liberty. Sharks #52136, #52143 and 52150 were recaptured after 27, 28 and 46 days at liberty, respectively, and PAT tags were recovered with complete archival records.

Salmon sharks tagged in this study averaged 233 ± 9 cm (mean \pm SD) straight total length and were mature based on size at maturity estimated for salmon sharks in the eastern North Pacific (Goldman and Musick In press). All sharks were female. In 2003, sharks were measured for curved fork length (CFL) and precaudal length (PCL) and these results were used to generate a CFL-PCL conversion equation (PCL = 0.88111 x CFL - 0.3; r² = 0.95). In other years, only CFL was measured, and the CFL-PCL conversion equation was used to estimate PCL. Total length (TL) was estimated from PCL using the equation of Nagasawa (Nagasawa 1998).

Sharks were captured from the R/V Montague and R/V Solstice in PWS, Alaska using handlines comprising a 10 mm rope, a 1.8 mm stainless steel leader covered with plastic tubing, and a circle hook. Hooks were baited with sardine, salmon or squid. Handlines were deployed directly from the research vessel or attached to polypropylene floats to control the depth of the bait. Sharks were hoisted out of the water by a stretcher deployed from the ship's crane. A soft moist cloth containing artificial anti-bacterial fish slime was placed over the eye to calm the animal and a saltwater hose was placed in the shark's mouth to irrigate the gills. The shark was restrained with straps during the period on board the vessel.

SPOT tags were attached to the dorsal fin such that the antenna and conductivity switch of the tag would be exposed in air when the animal swam at the surface. Tags were placed on the leading edge of the fin and as high up as possible while retaining

support from the fin structure. Attachments were made using small stainless steel bolts (3 mm x 40 mm) coated with plastic shrink-wrap so that no metal was in contact with the tissues of the animal. The ventral surface of the SPOT tag and the bolts were dipped in Betadine microbicide (Purdue Pharma L.P., Stamford, CT, USA) prior to attachment. Each PAT was attached to a titanium dart (59 mm x 13 mm) with a 15 cm segment of 136 kg monofilament line (300 lb test Extra-hard Hi-catch, Momoi Manufacturing, Japan). The titanium dart was dipped in Betadine and inserted into the dorsal musculature of the shark at the base of the first dorsal fin, such that the tag trailed behind the fin. A plastic loop was used to hold the tag in position and prevent interaction with the body of the shark.

For comparative purposes we tagged 27 blue sharks (*Prionace glauca*) with SPOT and PAT tags using the same methods described for salmon sharks. Blue sharks were captured from the R/V David Starr Jordan using a long line in the Southern California Bight during 2002-2004, and averaged 197 ± 23 cm (mean \pm SD) straight total length (Table 2-3).

SPOT tags transmitted to Argos satellites when the antennas were exposed to air, allowing the position of the animal to be calculated by the Argos satellite system. Argos provides error estimates for location events, which they term location classes (Anonymous 2003). Location classes 3, 2 and 1 are gives error estimates, while classes 0, A, B and Z are not rated (Table 2-2). In order to remove erroneous locations we filtered out those implying an unreasonable speed for the animal. To determine the threshold for reasonable speed, we estimated the maximum speed of sharks using only location classes 3, 2 and 1. We discarded locations that were placed near to each other in time because as the time elapsed between locations approaches zero, the speed error caused by location error approaches infinity. For animals tracked in this study, the distribution of speed as a function of elapsed time between locations is approximately level at high elapsed times, and becomes highly non-linear at elapsed times below 0.1 days. Therefore, we discarded all locations that were less than 0.1 days apart for the purposes of estimating the threshold speed. The speed threshold (1.75 m/s for salmon sharks and 1.25 m/s for blue sharks) was used to filter the entire dataset, including all

locations regardless of the elapsed time between them. All locations of class Z and those on land were discarded.

The *in situ* sea surface temperature (SST) for each salmon shark location was determined using eight-day averaged Pathfinder AVHRR satellite data obtained via the TOPP live access server, courtesy of NOAA/NESDIS/NODC. To illustrate the geographic variation in temperature experienced by blue sharks we created an average SST field for the eastern North Pacific for the duration of the tracking period (14-Jul-02 through 25-Jul-05). We used a 0.1 degree by 0.1 degree geographic grid and calculated the arithmetic mean temperature for each point, based on 8-day average Pathfinder AVHRR data provided by NOAA/NESDIS/NODC through December 31, 2004, and a comparable near real time data set from NOAA/NESDIS/OSDPD for the remainder of the period.

The habitat occupancy of salmon sharks during each meteorological season was analyzed with the kernel density method (ArcMap version 9, ESRI Inc., Redlands, CA, USA). The temporal frequency of geopositions obtained from SPOT tags varied between animals and locations, due to the coverage of the Argos system and the behavior of salmon sharks. Variations in temporal frequency of positions cause bias in the kernel density method, because locations where positions are obtained at high frequency are weighted more than those where positions are obtained at low frequency, even if the subject spent equal time in each location. To address these biases, we filtered tracks to one position per 24 hours. To account for spatial variation in the number of animals, we divided each value by the number of animals represented at that location. The resulting values were used to calculate kernel density with a smoothing radius of one degree.

PAT tags collected data at 1-minute intervals, summarized it into 12- or 24-hour bins and transmitted summary data to Argos satellites (PAT software version 1 in 1999; 2.08e in 2002; 3.01d in 2003; 4.01e in 2004; Wildlife Computers, Redmond, WA, USA). The time occupancy in each of twelve depth ranges and twelve temperature ranges was calculated on-board the tag to provide vertical and thermal distributions of habitat preference. These discrete values were used to make contour

plots of time-at-depth and time-at-temperature using MatLab (The MathWorks, Natick, MA, USA). Thermal profiles of the water column were constructed by measuring the minimum and maximum temperature at the surface, maximum depth, and six intermediate depths, for the deepest dive in each time interval. These profiles were used to create a time-series slice of the ocean along the track of the animal. Tags with 12-hour bins collected 16 points per day, while tags with 24-hr bins collected eight points per day, and transmitted PAT records yielded a total of 41,216 *in situ* measurements. The recovery of three PAT tags with 1-minute archival records yielded 193,604 *in situ* measurements of depth and temperature, such that the total number of *in situ* measurements was 234,820.

Subarctic and subtropical watermass designations were based upon the physical oceanography of the North Pacific, after Roden (1991): subarctic waters were defined as those north of the Subarctic Front where no thermocline existed, stability was low and surface temperatures were under 8°C; and subtropical waters were south of the Subtropical Front where surface and mixed layer waters exceeded 18°C, waters were thermally stratified and stability was high. Continental shelf waters of North America were defined as those less than 1000 m deep, denoted by a line on Figure 2-1and Figure 2-7.

Surface chlorophyll-a concentration was determined by comparing Argos positions for SPOT-tagged sharks with eight-day averages of chlorophyll concentration measured by the SeaWiFS sensor. Data was obtained via the TOPP live access server, courtesy of NASA/GSFC/DAAC and Orbimage Inc. Chlorophyll-a concentration was compared between three zones: the subArctic gyre (defined as waters north of 45°N), the transition zone (defined as waters between 28 and 45°N) and the subtropical gyre (defined as waters south of 28°N).

Six salmon sharks and four blue sharks were euthanized during 2002 and 2003 and samples of heart tissue obtained. Atria and ventricles were sliced into thin pieces, freeze-clamped in liquid nitrogen, and stored at -80°C. Fifteen adult Wistar rats (~300g) of both sexes were euthanized, their hearts were removed and the ventricles immediately freeze-clamped in liquid nitrogen and stored at -80°C. Heart tissues were

homogenized and microsomal fractions isolated by centrifugation (Landeira-Fernandez et al. 2004). SR Ca²⁺-ATPase (SERCA2) activity and protein expression were analyzed according to the methods of Landeira et al. (Landeira-Fernandez et al. 2004). The Ca²⁺ sensitive dye (fura-2) was used to measure microsomal Ca²⁺ uptake using a spectrofluorophotometer (Shimadzu, Japan). In addition, SR microsomal fractions were resolved on 3-12% SDS-PAGE gels for ryanodine receptor analysis or on 4-20% pre-cast Tris-Hepes-SDS polyacrylamide mini-gels (Pierce Biotechnology Inc, Rockford, IL, USA) for SERCA2 analysis. Gels were silver stained or blotted onto PVDF membranes and probed with a polyclonal antibody specific to either SERCA2 (Morrissette et al. 2003) or ryanodine receptor (Chugun et al. 2003). Densitometry was performed using NIH Image (National Institutes of Health, MD, USA). For the comparison of SERCA2 and RyR protein expression across species (Figure 2-9), we obtained mako shark (*Isurus oxyrinchus*) and white shark (*Carcharodon carcharias*) samples and used the methods described above.

2.3 Results and conclusions

The movements and behaviors of 48 salmon sharks (total length = 233 ± 9 cm, mean \pm SD) were recorded by tagging sharks in Prince William Sound (PWS), Alaska with two types of electronic tags. SPOT tags (n = 38) uplinked to Argos satellites, providing track lengths of 338 ± 37 days (mean \pm SE) and $8,605 \pm 748$ km (Figure 2-1and Figure 2-5). The longest distance traveled by an individual was 18,220 km over 640 days (shark 37380). By double tagging sharks with SPOT and PAT tags (n = 21) and by PAT tagging individuals (n = 10), we obtained 5,048 days of behavioral and environmental data (mean length 163 ± 14 days). Archival records were obtained from three sharks recaptured after tagging in the vicinity of their release location (Table 2-1). Salmon sharks provided 234,820 measurements of pressure and temperature from the surface to 832 m, demonstrating their value as platforms for oceanographic observations.

Salmon sharks undergo a striking seasonal migration from subarctic to temperate and sub-tropical regions, presumably to forage or give birth to their young (Goldman

and Musick In press) (Figure 2-1 and Figure 2-5). During summer and autumn the majority of tagged salmon sharks (all females) were foraging in PWS and the Gulf of Alaska (GOA). In winter, some sharks embarked on their migration to the subtropics while others remained in GOA waters. In spring their habitat extended as far south as Hawaii (22°N), a new record for the archipelago (J. Randall, personal communication), and from 170°W to the North American continental shelf, covering oligotrophic waters in the subtropical gyre (Figure 2-6) as well as productive waters of the California Current.

Salmon sharks have a broad thermal niche, and their subarctic winter habitat demonstrates tolerance to cold waters (Figure 2-2). Salmon sharks inhabited waters from 2-24°C, spending much of their time (68 ± 6%) in waters cooler than 10°C and 72 ± 3% of their time shallower than 50 m (Figure 2-3). Salmon sharks (n = 26) often remained in subarctic waters during winter where they occupied depths from 0-368 m in an unstratified water column (Figure 2-2) with ambient temperatures of 2-8°C. PAT tags (n = 13) showed occupancy of these waters for mean durations of 53 ± 7 days and up to 96 days (690 total days), with 98 ± 1% of the time shallower than 150 m. Periods of submergence occurred, sometimes associated with temperature inversions, causing gaps in SPOT records. Salmon sharks are known to eat salmon (Nagasawa 1998) and herring (Paust and Smith 1986). While salmon are abundant in PWS during summer and autumn, herring occur year-round (Norcross et al. 2001) and may be a prey species for sharks that overwinter. These data reveal that salmon sharks are major apex predators in Alaskan waters in all seasons and could improve ecosystem models of PWS (Hulbert 1999).

Upon migrating to the subtropical gyre salmon sharks (n = 19) encountered warmer waters (18-24°C) with increased thermal stratification (Figure 2-1 and Figure 2-2). PAT data (n = 4 averaging 43 ± 9 days) indicate distinct bimodal diving behaviors with one occupancy peak in the upper thermocline (100-200 m) at temperatures from 18-20°C, and another below the thermocline (300-500 m) in 6-8°C waters. In these warm waters salmon sharks remained submerged for long durations, possibly due to a physiological limitation, causing considerable gaps in SPOT records.

Sharks that moved into the eastern Pacific along the continental shelf (n = 12) occupied temperatures of 7-18°C and foraged from the surface to 356 m.

For comparison we tagged blue sharks (n = 27; total length 197 ± 23 cm, mean ± SD) in the eastern North Pacific (Figure 2-7 and Figure 2-8; Table 2-3), producing track lengths averaging 114 ± 14 days (2,970 total days). Blue sharks in the eastern North Pacific inhabit pelagic and neritic waters from 104-157°W and 4-37°N. Blue sharks carrying PAT tags (n = 15) spent 74 ± 6% of their time in waters of 14-27°C, with 67 ± 5% of their time above 50 m in the upper mixed layer. Blue sharks encountered sub-10°C temperatures only on brief dives beneath the thermocline, which comprised 6 ± 2% of their record (Figure 2-3). Over the range tracked, the occupancy of waters cooler than 10°C was significantly greater for salmon sharks than for blue sharks (Mann-Whitney test, W = 30.5, p = 0.001).

The distribution of salmon sharks and their prolonged occupation of sub-arctic waters indicate a capacity to sustain cardiac performance at cold temperatures. Salmon sharks are members of the family Lamnidae, renowned for their endothermic physiology (Carey et al. 1981). High metabolic rates combined with extensive counter-current heat exchangers (Carey et al. 1981) enable this species to maintain body temperatures up to 21.2°C above water temperature (Goldman et al. 2004). As in all endothermic fishes, the oxygen demands of warm, metabolically active tissues are supplied by a heart operating at ambient temperature (Brill and Bushnell 2001). We hypothesize that, as in the *Thunnus* lineage (Blank et al. 2004), an increased expression of the proteins required for excitation-contraction coupling (E-C coupling) in the heart may underlie the ability to maintain cardiac contractility in the cold. This physiological trait may be a key specialization enabling thermal and geographic niche expansion into productive subarctic seas.

We measured the activity and expression of the sarcoplasmic reticulum (SR) Ca^{2+} ATPase (SERCA2), a protein important for the maintenance of intracellular Ca^{2+} stores vital for beat-to-beat contractions. Salmon shark atrial SR vesicles have a high Ca^{2+} uptake rate, an order of magnitude greater than blue sharks (Figure 2-4). SERCA2-dependent Ca^{2+} uptake could be measured at temperatures as cold as 5°C in

salmon shark atrial and ventricular SR. Q_{10} values (15-25°C) for Ca²⁺ uptake in the atrial tissues were 2.6 ± 0.4 (mean ± SE) and 4.8 ± 0.02 for salmon shark and blue shark respectively. Ca²⁺ uptake was negligible in blue shark ventricular SR, so for comparison, we measured Ca²⁺ uptake rates in rat ventricular SR. At temperatures below 25°C, the activity of the SERCA2 enzyme in salmon shark ventricle microsomes was equivalent to that of rat ventricle. Activity dropped below that of the rat vesicles above 25°C. Q₁₀ values (15-25°C) of ~3.3 for Ca²⁺ uptake in ventricular tissues were similar in salmon shark and rat.

Analysis of SR protein content showed high expression of SERCA2 and SR Ca²⁺ release channel (RyR2) proteins in salmon shark cardiac tissues (Figure 2-4 inset), and in other sharks of the family Lamnidae (Figure 2-9). Densitometry indicated a 1.29 ± 0.72 fold greater SERCA2 expression in rat ventricle compared to salmon shark ventricle. The cold tolerance of salmon sharks may be directly related to this increased expression of SERCA2 and RyR2, which are crucial for maintaining rhythmic contractions, cardiac output and oxygenation of endothermic tissues.

Direct satellite telemetry from the dorsal fins of sharks reveals subarctic to subtropical migrations of salmon sharks over multiple years. The species' cardiac specializations and endothermy underlie its remarkable capacity to occupy a subarctic niche. Satellite tracking technologies can be used to rapidly map shark habitats worldwide, which is critical to their future protection.

	Length ¹	Tagging	SPOT	SPOT	Track	PAT Tag	Popup Date	e Lat	Lon	PAT days
	(cm)	Dale	rag	Days	(km)					
1	240	25-Jul-99			(iuii)	99-044	23-Oct-99	60.51	60.63	91
2	230	24-Jul-99				99-047	26-Sep-99	-146.90) -146.42	64
3	232	17-Jul-02	37374 ²	453	5672	03-163	DNR ³			
4	236	16-Jul-02	37375	486	15929	00-1002	13-Jan-03	57.32	-133.67	181
5	214	14-Jul-02	37376	248	12649	00-885	14-Nov-02	41.65	-124.92	123
6	219	17-Jul-02	37377	1078	10755					
7	234	15-Jul-02	37378	723	10940	00-1004	13-Jan-03	60.79	-146.69	182
8	230	16-Jul-02	37379	220	4196					
9	236	17-Jul-02	37380	640	18220	01-040	DNR			
10)225	14-Jul-02	37381	184	9123	00-775	15-Sep-02	41.66	-124.91	63
11	244	17-Jul-02	37382	620	14691					
12	2226	15-Jul-02	37383	338	10282	00-931	DNR			
13	3232	17-Jul-02				00-767	15-Sep-02	60.49	-147.00	60
14	227	18-Aug-03	41663	355	9396					
15	5219	15-Aug-03	41664	30	2047	03-164	21-Nov-03	28.62	-149.17	98
16	236	16-Aug-03	41665	685	11485					
17	231	17-Aug-03	41666	351	11363					
18	3234	15-Aug-03	41667	286	6957	03-165	16-Feb-04	35.48	-135.77	185
19	238	17-Aug-03	41669 ⁴	35	1861	03-168	20-May-04	59.60	-144.66	277
20)226	18-Aug-03	41670	279	10411	03-186	20-Feb-04	58.47	-147.13	186
21	247	19-Aug-03	41671	98	3881					
22	2223	17-Aug-03	41672	293	4453					
23	3247	19-Aug-03	41673	31	1503					
24	235	19-Aug-03	41674	67	3982	03-179	DNR			
25	5237	18-Aug-03	41675	319	10471	03-171	20-Feb-04	22.27	-160.24	186
26	236	19-Aug-03	41677	687	11107	03-176	20-Feb-04	31.53	-142.75	185
27	234	18-Aug-03	41679	289	9738	03-174	20-Feb-04	43.05	-134.25	186
28	3225	13-Jul-04	52136 ⁴	DNR		04-097	28-Aug-04	60.72	-146.07	46
29	230	11-Jul-04	52137	DNR		04-099	8-Nov-04	59.941	-148.00	120
30	235	14-Jul-04	52138	DNR						
31	206	12-Jul-04	52139	379	13091	04-105	9-Jan-05	57.194	-152.77	181
32	242	12-Jul-04	52140	DNR						
33	3241	13-Jul-04	52141	375	8887	04-108	9-Jan-05	57.9	-154.13	180
34	233	13-Jul-04	52142	377	11713	04-109	9-Jan-05	56.899	-153.10	180
35	5236	11-Jul-04	52143 ⁴	DNR		04-110	8-Aug-04	60.69	-146.59	28
36	242	13-Jul-04	52144	252	2791	04-111	9-Jan-05	59.29	-147.12	180
37	234	13-Jul-04	52145	38	1690	04-113	DNR			
38	3236	14-Jul-04	52146	375	9122	04-115	12-Mar-05	30.14	-134.63	241
39	247	14-Jul-04	52147	58	1703	04-101	DNR			
40)229	13-Jul-04	52148	36	1651	04-107	DNR			
41	220	13-Jul-04	52149	369	11804	04-118	10-Jan-05	34.16	-123.38	181

Table 2-1. Salmon sharks tagged with SPOT and PAT satellite tags

Length ¹	Tagging	SPOT	SPOT	Track	PAT Tag Popup Date Lat		Lon	PAT days	
(cm)	Date	Tag	Days	Distance					
				(KM)					
42232	12-Jul-04	521504	DNR		04-119	8-Aug-04	60.60	-146.60	27
43239	12-Jul-04	52151	348	11402	04-125	9-Apr-05	41.14	-145.36	271
44232	12-Jul-04	52152	300	5413	04-126	9-Apr-05	60.60	-147.29	271
45230	15-Jul-04	52153	376	10485	04-114	DNR			
46237	11-Jul-04	52154	380	17092	04-128	10-Apr-05	42.45	-124.75	273
47240	11-Jul-04	52155	380	9070	04-129	12-Apr-05	33.96	-120.81	275
48228	14-Jul-04				04-130	2-Mar-05	59.11	-152.62	231
49228	14-Jul-04				04-132	11-Nov-04	57.97	-152.21	120
50242	13-Jul-04				04-134	DNR			
51 226	15-Jul-04				04-136	8-Jan-05	45.63	-164.41	177

¹ Straight Total Length.
² This individual was tagged in 2002, then recaptured and retagged in 2003, so the tracks were combined.
³ Did not report.
⁴ Recaptured.

Argos LC	Proportion of All Locations	Proportion of All Locations	Error within	
	(Salmon Sharks)	(Blue Sharks)	1 SD	
3	0.07	0.09	<350 m	
2	0.29	0.25	<500 m	
1	0.23	0.16	<1000 m	
0	0.07	0.05	not reported	
Α	0.14	0.17	not reported	
В	0.20	0.27	not reported	

Table 2-2. Composition of Argos location classes obtained from SPOT tags on salmon sharks and blue sharks

	Length ¹ (cm)	Sex	Tagging Date	SPOT Tag	SPOT Days	Track Distance (km)	PAT tag	Popup Date	Lat	Lon	PAT days
1	199	Μ	01-Jul-02	36894	132	2218	00-695	26-Aug-02	33.00	-118.38	56
2	220	Μ	29-Jun-02	36895	148	4756	00-719	25-Oct-02	32.68	-117.48	118
3	225	Μ	24-Jun-02	37097	178	5735	00-762	26-Aug-02	33.58	-117.45	63
4	222	Μ	05-Jul-02	37098	18	769	00-702	1-Aug-02	33.02	-118.40	27
5	225	Μ	06-Jul-02	37099	142	3520	00-733	7-Dec-02	32.98	-118.30	154
6	260	Μ	01-Jul-03	37606	195	6342					
7	225	Μ	28-Jun-03	37607	DNR		02-652	DNR ²			
8	215	Μ	24-Jun-03	37608	161	7595	02-660	27-Dec-03	33.52	-119.28	186
9	193	Μ	26-Jun-03	37609	110	5168	02-653	DNR			
10	185	F	19-Jun-04	41678	DNR		03-395	DNR			
11	220	Μ	21-Jun-04	41680	7	189	03-294	DNR			
12	187	Μ	01-Jul-04	52127	93	3703	03-282	DNR			
13	175	F	17-Nov-04	52130	106	2218	04-247	15-Mar-05	27.13	-114.30	118
14	212	F	11-Oct-04	52216	287	10756	04-359	DNR			
15	208	Μ	13-Nov-04	52217	DNR		04-147	DNR			
16	179	F	13-Nov-04	53791	112	4886					
17	197	F	12-Nov-04	53792	91	3595	04-148	9-Feb-05	36.82	-122.00	89
18	199	F	15-Nov-04	53793	244	5120	04-246	DNR			
19	183	F	16-Nov-04	53794	87	3422	04-248	DNR			
20	174	F	16-Nov-04	53795	85	3130	04-116	DNR			
21	188	F	09-Nov-04	54579	39	1552	04-149	DNR			
22	164	F	08-Nov-04	54580	44	1602	04-146	27-Dec-04	35.13	-121.83	49
23	173	F	16-Nov-04	545813	32	1016	04-143	24-Dec-04	35.63	-121.32	38
24	189	F	16-Nov-04	54582	58	1470	04-152	4-Mar-05	5.74	-119.09	108
25	187	F	11-Nov-04	54583	139	5578	04-363	12-Feb-05	36.82	-122.00	93
26	186	F	12-Nov-04	545842	³ DNR		04-151	DNR			
27	195	F	09-Nov-04	54585	41	1647	04-362	25-Dec-04	35.40	-121.08	46
28	190	F	08-Nov-04	54586	242	8133	04-173	DNR			
29	188	F	10-Nov-04	54587	91	2315	04-150	5-May-05	7.28	-124.03	176
30	187	F	11-Nov-04	54588	88	3546	04-145	25-Dec-04	12.55	-121.15	44

Table 2-3. Blue sharks tagged with SPOT and PAT satellite tags

Straight Total Length.
 Did not report.
 Mortality.



Figure 2-1. Movements of salmon sharks in the eastern North Pacific. (A) Salmon sharks occupy a broad region of the eastern North Pacific. Animals were tagged in Alaskan waters in July 2002 (black), August 2003 (grey) and July 2004 (white). Photo: salmon shark with a SPOT3 tag on the dorsal fin. (B) Kernel density plots reveal extensive seasonal migrations. Salmon sharks utilized habitats near Alaska most heavily in the summer and autumn with some individuals overwintering. Sharks expanded their range southward in the winter and spring encompassing a wide range of habitat from Hawaii to the North American coast.





(A) Depth and temperature profiles of the water column along the track of a shark (41670) that overwintered in the GOA. The stratified summer water column cooled and the thermocline dissipated in the autumn. Black lines show latitude. Contour plots made from discrete measurements from PAT tags of (B) time-at-depth, and (C) time-at-temperature show a preference for the shallow mixed layer through November, followed by deeper diving when an inversion developed in December and mixed layer waters cooled to 5-6°C. (D) The thermal profile slice along the track of a shark moving from Alaska to the subtropics (#41675) shows an increase in temperature and strong thermal stratification. Depth (E) and temperature (F) habitat of the shark show a bimodal pattern in the warm subtropical gyre.



Figure 2-3 Thermal and depth habitats of salmon sharks and blue sharks. (A) Thermal habitat for 22 PAT-tagged salmon sharks shows a broad thermal niche of 2°C to over 22°C. (B) Salmon sharks spent $72 \pm 3\%$ of their time in the top 50 m. (C) PAT-tagged salmon sharks remaining in northern waters after the dissipation of the thermocline (n = 13) occupied 2-8°C waters, and (D) depth habitat predominantly shallower than 150 m. (E) Blue sharks (n = 15) showed a warmer thermal niche, preferring temperatures of 16-18°C and had (F) depth preferences with greater time near the surface than salmon sharks.



Figure 2-4. Rate of SR Ca²⁺ uptake in salmon shark heart. Temperature dependence of Ca²⁺ uptake catalyzed by SR Ca²⁺-ATPase (SERCA2) in microsomes from (•) salmon shark atrium; (•) salmon shark ventricle; (\blacktriangle) rat ventricle; and (•) blue shark atrium. Values represent mean ± SE of experiments performed with preparations from at least four individuals. Absence of the appearance of error bars indicates that the error bars are smaller than symbol. Inset: Immunoblot analysis of atrial (A) and ventricular (V) microsomes using a SERCA2-specific or RyR-specific polyclonal antibody.



Figure 2-5. Migrations of salmon sharks from subarctic to subtropical waters. (A) Shark #37382 moved from waters near Alaska into the pelagic eastern North Pacific during two consecutive annual migrations, utilizing similar pelagic regions in both years. Southward movements occurred during February and March and the animal returned to Alaska in May. (B) Shark #52139 departed Alaska in March and traveled to waters off California, arriving in April. It remained in the California Current System through September as it moved north along the margin of the North American continent. Argos positions (circles) are colored according to month with squares denoting the beginning of tracks and triangles denoting the end.



Figure 2-6. Low productivity of southern habitat utilized by salmon sharks. The oligotrophic waters visited by salmon sharks during spring suggest a non-foraging purpose for the migration, consistent with movements to pupping grounds. Surface chlorophyll-a concentration was significantly lower at the southern destinations of salmon sharks (subtropical gyre, south of 28°N) than in their northern habitat (subarctic gyre, north of 45°N) (Kruskal-Wallis test, H = 1540.96, DF = 2, P = 0.000). Inset: chlorophyll-a concentration decreases as salmon shark #37383 migrates to the south. Chlorophyll data courtesy of NASA/GSFC/DAAC and Orbimage Inc.









(A) Depth-temperature profiles along the track of a blue shark (#53792) in waters off California and Mexico show a 16-27°C mixed layer and thermocline waters cooling to 8°C. (B) Contour plots made from discrete measurements show that the thermal habitat of the blue shark is predominantly from 14-27°C in the mixed layer and upper thermocline, with only brief periods in waters cooler than 10°C. In comparison to salmon sharks, blue sharks inhabited waters with warmer surface temperatures, and spent less time in cold waters beneath the upper mixed layer.



Figure 2-9. SERCA2 and RyR protein expression in the hearts of lamnid sharks. Western blot analysis of atrial (A) and ventricular (V) microsomal preparations from salmon shark, mako shark, and white shark with blue shark and rat ventricle shown for comparison. (Upper panel): SERCA2- specific antibody labels a ~110 kDa band revealing high expression of the Ca²⁺ATPase among the Lamnidae family. (Lower panel): RyR-specific antibody labels a ~565 kDa band representative of the SR Ca²⁺ release channel protein.

3 Movements of a high trophic level predator between distant ecoregions

3.1 Introduction

3.1.1 Migration in pelagic marine vertebrates

The enormous scale and inhospitable nature of the pelagic ocean has limited our capacity to understand the biology of its most wide-ranging species. Recent technological advances are now providing insight into the lives of many large pelagic organisms, including mammals, birds, reptiles and fishes (DeLong et al. 1992; Morreale et al. 1996; Tuck et al. 1999; Block et al. 2001; Block et al. 2005; Weng et al. 2005). Enhanced knowledge of the long-range movements and aggregation areas of these species will improve our understanding of their life history, and of their relations to the physical and biotic environment. Home range size and movement patterns are important in understanding the demographic and genetic stock structure of populations, and also strongly influence the design and effectiveness of resource management actions.

Our knowledge of the migrations of air-breathing marine vertebrates has far outpaced that of fishes, as has our understanding of the life history functions of these migrations. We know that many species of marine mammals, birds and reptiles undertake large journeys between their favored feeding regions and their breeding and parturition areas. We have long know of the great migrations of the baleen whales from polar feeding grounds to low latitude calving grounds (Gilmore 1960), and bird migrations have been documented in great detail for decades, such as the migration of the short-tailed shearwater (*Puffinus tenuirostris*) from its breeding colony on Tasmania to feeding areas in the eastern North Pacific (Serventy 1967). Elephant seals breed and give birth at mid-latitude rookeries, but forage great distances away in high latitude pelagic and coastal waters (Le Boeuf and Laws 1994). Long distance migrations are known in fishes such as eels (Schmidt 1925), salmon (Scheer 1939) and

tunas (Orange and Fink 1963; Bayliff et al. 1991; Mather et al. 1995; Block et al. 2005), but have only recently been documented in lamnid sharks (Boustany et al. 2002; Bonfil et al. 2005; Weng et al. 2005; Bruce et al. 2006; Weng et al. In press; Weng et al. In review). Whether these migrations occur from parturition areas to feeding areas, or from feeding areas that are rich in one season to feeding areas that are rich in another, is unknown.

Whereas we can directly observe breeding and parturition in many pelagic birds, mammals and reptiles, our knowledge of these life history events in many pelagic fishes is based on inference rather than observation. We know the spawning areas of some tunas based on the capture of eggs and larvae in plankton trawls (Richards et al. 1989; Schaefer 1998), but for elasmobranchs, which have small numbers of young, our knowledge is less certain, and areas of parturition have been inferred from the capture of pregnant females and juveniles. For instance, pregnant white sharks have been captured near Japan, Taiwan, Australia, New Zealand, in the Mediterranean, and off Kenya (Bruce 1992; Fergusson 1996; Francis 1996; Uchida et al. 1996; Anonymous 1999), while young-of-the-year white sharks have been observed in these regions as well as near southern California and Baja California (Klimley 1985), the New York Bight (Casey and Pratt 1985), southeastern Australia (Bruce 1992) and South Africa (Cliff et al. 1996). Pregnant and juvenile salmon sharks have been captured across the north Pacific in a band to the north of the subarctic boundary (40-45°N) (Nakano and Nagasawa 1996), as well as in the coastal waters of Oregon, California and Baja California (Goldman and Human 2005), indicating the existence of at least two parturition areas. The problem with inferring parturition areas from the capture of pregnant and juvenile sharks is that both of these life history stages are highly vagile, so the location of capture may be distant from the location of birth.

3.1.2 Studying animal movement in the marine environment

The movements of pelagic animals can be studied using a variety of positioning methods, and error varies widely between them. The signal to noise ratio between the scale of animal movement and the scale of positioning error determines whether a particular method is sufficiently accurate to answer a question. If you want to know if

animals are in one 10 km cell vs. another, and your positions have an error of 100 km, then the method is not accurate enough to answer the question in a straightforward manner, and a statistical method is required to quantify uncertainty. If positions have an error that is considerably smaller than the cell size, then the method can answer the question with little uncertainty and therefore without the need for advanced statistical methods.

For the purposes of animal tracking Argos positions are considered to be of excellent quality, second only to the gold standard of GPS (Wormley 2007), and far superior to light- and SST-based geolocation (Figure 3-1). Teo et al. (2004) quantified errors in light- and SST-based geolocation using Argos data as the measure of the true position of animals, stating "The errors of Argos locations were probably 2 orders of magnitude smaller than the likely errors associated with light level and SST geolocation. Therefore, our assumption that the location estimates from Argos with $LC \ge 1$ represents the actual location of an animal is reasonable." Teo et al. (2004) provided error estimates for light- and SST- based geolocations on salmon sharks, which are compared to the error estimates for Argos positions (Hays et al. 2001; Vincent et al. 2002) in Table 3-1.

In most studies of wild animals using Argos, many positions are obtained at lower qualities than those used for reference in the Teo et al. (2004) study, such as in the study of Weng et al. (2005) in which only 59% of the positions were of Argos LC 1–3, and the remainder were of LC 0, A and B. A number of studies have quantified the accuracy of Argos positions, and the most important error is that associated with the lowest Argos quality, LC B. Published studies using fixed land transmitters and captive grey seals provide an RMS error for LC B of 7.8 km (Hays et al. 2001; Vincent et al. 2002), while testing by Kappes and Shaffer with fixed land transmitters showed and RMS error for LC B of 5.7 km (M. Kappes, personal communication). The accuracy of transmitters in fixed land positions, or on captive animals that cannot dive as deeply as in the wild, may be higher than for free-ranging animals. Tests comparing GPS and Argos positions on five wild elephant seals (Robinson et al., unpublished) revealed higher errors with RMS values of 11.8 km, and since this result

is based on a sample of 41 positions, it is unlikely to change much with the collection of additional data (D. Costa, personal communication).

The validity of using Argos data to determine the movements of animals is borne out by the numbers of publications that have used the technique (Priede 1984; McConnell et al. 1992a; Morreale et al. 1996; Eckert and Stewart 2001; Hyrenbach et al. 2002; Weng et al. 2005). Furthermore, the validity of Argos positions is borne out by their use to determine the sampling locations of animal-collected environmental data for inclusion in oceanographic databases (Boehlert et al. 2001; Fedak 2004).

While the behaviors of different animals have a profound effect on the nature of light curves obtained for light-based geolocation, as evidenced by the variation in errors between species reported by Teo et al. (2004), the behaviors of animals have little effect on the classification of Argos positions into location classes, since the latter is determined by the number of uplinks received from the tag during a satellite flyover. Vincent et al. (2002) used tags on grey seals, Robinson et al. (unpublished) used tags in wild elephant seals, whereas Hays et al. (2001) and Kappes et al. (unpublished) used tags placed at known fixed locations on land. These disparate techniques provided very similar error estimates ranging from 5.7 to 11.8 km for LC B.

The uncertainty in positioning error can be quantified using a variety of methods, and low quality positions can be removed with different types of filters. Speed filters have been used in a number of studies (McConnell et al. 1992a; Teo et al. 2004) while more advanced state-space methods have more recently been developed (Jonsen et al. 2003; Sibert et al. 2003; Royer et al. 2005; Nielsen et al. 2006), achieving results near to the theoretical limits to accuracy of light/SST geolocation (Figure 3-1). While advanced statistical techniques using state-space models can dramatically reduce errors, the theoretical minimum error of light/SST geolocation is far higher than the error in Argos and GPS positions. If the same individual animal were tracked with a light/SST geolocation tag (RMS error >100 km), as well as an Argos tag (RMS error ~ 7 km for LC B), and the light/SST track was then put through the best state-space Kalman filter in the world (theoretical minimum RMS error ~79 km), the Argos track

would still be far better, by about one order of magnitude (Figure 3-1). Put another way, if you were to ask a physical oceanographer who was considering whether to accept depth-temperature profiles taken by your animal into a database or model, the oceanographer would always prefer profiles associated with Argos positions over those associated with light/SST geolocations, regardless of the filtering and interpolation method applied to either positioning technique.

While the errors in light- and SST-based geolocation are very large compared to GPS and Argos, the technique can still be used effectively in cases where the scale of movement of animals is large enough to exceed position error. For instance, Block et al. (2001) and Block et al. (2005) effectively tracked Atlantic bluefin tuna using light- and SST-based geolocation, because the fish moved over scales of 7000 km (coastal US to Mediterranean), and thus the worst error in geolocation (latitude) was equivalent to 3% of the distance traveled (SST-based latitude error for Atlantic bluefin tuna is 1.89° or 210 km, Teo et al. 2004). In contrast, light- and SST-based geolocation could not be used to determine the movements of Atlantic bluefin tuna between different parts of the Outer Banks of North Carolina, since the scale of movements would be on the order of 300 km, and thus the proportional error would be 70%.

Over the scale of movement by salmon sharks in this study (eastern North Pacific Ocean, ~4500 km), the worst error in SPOT tracks (LC B for longitude, 7.5 km) is equivalent to 0.17% of the distance traveled. As such, the proportional errors in the studies of Block et al. (2001) and Block et al. (2005) are eighteen times as large as those of the present study. A comparison of the signal:noise ratio in various studies calculated as max movement distance/RMS error is provided in Figure 3-2. Another way to consider the ability of data to resolve movements is to consider the error in relation to the maximum distance moved by animals, provided in Figure 3-3.

The errors in positioning are an important consideration when querying environmental databases to determine oceanographic conditions for the time and place occupied by an animal. When using light/SST based geolocations, with their errors of 1 or 2°, the error in the position exceeds the size of the cell used in synoptic oceanographic databases (cell sizes for some common environmental data are: PP

0.1°, Blended SST 0.1°, Modis Chl-a 0.05°, SSH 0.25°). As a result it is necessary to construct an error distribution around the position, and then take environmental data from the multiple cells under this distribution and weight the values according to the probability distribution. This method is not a state-space technique, it is merely a probability-weighted average. In the case of Argos data, the position error (RMS error of 4 to 7 km for LC B, = 0.06°) is smaller than the cells used in all but the finest resolution oceanographic databases, so we know with reasonable confidence that the animals was actually in a particular cell. When there is little or no uncertainty, there is little need for advanced statistical methods (If you are right, you don't need statistics). The method used in this study to match oceanographic data to animal positions takes the average value in a 1° radius of the position in order to reduce the effect of missing and erroneous pixels in synoptic datasets (due to cloud cover and other errors). This means that the signal:noise is extended to the 1° search radius vs. the 0.06° RMS error of Argos LC B positions, which is a very good ratio.

Position errors are also an important consideration when calculating derived parameters such as speed and straightness. Argos provides positions that may be just a few minutes apart or days to months apart. If positions are just minutes apart, an error of 7 km on each position could yield an extremely high speed for a sensor than in reality was not moving at all. If positions are one day apart, the maximum false speed resulting from Argos LC B error (14 km/d) is much smaller than the maximum speed of a salmon shark (103 km/d, shark 59684), whereas the maximum false speed resulting from light/SST position (326 km/d) is much larger than the maximum speed of a salmon shark (Figure 3-4). It is evident from these data that daily speeds can be legitimately calculated from Argos data, but not from light/SST data.

3.1.3 The Lamnidae – endothermic sharks

The sharks of the family Lamnidae are apex pelagic predators occupying ranges throughout the polar, temperate and tropical oceans (Compagno 1984). The extant members of the Lamnidae are the shortfin mako shark (*Isurus oxyrhincus*), the longfin mako shark (*Isurus paucus*), the white shark (*Carcharodon carcharias*), the salmon

shark (*Lamna ditropis*) and the porbeagle shark (*Lamna nasus*) (Compagno 1984). The lamnid sharks possess the striking ability to maintain warm body temperatures (Carey and Teal 1969) and their endothermy may underlie many of their ecological traits, including long distance migrations (Casey and Kohler 1990), wide ambient temperature range (Carey et al. 1982; Nagasawa 1998; Weng et al. 2005), high performance swimming (Carey and Teal 1969; Graham et al. 1990; Bernal et al. 2005) and trophic specializations on large, fast prey species (Tricas 1985; Nagasawa 1998).

The difficulty in studying pelagic fishes has left many gaps in our understanding of the biology of lamnids. We know very little about their geographic range, migratory pathways or vertical movements. Most data on these species are derived from fishery-based research, which generally suffers from strong spatial and temporal bias in sampling effort. White sharks have been the subject of short term, local scale tracking studies, yielding high-resolution data on depth, temperature and vertical behavior (Carey et al. 1982; McCosker 1987; Strong et al. 1992; Goldman 1997; Klimley et al. 2002). Conventional tagging studies exist for the shortfin mako (Casey and Kohler 1992) but are limited for the white shark (Casey and Kohler 1990; Bruce 1992; Strong et al. 1992; Strong et al. 1998; Hulbert 2005).

The salmon shark, *Lamna ditropis* (Hubbs and Follett, 1947), is the least studied of the five lamnids (Anderson and Goldman 2001). Reaching over 3 m in length, it has a stout body, short snout, conical teeth with cusplets, secondary caudal keels, and spots on the ventral surface (Compagno 1984). Although the name salmon shark implies that it forages on salmon, studies of the gut contents indicate that they feed on a varied diet of Pacific salmon, herring, squid and a variety of benthic fishes (Sano 1960; Paust and Smith 1986; Nagasawa 1998). Salmon sharks have been captured over much of the north Pacific (Strasburg 1958; Nakano and Nagasawa 1996; McKinnell and Seki 1998) and have been observed to occur between 65 °N (Compagno 1984) and 35 °N (Strasburg 1958).

Fishery, acoustic and electronic telemetry studies show occupancy in waters between 3.5 and 22 °C (Strasburg 1958; Neave and Hanavan 1960; Nakano and

Nagasawa 1996; Nagasawa 1998; Weng et al. 2005). Recent acoustic tracking of salmon sharks for short periods of time indicates a constant elevation in stomach temperature to 25°C (Goldman et al. 2004). Satellite telemetry results show movements of individual sharks from Alaska to waters off California, Baja California and Hawaii (Weng et al. 2005).

3.1.4 Ecoregions of the eastern North Pacific

Salmon sharks inhabiting the eastern North Pacific move through a diverse environment, spanning broad ranges in temperature and productivity (Weng et al. 2005). The eastern North Pacific shows strong seasonal variations in temperature and productivity in the more northerly regions, and less seasonality in the southerly regions Figure 3-5, Figure 3-6, Figure 3-7). The eastern North Pacific can be divided into a number of oceanographic provinces or ecoregions, each with a characteristic pattern resulting from the physical forcing of light, wind and thermohaline circulation. Salmon sharks inhabit all of these ecoregions, which occupy both neritic and pelagic waters.

In the northern part of their range, the sharks swim in the Coastal Alaska Downwelling Region. This ecoregion covers the coastal waters of southern Alaska and British Columbia to approximately 150 km offshore. The southern margin of this region as it transitions from the continental shelf to slope merges into the West Wind Drift. Downwelling dominates this region, which has a low salinity surface layer and strong stratification, but topographically driven mixing causes high nutrient levels during spring and summer. Ephemeral upwelling occurs along the Alaska Peninsula during summer. Due to the seasonal light cycle, productivity is high in spring and summer, and very low in autumn and winter, with temperature warmest in summer and autumn and coolest in winter and spring (Longhurst 1998).

The second coastal region that attracts salmon sharks is the California Current Upwelling Region, which extends from 22–48°N and to 1000 km offshore (but narrower to the north). This ecoregion receives high levels of nutrients from the north, carried by the California Current itself, as well as nutrients upwelled by Ekman

transport along the coast, in cyclonic eddies, and along the divergent shear zone between the California Current and the poleward nearshore current. This region is strongly seasonal, with strong upwelling during late spring and early summer, and weak or no upwelling during winter. Productivity peaks during summer and autumn but remains high throughout the year (Bolin and Abbott 1963).

The remaining ecoregions occupied by salmon sharks are in pelagic waters. The Subarctic Alaska Gyre is a large body of pelagic water bounded on the south by the West Wind Drift (45°N), and to the north and east by the Coastal Alaska Downwelling Region. It is strongly influenced by high precipitation and therefore low surface salinity, causing a pycnocline that limits vertical mixing except during the stormy winter season (Roden 1991). The increase of primary production during spring and summer shows a weak or nonexistent signal in chlorophyll values due to the simultaneous increase in herbivorous plankton (Longhurst 1998). The Transition Zone marks the division between the subarctic and subtropical gyres, and is bounded to the north by the Subarctic Front (42–45°N), to the south by the Subtropical Front (30–32°N), and to the east by the bifurcation of the West Wind Drift into the Alaska Current and the California Current. It is characterized by lower stratification and stability than the waters to the north and south, and shows moderate productivity during all seasons except summer when the mixed layer is shallower than the photic zone (Roden 1991). The Subtropical Gyre lies between the Subtropical Front and the northern boundary of equatorial upwelling (10°N), and is bounded on the east by the California Current. It is a large body of uniform water with low nutrient levels and shows very little seasonality in temperature or productivity (Longhurst 1998).

3.1.5 Habitat use in a highly migratory marine vertebrate

In this study we seek to elucidate a number of ecological questions regarding the movement and habitat use of an abundant predator, the salmon shark, focusing on the following questions:

 How do salmon sharks move throughout the eastern North Pacific, and are these movements consistent from year to year?

- 2. Do the movements of salmon sharks correlate with our existing understanding of regional differences in productivity across the eastern North Pacific?
- 3. What life history functions appear to be fulfilled during the various phases of the migration cycle?
- 4. What ecological advantages, if any, are conferred by the migratory life history of salmon sharks, and how do the strategies of other high trophic level marine vertebrates compare?

3.2 Methods

3.2.1 Satellite telemetry

The movements of 68 salmon sharks were monitored using satellite telemetry. Thirtyeight of the animals included in this study were reported by (Weng et al. 2005). The SPOT tag (Wildlife Computers, Inc. SPOT versions 2.0, 3.0 and 4.0) transmitted to Argos receivers mounted on polar-orbiting NOAA weather satellites when sharks were at the surface. The Argos system calculated positions, based on the Doppler shift of transmissions from the tag (Taillade 1992), which are distributed to users via the Internet. Argos states that the standard deviation of errors for its positions are: quality 3, less than 150 m; quality 2, 150-350 m; quality 1, 350-1000 m. Estimates for qualities 0, A and B have been published in the literature, showing an RMS error for the worst position quality (LC B) of 7.8 km (Hays et al. 2001; Vincent et al. 2002).

Sharks were captured using hook and line in Prince William Sound, Alaska during the summers of 2002-2005. Circle hooks (L2045 20/0 circle hook, Eagle Claw, Denver, CO, USA) were used to avoid gut hooking. Hooks were baited with sardine, salmon or squid. All sharks tagged were female with lengths averaging 211 ± 10 cm, and ranging from 188 to 241 cm curved fork length, and were mature based on size at maturity data (Goldman and Musick 2006). Each SPOT tag was attached to the dorsal fin using small stainless steel bolts (3 mm x 40 mm) such that the antenna of the tag would be exposed in air when the animal swam at the surface. All bolts were coated with plastic shrink-wrap such that no metal was in contact with the tissues of the animal.

3.2.2 Environmental data

Environmental data were obtained for each space-time point in each track by referencing synoptic oceanographic datasets maintained by NOAA and AVISO. We obtained data for sea surface temperature, chlorophyll-a, primary productivity, and sea surface height deviation. Data were queried from the Oceanwatch Live Access Server and brought into MatLab using OPeNDAP. Sea surface temperature was blended from multiple sources to optimize coverage, comprising the Moderate Resolution Imaging Spectroradiometer (MODIS), Advanced Very High Resolution Radiometer (AVHRR), Imager, and the Advanced Microwave Scanning Radiometer (AMSR-E). Chlorophyll-a was measured by MODIS and obtained as 8-day averages. Primary productivity was estimated from chlorophyll-a measured by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and SST measured using AVHRR, using the method of (Behrenfeld and Falkowski 1997). Sea surface height deviation is based on altimetry measurements from multiple spacecraft, merged by the AVISO program and provided to NOAA. In order to quantify environmental gradients such as fronts or mesoscale flow features, we determined the standard deviation in temperature, chlorophyll, primary production and surface height deviation within a one-degree cell centered on the observation. The water depth at each position was determined using two-minute gridded global relief data (ETOP02) from the National Geophysical Data Center.

3.2.3 Analysis

The positions obtained from Argos for each animal were filtered to removed positions with Argos location class Z, those on land, and those exceeding a speed of 1.75 m/s (Weng et al. 2005). To avoid the bias introduced by variation in the frequency of sampling, the resulting tracks were then regularized to an even time spacing of one day, up to three day intervals, using the piecewise cubic hermite

interpolating polynomial (MatLab, The Mathworks, Natick, MA, USA), which had the highest accuracy of available methods in a recent study (Tremblay et al. 2006).

We conducted a seasonal kernel density analysis (Worton 1989) of daily positions to quantify variation in habitat utilization by salmon sharks, using the Animal Movement Extension (Hooge and Eichenlaub 1997) to ArcView version 3.3 (ESRI, Inc., Redlands, CA, USA). First we conducted the kernel analysis using the complete dataset of 68 individuals. The complete dataset contains many tracks that are much shorter than a year, thus biasing toward the tagging season and location. To avoid bias introduced by short tracks, we also conducted the kernel analysis with a subset of the data, comprising 34 individuals whose tracks averaged 360 (223-629) days. We use the 50% probability contour to show major focal regions of sharks, the 80% contour to show minor focal regions, and the 95% contour to show regions of low utilization. The complete range of salmon sharks during each season was represented using the minimum convex polygon technique (Burt 1943) implemented in Hawth's Tools (Beyer 2004) for ArcInfo version 9 (ESRI, Inc., Redlands, CA, USA). A normalized kernel density was produced by dividing the number of daily positions within each cell by the number of individuals within the cell.

Derived parameters were calculated from the filtered, interpolated position data to provide measures of shark behavior. Speed was calculated in MatLab using the distance function in the m-map toolkit of (Pawlowicz 2006), while an along-track index of straightness was calculated using the method of (Batschelet 1981). Speed and straightness were not calculated where gaps exceeded three days in length. First passage time, a measure of area restricted searching that is more robust to gaps in movement records (Fauchald and Tveraa 2003), was calculated using the implementation of (Robinson 2006). Focal area behavior, such as occurs during searching and foraging, was indicated by low speed, low straightness and high first passage time; whereas the opposite values indicated that animals were transiting through a region. In addition, we calculated the distance of each position from the coast of the North American mainland using the great circle method. We considered sharks to be in a migrating state when dy/dt > g, where y is latitude, t is time and g is a

gradient threshold, which we set at $0.25 \circ d^{-1}$. This condition was used to determine the event times for the starting and ending points of migration, and thus to determine the durations of northern, migrating and southern phases.

The movements of salmon sharks were compared to the major ecoregions of the eastern North Pacific Ocean. The boundaries of oceanic regions are not fixed in their positions over ground; rather they moved seasonally and with changes in oceanographic conditions. Therefore, the allocation of a particular time-space position into an ecoregion was conducted dynamically, after (Longhurst 1998)), as follows: the Subarctic Gyre was defined as waters 12°C or cooler; the Transition Zone comprised waters warmer than 12°C and cooler than 18°C; and the Subtropical Gyre comprised waters 18°C or warmer. Neritic regions were defined by their proximity to the coast, with the Coastal Alaska Downwelling Region being waters nearer than 150 km and north of 48°N; and the California Current Upwelling Region defined as waters south of 48°N and up to 1000 km from the coast at the southern margin, and 500 km from the coast at the northern margin. The occurrence of salmon shark positions in these ecoregions is shown in Figure 3-8. Frequency histograms of salmon shark occupancy of different regions for each month of the year were normalized by the total number of observations in each month to remove bias caused by observational variation. Averages are presented as mean \pm standard deviation for normal distributions, and median (first quartile-third quartile) for non-normal distributions.

3.3 Results

3.3.1 Salmon shark movements

3.3.1.1 Seasonality

Individual salmon sharks moved across a large range of the eastern North Pacific during their seasonal migrations, inhabiting both pelagic and neritic waters (Figure 3-9). The salmon sharks tracked in this study (n=34; Table 3-2) occupied waters from

22.3–61.0°N and from 117.9–168.6°W (Figure 3-10 and Figure 3-11). Salmon sharks made long distance migrations between subarctic foraging grounds in southern Alaska and subtropical destinations arrayed in a broad longitudinal band from 168°W to the North American continental shelf. Salmon sharks had a more northerly distribution during summer (median latitude 54°N (44–60°N)) and autumn (55°N (48–58°N)) and a more southerly distribution in winter (50°N (41–57°N)) and spring (42°N (37–49°N)). Use of subarctic foraging grounds was greatest in the summer, autumn and winter, with highest occupancy in Prince William Sound, the Alaska Peninsula and the Panhandle, with one animal entering the Bering Sea. The majority of migrations to the south occurred during autumn and winter, and the most southerly position of the population occurred in spring.

Salmon shark migrations or horizontal behaviors showed a high degree of variability between individuals. The variation in migration times between individuals was large, with sharks migrating south from the Coastal Alaska Downwelling region as early as 22 July and as late as 8 March, with a median date of 8 January (22 November–1 February). While migrating south, sharks swam as slow as 25 km/day and as fast as 103 km/day, averaging 68 (73–79) km/day. The duration sharks stayed in their southern destinations varied from 7 to 190 days, averaging 89 (51–129) days, and they began migrating north between 29 March and 13 October, averaging 4 May (16 April–90 June). Northward migration speeds were slightly slower than southward migration speeds, ranging from 21 to 83 km/day, and averaging 60 (47–69) km/day. Shark remained in their preferred northern habitat in the Coastal Alaska Downwelling region from 14 to 609 days, averaging 159 (120–238) days. Three animals did not undertake a southern migration, remaining in Coastal Alaska waters through the winter and spring (Table 3-3).

3.3.1.2 Habitat utilization intensity

The time-based habitat utilization intensity of salmon sharks was evaluated using kernel densities and minimum convex polygons. The complete dataset of 68 individuals contained many short tracks, which provided data for the tagging region
but did not record migration events; as a result, the kernel density using this dataset showed heavy usage of coastal Alaska waters in all seasons and the core 50% density contour never extended beyond this region (Figure 3-10). Using only longer tracks with average duration of approximately one year (n=34) ensured that the movements of sharks during all seasons were recorded, and the resulting kernel density showed much greater usage of regions further from the tagging site (Figure 3-11). During summer, salmon sharks were concentrated primarily in two regions. The focal region of salmon sharks, indicated by the 50% kernel density contour, was in waters of coastal Alaska while the 80% kernel density region occurred there as well as in the northern California Current region. Areas of low utilization, indicated by the 95% kernel density contour, occurred across stretches of coastal Alaska and British Columbia as well as in the northern California Current, with small regions in the Subarctic Gyre and Transition Zone. During autumn salmon sharks became slightly less concentrated, as the 50% contour extended across a larger area of coastal Alaska, and the 80% contour occurred there as well as along the Alaska panhandle, British Columbia, Washington and Oregon. The 95% contour extended beyond these regions into the eastern portions of the Subarctic Gyre and Transition Zone. Salmon sharks dispersed further during winter, with the 95% contour reaching the southern California Current region, but the 50% contour remained focused in coastal Alaska waters. In spring the greatest dispersion and most southerly distribution occurred, with the 50% contour showing focal areas in both coastal Alaska and the northern California Current. The 80% contour occurred in these regions as well as in isolated parts of the Transition Zone.

The areas of habitat used by salmon sharks were large, with total habitat occupancy (given by minimum convex polygons) ranging from a low of 5.8 million km² in autumn to a high of 13.1 million km² in winter, nearly the entire eastern North Pacific north of 22°N. In all seasons, utilization was concentrated into a small proportion of the total range. During summer, the total range of salmon sharks was 6.9 million km², but the 50% utilization contour occupied only 1.9% of this area, concentrated in coastal Alaska, with the 80% contour extending into the California

Current region. A similar pattern occurred during autumn, with slightly higher utilization of the California Current. During winter, when the total range was greatest, the 50% contour was only 1% as large, at 0.09 million km², and remained in a small region of coastal Alaska. During spring, when sharks had the most southerly distribution, the 50% contour also had its maximum extent, covering 0.3 million km² and 3% of the total range.

The utilization of habitat by salmon sharks was also represented by the number of individuals using an area regardless of the amount of time spent in the area (Figure 3-12). This showed the same pattern as the time-based kernel analysis, with large numbers of sharks in coastal Alaska waters in summer, autumn and winter, and lower numbers of sharks in other regions in all seasons except spring, when there was a concentration of salmon sharks in the California Current region. When the number of sharks per area was used to normalize the time-based kernel density, the density in coastal Alaska waters was reduced, and the density in other regions was increased (Figure 3-13 and Figure 3-14). Additionally, areas where single sharks spent large amounts of time were highlighted.

3.3.1.3 Speed

Salmon sharks traveled at speeds ranging from 0 to 129 km/day, with a median of 33 (11–62) km/day (Figure 3-15). While both high and low speeds occurred in all areas, there was a trend of higher speeds occurring in waters further from the coast (Spearman's rank correlation, r = 0.52), waters with lower chlorophyll-a (Spearman's rank correlation, r = -0.43), and waters with lower primary productivity (Figure 3-16; Spearman's rank correlation, r = -0.38). A very low correlation existed between speed and water temperature (Spearman's rank correlation, r = 0.13). Speed decreased slightly in regions with more variation in SST, indicative of thermal fronts (Spearman's rank correlation, r = -0.22). The correlation was very low between speed and sea surface height deviation (Spearman's rank correlation, r = 0.05), and between speed and variation in sea surface height deviation, indicative of mesoscale features such as eddies (Spearman's rank correlation, r = 0.003).

The behavior of salmon sharks, as measured by speed, was different between the major ecoregions they inhabited (Figure 3-17). In the Coastal Alaska Downwelling Region salmon sharks predominantly swam at low speeds, averaging 4 (12–35) km/day. Speeds were also low in the California Current, averaging 17 (35–57) km/day. Speeds were highest in the Subarctic Gyre, where sharks swam at an average speed of 41 (65–83) km/day, and intermediate in the Subtropical Gyre, averaging 26 (40–55) km/day, and the Transition Zone, averaging 27 (48–69) km/day.

3.3.1.4 Straightness

The movements of salmon sharks had a median straightness of 0.67 (0.37–0.88), and ranged from 0 to 1 (Figure 3-18), with 1 being a straight line. There was a trend of lower straightness occurring in waters near the coast (Spearman's rank correlation, r = 0.37), waters with higher chlorophyll-a (Spearman's rank correlation, r = -0.29), waters with higher variation in chlorophyll (Spearman's rank correlation, r = -0.32), waters with higher primary productivity (Spearman's rank correlation, r = -0.38), and waters with higher variation in primary productivity (Spearman's rank correlation, r = -0.26). A very low correlation existed between straightness and water temperature (Spearman's rank correlation, r = 0.10), and straightness and variation in SST (Spearman's rank correlation, r = -0.16). The correlation was very low between straightness and sea surface height deviation (Spearman's rank correlation, r = 0.03), and between straightness and variation in sea surface height deviation (Spearman's rank correlation, r = 0.10).

The behavior of salmon sharks, as measured by track straightness, was different between the major ecoregions they inhabited (Figure 3-19). In the Coastal Alaska Downwelling Region salmon sharks had an even distribution of straightness, averaging 0.49 (0.24–0.75). Straightness was broadly distributed in the California Current, averaging 0.61 (0.38–0.85), and the Subtropical Gyre, averaging 0.44 (0.28–0.67). However, in the Subarctic Gyre and the Transition Zone, sharks predominantly swam with straighter tracks, averaging 0.89 (0.68–0.97) and 0.79 (0.55–0.94), respectively.

3.3.1.5 First passage time

First passage time is an index of area-restricted searching (Fauchald and Tveraa 2003). The movements of salmon sharks had a median first passage time of 7.9 (3.7–23.0) days (Figure 3-20). There was a trend of higher first passage time occurring in waters nearer to the coast (Figure 3-21; Spearman's rank correlation, r = -0.43), waters with higher chlorophyll-a (Spearman's rank correlation, r = 0.38), waters with higher variation in chlorophyll (Spearman's rank correlation, r = 0.39), waters with higher primary productivity (Spearman's rank correlation, r = 0.33). A very low correlation existed between first passage time and water temperature (Spearman's rank correlation, r = -0.05), and a slightly higher correlation with variation in SST (Spearman's rank correlation, r = 0.19). The correlation was very low between first passage time and sea surface height deviation (Spearman's rank correlation, r = -0.03), and between first passage time and variation in SSH (Spearman's rank correlation, r = 0.05).

The behavior of salmon sharks, as measured by first passage time, was different between the major ecoregions they inhabited (Figure 3-22). In the Coastal Alaska Downwelling Region salmon sharks had a broad distribution of first passage time averaging 23 (7–46) days. In all other regions the distribution was strongly skewed toward low values, averaging 4 (3–7) days in the Subarctic Gyre, 6 (3–11) in the Transition Zone, 9 (5–20) days in the California Current, and 8 (5–55) days in the Subtropical Gyre. A secondary peak of high first passage times occurred in the Subtropical gyre as well as in the California Current.

3.3.1.6 Pelagic vs. neritic waters

The migration routes and destinations of salmon sharks fell into two broad categories, those in pelagic waters, and those in neritic waters. Sharks that moved into neritic waters (n=19) between southeast Alaska and Baja California initiated their southern migrations on 6 December (6 October–23 January), and arrived at their destinations in the California Current on 17 January (28 October–28 February). The

southern migration took 27 (25–32) days and covered 1975 (1599–2548) km at a speed of 66 (62–79) km/day. These sharks remained in their destination regions for 107 (51–136) days before initiating northern migrations on 4 May (26 April–5 August). The northern migration took 28 (20–46) days at a speed of 56 (42–66) km/day, and sharks arrived in the Coastal Alaska Downwelling region on 29 June (17 May–3 September). They remained in this region for 159 (82–239) days before initiating their next southern migration. The southernmost latitude for these sharks was 35 (30–38) °N, their median distance from the coast was 193 (97–361) km, and they occupied waters with a median depth of 2872 (2186–3480) m.

In comparison to the neritic migrators, sharks that moved into pelagic waters (n=12) initiated their migrations later, on 26 January (9 December–12 February), and arrived at their destinations in the Subtropical Gyre later, on 4 March (4 February–21 March). The southern migration occurred at a similar speed of 69 (67–78) km/day, but covered a longer distance of 2571 (1770–2978) km and thus took longer, averaging 40 (27–45) days. These sharks remained in their southern destination regions for a shorter period of time, 77 (52–95) days, before initiating northern migrations at an earlier date, 30 April (3 April–15 May). They returned the Coastal Alaska Downwelling region earlier, on 6 June (27 May–14 June), and traveled faster than the neritic migrators at a speed of 66 (51–71) km/day. The sharks remained in the Coastal Alaska Downwelling region for a longer period of time, 182 (137–224) days, before initiating their next southern migration. The southernmost latitude for these sharks was further south, 29 (28–32) °N, their median distance from the coast was greater, 621 (240–913) km, and they occupied deeper waters with a median depth of 4012 (2941–4649) m.

Salmon sharks traveled at higher speeds, with higher straightness and with lower first passage time when in pelagic waters, as compared to neritic waters (Figure 3-23). For all sharks, speed was significantly slower in the neritic zone (31 (10–59) km/day) than in the pelagic zone (54 (28–73) km/day) (Figure 3-24a; Wilcoxon rank sum test, h = 1, p = 0.00). The primary productivity of neritic waters inhabited by salmon

sharks was significantly greater than the productivity of pelagic waters (Figure 3-24b; Wilcoxon rank sum test, h = 1, p = 0.00).

Individual salmon sharks showed fidelity to their southern destination regions over multiple years. Among sharks that were tracked over multiple years (n=12), three animals visited the neritic waters of the California Current during both years; eight animals visited pelagic waters of the Subtropical Gyre and Transition Zone during both years; and one animal visited the California Current during the first year and the Transition Zone during the second.

3.3.2 Habitation utilization of major ecoregions within the eastern North Pacific

3.3.2.1 Coastal Alaska Downwelling Region

The Coastal Alaska Downwelling Region was the most highly utilized ecoregion for salmon sharks (Figure 3-11), often showing low speed and straightness and high first passage time while in the region (Figure 3-23). Salmon sharks inhabited the region during all seasons of the year, with the lowest utilization during spring (Figure 3-25). The seasonality of temperature, chlorophyll and primary production in this region is extreme, with very high levels of productivity during summer and autumn, and very low levels during winter (Figure 3-26). Strong, localized eddy activity occurred during all seasons and was most intense during autumn.

There was not a close correspondence between salmon shark utilization and environmental variables (Figure 3-25). Chlorophyll-a concentration showed a spring peak prior to the largest influx of salmon sharks during summer, and then dropped to a low level in winter. The increase in salmon shark abundance during summer occurred during the summer increase in primary productivity, but the high shark abundance continued through autumn and winter despite a precipitous decline in primary productivity during those seasons. The seasonal changes in this region did not show marked interannual variations (Figure 3-26).

3.3.2.2 Subarctic Alaska Gyre

Salmon sharks showed moderate utilization of the Subarctic Alaska Gyre (Figure 3-11), moving through the region rapidly (Figure 3-23). There was high variability in all seasons and peak utilization during autumn (Figure 3-27). This peak in utilization corresponded to the autumn peak in chlorophyll values and primary productivity for the region. The majority of occupancy occurred in the far eastern margin of the Gyre. There were no marked interannual variations in temperature, chlorophyll or primary productivity (Figure 3-28).

3.3.2.3 Transition Zone

Salmon shark showed moderate utilization of the Transition Zone (Figure 3-11), typically moving through the region rapidly (Figure 3-23). Utilization peaked in spring with moderate levels in winter and minimum levels during summer and autumn (Figure 3-29). The spring peak in utilization corresponded to the spring bloom, raising chlorophyll levels and primary productivity. However, the minimum utilization during autumn corresponded to the maximum levels of primary productivity. There were no marked interannual variations in temperature, chlorophyll or primary productivity (Figure 3-30).

3.3.2.4 California Current Upwelling Region

Salmon sharks showed high utilization of the California Current Upwelling Region (Figure 3-11). Shark frequently moved through the Subarctic Gyre and Transition Zone rapidly en route to the California Current, then slowed upon arrival (Figure 3-23), and used both the northern and southern portions of the ecoregion. Utilization of this ecoregion was highest in the spring, corresponding to a peak in chlorophyll concentration, but lowest in the summer and autumn when primary productivity is highest (Figure 3-31). There were no marked interannual variations in temperature, chlorophyll or primary productivity (Figure 3-32).

3.3.2.5 Subtropical Gyre

Salmon sharks showed low utilization of the Subtropical Gyre (Figure 3-11), though as noted above this may be an underestimate since sharks tend to submerge while in this habitat, preventing data transmission. Residency in the region was shorter than in the California Current ecoregion, and in some cases sharks began migrating north immediately upon reaching their southernmost point (Figure 3-23). Utilization of the habitat peaked in winter and spring with very little usage during summer and autumn, and did not correspond with the seasonality of productivity (Figure 3-33). Seasonality of temperature, chlorophyll and primary productivity were weak, with a slight increase in productivity during summer (Figure 3-34).

3.3.3 Weaknesses and biases in the data

The movement records of salmon sharks in this study contain gaps of varying length, such that we did not fully observe their habitat utilization. Time gaps of SPOT tag reporting averaged 2 (1–3) days, while the longest gap in each record was 38 (14-71) days.

Temporal gaps in the tracks of salmon sharks are concentrated in the northernmost and southernmost parts of the range, with very few in the mid-latitude and California Current regions. The distribution of gaps greater than 20 days in length, during which a salmon shark could complete a large portion of a meridional migration, is shown in Figure 3-35. Shorter gaps also occur throughout the range (Figure 3-36 and Figure 3-37). These gaps are by far the most numerous in the northern portion of salmon shark range, such that sharks are most poorly observed in the north, moderately observed in the south, and highly observed at mid-latitudes (Figure 3-38). When the observed distribution of salmon sharks is corrected for the missing days, the distribution increases in the north, decreases at mid-latitudes, and is unchanged at the southern margin of the range (Figure 3-39).

In additional to biases in the distribution of salmon sharks within their observed range, there may be error in the reported southern margin of salmon shark distribution. There are 7 records in which an animal disappeared during the southern phase; 10

tracks that end prior to the return migration, for a total of 17 incomplete tracks; 14 tracks with a complete southern migration; and 3 overwintering tracks (Table 3-3).

3.4 Discussion

Salmon sharks tagged with satellite tags, undertook long distance migrations on a seasonal basis between subarctic waters of coastal Alaska and southern destinations in the subtropical gyre and California Current, arrayed across the entire central and eastern North Pacific from the continental margin to the Hawaiian Islands. These movements mean that individual salmon sharks are vulnerable to fishing gear throughout this range (Strasburg 1958; McKinnell and Waddell 1993; Nakano and Nagasawa 1996; McKinnell and Seki 1998).

3.4.1 Sources of bias

The data used in this study contain a number of weaknesses that affect our ability to accurately describe salmon shark movements and determine seasonal distribution. First, the track lengths vary between animals, and many tracks are shorter than one year, such that they lack the power to elucidate seasonal movement through a full cycle. Second, the tracks contain gaps of varying length, some long enough to allow undocumented movements across much or all of the eastern North Pacific. To address the problem of varying track length, we conducted the seasonal kernel density analysis using only the longest tracks (n=34), averaging 360 days in length. Therefore, we will concentrate here on the issue of gaps in the records.

If the gaps are distributed randomly, then they should cause no bias in the final product, but if they are not randomly distributed, then the final analysis may not correctly represent reality. Therefore, we determined the distribution of gaps, using the 1-day interval regularized data described in the methods. Gaps in the tracks of salmon sharks are concentrated in the northernmost and southernmost parts of the range, with very few in the mid-latitude and California Current regions. When the observed distribution of salmon sharks is corrected for the missing days, the

distribution increases in the north, decreases at mid-latitudes, and is unchanged at the southern margin of the range.

While we can correct for a lower observation rate within a particular region, we cannot correct for the total absence of observations in a particular region. The possibility that sharks move further south than is reported by SPOT tags, as a result of their subtropical submergence behavior, raises the potential of a fundamental flaw in the kernel density analysis. Given that the number of incomplete tracks exceeds the number of complete southern migration tracks, we most likely suffer from both an under-reporting of the region as well as a misrepresentation of its extent. The former problem can be corrected, the latter cannot. Given that the correction shown above caused no change in the proportional utilization of the south, the kernel density estimates are likely to be reasonable, but their extent does not show the full southern extent of salmon shark movements.

The problem of long gaps in a record of animal movement cannot be solved using state-space or other techniques. If we do not know where an animal is, we do not know where it is. Jonsen et al. (2005) bridge gaps using a linear interpolation and state that this interpolation 'poses no difficulty for state transitions with reasonably short timesteps', meaning that it most definitely is a problem for long timesteps. Interpolation over the gap lengths in salmon shark records would amount to making up data (Jonsen, personal communication, 9 March 2007). The state-space technique used by Sibert et al. (2003) skips over gaps rather than interpolating (Sibert, personal communication, 5 March 2007); it does nothing to address gaps, and is not designed to. The best we can do is to present the uncertainly in the study clearly, thereby allowing readers to make informed interpretations of the results. If we could solve all of the problems in the dataset, then there would be little uncertainly.

3.4.2 Nature and repeatability of seasonal migrations

The spatial extent of seasonal movements by salmon sharks appears to be greater than for other elasmobranch and teleost fishes, reaching 13.1 million km², nearly the entire eastern North Pacific. Salmon sharks have a distinct seasonality in the timing of their migrations, though variation between individuals was large. Salmon sharks were

most aggregated and had the most northerly distribution during summer and autumn. Salmon sharks were most widely distributed across the eastern North Pacific during winter, encompassing waters from coastal Alaska to the Hawaiian Islands to northern Baja California. The maximum distribution of salmon sharks during this season resulted from some animals leaving coastal Alaska and embarking on southerly migrations into both pelagic and neritic waters. During spring, salmon sharks retained a distribution nearly as broad as during winter, but with an increase in the utilization intensity of the California Current region. Note that the most southerly movements of salmon sharks are most likely not represented by our data due to their submergence behavior while in subtropical waters (Weng et al. 2005). As a result, the distributions during winter and spring are likely to be even more southerly than shown here.

The use of different kernel density analysis techniques gave slightly different results for the seasonal distribution of salmon sharks. Using the complete dataset (n=68) showed high usage of waters near the tagging location, and low density in pelagic and southern regions. This result is biased toward the tagging location because the dataset contains many short tracks. By taking a subset of the dataset (n=34) comprising the longest tracks (average length 360 days) we were able to construct a kernel density analysis that represented all four seasons of the year. This version showed greater usage of waters distant from the tagging location, particularly the California Current region. Normalization of the dataset by the number of individuals in each area provided a sensitive measure of habitat utilization even if only a single individual was present in an area.

Variability in the timing, routing and destination of migration between individual sharks was large, indicating that the species probably does not undertake coordinated group migrations. Sharks initiated southern migrations across a wide range of the seasonal cycle, from 22 July to 8 March, and moved along paths toward Hawaii and Baja California and a wide range of intermediate directions. Sharks do not appear to migrate in order to avoid cold winter temperatures, as the wide variation in the timing of the southern migration means that many animals remain in subarctic waters during

the winter (Weng et al. 2005) and in some cases skip the southern migration for an entire annual cycle.

The differences in migratory behavior between sharks taking pelagic routes, and those taking neritic routes, is consistent with the contrast in productivity between neritic and pelagic waters of the eastern North Pacific. Salmon sharks that moved to neritic waters swam more slowly and remained for longer durations than sharks that moved to pelagic waters. Sharks undertaking neritic migrations that terminated in the California Current region likely encountered rich foraging regions that provided incentives to remain; and during their northward movements along the continental margin, their continued interaction with forage resources likely explains the slower northward migration speed of neritic migrators. Pelagic migrators spent more time in the Coastal Alaska Downwelling region than neritic migrators, potentially making up for the poorer resources they encountered during their southern movements.

Salmon sharks showed greater focal area behavior and habitat utilization intensity while in shallower waters and while nearer to the coast (Figure 3-23, Figure 3-24). These trends are most likely artifacts of the covariance of productivity with bathymetry and distance to the coast; productivity is most likely more important in the ecology of salmon sharks than the co-varying factors of bathymetry and distance to coast.

3.4.3 Utilization of ecoregions vs. productivity

Derived metrics of salmon shark foraging – speed straightness and first passage time – showed a correlation between the productivity of an ecoregion and the utilization intensity of salmon sharks. Speed was lowest in the Alaska Downwelling and California Current regions, and higher in the remaining regions; straightness was lowest in the Alaska Downwelling and California Current regions, and highest in the Subarctic Gyre and Transition Zone regions. The intermediate values of straightness in the subtropical gyre are increased by the fact that sharks turn around in this region since their migrations terminate here, leading to low straightness values. The highest values for first passage time occurred in the Alaska Downwelling and California Current regions, with intermediate values in the Subtropical Gyre and low values in the Subarctic Gyre and Transition Zone. Furthermore, the durations that salmon sharks spent in their southern destination regions were longer when sharks were in the neritic California Current region, and shorter when in pelagic waters of the Subtropical Gyre. Northern migration speeds were faster, and durations shorter, when salmon sharks moved north in pelagic waters, as compared to more productive neritic waters. The three metrics of salmon shark focal area behavior, as well as migration speeds and durations, agreed with the habitat utilization intensity estimates made using the kernel density method, allowing confidence in the conclusion that the most important habitats for salmon sharks are the Alaska Downwelling and California Current ecoregions.

The timing of salmon shark movements between the ecoregions of the eastern North Pacific shows some correlation between the seasonality of productivity in each ecoregion, but the correlation is not close. This may be explained by a number of factors: salmon sharks cannot be in all places all the time, so they may be required to forgo the peak season in one region if the benefit of being in another region at that time is greater; the seasonality of productivity in a region is not the same as the seasonality of prey species, due to trophic time lags and movements of prey species; or salmon sharks are fulfilling life history functions other than feeding during some parts of their migration cycle.

3.4.3.1 Coastal Alaska Downwelling Region

The primary focal area for salmon sharks is in the Coastal Alaska Downwelling region, where the 50% and 80% kernel density contours occurred during all seasons of the year. This ecoregion has the highest primary productivity of any ecoregion in the eastern North Pacific (Favorite et al. 1976). The high productivity of the Alaska Downwelling region results from the large supply of nutrients to the photic layer during spring and summer, as a result of high turbulence. This turbulence is created by the interaction of the Alaska Current with the continental shelf and coastal topography of the region, resulting in numerous eddies, filaments and jets that entrain nitrate rich waters from beneath the pycnocline and bring them into the photic zone (Okkonen 1992).

Salmon sharks have their lowest abundance in this ecoregion at the time of the spring bloom, but since they do not forage at the producer or low consumer trophic levels, there is no expectation that they would benefit directly from this productivity event. The increase in their utilization of the ecoregion through the summer and autumn is consistent with the flow of energy up the food web into trophic levels occupied by forage species such as herring, squid and demersal teleosts, which they are known to feed on during these seasons (Hulbert 2005). In addition, the maximum summer-autumn utilization of the ecoregion by salmon sharks coincides with the return of Pacific salmon to their natal rivers to spawn. Salmon aggregate in coastal waters near the mouths of rivers before embarking upon their upstream migrations, and during these staging periods are vulnerable to predation by salmon sharks (Hulbert and Rice 2002). Salmon sharks are known to be major predators of salmon (Nagasawa 1998) and are frequently observed feeding on them in Alaska waters.

During winter, the strength of the halocline prevents deep mixing in the coastal Alaska region, limiting the supply of nutrients to surface waters, and the short day length brings primary production to extremely low levels (Longhurst 1998). However, the lack of primary production does not mean that overwintering salmon sharks lack forage resources, and a variety of mid trophic level fishes remain in the region for the winter. Overwintering herring (*Clupea pallasi*) and walleye Pollock (*Theragra chalcogramma*) aggregate in nearshore bays, apparently because the slightly warmer thermal environment is more favorable than offshore waters or nearshore passages (Carlson 1980); (Stokesbury et al. 2000). These aggregated forage fishes may become vulnerable to salmon sharks, which maintain high body temperatures and activity patterns while in these cold waters (Goldman et al. 2004; Weng et al. 2005).

3.4.3.2 California Current

The California Current Upwelling ecoregion had the second highest utilization after coastal Alaska. The 50% kernel density contour occurred in this ecoregion during spring, and the 80% contour during spring, summer and autumn. This region is highly productive throughout the year as a result of the year-round availability of light at mid latitudes, and the supply of nutrients to the photic zone as a result of waters

entering the region from the West Wind Drift (Chelton et al. 1982) as well as strong wind driven upwelling. The southward flow of the offshore California Current includes extensive meandering, such that eddies spin off on both the seaward and landward sides, enhancing the mixing and nutrient supply, while interaction of the current with the coastal bathymetry leads to intense jets and plumes that entrain nutrients and carry them offshore (Burkov and Pavlova 1980). The dominant northwest winds of the region cause upwelling as a result of Ekman transport of surface waters away from the coast, bringing nutrients from below into the photic zone. The seasonal cycle of winds causes the most intense upwelling during spring and summer, with a relaxation during autumn and occasional reversals during winter than are accompanied by northward flow along the coast (Bolin and Abbott 1963). Higher productivity occurs in the California Current system when upwelling is intermittent, with pauses in upwelling allowing nutrients to be utilized by phytoplankton before being advected offshore. As a result, productivity lags behind upwelling such that summer and autumn have the highest productivity (Bolin and Abbott 1963).

The seasonality of habitat utilization by salmon sharks and the seasonality of productivity in the California Current region do not show close correspondence. The time of highest productivity, late summer and autumn, is also the time of minimum utilization by salmon sharks; whereas the low productivity in the spring corresponds to the peak utilization by salmon sharks. This asynchrony may result from tradeoffs in the foraging ecology of salmon sharks, in which they forego the optimum season in the California Current because the benefit of being in the Coastal Alaska Downwelling region at that time is greater. Alternately, it may indicate that the targeted forage species in the California Current region do not themselves occur in synchrony with seasonal changes in productivity. The region has large populations of teleost fishes including hake, anchovy, ocean whitefish, California barracuda, Pacific bonita, Pacific butterfish, mahi mahi, louvar, jack mackerel, Pacific mackerel, bullet mackerel, opah, Pacific sardine, white seabass, California sheephead, tunas, swordfish, wahoo and yellowtail (Hanan et al. 1993); and many elasmobranch fishes including bat rays,

pelagic rays, electric rays, mantas, angel sharks, blacktip sharks, blue sharks, cow sharks, dogfish, mako sharks, sevengill sharks, smoothhound, soupfin and thresher sharks (Hanan et al. 1993).

The spring timing of the peak utilization of the northern California Current region by salmon sharks may be related to the unusual life history of salmonids in this region. The run timing of salmonids is closely tied to river water temperatures and flow regimes (Miller and Brannon 1982). Whereas salmonids in Alaska and British Columbia typically undertake their upriver spawning runs once per year, during summer and fall when temperatures are warmer and flows higher (Burger et al. 1985), many rivers south of the Bella Coola and Fraser Rivers have multiple runs per year or early runs (Myers et al. 1998). The precipitation regime of Oregon and California means that some headwater spawning habitats are typically accessible to large spawning fish only during spring peak river flows (Kostow 1995). Salmon run during spring, summer and fall in many rivers of the region (Myers et al. 1998), and converge on coastal waters of Oregon and northern California prior to their run, potentially forming an important food source for salmon sharks that have migrated to the region from the north. The habitat suitability of the northern California Current region for salmon is broadest during spring (Hinke et al. 2005a), and the animals inhabit a narrow thermal range (Hinke et al. 2005a; Hinke et al. 2005b), potentially allowing the more eurythermal salmon sharks an advantage. In addition to the mature fish returning to the regions of their natal rivers, the spring season also sees the emigration of juvenile salmon from streams into the ocean, typically in their second or third year (Healey 1991), providing another large potential food source for salmon sharks.

3.4.3.3 Subarctic Alaska Gyre

The Subarctic Alaska Gyre was not used heavily by salmon sharks, as indicated by the fact that the 50% and 80% kernel densities contours did not extend into the ecoregion. The 95% contour extended into the region during all seasons. The Subarctic Alaska Gyre is intensely seasonal, with little light during the winter bringing primary production to extremely low levels. The high precipitation in the region causes a permanent halocline, which in turn results in a permanent pycnocline that

limits vertical mixing (Roden 1991). However, the intensity of storms during the winter season is able to bring nutrients into surface waters despite the strength of the pycnocline, such that when light becomes available primary productivity is moderate (Longhurst 1998).

The low usage of the ecoregion resulted from the high speeds of salmon sharks as they transited the region during both southward and northward migratory phases. Based on all measures of behavior – speed, straightness, first passage time and kernel density – salmon sharks rarely engaged in searching or focal behaviors in this ecoregion, particularly in the western portion. However, a wide range of potential prey species exist within the ecoregion, including smelts, capelin, euchalon, myctophids, bathylagids, sand lance, sandfish, gunnels and pricklebacks (Nelson 2003); and larger fishes including walleye pollock, Pacific cod, arrowtooth flounder, Pacific halibut, sablefish, big skate and Bering Skate (Yang et al. 2006). The rarity of focal area behavior within this ecoregion suggests that most salmon sharks in this study are using it for a non-feeding life history function, such as migration to more southerly foraging or parturition grounds.

3.4.3.4 Transition Zone

The Transition Zone ecoregion shows moderate primary productivity due to the availability of light at mid latitudes, combined with nutrient supply due to low stratification. The Transition Zone is formed by the margin between the two major wind regimes of the eastern North Pacific, the temperate Westerlies and the subtropical Easterlies, which, due to Ekman transport, cause a surface convergence throughout the region (Longhurst 1998). At its northern margin, typically 40–43°N, the subarctic front marks the southern edge of the Subarctic Gyre; to the north of this margin there is a strong halocline, whereas to the south in the Transition Zone itself the uniform salinity profile reduces density stratification. The southern margin of the Transition Zone is the subtropical front, typically at 28–35°N; to the south the waters of the Subtropical Gyre have high surface salinity and temperature, and strong stratification (Roden 1991). The reduced stratification of the Transition Zone is the

key factor that confers productivity to the region, with vertical mixing occurring in all seasons other than summer, bringing nutrients into the photic zone (Roden 1991). During summer, warming of the surface water cause enough reduction in density to establish a pycnocline, such that vertical mixing is shallower than the photic zone and nutrients become depleted.

The moderate productivity of the Transition Zone ecoregion makes it an important foraging region for a number of high trophic level pelagic vertebrates including turtles (Polovina et al. 2000), pinnipeds (Le Boeuf et al. 2000), fishes (Laurs and Lynn 1991) and squids (Pearcy 1991). The utilization of the Transition Zone by salmon sharks is known to be high based upon fishery catch data from high seas drift gillnets and longlines (Strasburg 1958; Nakano and Nagasawa 1996). In this ecoregion, salmon sharks are typically found in association with Pacific pomfret, Pelagic armorheads, Pacific salmon and various squid species, and may forage on these species (Pearcy 1991; McKinnell and Waddell 1993). The utilization of the Transition Zone by salmon sharks in the present study is low: the 50% kernel density contour never extends to the region, while the 80% contour occurs in small regions during spring, and the 95% contour occurs over small areas in the remaining seasons. This apparent contradiction may be explained by the fact that the salmon sharks reported in the above studies were predominantly juveniles, while the individuals reported in the present study are mature females, and salmon sharks may show ontogenetic changes in range and habitat utilization. As a result, the sharks in this study may be fulfilling different life history functions while in the region; in particular, if their primary purpose were not feeding then they would not necessarily be expected to respond to food resources (Dingle 1996).

3.4.3.5 Subtropical Gyre

The utilization of the Subtropical Gyre ecoregion by salmon sharks in this study was the lowest of all the ecoregions occupied. This is consistent with the low productivity of the system, resulting from strong density stratification that limits vertical mixing and nutrient supply (Roden 1991), keeping primary production low despite the large amount of available light. The Subtropical Gyre shows the lowest

seasonality of all the ecoregions occupied by salmon sharks, lacking major seasonal signals in productivity and chlorophyll (Longhurst 1998). Salmon sharks rarely showed focal area behaviors while in this ecoregion, and frequently initiated northern movements immediately after reaching their southernmost position, suggesting a non-feeding purpose for their movements into the region.

3.4.4 Life history functions of migration

The migrations of salmon sharks may occur for purposes of mating, parturition or foraging. All salmon sharks tracked in this study were reproductively mature females (Goldman and Musick 2006), allowing for the possibility of both mating and parturition. Alternately, mating could occur during autumn, which is thought to be the mating season in the western North Pacific (Nagasawa 1998). Both males and females occur in Alaska waters during autumn (Hulbert 2005) and fresh bite marks have been observed on females during this season, suggesting recent mating events (Goldman and Human 2005). Due to the sexual segregation of salmon sharks in the north Pacific (Sano 1960; Nagasawa 1998; Goldman and Musick 2006), with more females occurring to the east, and more males to the west, mating on the southern migration would likely require than males undertake a long movement from the western North Pacific to the subtropical eastern North Pacific, a distance greater than the movements undertaken by the females in this study.

Parturition on the southern migration, which is at its maximum extent during spring, is consistent with the springtime parturition of salmon sharks in the Western Pacific (Nagasawa 1998). The region in which young-of-the-year salmon sharks are reported includes a broad band across the Transition Zone (Nakano and Nagasawa 1996), as well as the continental margin of North America from the Alaska panhandle to northern Baja California (Goldman and Musick 2006), and these may be distinct parturition areas (Goldman and Musick In press). The highest concentration of young-of-the-year salmon sharks was reported during spring in California (Goldman and Human 2005), coinciding with the highest springtime abundance of adult female salmon sharks in this study. The spring timing of these movements may be advantageous to the young, as the initiation of upwelling starts at this time, leading to

a high productivity nursery region. The emigration of juvenile salmon to the sea may also be an important food resource for juvenile salmon sharks, in addition to the abundance of other forage fishes in the region.

Our results indicate that the Subtropical Gyre is not an important foraging region for salmon sharks, indicating that another life history function such as parturition may occur here. Female salmon sharks visiting the Subtropical Gyre undertake a longer migration that those visiting the California Current, yet remain in the area for short periods of time. The nursery region proposed by (Nakano and Nagasawa 1996) occurs along the boundary between the Subarctic Gyre and the Transition Zone, but the juvenile animals they observed were larger than young-of-the-year size, so it remains possible that parturition occurs in the Subtropical Gyre and neonates later swim north into the Transition Zone nursery. However, it does not seem necessary that females would have to swim as far south as the Subtropical Gyre in order to provide warm waters for their young, given that young-of-the-year salmon sharks are found in the California Current region where temperatures are typically cooler than 14°C.

The ability to undertake long distance migrations allows animals to integrate the resources regions that are separated in space and time, potentially conferring an ecological advantage over species that remain within a particular region throughout seasonal or ontogenetic timescales. Salmon sharks can alternate between the two most productive ecoregions of the eastern North Pacific – coastal Alaska and the California Current – potentially gaining an ecological benefit by integrating the available resources. Pacific bluefin tuna spawned near Japan and Taiwan are able cross the entire Pacific to take advantage of the rich resources of the California Current before returning to the western North Pacific as adults (Bayliff et al. 1991), and the number of bluefin that make this crossing appears to be related to the abundance of forage resources near Japan (Polovina 1996). The white shark makes long distance seasonal migrations between the coast of California and a region of the Subtropical Gyre midway between Baja California and Hawaii, though the life history functions of this migration are as yet unknown (Boustany et al. 2002; Weng et al. In review). The lamnid sharks and tunas, though related only in the very distant geological past, both

share a suite of adaptations to endothermy that increase the power of their muscles (Bernal et al. 2005) and may enable them to undertake these long migrations (Weng et al. 2005).

The long distance migrations of many marine birds, mammals and reptiles appear to occur because they have highly specific requirements for breeding and parturition, in areas that are distant from their foraging grounds (Gilmore 1960; Serventy 1967; Le Boeuf and Laws 1994; Morreale et al. 1996). Looked at another way, we may consider these animals capable of taking advantage of rich forage resources that are distant from their parturition areas, whereas less vagile species must forage near their parturition grounds. It appears that some teleosts and elasmobranch fishes, particularly with the endothermic lamnid and tuna groups, have also evolved these highly migratory strategies, though their precise life history functions remain to be elucidated.

latitude RMS error (km)	longitude RMS error (km)
163	99
4.6	7.21
5.23	7.79
4.915	7.5
0.157	0.295
0.12	0.32
0.1385	0.3075
0.030	0.076
0.001	0.003
	latitude RMS error (km) 163 4.6 5.23 4.915 0.157 0.12 0.1385 0.030 0.001

Table 3-1. RMS errors by positioning technique

Shark	TL							Mean	Max	
ID	(cm)	Start	End	Duratio	nNorthern	Southern	Positions/d	gap	Gap	Destination
37375	236	8-Sep-02	14-Nov-03	432	60.49	28.50	0.55	1.82	62	CC
37376	214	15-Jul-02	21-Mar-03	249	60.65	26.92	0.93	1.08	6	CC
37378	234	16-Jul-02	7-Jul-04	722	60.79	36.79	0.33	3.02	76	CC
37380	236	17-Jul-02	17-Apr-04	640	60.76	29.56	0.25	3.95	82	SubTropical
37381	225	18-Jul-02	14-Jan-03	180	60.53	26.64	0.92	1.10	6	CC
37382	244	7-Sep-02	28-Mar-04	568	60.51	31.84	0.37	2.73	113	SubTropical
37383	226	16-Jul-02	18-Jun-03	337	60.71	26.67	0.58	1.74	35	SubTropical
41665	236	7-Sep-03	23-Dec-05	838	60.85	36.78	0.35	2.88	129	CC
41666	231	14-Sep-03	2-Aug-04	323	60.74	38.26	0.79	1.27	14	CC
41667	234	20-Aug-03	27-May-04	281	60.73	30.96	0.25	4.07	106	SubTropical
41670	226	19-Aug-03	27-Apr-05	617	60.65	28.79	0.69	1.45	17	SubTropical
41672	223	3-Sep-03	5-Jun-04	276	60.90	55.43	0.38	2.65	40	Overwinter
41675	237	11-Sep-03	2-Jul-04	295	60.43	22.27	0.57	1.76	65	SubTropical
41679	234	21-Aug-03	9-Mar-06	931	60.78	29.76	0.61	1.65	24	SubTropical
52139	206	13-Jul-04	3-Apr-06	629	60.69	30.35	0.68	1.48	14	CC
52141	241	13-Jul-04	3-Apr-06	629	60.69	30.36	0.31	3.19	66	SubTropical
52142	233	13-Jul-04	31-Jul-05	383	60.75	38.11	0.59	1.69	42	CC
52146	236	20-Sep-04	27-Mar-06	553	60.79	34.06	0.28	3.61	92	CC
52149	220	12-Nov-04	17-Jul-05	247	59.77	32.89	0.78	1.29	10	CC
52151	239	18-Jul-04	2-Apr-06	623	60.47	39.14	0.37	2.70	85	SubTropical
52152	232	16-Jul-04	8-May-05	296	60.68	54.15	0.33	3.08	30	Overwinter
52153	230	15-Jul-04	2-Apr-06	626	60.72	37.01	0.58	1.72	56	CC
52154	237	11-Jul-04	3-Apr-06	631	60.71	27.60	0.54	1.85	72	CC
52155	240	11-Jul-04	2-Apr-06	630	60.71	27.47	0.52	1.94	40	CC
52941	252	4-Aug-04	23-Apr-05	262	60.74	28.56	0.44	2.28	63	SubTropical
59680	218	22-Aug-05	3-Apr-06	224	60.74	29.83	0.71	1.41	12	CC
59684	228	22-Aug-05	18-Feb-06	180	60.73	35.12	0.54	1.86	70	CC
59685	226	24-Aug-05	3-Apr-06	222	60.11	32.84	0.70	1.44	8	CC
59688	220	22-Aug-05	18-Mar-06	208	60.73	35.48	0.49	2.06	32	CC
59689	229	24-Aug-05	20-Mar-06	208	59.93	36.32	0.59	1.70	10	CC
59692	209	31-Aug-05	3-Apr-06	215	59.76	53.25	0.38	2.69	64	Overwinter
59697	227	24-Aug-05	28-Mar-06	216	60.73	28.38	0.43	2.37	54	SubTropical
59703	223	23-Aug-05	3-Apr-06	223	60.73	36.88	0.54	1.87	34	SubTropical
59706	230	31-Aug-05	31-Mar-06	212	60.18	29.36	0.88	1.14	6	CC
max	252			931	61	55	0.9	4	129	
min	206			180	60	22	0.2	1	6	
median	231			310	61	31	0.5	2	41	
Q1	225			223	61	29	0.4	2	15	
Q3	236			625	61	37	0.7	3	69	

Table 3-2. Salmon sharks tracked in the eastern North Pacific Ocean, 2002-2006

Gap in south	Ends during migration	Complete migration	Complete overwinter
37375	37376	37382	41672
37380	37378	37383	52152
41667	37381	41665	59692
41675	41666	41670	
52141	59680	41679	
52146	59684	52139	
52941	59688	52142	
	59697	52149	
	59703	52151	
	59706	52153	
		52154	
		52155	
		59685	
		59689	

Table 3-3. Degree to which salmon shark movements were captured by SPOT data



Figure 3-1. RMS errors for a variety of positioning methods and filters



Figure 3-2. Signal: Noise ratios in various studies of pelagic fish movement



Figure 3-3. Scale or RMS position error in relation to maximum animal movement distance in various studies of pelagic fish movement



Figure 3-4. RMS errors in daily speed introduced by different positioning techniques compared to maximum speed of salmon sharks



Figure 3-5. Seasonality of temperature in the eastern North Pacific during 2004-5



Figure 3-6. Seasonality of Chlorophyll-a in the eastern North Pacific during 2004-5



Figure 3-7. Seasonality of primary productivity in the eastern North Pacific during 2004-5



Figure 3-8. Occurrence of salmon sharks in the major ecoregions of the eastern North Pacific: Coastal Alaska Downwelling Region (green), California Current Upwelling Region (magenta), Subarctic Gyre (cyan), Transition Zone (blue) and Subtropical Gyre (red).



Figure 3-9. Migration of salmon sharks in the eastern North Pacific to (a) neritic and (b) pelagic destinations. Color denotes speed in km/day.



Figure 3-10. Kernel density of salmon shark (n=68) daily positions during 2002-2006. Color scale shows seasonal change in habitat utilization intensity of salmon sharks, while the complete range during each season is shown by the minimum convex polygon.



Figure 3-11. Kernel density of salmon shark (n=34) daily positions during 2002-2006. Color scale shows seasonal change in habitat utilization intensity of salmon sharks, while the complete range during each season is shown by the minimum convex polygon.



Figure 3-12. Number of individual salmon sharks (n=34) per 1° cell during 2002-2006.


Figure 3-13. Kernel density of salmon shark daily positions during 2002-2006 (n=34). Color scale shows seasonal change in habitat utilization intensity of salmon sharks.



Figure 3-14. Kernel density of salmon shark daily positions divided by number of individuals during 2002-2006 (n=34). Color scale shows seasonal change in habitat utilization intensity of salmon sharks; dividing by the number of individuals highlights regions where a small number of individuals spent larger amounts of time, while reducing density in regions inhabited by large numbers of salmon sharks.



Figure 3-15. Daily movement rate for all salmon sharks (n=34). Color denotes speed in km/day.



Figure 3-16. Speed of salmon sharks vs. primary productivity. Color denotes number of observations.



Figure 3-17. Speed distributions of salmon sharks in the major ecoregions of the eastern North Pacific Ocean.



Figure 3-18. Track straightness for all salmon sharks. Straightness is denoted by color, on a dimensionless scale (1 =straight line), calculated using the method of Batschelet (1981).



Figure 3-19. Track straightness distributions of salmon sharks in the major ecoregions of the eastern North Pacific Ocean.



Figure 3-20. First passage time for all salmon sharks, denoted by color in days. First passage time is a measure of area-restricted searching (Fauchald and Tveraa, 2003).



Figure 3-21. First passage time vs. distance to coast for all salmon sharks. Color denotes number of observations.



Figure 3-22. First passage time distributions of salmon sharks in the major ecoregions of the eastern North Pacific Ocean.



Figure 3-23. Speed, first passage time and straightness of three salmon sharks in pelagic, neritic and combined pelagic-neritic migrations. Speed is in km/day, first passage time in log(days) and straightness in a dimensionless index (1 = straight line).



Figure 3-24. (a) Speed of salmon sharks while in neritic and pelagic waters and (b) primary productivity of neritic and pelagic waters inhabited by salmon sharks. Boxplots are: centerline, median; edges of box, 1st and 3rd quartiles; whiskers, data points within the range Q1 - 1.5(Q3-Q1) to Q3 + 1.5(Q3-Q1).



Figure 3-25. Seasonality of utilization (bars) of the Coastal Alaska Downwelling Region compared to monthly median chlorophyll-a concentration in $\log mg/m^3$ (green) and primary production in $mgC/m^2/day$ (blue).



Figure 3-26. Hovmöller diagrams showing temporal changes in temperature (°C), chlorophyll-a (log mg/m³), primary production (mgC/m²/day) and surface height deviation (m) in the Coastal Alaska Downwelling Region at 58°N.



Figure 3-27. Seasonality of utilization (bars) of the Subarctic Alaska Gyre compared to monthly median chlorophyll-a concentration in $\log mg/m^3$ (green) and primary production in $mgC/m^2/day$ (blue).



Figure 3-28. Hovmöller diagrams showing temporal changes in temperature (°C), chlorophyll-a (log mg/m³), primary production (mgC/m²/day) and surface height deviation (m) in the Subarctic Alaska Gyre at $51^{\circ}N$



Figure 3-29. Seasonality of utilization (bars) of the Transition Zone compared to monthly median chlorophyll-a concentration in $\log mg/m^3$ (green) and primary production in $mgC/m^2/day$ (blue).



Figure 3-30. Hovmöller diagrams showing temporal changes in temperature (°C), chlorophyll-a (log mg/m³), primary production (mgC/m²/day) and surface height deviation (m) in the Transition Zone at $37^{\circ}N$



Figure 3-31. Seasonality of utilization (bars) of the California Current ecoregion compared to monthly median chlorophyll-a concentration in $\log mg/m^3$ (green) and primary production in $mgC/m^2/day$ (blue).



Figure 3-32. Hovmöller diagrams showing temporal changes in temperature (°C), chlorophyll-a (log mg/m³), primary production (mgC/m²/day) and surface height deviation (m) in the California Current Upwelling Region at 40°N



Figure 3-33. Seasonality of utilization (bars) of the Subtropical Gyre ecoregion compared to monthly median chlorophyll-a concentration in $\log mg/m^3$ (green) and primary production in $mgC/m^2/day$ (blue).



Figure 3-34. Hovmöller diagrams showing temporal changes in temperature (°C), chlorophyll-a (log mg/m³), primary production (mgC/m²/day) and surface height deviation (m) in the Subtropical Gyre at $20^{\circ}N$



Figure 3-35. Distribution of gaps exceeding 20 days in length in the movement records of 34 salmon sharks used for kernel density analysis



Figure 3-36. Distribution of gaps exceeding 10 days in length in the movement records of 34 salmon sharks used for kernel density analysis



Figure 3-37. Distribution of gaps exceeding 4 days in length in the movement records of 34 salmon sharks used for kernel density analysis



Figure 3-38. Latitudinal distribution of salmon sharks. (a) Observed number of days, (b) missing data, (c) fraction of days observed and (d) distribution corrected for missing data.



Figure 3-39. Distribution of salmon sharks according to raw data (white) and data corrected for missing observations (black).

4 Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern North Pacific Ocean²

4.1 Introduction

The sharks of the family Lamnidae are apex pelagic predators that range into temperate, tropical and polar oceans (Compagno 1984), and comprise the shortfin mako shark (*Isurus oxyrhincus*), the longfin mako shark (*Isurus paucus*), the white shark (*Carcharodon carcharias*), the salmon shark (*Lamna ditropis*) and the porbeagle shark (*Lamna nasus*) (Compagno 1984). The Lamnidae are unique among sharks due to the presence of counter-current heat exchangers, centralized slow-twitch muscle and elevated metabolic rates. These physiological attributes enable these sharks to maintain warm body temperatures (Carey et al. 1982; Graham et al. 1990), which may underlie many of their ecological traits, including wide thermal tolerance, high performance swimming (Bernal et al. 2005), niche expansion into northern latitudes (Weng et al. 2005), and the ability to capture marine mammals (Ainley et al. 1985).

White sharks live in temperate and tropical waters with a distribution that spans coastal to pelagic habitats. Adult white sharks feed on fishes and marine mammals (Compagno 1984). Aggregations of white sharks near pinniped rookeries have been documented in a number of areas, including northern California (Ainley et al. 1985), southern Australia (Bruce 1992), eastern Canada (Brodie and Beck 1983) and South Africa (Ferreira and Ferreira 1996). White sharks have been observed poleward of 50° in both hemispheres and in tropical waters (Compagno 1984). Conventional tagging studies have shown movements up to 1445 km from the point of release (Kohler and Turner 2001), while photographic identification of individual sharks has revealed movements of 700 km (Anderson and Goldman 1996). Acoustic tracking

² The content of this thesis chapter is based on a manuscript that is in review at the journal Marine Biology: Weng et al., Migration and Habitat of White Sharks (*Carcharodon carcharias*) in the Eastern Pacific Ocean.

studies have shown that white sharks have average stomach temperature elevations of 10.8°C in 15 to 18°C waters (Goldman 1997).

Recent satellite tracking studies have rapidly expanded our knowledge of the horizontal movements and diving behaviors of white sharks. Satellite tags placed on adult white sharks in the Pacific and Indian Oceans (Boustany et al. 2002; Bonfil et al. 2005; Bruce et al. 2006) have provided new detail of the long-range movements and vertical habitat distribution. Boustany et al. (2002) demonstrated that white sharks tracked from the central California coast moved into an offshore region between Hawaii and Baja, as well as to the Hawaiian Islands. Bonfil et al. (2005) reported a transoceanic migration from South Africa to western Australia and back, as well as fine-scale coastal movements in South Africa and Mozambique. Bruce et al. (2006) showed that white sharks make long distance movements along the west, south and east coasts of the Australian continent, and reported one shark moving from South Australia to the north island of New Zealand. These studies rejected the widely held belief that white sharks were coastal or neritic, and raised a number of new questions about their behaviors and life history, including the purposes of nearshore and pelagic phases, the portions of the year spent in each habitat, and the predictability of long distance movements.

In California, white sharks are known to aggregate at pinniped rookeries during autumn (September–November) and winter (December–February) when the abundance of immature elephant seals is at a maximum (Ainley et al. 1985). Their absence from these rookeries during the spring (March–May) influx of elephant seals was thought to be a result of mature sharks moving into the Southern California Bight to mate or give birth (Klimley 1985). Parturition in the Southern California Bight is supported by the existence of young-of-the-year sharks in that region (Klimley 1985; Weng et al. In press), but no pregnant females have ever been observed there (Francis 1996). The results of Boustany et al. (2002) were not consistent with this hypothesis, and suggested the possibility of offshore movements for parturition, mating, and foraging. Anderson and Pyle (2003) found that females return to the Farallones on a

two-year cycle, while males return annually, and speculated that females may travel large distances to give birth.

The discovery that top-down processes can have fundamental structural impacts on ecosystems (Hunter and Price 1992) highlights the need to understand the biology of apex predators such as the white shark. The use of new electronic tagging technologies to track pelagic animals has yielded numerous insights into the biology of species such as salmon sharks (Weng et al. 2005), bluefin tuna (*Thunnus thynnus*) (Block et al. 2005), elephant seals (Mirounga angustirostris) (DeLong et al. 1992) and marine birds (Weimerskirch et al. 2002). Enhanced knowledge of the long-range movements and aggregation areas of pelagic species will improve our understanding of their life history, and of their relations to the physical and biotic environment. This knowledge is essential to the management of white shark populations, which are threatened globally (Stevens et al. 2000). White sharks, while protected along the California coast, are considered a threatened species and it is essential to obtain information on the critical habitat utilization for future management efforts. In this paper we investigate the seasonal movements of eastern North Pacific white sharks, compare their utilization of neritic and pelagic waters, and discuss the biological functions that they may be fulfilling in these distant habitats.

4.2 Materials and methods

4.2.1 Satellite telemetry of sharks

White sharks were tagged at Southeast Farallon Island (37.70°N, 123.00°W), which lies 30 km west of the entrance to San Francisco Bay, California, USA. Pop-up archival transmitting tags (PAT tag firmware versions 2.0, 3.0 and 4.0; Wildlife Computers, Redmond, Washington, USA) were deployed on white sharks during the autumn months of 1999-2004. Each PAT tag was attached to a titanium dart with a 20 cm segment of 136 kg monofilament line (300 lb test Extra-hard Hi-catch, Momoi Manufacturing, Japan) coated with shrink-wrap. The titanium dart was custom-made, measuring 59 mm x 13 mm x 1.5 mm, with the trailing 10 mm canted at a 17° angle. The dart was inserted 17 cm into the dorsal musculature of the shark at the base of the

first dorsal fin using a 2 m aluminum pole. Sharks were not captured, but were tagged during predatory events as they swam near the research boat, a 4.3 m whaler. No chum was used to attract sharks. Sizes were estimated and underwater and above water video and photos were taken to determine sex and aid in visual identification of individual sharks.

PAT tags remain attached to a study animal for a pre-determined duration, and then activate a release mechanism via electrolysis. The tag's syntactic foam float lifts it to the surface, and the PAT tag transmits data to the Argos satellite system. PAT tags in this study were programmed to archive depth, temperature and light level data at 1- or 2-minute intervals. If the tag was recovered it was possible to download the entire archival dataset. The archival data were compressed into bins of 12 or 24 hours for transmission to Argos satellites. For each time period the tag produced a depthtemperature profile and two histograms, one of time-at-depth and one of time-at temperature. In addition, 12 light level data points were transmitted for both dawn and dusk of each day.

4.2.2 Data recovery

Of the 29 PAT tags deployed, 20 successfully transmitted data on the movements and habitat preferences of white sharks. Three PAT tags were recovered (2-M, 17-U and 18-F) and the full archival tag records obtained (525 d total). The PAT tag on white shark 2-M detached and transmitted from waters near the Farallon Islands, California, drifted to shore and was found, yielding a 26 d archival record. Tag 17-U popped up and transmitted from waters near Año Nuevo, California and was recovered at sea, yielding a 305 d archival record. Tag 18-F never transmitted, and was found near Sea Ranch, California, yielding a 194 d archival record. Subsequent analysis revealed that the battery of tag 18-F failed during the track.

For all 20 sharks, the tracking duration (the time the PAT tag remained attached to the shark) averaged 167 ± 96 d with a maximum tracking period of 367 d. We obtained 19 satellite tag endpoint locations from Argos, and 906 geolocations based on light-based longitudes and SST-based latitudes, of which 395 were obtained from archival records. Including the known deployment locations, the total location dataset

includes 945 positions. Visually estimated total lengths (TL) for the sharks in this study averaged 443 ± 49 cm. Using TL maturity thresholds of 3.8 m for males (Pratt 1996) and 4.5 m for females (Francis 1996), we estimate that 68% of the sharks we tracked were sexually mature, comprising nine males, three females and one of unknown sex larger than the female threshold. Of the remaining sharks, one was an immature male, three were immature females and two were of unknown sex. Three of the 20 sharks in this study (1-M, 2-M and 3-M) were included in an earlier publication (Boustany et al. 2002).

4.2.3 Analysis

To determine the movements of each shark, we estimated longitude for each day based on threshold techniques for assessing position with ambient light levels (Hill and Braun 2001). Latitude was estimated for each day by comparing sea surface temperature measured by the tag with that measured by satellite sensors along the light-based longitude estimation (Teo et al. 2004). A speed filter of 2 m s⁻¹ was used to discard points requiring movements that were not biologically feasible, based on published speeds from electronic tagging studies for white sharks of 1.2 m s^{-1} (Klimley et al. 2001a) and 1.3 m s⁻¹ (Bonfil et al. 2005). Teo et al. (2004) estimated the root mean square (RMS) error of light-based longitude to be within 0.89 degrees, and the RMS error of SST-based latitude to be within 1.54 degrees, for double tagging experiments (PAT and SPOT) on salmon sharks and blue sharks. We also directly estimated errors for white sharks in this study by comparing known deployment or endpoint locations to light/SST geolocations up to one day away (Table 2-2). For the purposes of error estimation we did not use a speed filter, so as to avoid artificially reducing errors. The straightness of tracks was calculated using the method of (Batschelet 1981), in which the straightness index is the ratio of the straight distance between two points and the actual path traveled between them, such that a straight line has a value of one. Straightness was calculated only for the tracks of the two sharks with archival records that moved offshore. Sharks with transmitted records had insufficient positions to calculate straightness with confidence.

The habitat use of white sharks was quantified using the kernel density method (Silverman 1986) implemented in the Animal Movement extension (Hooge and Eichenlaub 1997) for ArcView 3.2 (ESRI, Inc., Redlands, California, USA). Kernel densities were calculated for each meteorological season using a search radius equal to the mean latitude position error for our tags (1.73°). Variability in the temporal frequency of positions can bias density estimation (Aebischer et al. 1993) so we regularized our tracks to one position d⁻¹. We used the piecewise cubic hermite interpolating polynomial (Matlab, The Mathworks, Natick, MA, USA), which had the highest accuracy of available methods in a recent study (Tremblay et al. 2006). Kernel density was presented as percent of all positions, with 25%, 50% and 95% contours overlaid on color-mapped data. The 25% contour was used to highlight core regions of occupancy, while 50% and 95% contours showed regions of decreasing usage.

We classified our data into five phases according to the movements of the sharks: nearshore, traveling, in the offshore focal area, near Hawaii, traveling to the south of Hawaii, and in an offshore focal area south of Hawaii. Sharks were considered to be nearshore from the date of tagging until they dove to 200 m or greater and were thus off the continental shelf, signifying departure. A dive threshold was used rather than light/SST geolocation because dive data were more temporally continuous than geoposition data. Sharks were considered to be traveling while their longitude-time trajectory showed monotonic westward motion, and to have reached their destination, either in the offshore focal area or near Hawaii, at the first inflection in this trajectory. The straight distance between the departure and arrival positions was used to determine speed, which was thus an estimate of minimum speed. Longitude was used as an indicator of migration rather than position, because we obtained far fewer latitudes than longitudes, and thus had fewer positions than longitudes. Sharks were considered to be offshore or near Hawaii until another monotonic movement eastward occurred.

We characterized the depth and temperature preferences of the sharks using the histograms transmitted by PAT tags, which aggregated all observations into

preprogrammed intervals. The means and standard deviations for each interval were calculated from the mean values at that interval for each shark, such that error bars represent variation between individuals. Distributions were Gaussian, so comparisons are made with parametric Student's t-tests.

Estimates of surface mixed layer depth, Z_{ML} , were made using the temperature, *T*. We used pressure-temperature data collected by the tags to determine the local maximum in the second derivative of the depth-temperature profile, C_{ZT} , (Brainerd and Gregg 1995), given by

$$C_{ZT} = \frac{d(dT/dZ)}{dZ}$$
 and $Z_{ML} = Z$ at max{ C_{ZT} }

Where archival records were available we then calculated the amount of time sharks spent within the surface mixed layer and below it. Where transmitted records were available such calculations were not possible since depth and temperature occupancy data were aggregated into predetermined intervals that did not correspond to mixed layer depth.

For the three sharks with archival records (2-M, 17-U and 18-F), more detailed analyses were possible, so we assigned measurements to diel periods based on the light record (Weng et al. In press), and characterized the depth and temperature preferences of the sharks during these periods. Vertical excursions were the greatest depths reached every 1/10th of an hour. Due to the non-Gaussian distribution of the data, we use median (1st quartile–3rd quartile) to summarize the results, and the nonparametric Wilcoxon rank sum test for comparisons. We compared behavior across the five movement phases defined above.

The migration route was characterized in terms of factors that could potentially aid in navigation, such as bathymetry, magnetism and gravity. Bathymetry data were obtained from (Smith and Sandwell 1997). Gravity data were obtained from (Sandwell and Smith 1997). Magnetic declination and inclination data were obtained from (Peddie 1993), while magnetic anomaly data were obtained from (Bankey et al. 2002). Data were imported into ArcGIS version 9 for comparison with shark movements.

4.3 Results

4.3.1 Timing of movements and focal areas

We obtained 3336 d of observation for 20 white sharks tagged off the central California coast. The geolocation data alone provide evidence for a seasonal pattern of nearshore residency during autumn and winter, followed by a pelagic phase during spring and summer (June–August), in which sharks move as far west as the Hawaiian archipelago (Figure 4-1). Offshore movements away from the coast of California were recorded for 15 sharks (Figure 4-2). A single individual (17-U) was tracked from the tagging location near the Farallon Islands to an offshore focal area between the Baja Peninsula and Hawaii, and back to the coast of California, over a period of 305 d. Eleven sharks moved to an offshore region, southwest of the deployment position, approximately 2500 km west of the Baja Peninsula. Four sharks traveled to waters near the main Hawaiian Islands. One shark was moving offshore from the California coast when the tag released. The remaining four sharks were tracked for durations of 14 to 67 d and remained near the coast over the tracking period.

All 20 electronically tagged white sharks remained near the coast of California for a period of time after tagging. During this period, sharks inhabited waters ranging from $32-38^{\circ}N$ and from the coast of California to $125^{\circ}W$. For the 15 sharks that undertook offshore migrations, the duration of the nearshore phase was 57 ± 35 d. Four sharks had the tags release and transmit while the individuals were still near the coast, while a fifth (12-M) did not transmit position data, so the duration of the nearshore phase for these sharks could not be determined. Sharks were in nearshore waters for unknown duration prior to tagging, so these results underestimate the duration of the nearshore phase. One shark was tracked through a full return migration (17-U), so we recorded the date of its arrival back at the coast of California, and if we assume that it departed on the same date as the previous year, its coastal phase would be 117 d.

Offshore migrations for the 15 sharks that departed the coast began on a mean date of 2 January (earliest 19 November, latest 24 March). Female sharks (n=4)

embarked on migrations on a mean date of 15 February (earliest 25 December, latest 24 March), later than male sharks (n=8), which departed on a mean date of 11 December (earliest 19 November, latest 23 January), but the difference was not significant (Student's t-test: t = 2.36, p = 0.07).

The dates on which sharks (n=15) initiated offshore migrations followed periods of decreasing pinniped abundance at Southeast Farallon Island (Figure 4-9), and the abundance on those dates was significantly lower than the median abundance during the month preceding the departure (Wilcoxon rank sum test, h = 1, p = 0.03).

Movements of white sharks to an offshore focal area 2500 km west of Baja California, centered at 23°N, 134°W, and ranging from 18–26°N and 125–140°W, were undertaken by male and female, and mature and immature sharks (Table 4-1). Sharks arrived at the offshore focal area between 2 December and 12 April, with a mean date of arrival of 28 January over all years. Female sharks arrived on 8 March (earliest 11 January, latest 12 April), while male sharks arrive significantly earlier on 30 December (earliest 1 December, latest 21 February) (Student's t-test: t = 3.07, p = 0.02).

All sharks but one (17-U) were located in the offshore focal area when their tags released, 109 ± 58 d later. The longest offshore residency in this area was 167 d (shark 9-M). The offshore migrations to the focal area traversed straight-line distances of 1961 ± 406 km over 23 ± 5 d at an average minimum speed of 88 ± 14 km d⁻¹ (0.23 ± 0.05 TL s⁻¹). The fastest migration (14-M) occurred at a minimum speed of 119 km d⁻¹ (0.30 TL s⁻¹).

Return migration to foraging areas on the coast of California was exhibited by a single shark (17-U) that was tracked for 305 d. This shark was tagged at the Farallones on 5 November 2004, remained near the coast for 103 d, and embarked on the westward migration on 16 February 2005. Its movement to the offshore focal area covered a straight-line distance of 2234 km, and took 27 d at an average speed of 90 km d⁻¹. It remained in the offshore focal area for 137 d before initiating its return migration to the North American coast on 31 July 2005, which occurred in 22 d, at an average speed of 75 km d⁻¹. The shark inhabited shallow nearshore waters between
35–38°N from 21 August 2005 until the tag released and transmitted on 6 September 2005, 10 km from Año Nuevo Island.

Directed movements to waters near the Hawaiian Islands were undertaken by four white sharks, along routes that did not pass through the offshore focal area, and included male and female, mature and immature sharks. Sharks occupied waters from 18–23°N and 154–163°W. The migration to the islands covered 3713 ± 56 km and occurred in 37 ± 2 d at 101 ± 6 km d⁻¹ (0.27 \pm 0.03 TL s⁻¹) (*n*=3). Sharks remained near the Islands of Kauai, Maui, Lanai, Kahoolawe and Hawaii for 62 ± 50 d. One shark (3-M) inhabited these waters from 26 December 2000 until its tag released 122 d later on 16 April 2001, when it was in the Kealaikahiki Channel between Kahoolawe and Lanai (Boustany et al. 2002), 11 km from Lanai. Another shark (4-M) inhabited waters of Molokai and Maui for 61 d from 15 January-17 March 2002, before heading east from the Islands into the offshore focal area, the only shark that visited both offshore aggregation areas. The tag on a third shark (12-M) released and transmitted 5 km from the north shore of Maui near Paia on 23 June 2004. Shark 18-F utilized waters near Lanai and Kahoolawe for 13 d from 22 March - 4 April 2005, before moving south to a region 700 km to the south of the island of Hawaii (Fig. 1). This southern migration extended to 11°N, and the traveling period lasted eight d, with a speed of 87 km d^{-1} (0.26 TL s⁻¹). It was in these waters 57 d later when the battery failed.

The kernel density analysis (Figure 4-2) indicates that white sharks (n=15) were aggregated near the Farallones in the autumn and early winter, and in the offshore focal areas in the spring and summer. During autumn the 25% utilization contour area was centered on the nearshore Central California region ($37.3^{\circ}N$, $123.2^{\circ}W$), and the 50% contour ranged from $35.3-39.2^{\circ}N$ and from the coast to $125.1^{\circ}W$. During the winter the 25% contour core area remained in central California (centered at $36.0^{\circ}N$, $123.0^{\circ}W$) but the 95% contour outlined an elongated band of waters oriented northeast to southwest, 450 to 700 km wide and 1700 km long, a corridor used by the sharks during their offshore migration. The 50% contour showed the early phase of residency in the offshore focal area ($23.1^{\circ}N$, $134.1^{\circ}W$), while a sub-region outlined by

the 95% contour showed occupancy of Hawaiian waters, extending southward to 11.1°N. In spring, the 25% density core region was centered in the offshore focal area (23.7°N, 133.6°W), with a subregion of the 95% contour around Hawaii and extending to 12.9°N, and a smaller subregion of the 95% contour in central California (34.9°N, 123.0°W). In summer, the core 25% contour region remained offshore (22.4°N, 132.0°W) but was connected to central California by an elongate band outlined by the 95% contour as a result of the return migration by shark 17-U. A minor subregion outlined by the 95% contour remained south of Hawaii (11.2°N, 159.9°W).

Focal areas were strongly differentiated from migration routes by the straightness of tracks, quantified using the straightness index (Batschelet 1981), based on the tracks for the two sharks with archival records that traveled into offshore waters. Migration phases between the central coast of California and the offshore focal area or the islands of Hawaii had straightness indices of 0.78 ± 0.12 , significantly greater than the straightness indices for the Farallones, the offshore focal area and the Hawaiian Islands of 0.16 ± 0.21 (Student's t-test, t = -5.88, p = 0.0003). Shark 17-U inhabited three focal areas, the Farallones, the offshore focal area, and Año Nuevo (37.11°N, 122.34°W); and undertook two migrations, one away from the coast of California to the offshore focal area, and another returning to the California coast. Shark 18-F utilized a focal area at the Farallones, another near the Main Hawaiian Islands, and a third 700 km south of Hawaii. The paths taken by white sharks during migration did not show clear relationships with magnetic features of the earth's crust (Figure 4-10).

The errors in light- and SST-based geolocations were estimated by comparison to known tagging positions and satellite tag endpoint positions determined by the Argos system (Table 2-1). Of the 20 white shark tags that reported data, light and SST geolocation estimates were obtained within one day of the start and endpoints for seven of 38 possible events. Longitude errors ranged from -0.77° (west) to 0.46° (east), with absolute values averaging $0.42 \pm 0.23^{\circ}$ (mean \pm SD). Latitude errors ranged from -4.17° (south) to 3.6° (north), with absolute values averaging $1.73 \pm 1.63^{\circ}$.

4.3.2 Nearshore California

In nearshore California waters white sharks (n=16) spent 99 ± 3 % of their time at depths shallower than 50 m, but only 22 ± 16 % of their time in 0–5 m depths (Figure 4-3, Figure 4-6a). These sharks spent 92 ± 10 % of their time in ambient temperatures of 10–14 °C (Figure 4-6b). Mixed layer depths averaged 36 ± 18 m.

Archival records for sharks near the Farallon Islands (n=3) and Año Nuevo Island (n=1), California provided a detailed look at these behavioral patterns (Table 4-3), with sharks spending $82 \pm 28\%$ of their time in the mixed layer of 26 ± 16 m, where temperatures were 13.3 ± 0.2 °C, and the remainder below the mixed layer where temperatures were 12.7 \pm 0.4°C. Sharks moved below the surface mixed layer 2.9 \pm 2.9 times d⁻¹, up to a maximum of 7.7 ± 6.7 times d⁻¹. There were no strong diel patterns in behavior (Figure 4-4a and Figure 4-5a). The sharks had median depths of 11 m (10–12 m) during day, where ambient temperatures were 13.1°C (12.9–13.2°C); and 10 m (8–10 m) during night, where ambient temperatures were 13.1°C (12.9–13.2°C) (Table 4-4). These patterns reflected their limited vertical movements, as well as the rarity of visits to the surface. Diel differences in depth (Figure 4-7a, e and Figure 4-8a) and temperature were not significant (Wilcoxon rank sum tests: depth, W = 21.0, p = 0.47; temperature, W = 18.0, p = 1.00). Vertical excursions had median values of 38 m (33–48 m) during day, where temperatures were 11.6°C (11.4–11.8°C); and 46 m (38–51 m) during night, where temperatures were 11.7°C (11.4–12.0°C) (Table 4-5). Diel differences in vertical excursions were not significant (Wilcoxon rank sum tests: depth, W = 17.0, p = 0.89; temperature, W = 16.5, p =0.77).

4.3.3 Traveling

During migratory phases (n=10) sharks spent 57 ± 7 % of their time shallower than 5 m, but also undertook dives to 736 m, and spent 15 ± 10 % of their time deeper than 300 m (Figure 4-3, Figure 4-6c). Ambient temperatures showed a broad distribution with 20 ± 14 % of the time spent at 20–22 °C and 19 ± 10 % spent at 6–10 °C,

reflecting the combination of surface swimming behavior and deep diving (Figure 4-6d). During the traveling phase sharks spent significantly more time near the surface (Student's t-test, t = 7.64, p = 0.00) and more time deeper than 300 m (Student's t-test, t = 5.25, p = 0.00) than they did during the nearshore phase (Figure 4-6). Mixed layer depths averaged 110 ± 28 m.

Archival records for the migratory phase away from the coast of California (n=2) and the return migration back to the coast of California (n=1) showed that sharks spent 71 \pm 5% of their time in the mixed layer of 112 \pm 37 m, where temperatures were 18.9 ± 1.2 °C, and the remainder below the mixed layer where temperatures were 10.8 ± 1.6 °C. Sharks moved below the surface mixed layer $8.0 \pm$ 3.9 times d⁻¹, up to a maximum of 23.7 ± 12.0 times d⁻¹. The sharks had a strong preference for the surface, which was consistent through their initial westward migrations through the California Current (Figure 4-4b and Figure 4-5b) as well as the later stages of migration in the subtropical gyre (Figure 4-4c and Figure 4-5c). Median depths were 2 m (2-3 m) during daytime, with temperatures of 18.5°C (18.2–19.4°C); and 2 m (1–15 m) during nighttime, with temperatures of 18.0°C (17.3–18.3 °C). The habitat preferences reflected the behavior of sharks returning to the surface between vertical movements, and remaining there for periods up to 1.5 d (shark 17-U). Diel differences (Figure 4-7b and Figure 4-8b) were not significant for depth (Wilcoxon rank sum test, W = 10.5, p = 1.00) or temperature (Wilcoxon rank sum test, W = 12.5, p = 0.51). Vertical excursions had median depths of 460 m (450–480 m) during daytime, with temperatures of 6.7°C (6.6–7.1°C); and 408 m (370–442 m) during nighttime, with temperatures of 7.2°C (6.9–9.0°C). Diel differences were not significant for depth (Wilcoxon rank sum test, W = 13.0, p =0.38) or temperature (Wilcoxon rank sum test, W = 6.0, p = 0.08).

Variations in magnetic intensity in the region of the migration corridor exceed variations measured by (Klimley 1993), which were correlated with directed movements of hammerhead sharks (*Sphyrna lewini*), suggesting that magnetic navigation is possible. (Klimley 1993) hypothesized that vertical movements of hammerhead sharks would allow them to sense altitudinal variations in the earth's

magnetic field, and migrating sharks did undertake such movements, though not in a regular pattern. Magnetic inclination and declination vary gradually across the region (Peddie 1993), and could provide direction but no obvious landmarks. The track of shark 18-F, for which geolocations were obtained almost daily during the migration, and magnetic anomaly fields of the region, show little correlation (Figure 4-10). The winter 95% density contour, showing the migration corridor for all sharks, was in agreement with the track of shark 18-F, forming an envelope around it. The pattern of movement evident from both 18-F's track and the 95% density contour show oblique movement across the magnetic anomaly lineations created by the Cenozoic spreading center of the east Pacific, which are oriented approximately north-south in the eastern portion of the migration corridor. Further west the magnetic anomaly data become increasingly sparse, but lineations appear to be oriented northwest-southeast, again meaning that shark movements are oblique. The final movements of shark 18-F to the Main Hawaiian Islands were beyond the extent of the magnetic anomaly data. The offshore focal area lies over the Molokai Fracture Zone, and has a complex pattern of magnetic lineations in different orientations as well as zones without lineations.

Gravity anomalies show lineations along the major fracture zones of the eastern North Pacific (Figure 4-10), which are oriented east-west (Sandwell and Smith 1997; Smith and Sandwell 1997). The migration to the offshore focal area does not line up with any of these lineations, crossing the Murray fracture zone, while the latter part of shark 18-F's migration to Hawaii occurs over the Molokai Fracture Zone. The Clarion fracture zone lies to the south of the offshore focal area. A direct movement from California to Hawaii would occur along the Molokai Fracture Zone, so the track of shark 18-F is not considered to be strong evidence for the use of bathymetric lineations in navigation.

4.3.4 Offshore focal area

Sharks in the offshore focal area (n=9) occupied a broad depth and temperature range (Figure 4-3), spending 54 ± 18 % of the time shallower than 100 m, and 46 ± 22 % of the time deeper than 100 m (Figure 4-6e). Sharks spent 58 ± 13 % of the time in

20-24°C waters and 42 ± 13 % of the time in 4-20°C waters (Figure 4-6f). Sharks spent 29 ± 10 % of the time in 0-5 m waters while in the offshore focal area, significantly more than while traveling (Student's t-test, t = 7.74, p = 0.00). Mixed layer depths averaged 132 ± 20 m.

The archival record of shark 17-U revealed a remarkable oscillatory behavior pattern when the shark was in the offshore area, with vertical excursions occurring throughout the diel cycle, from the surface to 644 m. The shark experienced ambient temperatures from 5.4 to 24.2°C (Figure 4-4d), and spent 55% of its time in the 104 m deep mixed layer, where temperatures were $21.5 \pm 1^{\circ}$ C, and the remainder in deeper waters where temperatures were 14.3 ± 4.3 °C. The shark moved below the surface mixed layer 30.3 ± 19.2 times d⁻¹, up to a maximum of 96 times d⁻¹ (Figure 4-4e). The median depths occupied were 60 m (2–220 m) during day, at temperatures of 20.7°C (13.1–21.8 °C); and 83 m (23–154 m) during the night, at temperatures of 20.6°C (18.5–21.6 °C), reflecting the continuous movements as well as the avoidance of near surface waters on some nights. Median depths during the day were significantly shallower (Wilcoxon rank sum test, W = 4.72, p = 0.00) than during the night, although the shark remained in the mixed layer during both diel periods. However, despite the deeper median position during night, the depth of vertical excursions was greater during day (Figure 4-7c), reaching 500 m (492–516 m), at a temperature of 6.8°C (6.5–6-9°C); compared to the nighttime median of 348 m (316–380 m), at temperatures of 9.8°C (8.9–10.1 °C). Vertical excursions during the day were significantly deeper (Wilcoxon rank sum test, W = 10.2, p = 0.00) and cooler (Wilcoxon rank sum test, W = 10.17, p = 0.00) than during the night, and beneath the surface mixed layer during both diel phases.

4.3.5 Hawaii

Depth and temperature data were obtained for three of the four sharks that moved to the Hawaiian Islands. These sharks showed a broad depth distribution, spending 48 ± 27 % of the time shallower than 100 m and 52 ± 27 % of the time deeper than 100 m, but avoided the surface, spending only 7 ± 1 % of the time in 0–5 m waters (Figure

4-6g). Surface mixed layer depths averaged 113 ± 17 m, suggesting that equal division of time above and below the preprogrammed 100 m histogram threshold corresponded approximately to time in and below the mixed layer. The time in 0–5 m waters in Hawaii (*n*=3), where temperatures were 24.8 ± 0.1°C, was significantly lower than during the nearshore California phase (7% vs. 22%; Student's t-test, t = 3.60, p = 0.00); and time deeper than 50 m was significantly higher (79% vs. 1%; Student's t-test, t = -27.8, p = 0.00). Temperature distribution was broad, with 36 ± 31 % of the time spent in waters warmer than 24 °C, and 5 ± 8 % of the time in waters cooler than 14 °C (Figure 4-6h).

A single archival record was obtained (18-F) providing more detailed time series records for the occupation of the Hawaiian focal area (Figure 4-3b, Figure 4-5d). The shark spent 55% of its time in the 100 m deep surface mixed layer, in average temperatures of 24.4 ± 0.3 °C; and the remainder beneath the surface mixed layer in temperatures of 21.0 ± 2.1 °C. The shark moved below the surface mixed layer 3.5 ± 2.9 times d⁻¹, up to a maximum of 12 times d⁻¹. The archival record for shark 18-F had median depths of 63 m (49–76 m) during day, with temperatures of 24.5°C (24.3–24.6°C); and 94 m (57–162 m) during night, at temperatures of 24.0°C (21.2–24.5 °C) (Figure 4-5d), and these depths were within the surface mixed laver during both diel periods. The median daytime distribution was significantly shallower (Wilcoxon rank sum test, W = 41.9, p = 0.00) and warmer (Wilcoxon rank sum test, W = 38.4, p = 0.00) than the median nighttime distribution (Figure 4-8c). These patterns reflected a deeper position than nearshore California behaviors, and the reduced number of visits to surface waters, which had temperatures of 25.1 ± 0.4 °C. Vertical excursions reached 126 m (101-213 m) during day, where temperatures were 22.8°C (18.3–22.7°C); and 208 m (200–228 m) during night, at temperatures of 17.9°C (17.3–18.3 °C). These depths were beneath the mixed layer during both diel periods. These patterns reflected the dominance of nocturnal diving during this period (Figure 4-5d). During the nighttime, vertical excursions were significantly deeper

(Wilcoxon rank sum test, W = 6.8, p = 0.00), and cooler (Wilcoxon rank sum test, W = 7.0, p = 0.00), than during the daytime.

4.3.6 Travel south of Hawaii

During movement from waters near Maui to the focal area 700 km to the south (centered at 11.20°N, 159.88°W), shark 18-F used waters from the surface to 708 m, and from 25.8–5.9°C (Figure 4-3b, Figure 4-5e). The shark spent 47% of its time in the 120 m deep surface mixed layer, in average temperatures of 25.0 ± 0.5 °C; and the remainder beneath the surface mixed layer in temperatures of 12.9 ± 4.9 °C. The shark moved below the surface mixed layer 6.2 ± 2.0 times d⁻¹, up to a maximum of 8 times d^{-1} . Median depths were 46 m (1–428 m) during the day, with temperatures of 24.5 °C (9.2–25.2 °C); and 91 m (2–212 m) during the night, with temperatures of 24.5 °C (18.6–25.1 °C) (Figure 4-8d), and were within the mixed layer during both diel periods. The median daytime distribution was significantly shallower (Wilcoxon rank sum test, W = 2.3, p = 0.02) and warmer (Wilcoxon rank sum test, W = 10.3, p = 0.00) than the median nighttime distribution. Vertical excursions averaged 468 m (460-476 m) during daytime, with temperatures of 8.1° C ($8.0-8.3^{\circ}$ C); and 288 m (253-340 m) during nighttime, with temperatures of 13.4°C (10.7–15.6°C), and were beneath the mixed layer during both diel periods. During the daytime, vertical excursions were significantly deeper (Wilcoxon rank sum test, W = 10.7, p = 0.00), and cooler (Wilcoxon rank sum test, W = 10.6, p = 0.00), than during the nighttime. The shark's behavior was similar to the traveling periods from California, as the shark returned to and remained at the surface after vertical excursions, but these surface periods were shorter, and its median depth was much deeper than during migrations from California during both day and night.

4.3.7 Offshore focal area south of Hawaii

At a focal area centered 700 km south of Kauai, shark 18-F inhabited the warmest surface waters recorded in this study, where temperatures were up to 27.2°C (Figure 4-3b). It spent 60% of its time in the 131 m deep surface mixed layer, in average

temperatures of $25.0 \pm 0.9^{\circ}$ C; and the remainder beneath the surface mixed layer in temperatures of 12.4 ± 5.1 °C (Figure 4-5f, Figure 4-6i, j). The shark moved below the surface mixed layer 3.8 ± 2.5 times d⁻¹, up to a maximum of 11 times d⁻¹. The shark used a broader vertical habitat in the day, with median depths of 48 m (16–404 m), and temperatures of 24.8 °C (9.5–25.5 °C); and a narrower habitat during nighttime, with median depths of 104 m (21–212 m), and temperatures of 23.3 °C (18.5–24.9 °C) (Figure 4-8e). The median daytime distribution was significantly shallower (Wilcoxon rank sum test, W = 6.8, p = 0.00) and warmer (Wilcoxon rank sum test, W = 21.4, p = 0.00) than the median nighttime distribution. Vertical excursions averaged 580 m (564–612 m), with temperatures of 6.2 °C (6.0–6.5 °C) during the day; and 456 m (420–500 m), with temperatures of 8.5 °C (7.7–9.3 °C) during the night. During the daytime, vertical excursions were significantly deeper (Wilcoxon rank sum test. W = 10.3, p = 0.00), and cooler (Wilcoxon rank sum test, W = 10.4, p = 0.00), than during the nighttime. On 24 April the shark made one movement deeper than the limit of the depth sensor (980 m), where the temperature was 4.5°C. The pattern of having a shallower median position during the day, but deeper vertical excursions during the day was the same for this shark and shark 17-U in the offshore focal area.

4.4 Discussion

White sharks electronically tagged in the waters off central California, USA made long distance offshore movements on a seasonal cycle. White sharks aggregated in the coastal waters of central California during autumn and winter, and undertook offshore migrations into oceanic waters during winter and spring. The satellite telemetry results indicate that white sharks occupy neritic zones for about half the year and pelagic habitats for the remaining period. Between the two phases we identify a migration of approximately three weeks that links the two habitats (Figure 4-1, inset; Figure 4-3a). The offshore focal area used by white sharks is an area of low productivity and may be a region used for foraging, mating, or parturition. We observed similar migration routes and destinations in male and female, as well as mature and subadult sharks, though there were sex-specific differences in migration

timing. The neritic-pelagic migration cycle observed in this study differs from seasonal movement patterns of Australian sharks. Bruce et al. (2006) reported that white sharks spent the majority of time near the coast, but reported a single pelagic movement from Australia to New Zealand. White sharks occupied the Great Australian Bight during spring and summer, made northward movements during autumn and winter along the east coast through New South Wales and Queensland, and returned to the southern region by early summer. Bonfil et al. (2005) reported the movement of a white shark between South Africa and Australia but further research is needed before we will know if this is a rare movement or a seasonal pattern.

4.4.1 Nearshore habitat

The coastal habitat of adult and subadult white sharks appears to be important for foraging. The relationship between white shark movements to the Farallones and the existence of pinniped rookeries is well known (Ainley et al. 1985), and individually identified sharks return in subsequent years at this location (Anderson and Pyle 2003) as well as at the pinniped rookery at Guadalupe Island, Mexico (Domeier and Nasby-Lucas 2007) and Seal Island in South Africa (Martin et al. 2005). White sharks begin to aggregate at the Farallones in late August (Pyle et al. 1996) so the duration of this phase is likely to be substantially longer than the mean duration of 57 d in this study. since sharks were at the Farallones for unknown duration prior to tagging. The shark tracked through a full offshore-onshore migration cycle in this study (17-U) was estimated to have a 177 d nearshore phase. The nearshore vertical behaviors of white sharks in this study are consistent with a hunting strategy for pinnipeds (Figure 4-3c, Figure 4-4a and Figure 4-5a). The sharks patrol at a depth of 11 m (10–12 m) and rarely visit the surface waters, reflecting the behavior of looking for silhouettes from below and attacking by surprise (Goldman and Anderson 1999). Bruce et al. (2006) reported that white sharks foraging on teleosts and elasmobranchs in shallow regions swam along the bottom with few visits to the surface.

Sharks returning to the continental margin may forage on harbor seals and sea lions prior to their arrival at elephant seal rookeries. We recorded a white shark returning to the California coast from the offshore focal area (17-U) during August,

and inhabiting waters between Bodega Bay, California and Big Sur, California before the pop up satellite tag transmitted near Año Nuevo Island, California. Long et al. (1996) showed a peak in predation on harbor seals and sea lions in August, which occurred in coastal areas away from elephant seal rookeries.

4.4.2 Traveling

The timing of departure of white sharks from the Farallones may be related to the decline in abundance of pinnipeds. In this study, electronically tagged white sharks departed the California coast on a mean date of 2 January, shortly after the peak in abundance of young-of-the-year elephant seals that use the islands for their first haulout period and then depart as adult male seals arrive to establish mating territories (Le Boeuf and Laws 1994). Sharks left after periods of decreasing pinniped abundance that may have resulted in decreased hunting success (Figure 4-9). In years where multiple departures were recorded, we did not see a coordinated departure of sharks following a single decline in abundance.

There was a distinct difference in the date of departure based on sex, with females (n=4) leaving on 15 February (earliest 25 December, latest 24 March), and males (n=8) leaving on 11 December (earliest 19 November, latest 23 January). This result is consistent with a higher energy demand for females and potentially a need to remain in the Farallones for additional caloric benefit, given that the oligotrophic offshore focal area may offer reduced foraging opportunities, though without knowledge of arrival dates we do not know if females stay near the Farallones longer, or are shifted later with respect to males. Anderson and Pyle (2003) noted a biannual visitation of individually identified females to the Farallones, suggesting a two-year reproductive cycle, while Domeier and Nasby-Lucas (2007) recorded smaller female sharks visiting in consecutive years and larger visiting at multi-year intervals.

Occasionally, the departure of white sharks from the Farallones may be governed not by availability of forage or the need to move to a breeding or parturition area, but by predator avoidance. After an orca (*Orcinus orca*) killed a large prey item believed to be a white shark on 19 November 2000, no white sharks, attacks on pinnipeds, or interactions with decoys were observed again until 10 December 2000 (Pyle and

Anderson, unpublished). The data for shark 3-M tagged on 16 October 2000 shows depths shallower than 77 m until the day of the orca attack, when a dive to 484 m occurred, indicating the shark had left shelf waters close to the Farallones. Geolocation data indicated that the shark (3-M) traveled to the west until it reached the Main Hawaiian Islands. These data are consistent with the findings of (Pyle et al. 1999), who observed an orca kill a white shark at the Farallones on 4 October 1997, and subsequently saw only two white sharks through the duration of observations on 1 December 1997.

Geolocation and speed data for 15 white sharks provide evidence for a distinct migration corridor in the eastern North Pacific that connects the coastal and pelagic aggregation areas. Straightness and minimum velocity estimates for the migratory phases of white sharks indicate directed movements from coastal to offshore focal areas in the eastern Pacific and Hawaii, rather than sinuous or nomadic movements. Straightness indices for sharks that visited the offshore focal area (17-U) and the Main Hawaiian Islands (18-F) showed directed migrations, being 0.77 ± 0.12 while the sharks were moving between coastal and offshore focal areas, compared to 0.16 ± 0.21 for focal areas. For comparison, Atlantic bluefin tuna had straightness indices of 0.84 \pm 0.07 and 0.57 \pm 0.13 during migration to the Gulf of Mexico, and breeding activity, respectively (Teo et al. 2006). Wandering albatrosses (Diomedea exulans) had straightness indices of 0.65 ± 0.09 and 0.29 ± 0.08 while moving between and within foraging regions, respectively (Weimerskirch et al. 2002). Bruce et al. (2006) noted that white sharks in Australian waters spend extended periods at a foraging area then switch to a directed swimming behavior and use 'common highways' for travel to the next foraging area.

Estimates of minimum speed during the migratory phase also indicate that movements were directed rather than sinuous. To avoid bias caused by differences in shark size, comparisons are made using relative speed in TL s⁻¹. Our minimum speed estimates of 0.23 ± 0.05 TL s⁻¹ (88 ± 14 km d⁻¹) for the migration to the offshore focal area, and 0.27 ± 0.03 TL s⁻¹ (101 ± 6 km d⁻¹) for the migration to Hawaii, are similar to speed estimates from published acoustic and satellite tracking studies. While

following acoustically tagged adult white sharks, (Carey et al. 1982) measured a speed of 0.19 TL s⁻¹ (77 km d⁻¹), while (Strong et al. 1992) obtained speeds of 0.21–0.25 TL s⁻¹ (78 ± 41 km d⁻¹). (Klimley et al. 2001a) used a radio-acoustic positioning array to measure swimming speeds of 0.22 TL s⁻¹ (104 km d⁻¹). Bonfil et al. (2005) measured a transoceanic migration using a PAT tag, with a minimum speed of 0.34 TL s⁻¹ (113 km d⁻¹), a higher relative speed, but a lower absolute speed, than the fastest migration in our study of 0.30 TL s⁻¹ (119 km d⁻¹; shark 14-M). Bruce et al. (2006) used finmounted satellite transmitters on four white sharks with a mean traveling speed of 0.31 TL s⁻¹ (74 km d⁻¹). If the sharks in our study had taken sinuous migration routes, their actual speeds would have been considerably higher than our estimates, and considerably higher than the published values for white shark swimming speeds.

During offshore migrations, sharks passed from California Current waters into transition zone waters, and through the subtropical front (Roden 1991) and the transition zone chlorophyll front (Polovina et al. 2001). Once south and west of these features, synoptic ocean color measurements show very low chlorophyll concentration, but the region maintains moderate productivity due to the subduction of nutrient rich waters from the north (Seki et al. 2002). Once white sharks moved south of the south subtropical front they entered the subtropical gyre, where they remained for the duration of their offshore periods. In this region the mixed layer deepens and as a result, there is a very low rate of vertical advection of nutrients into the euphotic zone (Seki et al. 2002). The subsurface chlorophyll peak weakens and deepens considerably and primary production is extremely low (Polovina et al. 2001). The lack of minor focal areas during the migration phase suggests that white sharks did not feed extensively en route.

During all traveling phases undertaken by the two sharks with archival records, the sharks returned to and remained directly at the surface after each vertical movement (Figure 4-4b, c and Figure 4-5b, c and e), in contrast with their behaviors at neritic and pelagic focal areas (Figure 4-4a, d and Figure 4-5a, d, f). The frequent and long periods of time spent at the surface could allow a shark to use celestial cues for navigation (Able and Able 1990). While returns to shallow, warm water following

dives may serve a thermoregulatory purpose (Brill and Bushnell 2001), such warming phases require only a return to the mixed layer, not a return to the surface. No clear indication of the use of geological features for navigation was evident (supplement).

4.4.3 Offshore focal area

The purpose of the migration to the offshore focal area is unknown, and may be foraging, mating, or parturition. Direct evidence for any of these hypotheses is lacking, such as observations of mating or parturition, and data on stomach contents or stomach temperature records. However, the behavioral data in our study contrast this region strongly from all other regions, and suggest either a foraging strategy on a distinctly different prey than in inshore areas or a non-foraging purpose for the time spent in the offshore focal area.

The offshore migrations of white sharks took them from the eutrophic waters of the California Current system into the oligotrophic subtropical gyre, where food resources appear to be sparse and pinnipeds are absent. The offshore focal area is south of the pelagic regions used by elephant seals, which feed in productive transition zone waters to the north (Le Boeuf and Laws 1994). The area is west of the migration routes of humpback whales between Hawaiian breeding/calving grounds and subarctic Pacific feeding grounds (Mate et al. 1998). This area is south of the trans-pacific migration corridor currently identified for bluefin tuna (Perle et al. unpublished data).

Large pelagic fishes occur in this area, but at much lower concentrations than in other parts of the eastern North Pacific (Okamoto and Bayliff 2003). The dominant large pelagic fishes in the area are albacore (*Thunnus alalunga*), yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*) tuna and swordfish (*Xiphius gladius*), with lower levels of other billfishes and sharks (Okamoto and Bayliff 2003). Abundance of tunas and swordfish peaks in the winter and spring during the time that the white sharks are there, whereas abundance of billfishes (*Istiophorus, Makaira, Tetrapturus spp.*) peaks in summer and fall (Okamoto and Bayliff 2003). Sharks include blue (*Prionace glauca*), silky (*Carcharhinus falciformis*), oceanic whitetip (*Carcharhinus longimanus*), shortfin mako, longfin mako, salmon shark, bigeye thresher (*Alopias superciliosus*) and pelagic thresher (*Alopias pelagicus*), with abundance peaking in the

winter and spring (Okamoto and Bayliff 2003). Recent longline data suggests that bigeye tuna fishermen have increased effort in these regions (IATTC, 2006).

The area is southwest of the subtropical summer blooms noted by (Wilson 2003), and a developing food chain in such a productivity center would not be advected into the area, given the westerly currents in the region (Roden 1991). The region of temporally stable negative wind stress curl where floating debris accumulates, and which may concentrate whale carcasses, lies directly to the north of the mid-zone but does not overlap with it.

The oscillatory pattern of shark 17-U (Figure 4-4e), which undertook up to 96 daily excursions below the mixed layer, is consistent with a searching pattern in which olfactory cues that disperse along horizontal shear layers would be encountered with the highest probability (Klimley et al. 2002). However the deep nocturnal diving differs from behaviors observed for other upper trophic level pelagics. Whereas shark 17-U made oscillatory movement at night to median depths of 348 m (Figure 4-4d), many large pelagic fishes cease diving at night, remaining in shallow waters. Such a pattern has been documented in tunas (Holland et al. 1992); billfishes (Carey and Robison 1981); and a variety of other shark species (Weng and Block 2004). The shallow nighttime distributions of most of these fishes are thought to be the result of the shallow distribution of prey species associated with the deep scattering layer, which approach the surface at night (Josse et al. 1998). The pattern of white shark 17-U suggests either a different foraging strategy necessitated by a prey that does not ascend to the surface at night, or a function other than foraging for the oscillatory movements.

The offshore focal area may be used for parturition, mating, or both. The rapid oscillatory dives of shark 17-U (Figure 4-4e) could be a courtship activity. Bluefin tuna show distinct oscillatory diving while on their breeding grounds in the Gulf of Mexico (Teo et al. 2006). The fact that both males and females are in the focal area is not consistent with it being solely a parturition area. In some shark species females mate shortly after giving birth, such that the same region is used for both functions (Carrier et al. 2004). The possibility of mating or parturition during annual visits to

the offshore focal area would be consistent with a one-year reproductive cycle; however, female sharks appear to visit the Farallones biannually, providing evidence for a two-year cycle (Anderson and Pyle 2003). Based on the seasonality of parturition, (Francis 1996) hypothesized that the gestation period was more than one year; (Mollet et al. 2000) hypothesized an 18-month gestation cycle. The visitation of the offshore focal area by subadult sharks is not consistent with a purely reproductive function for the migration.

4.4.4 Hawaii and vicinity

The visitation of white sharks to the waters surrounding the islands of Kauai, Maui, Lanai, Kahoolawe and Hawaii indicates these areas may be used for foraging. While in this region, shark 18-F showed significantly deeper diving during nighttime than daytime (Figure 4-5d), in contrast to diel patterns observed during other phases. The diel pattern of vertical movements near Hawaii contrasts with most patterns observed for a wide variety of pelagic sharks and fishes, in which sharks make deeper movements during day than night (Weng and Block 2004).

The pattern of shark 18-F is consistent with foraging in nearshore waters during day, and moving away from land at night. The pattern of aggregating during the day and dispersing at night has been observed in tunas at fish aggregating devices (Holland et al. 1990b) and seamounts (Klimley et al. 2003). However, due to the inherent limitations in light- and SST-based geolocation, we do not know the precise locations of the shark during daytime and nighttime. The white shark rarely visited the surface, which is consistent with a silhouette-based hunting strategy, but the median positions during day (63 m) and night (94 m) are likely too deep to see silhouettes of animals at the surface. White sharks have been observed near aggregation sites for spinner dolphins (*Stenella longirostris*) on the west side of Oahu, as well as near Hawaiian monk seal (*Monachus schauinslandi*) colonies on Niihau, and their presence in Hawaii corresponds to the timing of birth for humpack whales (*Megaptera novaeangliae*), allowing for the possibility of feeding on placentas (John Naughton, personal communication). Sharks may also forage on fishes, sharks and squids while near the Islands. Teleost and elasmobranch fishes are important food sources for white sharks

in Australian waters (Malcolm et al. 2001), and may also be important in waters around Guadalupe Island, Mexico (Domeier and Nasby-Lucas 2007). Bruce et al. (2006) reported a similar pattern of shallow daytime and deep nighttime swimming while a white shark was near the Neptune Islands, where pinniped colonies occur.

While in the focal area south of Hawaii, shark 18-F had a very different vertical diving behavior than shark 17-U in the offshore focal area between Hawaii and Baja. Whereas the offshore focal area behavior of shark 17-U showed high frequency vertical oscillations up to a maximum of 96 oscillations d^{-1} , shark 18-F south of Hawaii only undertook 3.8 ± 2.5 vertical oscillations d^{-1} (Figure 4-5f). In addition, the shape of dives differed between the two regions. South of Hawaii shark 18-F showed dive profiles with long basal periods, consistent with a dive to a target depth followed by a period of searching for prey (Josse et al. 1998), whereas shark 17-U initiated ascent immediately upon reaching the maximum depth of a dive.

4.4.5 **Population structure**

Genetic studies comparing the southwest Pacific and southwest Indian Oceans have shown separate populations of white sharks based on mitochondrial markers, but a lack of differentiation based on nuclear markers, leading to the hypothesis of greater trans-oceanic movement by males than females (Pardini et al. 2001). Satellite telemetry showed a trans-oceanic movement between these white shark populations by a female (Bonfil et al. 2005), raising the possibility that long-distance transfer of male gametes could occur through the movements of adult females. The population structure of white sharks in the Pacific Ocean is unknown, and no genetic studies have been published for this ocean basin. The present study and others based in Mexico (Domeier and Nasby-Lucas 2006) and the Southern California Bight (Weng et al., In press) have recorded movements via satellite telemetry. Adult and subadult white sharks tracked from both Central California and Guadalupe Island, Mexico have visited the offshore focal area highlighted in this study, raising the possibility of connections between these two groups. Juvenile white sharks tracked from Los Angeles, California have moved along the coast northward to Point Reyes, California, and southward to Sebastian-Vizcaino Bay, Baja California, Mexico. The movements

of western Pacific white sharks are unknown, so it remains possible that they make long-range movements into habitats shared by eastern Pacific white sharks. Further research into both the genetics and movements of white sharks is required to elucidate the evolutionary and ecological relationships of white sharks globally and within the Pacific basin, and to determine the role of the unusual movements to the offshore focal area highlighted in this study.

Shark	Tagging date	Total Length (cm)ª	Sex	Maturity	Pop-up Date	Track Days	Longitude	Latitude	Comment
1-M	19-Oct-99	402	М	Mature	02-Nov-99	14	-124.49	38.95	Nearshore
2-M	30-Oct-99	366	М	Adolescent	25-Nov-99	26 ^b	-125.97	38.69	Nearshore
3-M	16-Oct-00	457	М	Mature	16-Apr-01	182	-156.80	20.67	To Hawaii
4-M	05-Nov-01	457	М	Mature	06-May-02	182	-141.47	26.39	To Hawaii
5-F	05-Nov-01	488	F	Mature	19-Jul-02	256	-133.25	21.13	Offshore focal area
6-M	05-Nov-01	427	М	Mature	07-Aug-02	275	-138.83	26.50	Offshore focal area
7-F	05-Nov-01	442	F	Adolescent	10-Dec-01	35	-123.09	37.07	Nearshore
8-M	15-Nov-01	380	М	Mature	14-Jan-02	60	-131.71	34.93	Initiated migration
9-M	15-Nov-01	450	М	Mature	12-Jun-02	209	-134.22	25.04	Offshore focal area
10-F	15-Nov-02	530	F	Mature	14-Feb-03	91	-134.69	26.81	Offshore focal area
11-U	24-Sep-03	427	?	n/a	24-Mar-04	182	-134.18	25.20	Offshore focal area
12-M	27-Oct-03	396	Μ	Mature	23-Jun-04	240	-156.39	20.97	Hawaii; pop-up position only
13-U	31-Oct-03	488	?	Mature	01-Nov-04	367	-147.10	24.80	Offshore focal area
14-M	05-Nov-04	457	М	Mature	09-Apr-05	155	-124.20	22.30	Offshore focal area
15-M	05-Nov-04	457	М	Mature	10-Apr-05	156	-132.29	22.67	Offshore focal area
16-M	05-Nov-04	427	М	Mature	10-May-05	186	-127.71	22.06	Offshore focal area
17-U	05-Nov-04	360	?	n/a	06-Sep-05	305 ^b	-122.45	37.10	Return migration
18-F	30-Nov-04	396	F	Adolescent	12-Jun-05	194 ^b	n/a	n/a	To Hawaii
19-F	30-Nov-04	490	F	Mature	03-May-05	154	-136.73	27.59	Offshore focal area
20-F	03-Dec-04	426	F	Adolescent	08-Feb-05	67	-122.87	37.77	Nearshore

Table 4-1. White sharks tracked from Southeast Farallon Island, California, USA, 1999-2004

^a Total length was estimated visually.

^b Tag recovered and archival record obtained.

Known Position	Shark	Longitude Error (°)	Latitude Error (°)
Popup	3-M	0.34	0.09
Deployment	9-M	0.461	1.111
Deployment	7-F	-0.683	-0.595
Deployment	20-F	-0.26	-2.17
Deployment	16-M	0.23	3.6
Popup	18-U	-0.77	-0.35
Deployment	19-F	-0.19	-4.17

Table 4-2. Comparison of tagging locations and Argos popup locations with light- and SST-based geolocations

Phase	Mixed Layer (m)	Mixed Layer (°C)	Time in ML (%)	Time Below ML (%)	Movements below ML	Max movements below ML
Nearshore	26 ± 16	13.3 ± 0.2	82 ± 28	12.7 ± 0.4	2.9 ± 2.9	7.7 ± 6.7
Traveling	112 ± 37	18.9 ± 1.2	71 ± 5	10.8 ± 1.6	8.0 ± 3.9	23.7 ± 12.0
Offshore focal area	104	21.5 ± 1	55	14.3 ± 4.3	30.3 ± 19.2	96
Hawaii	100	24.4 ± 0.3	55	21.0 ± 2.1	3.5 ± 2.9	12
Travel south of Hawaii	120	25.0 ± 0.5	47	12.9 ± 4.9	6.2 ± 2.0	8
Offshore focal area south of Hawaii	131	25.0 ± 0.9	60	12.4 ± 5.1	3.8 ± 2.5	11

Table 4-3. Mixed layer properties for sharks with archival records

Phase	Median Day (m)	Median Night (m)	Median Day (°C)	Median Night (°C)
Nearshore	11 (10-12)	10 (8-10)	13.1 (12.9-13.2)	13.1 (12.9-13.2)
Traveling	2 (2-3)	2 (1-15)	18.5 (18.2-19.4)	18.0 (17.3-18.3)
Offshore focal area	60 (2-220)	83 (23-154)	20.7 (13.1-21.8)	20.6 (18.5-21.6)
Hawaii	63 (49-76)	94 (57-162)	24.5 (24.3-24.6)	24.0 (21.2-24.5)
Travel south of Hawaii	46 (1-428)	91 (2-212)	24.5 (9.2-25.2)	24.5 (18.6-25.1)
Offshore focal area south of Hawaii	48 (16-404)	104 (21-212)	24.8 (9.5-25.5)	23.3 (18.5-24.9)

Table 4-4. Depth and temperature preferences for sharks with archival records

Phase	Excursion Day (m)	Excursion Night (m)	Excursion Day (°C)	Excursion Night (°C)
Nearshore	38 (33-48)	46 (38-51)	11.6 (11.4-11.8)	11.7 (11.4-12.0)
Traveling	460 (450-480)	408 (370-442)	6.7 (6.6-7.1)	7.2 (6.9-9.0)
Offshore focal area	500 (492-516)	348 (316-380)	6.8 (6.5-6-9)	9.8 (8.9-10.1)
Hawaii	126 (101-213)	208 (200-228)	22.8 (18.3-22.7)	17.9 (17.3-18.3)
Travel south of Hawaii	468 (460-476)	288 (253-340)	8.1 (8.0–8.3)	13.4 (10.7–15.6)
Offshore focal area south of Hawaii	580 (564-612)	456 (420-500)	6.2 (6.0-6.5)	8.5 (7.7-9.3)

Table 4-5. Vertical excursions for sharks with archival records

Tagging date	Total Length (cm)	Sex	Maturity
16-Oct-00	518	?	Mature
16-Oct-00	518	F	Mature
09-Nov-00	518	F	Mature
09-Nov-00	381	?	n/a
12-Nov-02	430	Μ	Mature
08-Oct-03	442	Μ	Mature
23-Oct-03	n/a	F	n/a
31-Oct-03	488	Μ	Mature
13-Oct-04	381	?	n/a

Table 4-6. Satellite tags that failed to report, 1999-2004

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Figure 4-1. Movement patterns for two out of 20 white sharks tracked from 1999-2005. Sharks 17-U (\circ) moved from the tagging location in California (arrow) to the offshore focal area and back to California where the tag popped up (O); white shark 18-F (Δ) moved from California to Hawaii, where the tag stopped recording data (Δ). Colors denote month. Pie diagram shows days of the year spent in four phases by shark 17-U.



Figure 4-2. Kernel density estimates for white sharks that made offshore movements (n=15). Contours encompass 25%, 50% and 95% of all positions.



Figure 4-3. Ambient temperature-depth profiles taken by (a) shark 17-U during movements from the Farallones, California to the offshore focal area and back to Año Nuevo, California; (b) shark 18-F during movements from the Farallones, California to waters near the Hawaiian Islands; and (c) shark 2-M while near the Farallones, California. Color denotes ambient temperature; black line shows median daily depth of the shark.



Figure 4-4. One week time series of depth (line) and temperature (color) for white shark 17-U (a) Nearshore, off the Farallon Islands, California, (b) traveling west through the California Current, (c) traveling through the subtropical gyre, (d) in the offshore focal area, and (e) a single day in the offshore area. Dark grey denotes nighttime, light grey denotes twilight.



Figure 4-5. One week time series of depth (line) and temperature (color) for (a) white shark 18-F nearshore, off the Farallon Islands, California, (b) traveling west through the California Current, (c) traveling west through the subtropical gyre, (d) near the Main Hawaiian Islands, (e) traveling south from Hawaii, and (f) at a focal area between Hawaii and Kiribati. Dark grey denotes nighttime, light grey denotes twilight.



Figure 4-6. Depth and temperature distribution for white sharks (n=16) while nearshore (a, b), traveling (n=10) (c, d), in the offshore focal area (n=9) (e, f), and near the Main Hawaiian Islands (n=3) (g, h), and south of the Hawaiian Islands (n=1) (i, j). Bars show mean, lines show standard deviation.



Figure 4-7. Diel distribution of shark 17-U (a) near the California coast, (b) traveling west from California, (c) in the offshore focal area, (d) traveling east back to California, and (e) near the California coast. Color denotes % time spent at each depth (log scale). White line shows the diel cycle of light intensity in arbitrary units.



Figure 4-8. Diel distribution of shark 18-F (a) near the California coast, (b) traveling west from California, (c) near the Main Hawaiian Islands, (d) traveling south from Hawaii, and (e) at a focal area between Hawaii and Kiribati. Color denotes % time spent at each depth (log scale). White line shows the diel cycle of light intensity in arbitrary units.



Figure 4-9. Abundance of pinnipeds at Southeast Farallon Island (black) are significantly correlated with the departure dates of 15 white sharks (blue). Arrow shows the date of an orca attack on a white shark.



Figure 4-10. The track of shark 18-F (black) and the winter 95% density contour for all sharks (grey) over (a) magnetic anomalies, and (b) gravity anomalies for the eastern North Pacific.



Figure 4-11. Archival data for shark 17-U comprising (a) depth, (b) temperature and (c) light during the 305 d track. Vertical axes show time of day, horizontal axes show time.



Figure 1-12. Archival data for shark 18-F comprising (a) depth, (b) temperature and (c) light during the 194 d track. Vertical axes show time of day, horizontal axes show time.
5 Movements, behavior and habitat preferences of juvenile white sharks in the eastern Pacific as revealed by electronic tags³

5.1 Introduction

The white shark (*Carcharodon carcharias*) is an apex predator with a cosmopolitan distribution in temperate and tropical waters of both hemispheres (Compagno 1984) and occurs rarely at boreal latitudes (Martin 2004). Recent advances in our understanding of adult white shark movements and habitat utilization have come through the use of electronic tag technologies. Short-term acoustic tracks revealed that sharks prefer shallower depths (0–50 m) on the continental shelf of North America (Carey et al. 1982; Goldman et al. 1996; Goldman 1997; Klimley et al. 2001b). Longer satellite tracks revealed that adult white sharks made large-scale pelagic movements from the coastal waters of California into the eastern and central Pacific as far west as Hawaii (Boustany et al. 2002). During these offshore excursions the white sharks occupied depths from the surface to over 980 m and encountered ambient temperatures from 4–24°C. Satellite tracking of white sharks in South Africa (Bonfil et al. 2005) using fin-mounted Argos position tags also revealed coastal and pelagic movements, with one shark making an extensive trans-oceanic journey from South Africa to Western Australia.

Few studies have focused on the juvenile life stages of white sharks (Klimley et al. 2002; Dewar et al. 2004). Klimley et al. (2002) acoustically tracked a single young-of-the-year (YOY) white shark for 3.6 hours near La Jolla, California, USA. This shark made oscillatory movements between the surface and 25 m depth. Over this

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depth range the temperature dropped from 21 to 15°C. Dewar et al. (2004) tracked an individual YOY white shark with a pop-up satellite tag for 28 days near Long Beach, California. This shark preferred mixed layer waters of 16–22°C but made frequent movements through the thermocline to temperatures as low as 9°C and depths of 240 m. Neither animal moved out of the Southern California Bight (SCB), however both were tracked for short durations.

Little is known about the breeding, parturition and early life history phases of white sharks. Pregnant white sharks have been captured near Japan, Taiwan, Australia, New Zealand, in the Mediterranean, and off Kenya (Bruce 1992; Fergusson 1996; Francis 1996; Uchida et al. 1996; Anonymous 1999). YOY white sharks, having total lengths under 176 cm (Cailliet et al. 1985), have been observed in these regions as well as in the SCB and Baja California (Klimley 1985), the New York Bight (Casey and Pratt 1985), southeastern Australia (Bruce 1992) and South Africa (Cliff et al. 1996). In the eastern Pacific, the nursery habitat is hypothesized to include the coast of North America south of Point Conception (Klimley 1985). YOY white sharks have been captured in commercial and recreational fisheries along this coast relatively close to shore (Klimley 1985), but no pregnant females have been captured in the region (Francis 1996), and the breeding and parturition locations for white sharks in the eastern Pacific remain unknown.

White sharks, like many large pelagic fishes, are under increasing fishing pressure (Baum et al. 2003). The species is listed as vulnerable by the International Union for Conservation of Nature and Natural Resources (Fergusson et al. 2000) and is on Appendix II of the Convention on International Trade in Endangered Species (Inskipp and Gillett 2005). Understanding the biology of both adult and juvenile white sharks is essential to the development of effective management strategies. The early life history stages of a low-fecundity species such as the white shark are particularly important, as fishing mortality is a more important factor in population dynamics than for a high fecundity species (Mollet and Cailliet 2002). Juvenile white sharks are captured in commercial fisheries off California (Klimley 1985) and Baja California,

Mexico (O. Sosa-Nishizaki, CICESE, pers. comm.), and in this study we identify important habitats of juvenile white sharks in this region of the eastern Pacific.

5.2 Methods

5.2.1 Satellite tagging of sharks

Pop-up satellite archival tags (PAT 2.0 and 4.0, Wildlife Computers, Redmond, WA, USA) were deployed on six juvenile white sharks during 2002 to 2004 (Table 5-1). The tags were programmed to archive data at 30- or 60-second intervals. The archival data were compressed into bins of two, six or twelve hours for transmission to Argos satellites. For each bin the tag produced a depth-temperature profile and two histograms, one of time-at-depth and one of time-at temperature. In addition, a dawn and dusk light curve was transmitted for each day.

Tags were deployed in the SCB on white sharks that were captured in bottomset gillnets as bycatch (Table 5-1). Each PAT was attached to a titanium dart (59 mm x 13 mm) with a 15 cm segment of 136 kg monofilament line (300 lb test Extra-hard Hi-catch, Momoi Manufacturing, Japan) covered with shrink-wrap (Block et al. 1998). The dart was cleaned with Betadine microbicide (Purdue Pharma L.P., Stamford, CT, USA) and inserted into the dorsal musculature at the base of the first dorsal fin using a stainless steel applicator, such that the satellite tag trailed behind the fin. To ease the insertion of the dart, a small slit in the skin was made using a surgical scalpel.

We obtained data from all six of the white sharks tagged. Four PAT tags were recovered after releasing from sharks or when sharks were recaptured, providing full archival records of depth, temperature and light, while the two remaining tags transmitted summary data (Table 5-1).

5.2.2 Estimation of geopositions

To determine the movements of each shark between the start and end positions, longitude was calculated from light levels (Hill and Braun 2001) using software provided by the manufacturer (WC-GPE version 1.01.0005) and latitude was estimated by matching sea surface temperature (SST) measured by the tag to SST measured by satellites along the estimated longitude (Smith and Goodman 1986; Teo et al. 2004) using MatLab (The MathWorks, Inc. Natick, MA, USA). A speed filter of 2.7 km/h was used to filter the position data, based on the speed for a juvenile white shark obtained by Klimley et al. (2002) during an acoustic track. Given that this shark would travel 2.7 km/h if it made no turns or vertical movements, this speed filter is conservative.

Potential errors in geolocation were estimated by comparing known deployment or endpoint locations to estimated geolocations within one day. For error calculations, the geolocation algorithm was run with no limit on daily movements rates so that there would be no confounding effects of the speed filter.

5.2.3 Quantification of vertical and thermal habitat preferences

The depth and temperature habitats of the sharks were described using pressure and temperature data collected by the tags, and characterized in terms of the surface mixed layer and thermocline. Ideally, surface mixed layer depth is calculated according to density, but since our tags do not measure salinity, we used a definition of $\Delta 1^{\circ}$ C from the surface (Rao et al. 1989). This depth was used to calculate the average temperature of the surface mixed layer and the thermocline. Time spent within the surface mixed layer and the thermocline was calculated for animals with archival records (YOY-1, YOY-2, YOY-4 and 3YR-1); for transmitted records, bin margins for the time-at-depth histograms typically did not correspond to the surface mixed layer depth, so similar calculations were not performed. However, in the case of shark 3YR-2, a time-at-temperature histogram bin (20°C) corresponded closely to the mixed layer temperature in the summer and autumn (19.8°C); and a time-at-depth bin (50 m) corresponded closely to the winter mixed layer depth (55 ± 1 m), so these values were used.

5.2.4 Quantification of diel differences in depth and temperature

To investigate diel patterns in habitat preferences, we used the light record in archival records to divide the 24-hour cycle into dawn, day, dusk and night periods, and then determined depth and temperature preferences within these four periods,

using MatLab. The light record was corrected for light attenuation with depth using the following light attenuation relationship:

$$L_{\rm Z} = L_{\rm s} \cdot e^{-KZ}$$
 such that $L_{\rm s} = \frac{L_{\rm Z}}{e^{-KZ}}$

where Z is the depth, L_s is the light at the surface, L_Z is the light measured by the tag at depth Z, and K is the light attenuation coefficient. To allow the use of a threshold value to separate twilight from day (or night), between-day variation in L_s was removed as follows:

$$L_{sc} = L_s - \overline{(L_s)_w}$$

where *w* is the width of the moving average of L_s , set to the number of records per day. L_{sc} is then L_s without interdiel trend and centered about zero. We defined the periods of the diel cycle as follows:

$$dawn : \frac{\Delta L_s}{\Delta t} \ge G_{dn}$$

$$day : \left(\frac{\Delta L_s}{\Delta t} < G_{dn}\right) \land \left(\frac{\Delta L_s}{\Delta t} > G_{dk}\right) \land \left(L_s > L_d\right)$$

$$dusk : \frac{\Delta L_s}{\Delta t} \le G_{dk}$$

$$night : \left(\frac{\Delta L_s}{\Delta t} < G_{dn}\right) \land \left(\frac{\Delta L_s}{\Delta t} > G_{dk}\right) \land \left(L_s < L_d\right)$$

where t is time, $G_{dn} = \frac{\Delta L_s}{\Delta t}$ during dawn, $G_{dk} = \frac{\Delta L_s}{\Delta t}$ during dusk, and L_d is the

minimum L_s during day.

We conducted an analysis to determine if the light of the moon affected the vertical distribution of juvenile white sharks during nighttime periods. We selected nighttime depths based on the light level measured by the tag, as described above, and within these data compared three-day periods centered on the full moon with three-day periods centered on the new moon, as determined from astronomical tables (Anonymous 2006).

5.3 Results

5.3.1 Geographic movements

Six juvenile white sharks were tagged and released in the SBC between July 2002 and August 2004, and moved within waters offshore of California and Baja California, Mexico (Fig. 4–1). YOY sharks were tracked for 46 ± 19 days (184 total days) while three-year-old sharks were tracked for 175 ± 10 days (350 total days) (Table 5-1). The ranges of YOY and three-year-old sharks overlapped in the SCB but YOY sharks traveled further south, and three-year-old sharks moved further north. The two YOY sharks for which we have data in the summer and early autumn (YOY-1 and YOY-2) remained within the SCB for the duration of their tracks (July and August to September, respectively). YOY-1 was recaptured near Ventura, California, and YOY-2's satellite tag popped up near Hermosa Beach, California. The remaining YOY sharks were tracked during autumn and traveled south into Mexican waters. Shark YOY-3 moved from the SCB to Vizcaino Bay, Baja California between late September and mid October, traveling 700 km. Shark YOY-4 left the SCB during late November and was captured near Ensenada shortly thereafter. The three-year-old sharks were tracked during autumn and winter (Table 5-1). Shark 3YR-1 was tagged off the SCB and remained within the SCB and waters off northern Baja California for the 168 days of the track. The satellite tag popped up near El Segundo, California on 25 January 2005. Shark 3YR-2 remained in the SBC and waters off northern Baja California from August to October and then moved north of Point Conception during the first nine days of November 2004. During the remainder of the 182-day track the animal inhabited waters off central and northern California, and the tag released near Point Reyes on 25 January 2005, 600 km from the tagging location and 4° farther north.

5.3.2 Accuracy of geolocations

Of the six sharks tagged in this study, light and SST geolocation estimates were obtained within one day of the start and end points for six of twelve possible pop-up endpoint events (Fig. 5-2). For these six events, the longitude errors ranged from 80 km west to 103 km east, with absolute error values averaging 54 ± 36 km (mean \pm SD). Latitude errors were all south, ranging from 17 to 434 km, with an average of 231 ± 159 km.

5.3.3 Vertical movements and diel patterns in behavior

Juvenile white sharks showed strong diel patterns in behavior. During summer and autumn, when data were available for all four animals with archival records (sharks YOY-1, YOY-2, YOY-4 and 3YR-1), mean depths were within the thermocline during dawn $(31 \pm 19 \text{ m})$, day $(26 \pm 16 \text{ m})$ and dusk $(22 \pm 10 \text{ m})$, but in the surface mixed layer at night $(6 \pm 3 \text{ m})$ (Fig. 5-3 and Fig. 5-4); these depths were significantly shallower at night than during other periods of the day (Paired t-tests, p < 0.05; Table 5-2). Consequently, the mean ambient temperatures were cooler during dawn $(15.8 \pm 0.4^{\circ}\text{C})$, day $(16.8 \pm 0.4^{\circ}\text{C})$ and dusk $(16.6 \pm 0.3^{\circ}\text{C})$ than during night $(18.2 \pm 0.4^{\circ}\text{C})$ (Fig. 5-5 and Fig. 5-6). These temperatures were significantly warmer during night than during other periods of the day; in addition, dawn was significantly cooler than day and dusk (Paired t-tests, p < 0.05; Table 5-2). During winter, archival data were only available for shark 3YR-1, a three-year-old, and it showed no diel patterns in depth or temperature. The animal remained at a depth of 4 ± 1 m and a temperature of $15.5 \pm 0.1^{\circ}$ C, which was in the surface mixed layer.

In addition to comparing the average depths and temperatures between periods of the day, we compared the distributions of time-at-depth and time-at-temperature between the four diel periods by summarizing these variables into evenly spaced depth and temperature bins. The same diel patterns emerged for all four sharks. During summer and autumn, when data were available for all four sharks, the shallower (Fig. 5-3 and Fig. 5-4) and warmer (Fig. 5-5 and Fig. 5-6) nighttime distributions were significantly different from other periods of the diel cycle (p < 0.05, Kolmogorov-Smirnov tests, Table 5-3). A secondary peak of occupancy at depth occurred during dawn, day and dusk for all four animals, though the depth of this secondary peak was shallower for YOY sharks (47 + 23 m) than for the three-year-old (240 m). 3YR-2

had a secondary peak in the 200-300 m bin, showing agreement with the archival data for 3YR-1. This secondary peak of occupancy caused a secondary peak in temperature occupancy during dawn, day and dusk, at 12.8 ± 1.9 °C for YOY sharks and 9.7 ± 0.3 °C for the three-year-old shark. During winter, archival data were available only for shark 3YR-1, and this animal showed neither diel patterns nor a secondary peak of occupancy in the thermocline.

During the course of their tracks, the three YOY sharks undertook 2493 vertical excursions below the surface mixed layer, while the three-year-old shark (3YR-1) undertook 1751 vertical excursions. The frequency and duration of these vertical excursions did not differ markedly between YOY and three-year-old sharks, while the mean depth of excursions was shallower for the YOY animals. YOY sharks made 21 \pm 9 vertical excursions per day, while the 3YR-1 made 20 \pm 11 vertical excursions per day, and the difference was not significant (Paired t-test, p = 0.69). The duration of excursions below the surface mixed layer was similar for YOY sharks (0.7 ± 1.3) hours) and the three-year-old shark (0.8 ± 1.5 hours) (Paired t-test, p = 0.30). However, the duration of the longest excursion during each day was significantly greater for the three-year-old shark (5.1 \pm 3.0 hours) than the YOY sharks (3.9 \pm 3.2 hours) (Paired t-test, p = 0.01). Maximum depths were greater during dawn, day and dusk $(157 \pm 80 \text{ m})$ than during night $(56 \pm 40 \text{ m})$ for the four animals with archival records (Paired t-test, p < 0.01) (Fig. 5-7). Minimum temperatures were significantly cooler during dawn, day and dusk $(10.2 \pm 1.1^{\circ}C)$ than during night $(12.2 \pm 1.7^{\circ}C)$ (Paired t-test, p = 0.05). There was a strong contrast in the depth of excursions into the thermocline between age classes, with YOY sharks having significantly shallower excursions $(100 \pm 59 \text{ m})$ than the three-year-old shark $(226 \pm 81 \text{ m})$ (Paired t-test, p = 0.02). The three-year-old shark reached significantly cooler temperatures during excursions into the thermocline $(9.2 \pm 0.9^{\circ}\text{C})$ than the YOY sharks $(11.2 \pm 1.4^{\circ}\text{C})$ (Paired t-test, p < 0.01). The greatest depth and coolest temperature reached by each animal during its track was deeper and cooler for three-year-olds (394 \pm 14 m; 8.4 \pm 0.3°C) than for YOY animals $(241 \pm 82 \text{ m}; 9.4 \pm 0.6^{\circ}\text{C})$ (Paired t-test for depth, p = 0.02; Paired t-test for temperature, p = 0.03).

We compared nighttime depths between full moon and new moon periods (Fig. 5-8). The median nighttime depths were greater during full moon periods than new moon periods for three of the four sharks (sharks YOY-2, YOY-4 and 3YR-1). For sharks YOY-2, YOY-4 and 3YR-1, nighttime full moon depths (7 ± 4 m) were significantly greater than nighttime new moon depths (3 ± 2 m) (Wilcoxon rank sum tests, p < 0.05). Shark YOY-1 did not show greater nighttime depths during full moon periods.

Potential benthic foraging events, as indicated by vertical excursions to consistent or gradually changing bottom depths (Fig. 5-8b), were noted on $63 \pm 10\%$ of all days for juvenile white sharks for which archival data were obtained (sharks YOY-1, YOY-2, YOY-4 and 3YR-1). YOY sharks undertook benthic foraging on 67 \pm 3% of all days, compared to 48% for the three-year-old shark. The value for 3YR-1 remained the same if the comparison was conducted during summer and autumn only.

5.3.4 Depth and temperature preferences

The pressure and temperature data recorded on the PAT tag enabled reconstruction of the vertical thermal structure along the tracks of the sharks (Fig. 5-9). YOY sharks occupied waters with surface temperatures ranging from $15.0-23.4^{\circ}$ C, and the surface mixed layer had an average depth of 8 ± 2 m (mean \pm SD) and an average temperature of $18.8 \pm 0.2^{\circ}$ C. Below the surface mixed layer, waters occupied by YOY sharks averaged $13.8 \pm 1.7^{\circ}$ C. YOY sharks spent $64 \pm 19\%$ of their time in the surface mixed layer, and $36 \pm 19\%$ of their time in the thermocline. Temperatures encountered by YOY sharks ranged from 23.4° C (shark YOY-2) to 8.6° C (shark YOY-3).

Three-year-old sharks (3YR-1 and 3YR-2) inhabited waters similar to those of YOY sharks during the summer and autumn, spending $53 \pm 0\%$ of the time in the surface mixed layer with an average depth of 9 ± 0 m and an average temperature of 19.2 ± 0.8 °C, and $47 \pm 0\%$ of the time in thermocline waters averaging 13.4 ± 1.6 °C. During the winter (December-February) the three-year-old sharks spent $93 \pm 9\%$ of their time in a deeper, colder surface mixed layer averaging 45 ± 15 m and 14.3 ± 1.6 °C.

1.8°C; and $7 \pm 9\%$ of their time in the thermocline in average temperatures of 13.0 ± 0.1 °C. Temperatures encountered by three-year-old sharks ranged from 24.0°C (shark 3YR-2) to 8.4°C (shark 3YR-1).

The depth and temperature distributions of the juvenile white sharks showed differences between YOY and three-year-old age classes. YOY sharks inhabited temperatures below 10°C only $1 \pm 2\%$ of the time, compared to $10 \pm 1\%$ of the time for three-year-old sharks during the same seasons (Paired t-test, p < 0.01).

5.3.5 Seasonal patterns of mixed layer occupancy and maximum depth

Vertical and thermal habitats were compared across seasons (autumn and winter) for the two three-year-old sharks that were tracked into the winter months. For 3YR-1 and 3YR-2 a seasonal cooling of the mixed layer in winter, as well as during movements north of Point Conception, coincided with a near cessation of vertical movements into the thermocline resulting in a constriction of the habitat to the surface mixed layer (Fig. 5-10). During summer and autumn, when mixed layer temperatures averaged 19.2 ± 0.8 °C, both sharks frequently made excursions to 300 m or more where water temperatures averaged 13.4 ± 1.6 °C, and spent $18 \pm 2\%$ of the time in waters cooler than 12°C (a calculation of time within thermocline waters was not possible for shark 3YR-2, so 12°C was used as a threshold instead). During winter, when mixed layer temperatures averaged 14.3 ± 1.8 °C, the two sharks avoided thermocline waters even though the temperature of this layer $(13.0 \pm 0.1^{\circ}C)$ was similar to its temperature during summer and autumn, spending only $0.4 \pm 0.0\%$ of the time in waters cooler than 12°C (Paired t-test, p = 0.05). The maximum depth reached by the sharks was positively correlated with surface temperature (Least squares regression, $r^2 = 32.7$, p < 0.01).

5.3.6 By-catch of juvenile white sharks in fisheries

In this study, four YOY white sharks were caught in US and Mexican bottom-set gillnets six times (Table 5-1). All YOY sharks were initially captured in gillnets and two sharks (YOY-1 and YOY-4) encountered gillnets a second time. Shark YOY-1

encountered a gillnet near Ventura, California and escaped, but left its satellite tag behind in the net. Shark YOY-4 was recaptured by a gillnet fisherman near Ensenada, Baja California, Mexico.

5.4 Discussion

5.4.1 Nursery region of white sharks in the eastern North Pacific

In this paper we track six juvenile white sharks in the eastern North Pacific over durations of 24 to 182 days and provide new information on their seasonal movements, behavior and habitat utilization. The apparent residency of sharks in the California Current System off California and Baja California suggests that this region is an important nursery habitat for juvenile white sharks. YOY sharks tracked during summer (Sharks YOY-1 and YOY-2) remained within the SCB, whereas YOY sharks tracked in autumn (YOY-3 and YOY-4) moved south into waters of Baja California, Mexico. The two three-year-old sharks were tracked from late summer through winter, with one remaining in the SCB and northern Baja California waters (3YR-2), overlapping the range of the YOY sharks, and the other moving north of Point Conception into central and northern California waters (3YR-1).

The results presented here extend the nursery region for white sharks south of the SCB, expanding the area described by Klimley (1985), and indicating that juvenile white sharks located in US and Mexican waters are most likely part of the same population. Juvenile white sharks have also been captured inside the Gulf of California (Klimley 1985); O. Sosa-Nishizaki, CICESE, pers. comm.). Our results suggest that the expansion of the nursery may be associated with season, as YOY sharks tracked in the summer remained in the SCB, while those tracked in the autumn moved south into Mexican waters. Longer tracks are required to determine the full extent of the nursery grounds in the eastern Pacific and whether subpopulations exist.

Putative nursery areas exist in other regions of the world, and in both the northern and southern hemispheres, captures of pregnant and YOY sharks occur most frequently during spring and summer (Casey and Pratt 1985; Bruce 1992; Cliff et al.

1996; Fergusson 1996; Francis 1996; Uchida et al. 1996). In our study, sea surface temperatures occupied by YOY sharks ranged from 15.0–23.4°C. For the seasons of YOY and pregnant shark captures in other putative nursery areas, climatological temperatures are 19–22°C in southern Japan; 20–22°C in Taiwan; 21–26°C in eastern South Africa; 20–23°C in southeastern Australia; 16–20°C in northern New Zealand; 20–26°C in the central Mediterranean; and 17–24°C in the Mid-Atlantic Bight (Anonymous 2005). The similarity in water temperature in all of these regions suggests that there may be an optimal thermal environment for YOY white sharks.

Larger juvenile white sharks appear to have a different geographic range and seasonal pattern than YOY animals. While both year classes of sharks appear to enter Mexican waters at various points, three-year-old animals returned to California waters and remained there during the winter. Shark 3YR-2 moved north of Point Conception, into the primary nearshore habitat of adult white sharks. Since this individual was a three-year-old of 2.5 m length, and fishes predominate in the diets of white sharks smaller than 3 m in length (Tricas and McCosker 1984), the northward movements of juvenile sharks are probably not associated with the addition of mammals to the diet (Klimley 1985). Differences in track duration may bias the geographic ranges covered (Block et al. 2005), so longer tracks on YOY sharks may show more overlap with the three-year-old sharks. Conversely three-year-old sharks may be revealing a niche expansion to the north that YOY sharks cannot physiologically tolerate (Weng et al. 2005).

5.4.2 Accuracy of geopositions

Long distance movements of individual sharks between the SCB, Baja California, and northern California were demonstrated by satellite-derived pop-up endpoint positions and recapture positions, with intermediate positions calculated using light and SST based geolocation. The geoposition errors for juvenile white sharks in this study, of 54 ± 15 km zonally, and 231 ± 64 km meridionally (Fig. 5-2), meant that the data were useful in characterizing movements out of the SCB, but not within the SCB. As in the validation study of Teo *et al.* (2004), longitude errors for juvenile white

sharks are smaller than latitude errors. However, the latitude errors for juvenile white sharks are all to the south, indicating a systematic bias which was not observed by Teo *et al.* (2004). The use of SST to determine latitude (Smith and Goodman 1986) is most accurate in regions where greater north-south gradients in SST exist; the gradient is monotonic over scales greater than a degree of latitude; there are no large gaps in SST data, as occur in areas with high cloud cover or near land; and the scale of movements is much larger than the scale of errors. Teo *et al.* (2004) estimated root mean square latitude errors of 163 km, 129 km and 100 km for salmon sharks (*Lamna ditropis*), blue sharks (*Prinace glauca*) and bluefin tuna (*Thunnus thynnus*), respectively. These highly migratory pelagic species travel hundreds or thousands of kilometers in primarily offshore waters. The present study takes place in coastal, upwelled waters with a much finer scale of variability in SST, which likely explains the slightly higher error estimates we obtained. Furthermore, the high cloud cover in the region reduces the coverage of satellite data.

5.4.3 Diel Patterns in depth and temperature

The 30-second and 60-second archival data sets obtained from four white sharks provided the opportunity to conduct a detailed analysis of behavior over diel and lunar time scales, across a range of habitats. Juvenile white sharks make deeper vertical movements during day, dawn and dusk than during night (Fig. 5-3 and Fig. 5-4). Dewar et al. (2004) also noted a peak in activity in a juvenile white shark in the SBC at sunrise. Twilight activity has been noted in a wide range of pelagic fishes including tunas (Thunnini) (Dagorn et al. 2000; Kitagawa et al. 2000); (Schaefer and Fuller 2002), billfishes (Xiphidae, Istiophoridae) (Carey and Robison 1981; Holland et al. 1990a) and mako sharks (*Isurus oxyrinchus*) (Sepulveda et al. 2004). Stomach content analysis indicates that these dawn/dusk activity peaks are often associated with feeding (Buckley and Miller 1994; Scott and Cattanach 1998), although feeding may also occur during the day (Reintjes and King 1953) or night (Holland et al. 1990b). Vertical excursions into the thermocline comprise a small portion of the animals' time, but may be ecologically important if they are foraging behaviors. (Sepulveda et al. 2004) used stomach temperature data to confirm feeding events on vertical excursions

by mako sharks. Similar studies on juvenile white sharks would help to confirm if these behaviors are for foraging.

During the nighttime, the moon phase influenced the occurrence and depth of vertical excursions by juvenile white sharks (Fig. 5-8). Vertical excursions into the thermocline occurred more frequently and to greater depths during full moon nights as compared to new moon nights. Increased depth during full moon periods may be associated with the deeper depth of the prey species (squids, fishes and zooplankton), which undergo light-mediated vertical migrations (Ringelberg and van Gool 2003). This also suggests that during the full moon, the juvenile white sharks are foraging at night.

5.4.4 Depth and temperature preferences

Tagging data indicate that the primary habitat of juvenile white sharks is in the surface mixed layer, but that they make extensive use of the cooler waters of the thermocline. The preference for surface mixed layer waters results in occupancy of the warmest waters within the California Current, ranging from 16-20°C (Fig. 5-5 and Fig. 5-6). This habitat preference is similar to those of the sharks tracked by Klimley et al. (2002) and Dewar et al. (2004), which showed a preference for waters of 15–21°C and 16–22°C, respectively. These temperatures are characteristic of nearshore SCB waters during summer and autumn (Venrick et al. 2003). Occupancy of cooler waters in the thermocline by juvenile white sharks was higher in this study than in previous studies. During summer and autumn, YOY white sharks spent $32 \pm$ 20% of their time in waters cooler than 16°C, as compared to 11% of the time for the white shark tracked by Dewar et al. and 25% by the white shark tracked by Klimley et al. The greater occupancy of cooler waters observed here likely results from the longer tracks capturing a wider variety of behaviors (46 ± 19 days in the present study, vs. 0.15 days and 28 days in the studies of Klimley and Dewar, respectively). The lack of data for YOY sharks during the winter leaves open the possibility that this age class may encounter cooler habitats if tracked during this period.

The three-year-old sharks tracked in this study inhabited similar water masses to the YOY sharks during summer and autumn, but utilized the habitat differently. These older and larger sharks made deeper vertical excursions, and as a result, their depth distributions were significantly deeper (Fig. 5-4) and temperature distributions significantly cooler (Fig. 5-6). A similar result was found for juvenile mako sharks by (Sepulveda et al. 2004). The niche expansion of white sharks into cooler habitats appears to continue beyond the three-year-old phase, as adult white sharks occupy waters ranging from 4–25°C (Lowe and Goldman 2001; Boustany et al. 2002) and enter boreal habitats (Martin 2004).

In contrast to juvenile white sharks, adult white sharks occupy both colder and warmer waters, suggesting that thermal niche breath increases along with body size and endothermic capacity as individuals grow. White sharks inhabit waters up to 27.2°C while in the tropics, waters of 10–14°C while nearshore, and waters as cool as 4°C during deep dives. This increased thermal niche breadth allows larger white sharks access to a range of habitats that are not used by juveniles.

Large body size may have been a precursor to the evolution of anatomical and physiological specializations to endothermy. In the ancestors of the lamnid sharks, which presumably had much lower aerobic capacity than extant lamnids, the low conductance resulting from large body size could offset the lower heat production, facilitating the evolution of mechanisms for reducing conductivity, such as countercurrent heat exchangers.

5.4.5 Foraging habitat of juvenile white sharks

The large proportion of time juvenile white sharks spent in the surface mixed layer indicates that this may be an important foraging habitat. Stomach content analysis shows that nearshore pelagic fishes are in the diet of juvenile white sharks, including Pacific sardine (*Sardinops sagax*), king salmon (*Oncorhynchus tshawytscha*), white seabass (*Cynoscion nobilis*) and striped bass (*Morone saxatilis*) (Klimley 1985). Other potential prey species that inhabit the water column in the study area include grunion (*Leuresthes tenuis*), surfperch (*Hyperprosopon* spp.), smelt (*Atherinops* spp.), croaker (*Genyonemus* spp.), mackerel (*Scomber* spp.), barracuda (*Sphyraena argentea*), and market squid (*Loligo opalescens*).

Our data indicate that benthic foraging is also important for juvenile white sharks (Fig. 5-8b). Behaviors indicating benthic foraging were observed on $63 \pm 10\%$ of all days for sharks with archival records. Similar behaviors were noted by Dewar et al. (2004), and stomach content studies show a variety of demersal fishes in the diet of juvenile white sharks including the bat ray (*Myliobatis californica*), cabezon (Scorpaenichthys marmoratus), soupfin shark (Galeorhinus zygopterus), grey smoothhound (Mustelus californicus), spiny dogfish (Squalus acanthius), lingcod (Ophiodon elongatus), rock crab (Cancer antennarius), and rockfishes (Sebastes spp.) (Klimley 1985). The secondary peak of occupancy at depth (47 + 23 m for YOY sharks, Fig.)5-3; and 240 m for three-year-olds, Fig. 5-4) is the aggregate time of vertical excursions, and may be an indicator of foraging effort. There are large depthassociated changes in the species assemblages of fishes off California and Baja California, so the depth range of a predator determines the forage species it can access. At the depth range of the secondary occupancy peak for YOY sharks, other potential forage species include shallow-living soft-substrate demersal fishes such as halibut (Paralichthys californicus), sanddabs (Citharichthys spp); shallow hard-substrate fishes such as copper rockfish (Sebastes caurinus), vermilion rockfish (S. miniatus), lingcod (Ophiodon elongatus) and painted greenling (Oxylebius pictus); or elasmobranches such as round stingray (Urobatis halleri), California skate (Raja inornata), and leopard shark (Triakis semifasciata) (Bond et al. 1999; Love et al.

2000). Forage species accessible to three-year-old sharks could include deeper-living soft-substrate fishes such as turbot (*Hypsopsetta* spp., *Pleuronichthys* spp.), and sole (*Microstomus* spp.); and deep-living hard-substrate fishes such as greenspotted rockfish (*S. cholorostictus*), flag rockfish (*S. rubrivinctus*) and bocaccio (*S. pausispinus*) (Bond et al. 1999; Love et al. 2000).

The closely related shortfin mako shark, which is abundant in the SCB, appears to utilize thermocline waters less than juvenile white sharks. Shortfin mako sharks of a size intermediate between YOY and three-year-old sharks in this study (1.8 m), tracked in waters of the SCB, showed only occasional use of the thermocline and spent only $3.7 \pm 3.2\%$ of the time in waters cooler than 16° C (Holts and Bedford 1993). This suggests that there may be some resource partitioning between these species, with mako sharks utilizing epipelagic resources and white shark potentially making use of both epipelagic and demersal resources.

5.4.6 Thermal limitation of habitat

A number of results in this study are consistent with thermal limitation in juvenile white shark habitat utilization, and a niche expansion into cooler habitats with growth. The southward movement of YOY animals during the autumn, when mixed layer temperatures in the SCB are falling, is consistent with movements to avoid cooler winter temperatures. The greater depths and cooler temperatures of vertical excursions undertaken by three-year-olds, in comparison to YOY sharks occupying the same region during the same season (summer and autumn in the SCB), are consistent with an expansion of thermal habitat with body size. The northward movement of one three-year-old shark into waters north of Point Conception, where YOY animals are rare (Klimley 1985), is consistent with a thermally mediated geographic range expansion with body size. The cessation of excursions into the thermocline by three-year-old sharks when surface mixed layer temperatures fall below 16°C is consistent with behavioral thermoregulation (Carey and Scharold 1990; Holland et al. 1992). However, the observation could also be explained by patterns in the vertical distribution of prey. It is important to note the bias caused by the longer tracks of three-year-olds, extending into the winter, as compared to the tracks of YOY

sharks that were limited to summer and autumn. However, comparisons of depth and temperature using only data for summer and autumn did reveal deeper and cooler habitat utilization by three-year-olds.

Recent physiological studies have indicated that pelagic fishes may have cardiac limitations when entering cold waters. A cold induced bradycardia is evident in tunas (Korsmeyer et al. 1997; Blank et al. 2002; Blank et al. 2004). Although few studies have investigated the influence of cooler temperatures on *in vivo* cardiac performance in lamnid sharks, it is possible that a similar cold-induced bradycardia occurs. We have identified a high expression of calcium cycling proteins in the cardiac myocyctes of lamnid sharks including the white shark (Weng et al. 2005). These results suggest that white sharks have the potential to maintain cardiac output at cooler temperatures, but the relation of this capacity to body size remains unknown.

5.4.7 Fishing mortality and management

In this study, four juvenile white sharks were captured by US and Mexican fishermen six times. Dewar et al. (2004) reported that a single juvenile white shark was captured twice in the SCB. The capture rate of juvenile white sharks in bottom-set gillnet fisheries in US and Mexican waters suggests that fishing mortality on juvenile white sharks in the Eastern Pacific may be significant and that management actions may be warranted to protect these vulnerable life history stages. Efforts to reduce fishing mortality will be most effective if management efforts occur in both US and Mexican waters.

The geographic range of species and individuals is important in understanding population dynamics (DeMartini 1993; McNeill and Fairweather 1993; Russ and Alcala 1996). Futhermore, the fisheries that animals are likely to encounter, and the required scale of management actions, changes with ontogeny and season (Block et al. 2001; Block et al. 2005). In addition to understanding geographic range, knowing the vertical distribution of animals in the water column allows assessment of the vulnerability of juvenile white sharks to different types of fishing gear. Vertical habitat data showing a preference for the surface mixed layer and upper thermocline indicate that juvenile white sharks may be most susceptible to fishing gear deployed at these

depths. Furthermore, the diel pattern showing greater vertical movements during daylight indicates that they are more likely to be captured in bottom-set gillnets during daylight, as noted by Dewar et al. (2004). This implies that a shift toward nocturnal gillnet effort could reduce bycatch of juvenile white sharks. In regions where mixed layer temperatures are cooler than 16°C, juvenile white sharks rarely make vertical excursions and thus should be less vulnerable to deeper gear. Northward movements of larger juveniles may reduce the risk of encountering bottom set gillnets, as this gear is presently banned north of Point Conception, California.

		Length	Mass										
Individual	Sex	(cm) 1	(kg) ²	Age (yr) ³	Days	Start	Start Location	Latitude	Longitude	End	End Location	Latitude	Longitude
							Channel Islands						
YOY-1	F	147	27	0.2	248	2-Jul-02	Harbor, CA ⁴	34.08°N	119.23°W	12-Aug-02	Ventura, CA4	34.25°N	119.42°W
											Hermosa Beach,		
YOY-2	F	155	32	0.4	63	29-Jul-03	Ventura, CA ⁴	34.01°N	118.77°W	30-Sep-03	CA ⁶	33.85°N	118.45°W
											Vizcaino Bay,		
YOY-3	Μ	156	32	0.4	60	8-Sep-03	Long Beach, CA ⁴	33.68°N	118.24°W	7-Nov-03	BCN ⁷	28.49°N	114.29°W
YOY-4	М	155	32	0.4	37	20-Oct-03	Port Hueneme, CA4	34.13°N	119.23°W	26-Nov-03	Ensenada, BCN ⁴	31.92°N	116.83°W
							Will Rogers State				·		
3YR-1	F	248	143	3.2	168	11-Aug-04	Beach, CA⁵	34.03°N	118.54°W	25-Jan-05	El Segundo, CA6	33.88°N	118.50°W
						0	Will Rogers State				Point Reyes,		
3YR-2	F	250	146	3.3	182	12-Aug-04	Beach, CA ^₅	34.03°N	118.54°W	10-Feb-05	CA ⁷	37.98°N	122.87°W

Table 5-1. Juvenile white sharks tagged during 2002-2004

¹ Total length.

² After (Kohler et al. 1995). ³ After Cailliet et al. (1985).

³ After Cannet et al. (1985).
⁴ Captured in a commercial gillnet.
⁵ Captured by hook and line.
⁶ Tag popped up and was recovered.
⁷ Tag popped up and was not recovered.
⁸ The shark was at liberty for 41 days, but the tag recorded only until 26-Aug-02, yielding a 24-day track.

Table 5-2.	P-values ¹	for average	depth and	temperature	during d	iel periods

Test	dawn-night	day-night	dusk-night	dawn-day	dawn-dusk	dusk-day
Depth (a>b)	0.04*	0.05*	0.03*	0.36	0.22	0.66
Temperature (a <b)< td=""><td>0.00*</td><td>0.00*</td><td>0.00*</td><td>0.01*</td><td>0.00*</td><td>0.24</td></b)<>	0.00*	0.00*	0.00*	0.01*	0.00*	0.24

¹ Paired t-tests. Data is for sharks YOY-1, YOY-2, YOY-3 and 3YR-1 during summer and autumn. * Statistically significant.

Tag	Variable	dawn-night	day-night	dusk-night
YOY-1	Depth	0.155	0.797	0.797
YOY-2	Depth	0.000*	0.000*	0.000*
YOY-4	Depth	0.000*	0.000*	0.000*
3YR-1 autumn	Depth	0.000*	0.000*	0.001*
3YR-1 winter	Depth	1	1	1

Table 5-3. P-values¹ for distributions of time-at-depth and time-at-temperature during diel periods

¹ Kolmogorov-Smirnov tests. * Statistically significant.



Fig. 5-1. *Carcharodon carcharias*. (a) Start and end positions for juvenile white sharks tracked off southern California, USA and Baja California, Mexico. (b) Daily positions of juvenile white sharks based on light- and SST-based geolocations. Grey line shows 1000 m depth contour.



Fig. 5-2. *Carcharodon carcharias*. Error estimates for light- and SST-based geolocations for six juvenile white sharks. Positive values represent east and north; negative values west and south. Boxplots are: centerline, median; edges of box, 1^{st} and 3^{rd} quartiles; whiskers, data points within the range Q1 – 1.5(Q3-Q1) to Q3 + 1.5(Q3-Q1).



Fig. 5-3. *Carcharodon carcharias*. Diel changes in vertical movements for one young-of-the-year white shark (YOY-2). (a) Timeat-depth through the 24-hour cycle during summer in the Southern California Bight. Color denotes amount of time spent at each depth. White line shows light intensity at the surface in arbitrary units. Time-at-depth histograms for (b) day and night and (c) dawn and dusk. Blue lines show depth-temperature profile.



Fig. 5-4. *Carcharodon carcharias*. Diel changes in vertical movements for one three-year-old white shark (3YR-1). (a) Time-atdepth through the 24-hour cycle during autumn in the Southern California Bight. Color denotes amount of time spent at each depth. White line shows light intensity at the surface in arbitrary units. Time-at-depth histograms for (b) day and night and (c) dawn and dusk. Blue lines show depth-temperature profile.



Fig. 5-5. *Carcharodon carcharias*. Diel changes in temperature preferences for a young-of-the-year white shark (YOY-2). (a) Time-at-temperature through the 24-hour diel cycle during summer in the Southern California Bight. Color denotes amount of time spent at each temperature. White line shows light intensity at the surface in arbitrary units. Time-at-temperature histograms for (b) day and night and (c) dawn and dusk.



Fig. 5-6. *Carcharodon carcharias*. Diel changes in temperature preferences for a three-year-old white shark (3YR-1). (a) Time-attemperature through the 24-hour diel cycle during autumn in the Southern California Bight. Color denotes amount of time spent at each temperature. White line shows light intensity at the surface in arbitrary units. Time-at-temperature histograms for (b) day and night and (c) dawn and dusk.



Fig. 5-7. *Carcharodon carcharias*. Maximum depths during dawn, day, dusk and night for a juvenile white shark (YOY-2). Boxplots are: centerline, median; edges of box, 1^{st} and 3^{rd} quartiles; whiskers, data points within the range Q1 – 1.5(Q3-Q1) to Q3 + 1.5(Q3-Q1); asterisks, points lying outside this range.



Fig. 5-8. *Carcharodon carcharias*. Vertical movements of a juvenile white shark (YOY-2) for two 48-hour periods during (a) the full moon and (b) the new moon. Lines show depth measured at 60-second intervals, grey boxes denote nighttime.



Fig. 5-9. *Carcharodon carcharias*. Timeseries of water column thermal structure for (a) shark YOY-2 and (b) shark 3YR-1. The extent of the profile is the maximum depth reached on a given day. Color denotes ambient water temperature.



Fig. 5-10. Frequency of depth-temperature observations for two three-year-old white sharks (3YR-1 and 3YR-2). Color denotes the number of observations at each depth and temperature.

6 Conclusions

Our knowledge of the biology of lamnid sharks, and of pelagic vertebrates in general, has been limited by the inaccessibility of their environment, such that the methods traditionally available to biologists, such as direct observation and sampling, are difficult or impossible to apply to these species. As a result, our knowledge has been based on direct observations of animals during periods when they occupy habitats near land, or upon data obtained through fisheries, which suffer from great biases in sampling and frequently contain errors in species identification. Understanding the biology of pelagic vertebrates is essential to our understanding of the function of pelagic ecosystems. It is now clear that upper level predators can exert profound structuring influences on the underlying trophic pyramid, affecting community composition, demographics and energy flows.

Revolutions in electronics, information technology and synoptic earth observation have opened a new field of study of pelagic organisms, allowing biologists to take measurements without being in the field themselves, thus overcoming the many of the costs and difficulties of working in the harsh open ocean environment. Acoustic and satellite telemetry tags, as well as archival data loggers, can be attached to or implanted in a wide variety of organisms to measures a variety of environmental and physiological variables, such as position, depth, ambient temperature and body temperature, sometimes over multi-year periods. The longer records now being obtained for animal movement and behavior are shedding light on the seasonal and even ontogenetic patterns in habitat utilization of pelagic organisms, and when combined with the synoptic environmental data available from earth-observing satellites, can help us to understand their spatial ecology. In this thesis I have conducted a number of studies of the movement and behavior of white sharks and salmon sharks, elucidating the ways in which these high trophic level animals use their environment. I focused on four questions during the course of my research. How do lamnid sharks utilize their environment? Does endothermy allow lamnid sharks to expand their niches, either thermally or geographically? How does body size affect niche breadth? How do lamnid sharks overcome the paradox of having a warm body

and an ambient temperature heart? What are the ecological and conservation implications of the wide-ranging behavior or lamnid sharks?

Both salmon sharks and white sharks undertake long distance migrations on a seasonal cycle in the eastern North Pacific. The scale and rapidity of these migrations exceed those known for other elasmobranchs. Salmon sharks undertake primarily meridional migrations from foraging grounds in coastal Alaska to pelagic and neritic regions of the subtropics between Hawaii and the North American continent. These migrations allow salmon sharks to take advantage of some of the most productive waters in the entire ocean basin, Prince William Sound, the Alaska downwelling region and the California Current upwelling region. Salmon sharks also migrate to oligotrophic regions in the subtropical between Hawaii and the west coast of North America. White sharks undertake predominantly zonal migrations between coastal California and an offshore focal area between Hawaii and Baja where productivity is very low. The migrations of salmon sharks and white sharks may include both foraging and reproductive functions. There is evidence that salmon sharks may give birth in both the subtropics and the California Current system, while white sharks may mate or give birth in their offshore focal area.

Among the Lamnidae, there is a hypothesized gradient in endothermic capacity, based on morphological and physiological specializations, with salmon sharks being the most endothermic and white sharks occupying an intermediate position (Carey et al. 1985). We have hypothesized that a higher capacity for endothermy would allow an animal to inhabit cooler environments, and in this thesis I provide empirical evidence that demonstrates salmon sharks do have a broader and cooler thermal niche than white sharks. Salmon sharks can withstand the subarctic winter, inhabiting 2–8°C waters for periods up to 96 days. Salmon sharks can also travel rapidly across great distances to subtropical waters as warm as 24°C, thereby inhabiting a very broad thermal niche. White sharks also inhabit a broad thermal range, though not to the cold extremes of salmon sharks. Adult white sharks reach waters as cool as 4°C during deep dives, and occupy these thermal environs briefly, and over 27°C while in subtropical waters offshore. Juvenile white sharks inhabited waters ranging from

9–23°C, a narrower range than adult white sharks, suggesting that the small body size of juveniles reduces their endothermic capacity and narrows their thermal niche relative to adults.

Lamnid sharks, as well as tunas, are able to maintain higher body temperatures than the environment, but their hearts receive blood directly from the gills, at ambient temperature. This presents a paradox, since in cold waters the cold heart must maintain oxygen supply to the warm tissues. Lamnid sharks show exceptionally high expression and activity of key calcium handling proteins than help to maintain contractility of heart myocytes at low temperatures (Blank et al. 2004; Weng et al. 2005). Furthermore, the expression and activity of these proteins is greatest in the most endothermic and cold-adapted species, the salmon shark, and intermediate in the white shark.

In this thesis I demonstrate that salmon sharks and white sharks move seasonally over major portions of the largest ocean basin on earth, the Pacific. The data indicate these top predators have trophic impacts that are not restricted to the narrow coast regions where humans most frequently observe them. By structuring the demographics and behavior of more abundant lower level consumers such as pinnipeds, salmon and squid, these predators likely have profound effects on system as a whole. The spatial ecology of sharks is also of great conservation importance due to the high fishing mortality that this group is suffering on a global scale, and low resilience of the group due to its k-selected life history strategy. White sharks are listed on Appendix II of the Convention on International Trade in Endangered Species, and are protected in Australia, South Africa, and California, USA. Despite these protections, I showed in chapter four that juvenile white sharks are vulnerable to gillnet fisheries in the US and Mexico and that management actions are likely required to protect the eastern North Pacific population. Effectively managing shark populations, while minimizing the economic and social costs of such management, requires that we obtain the biological knowledge to optimize our management actions. Satellite telemetry can provide detailed information on the horizontal and vertical habitat utilization of organisms in time and space, allowing us to understand where

and when they are most vulnerable to fisheries, and how best to adjust those fisheries to minimize mortality and bycatch.
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